SOUNDS, ACOUSTIC BEHAVIOUR AND GILLNET ENTANGLEMENT OF HECTOR'S DOLPHIN

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Abstract

Vocalisations of free-ranging Hector's dolphins were recorded with wideband recording equipment. Preliminary analyses of these sounds showed them to be high-frequency clicks centred around 120-125kHz. Digital signal processing methods were used to automatically measure many features of the sounds and, in combination with multivariate statistical methods, to provide a quantitative analysis of the acoustic repertoire of Hector's dolphins. Almost all of the sounds made were narrowband, high-frequency clicks of comparatively simple structure. Hector's dolphins make very few audible sounds, the most common of which is made up of high-frequency clicks emitted at such high repetition rates that the repetition rate is audible as a tonal "cry" or "squeal". Multivariate analyses of the automatically measured data revealed different types of high-frequency clicks according to their frequency and timing characteristics. The sounds are described in detail, as are the techniques used to automate the digital measurement process. To gain an insight into the possible role of these signals as echolocation signals, the ambiguity functions of different types of click are presented. With any simple sonar signal, the structural demands of range measurement and resolution of target velocity are in conflict. These analyses show that Hector's dolphin sonar signals are poorly suited to determining target velocity, but are well suited to resolving target range. Information about target velocity is accessible to the dolphin only from the trend of range measurements during a sequence of clicks.

To explore whether click types have different communicative meaning, I analysed whether certain click types were used disproportionately in different behavioural contexts. Hector's dolphin clicks do not appear to be used solely in sonar. Click types with complex spectra were used more often in large groups than in small ones, and double pulses (in the time domain) were used more often in "surface active" groups than in "long-diving" ones, suggesting they have some social significance. High repetition rate sounds ("cries") were much more commonly associated with aerial behaviours than with feeding, and appear to indicate excitement. I conclude that there is a general association between sounds and behaviour, and hypothesise that dolphins may have developed a communication system based on the ability to interpret each other's sonar echoes.

Several workers have suggested that gillnet entanglement is essentially an acoustic problem, as the dolphin's sonar apparently fails to detect the nets. The Pegasus Bay/Canterbury Bight gillnet fishery was studied to investigate gillnet entanglement. Over the four years of the study, 230 Hector's dolphins were reported killed in gillnets. Most dolphins (89%) were caught within four miles of the shore, and over the summer months of November to February (91%). The acoustic aspects of this problem were explored in an analysis of proposals to reduce entanglement by modifying gillnets. I show that neither making the nets more reflective to dolphin sonar nor warning of their presence by attaching sound emitters has proved successful, and argue that they are unlikely to be successful because of logical and practical difficulties with the concepts. I conclude that the best management strategy for the reduction of gillnet entanglement is the closure of specific areas to gillnetting.

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General Introduction

Hector's dolphin (*Cephalorhynchus hectori*) is the only truly endemic cetacean species in New Zealand waters (Baker, 1978; Dawson, 1985). Its total population size is small (3000-4000), and its distribution is essentially limited to the inshore waters of the South Island of New Zealand (Dawson and Slooten, 1988; Slooten and Dawson, 1988 and In press). Before 1984 this species had been little studied, and almost nothing was known of its acoustic behaviour. As part of a study of the biology and behaviour of this species, I studied its sounds, acoustic behaviour, and associated problems with entanglement in inshore gillnets.

Cetacean sounds and acoustic behaviour

Although sailors had for many years been aware of sounds made by marine mammals, it was underwater warfare during World War II that made these sounds a topic of considerable interest. Wartime developments of suitable listening equipment made possible the first scientific studies of marine mammal sounds (Watkins and Wartzok, 1985). Scientific interest in these sounds started in earnest with the recording by Schevill and Lawrence (1949) of belugas (*Delphinapterus leucas*) in the Saguenay River, Quebec. These recordings, made via a custom-built salt crystal hydrophone, three tube amplifier and a dictation machine, were the first underwater recordings of an identified species of marine mammal in the wild (Watkins and Wartzok, 1985).

Freed from having to support their bulk in air, cetaceans encompass a greater size range than any other mammalian order, from almost 30 m for female blue whales to around 1.4 m (a large Hector's dolphin). Accordingly, cetacean sounds cover a wide frequency spectrum. The largest cetaceans, blue and fin whales (*Balaenoptera musculus, B. physalus*), make sounds which are usually less than 200 Hz extending down into infrasonic frequencies (<20 Hz) (Cummings and Thompson, 1971; Edds, 1982; Watkins and Wartzok, 1985). In contrast, many of the smaller toothed whales (odontocetes) use broadband sonar pulses which often contain frequencies up to 150 kHz, and in an exceptional case as high as 256 kHz (*Steno bredanensis*; Norris and Evans, 1967).

High frequencies can potentially carry more information than low frequencies, but are attentuated quickly in seawater, while low frequencies propagate over long distances (Payne and Webb, 1971). This imposes a trade-off between using low frequencies for long-range communication but low information content, or high frequencies for high information content, but only over a short range. Body size is an important constraint, since large sound producing organs are needed to make low frequencies. Hence small cetaceans do not have the necessary vocal apparatus to communicate over long distances. The loud, infrasonic (20 Hz) tones made by fin whales (the second largest cetacean) are thought to act as long range contact calls which may be effective over as much as 80 km, or much more if made in a deepwater channel (Payne and Webb, 1971).

Many studies have described the sounds made by various species (see Watkins and Wartzok, 1985, for review). The acoustic repertoire of some is remarkably varied and includes a large repertoire of audible sounds including whistles, squawks, barks, burst pulses, "raspberries" and broadband sonar pulses (e.g. Bottlenose dolphins *Tursiops truncatus*, Lang and Smith, 1965; Popper, 1980).

The two orders of living whales, baleen whales (Mysticetes) and toothed whales (Odontocetes), make different sounds, but fewer generalisations are possible than might be expected. Each group makes both tonal and pulsive sounds, although Mysticete sounds are generally of lower frequency, narrower bandwidth and longer duration (Norris, 1969). Clark's (1982) analysis of right whale (*Eubalaena australis*) sounds revealed both pulsive and tonal sounds (and hybrids that were both tonal and pulsive), all of which had fundamental frequencies below 500 Hz. Mysticete sounds might appear generally simpler than Odontocete sounds were it not for humpback whales (*Megaptera novaeangliae*), which produce a wide variety of sounds repeated in a consistent sequence to form a "song" (Payne and McVay, 1971).

Odontocete vocalisations are divisible into three major classes; clicks, burst pulse sounds and tonal sounds (Norris, 1969). Clicks are short (usually <1 ms) phonations which are broadband in most species (Evans, 1973) but narrowband in a few (Kamminga and Wiersma, 1982; Evans et al., 1988; Dawson, 1988). Burst pulses are patterned sequences of pulses at high repetition rates, which are audible as screams, cries, squawks, barks, and moans (e.g. beluga, Sjare and Smith, 1986a). Unpulsed, tonal sounds are most commonly referred to as whistles, and are made by most dolphin species, but apparently not by porpoises, sperm whales, river dolphins or beaked whales (Herman and Tavolga, 1980). Whistles are more or less pure tones which are often frequency modulated, forming complex signals rich in harmonics (e.g. beluga, Sjare and Smith, 1986a). Of the vast variety of sounds made by cetaceans, there appears to be only two types which are not shared in some form by Odontocetes and Mysticetes, and both of these are related to the size of the animals involved. Mysticete whales do not appear to make ultrasonic clicks (but see Beamish and Mitchell, 1971), and Odontocetes do not make the low-frequency moans of blue and fin whales.

Cetacean sounds are particularly interesting for three major reasons.

1. Some of the signals are extraordinarily complex. Humpback whales congregating on low latitude breeding grounds sing long (3-30 min), often complex, highly organised, songs which vary between season (Payne and McVay, 1971; Payne and Payne, 1985). These songs are arguably the most complex non-human vocal signals. It appears that singers are male (Tyack, 1983), and all singers on a particular breeding ground sing a version of the same song (Payne and Payne, 1985). The whales' behaviour suggests that song is used in mate attraction (Tyack, 1981, 1983).

2. Odontocete cetaceans are known to echolocate. In echolocation, or active sonar (an acronym for SOund Navigation And Ranging), pulses of sound are emitted, and are reflected by "targets". Returning echoes potentially contain information about the target's range (from their delay), velocity (from any frequency shift in the echo, via the doppler effect) and target composition (via amplitude and frequency characteristics of the echo).

   McBride (published posthumously, 1956) noted in 1947 that bottlenose dolphins could avoid nets in darkness and in turbid water, and suggested echolocation as an explanation. Formal trials (Schevill and Lawrence, 1956; Kellogg, 1958; Norris et al., 1961) confirmed this, stimulating a large number of studies exploring the echolocation abilities of various species (e.g. Evans, 1973; Norris, 1969; Au et al., 1974, Turl et al., 1987).

While all echolocating cetaceans use short, sharp onset, pulsed sounds with fast rise times, the signals vary widely among species. Bottlenose dolphin sonar pulses are typically broad-band emissions of about 50 µs in duration, whose spectral shape can be altered to suit different sonar tasks (Au et al., 1974). Belugas appear to have a dual component sonar system, in which composite pulses of 1.6 and 60 kHz are emitted (Kamminga and Wiersma, 1981). Harbour porpoise (*Phocoena phocoena*), Dall's porpoise (*Phocoenoides dalli*) and Commerson's dolphin (*Cephalorhynchus commersonii*) are unusual in that their signals are *narrow*-bandwidth pulses which are centred around 120-130 kHz (Møhl and Andersen, 1973; Evans et al., 1988). Echolocation pulses are typically emitted in "trains" of a few to several hundred clicks. Normally these are spaced so that the previous pulse's echo returns before the next pulse is emitted (Au et al., 1982; for review see Turl and Penner, 1989), although this is not always true (e.g. belugas, Au et al., 1987).

There has been a further suggestion that Odontocetes may use intense sonar sounds to stun prey (Norris and Møhl, 1983). Berzin (1971) proposed acoustic stunning of prey after noting that few items of food from sperm whale stomachs bore tooth marks, and that even sperm whales with badly deformed lower jaws appeared healthy and well fed when caught by whalers. Additionally, sperm whale teeth do not erupt until sexual maturity, so clearly are not essential to feeding before then. Hult (1982) noted that captive bottlenose dolphins disorient schooling fish, apparently by using intense click trains. Maximum sound pressure levels of clicks made by a bottlenose dolphin attempting to detect a distant target were exceptionally high (220 dB re 1 µPa: Au et al., 1974, 1978), as were those made by a beluga in a similar experiment (218 dB re 1 µPa, Au et al., 1987). However, even these levels are about 10-25 dB below those required to stun fish (Zagaeski, 1987), so the validity of the prey-stunning hypothesis remains an open question (see also Mackay and Pegg, 1988).

It is probable that all dolphins and porpoises, and possibly all Odontocetes, echolocate (see Norris, 1969). Although bowhead whales (*Balaena mysticetus*) may be able to use surface reverberation cues while navigating under arctic ice (Ellison et al., 1987), it is unknown whether any of the Mysticetes or Pinnipeds echo-locate (Watkins and Wartzok, 1985).

3. The large brains (Morgane et al., 1986) and complex behaviour of some species (particularly delphinids; Conner and Norris, 1982; Würsig, 1986) suggests that they may possess a sophisticated communication system. It is generally assumed that most animal vocalisations are communicative (Sebeok, 1977), and that the meaning of sounds can be broadly deduced from the contexts in which they are made (e.g. Tyack, 1981; Clark, 1983; Sjare and Smith, 1986b). Right whales use different sounds in different behavioural contexts (Clark, 1982, 1983), and react more to playbacks of conspecific sounds than to other sounds (Clark and Clark, 1980). Humpback whales react differently to playback of conspecific social sounds and song (Tyack, 1983), and to sounds made on the summer feeding grounds and winter breeding grounds (Mobley et al., 1988). These studies show that, at least in humpback whales, different types of vocalisations have different communicative meaning.

   Few studies have addressed whether free-ranging Odontocetes use different sounds in different contexts. Sjare and Smith (1986b) showed a general association between sounds and behaviour in belugas. The number of click series varied with behavioural context and certain specific sounds (e.g. "squawks" and "blare-type" sounds) occurred most often in social contexts (Sjare and Smith, 1986b). Weilgart and Whitehead (In press) found that North Atlantic pilot whales (*Globicephala melas*) used different whistle types in different contexts. To my knowledge no published studies have attempted to confirm hypothesised meanings of Odontocete sounds via playback experiments.

There has been a prevalent, but usually unstated, assumption that dolphins use their often rich repertoire of audible sounds in communication (e.g. Lang and Smith, 1965) and their high-frequency pulses solely in echolocation. Researchers interested in communication have thus concentrated their energies on recording the sounds audible to them, ignoring the high frequencies. This approach is certainly easier, as audio recording equipment is readily available and much less expensive than wideband equipment. Whether the assumption is correct or not, Hector's dolphin is a particularly interesting species to study. Unlike many other dolphins, Hector's dolphin does not whistle. It has only two types of audible sounds, both of which are rare. Tonal sounds (called "cries" by Watkins et al., 1977) are caused by high-frequency pulses at fast repetition rates. The second type of audible sound is uncommon, and comprises broadband clicks in which the bottom emphases are audible. If there is acoustic communication between individual Hector's dolphins, it seems likely to involve their high-frequency clicks.

Previous acoustic work on *Cephalorhynchus*

The genus *Cephalorhynchus* comprises four species of small, coastal dolphins, each of which has an unusually limited distribution. Heaviside's dolphin (*C. heavisidii*) is restricted to the tip of South Africa. As its name suggests the Chilean dolphin (*C. eutropia*) occurs in Chile. Hector's dolphin (*C. hectori*) is found solely in New Zealand waters, and is largely restricted to South Island coasts. Commerson's dolphin (*C. commersonii*) is more widely distributed than the others, and occurs along Argentine coasts, in the Falkland islands, and has an apparently small, isolated population in the Kerguelen Islands in the Indian Ocean.

Description of the acoustic repertoire is a necessary precursor to any thorough investigation of how sounds are used. Prior to this study the only bioacoustic attention Hector's dolphin had received was Watkins et al.'s (1977) one day of recording in 1964 off Oaro (near Kaikoura) using audio equipment of very limited bandwidth (60 Hz to 10 kHz). They noted only a few tonal cries which represented the fast repetition rates of high-frequency pulses beyond the range of their equipment. As their equipment could not record the vast majority of Hector's dolphin's signals, their description provides a distorted picture of this species' sounds.

The acoustic behaviour of the other three species of *Cephalorhynchus* has also been neglected. Watkins et al. (1977) described the sounds made by four Heaviside's dolphins held temporarily in a rock pool. They noted low-level clicks with major emphases around 800 Hz and secondary emphases between 2 to 5 kHz, and "cries" caused by clicks with high repetition rates. They also reported that they had heard similar sounds in the presence of the Chilean dolphin. However, their inadequate recording equipment (as above) dictates that their descriptions of click characteristics need to be treated with extreme caution. Watkins and Schevill (1980) made similar observations from four captive Commerson's dolphins, but again the upper limit of the recording equipment (100 kHz) prevented recording the high-frequency clicks.

The sounds made by Commerson's dolphin are better known, chiefly because the species has been captured from South American waters and kept in captivity. Wideband recordings of these dolphins have been studied by Kamminga and Wiersma (1982) and Shochi et al. (1982). In addition, sounds from two groups of 6-8 free-ranging Commerson's dolphins were recorded by Evans et al. (1988) in the Falkland Islands. The three studies show that Commerson dolphin clicks are high-frequency single and double pulses centred around 120-130 kHz. Shochi et al. (1982) used two hydrophones, a very sensitive one optimised for low frequencies, and another (of necessity small, and rather insensitive) to capture high frequencies. They found a very weak, lower-frequency component of 1.6 to 2 kHz in the clicks, as well as the high-frequency component at 130 kHz. Their finding helps explain what was reported by Watkins et al. (1977).

Finding the free-ranging Commerson's dolphins of the Kerguelen Islands difficult to record, Dziedzic and DeBuffrenil (1989) captured two, which were kept in a floating metal cage while recordings were made. Even this recent study used recording equipment that could not faithfully record the spectrum of the high-frequency clicks (the recorder had a bandwidth of 120 kHz, while Commerson's dolphin signals are centred on 125 kHz [Kamminga and Wiersma, 1982]). Only the studies of Commerson's dolphins by Kamminga and Wiersma (1982), Shochi et al. (1982), Evans et al. (1988) and of Hector's dolphins by Dawson (1988; Chapter 1 in this thesis) have used equipment that could record the high-frequency sounds of these species with appropriate fidelity. None of these studies was extensive enough to allow investigation of whether different sounds are used in different contexts.

The high-frequency vocalisations of Hector's dolphins remained unrecorded until this study. The recording equipment I used has a minimum overall frequency response of 300 Hz - 150 kHz +/- 3 dB. Most of my recordings were made at a tape speed of 60 ips, in which case the upper frequency response was limited by the hydrophone (-10 dB at 200 kHz). To my knowledge this study is the first detailed, wideband study of the sounds made by free-ranging dolphins.

Acoustic factors affecting gillnet entanglement

Several researchers have suggested that gillnet entanglement is essentially an acoustic problem: That the dolphins are caught because their sonar cannot detect the nets (e.g. Awbrey et al., 1979; Gaskin, 1984; Hatakeyama, 1986a; Hembree and Harwood, 1987; Jefferson, 1987). This suggestion provided some of the motivation for my work on the physical characteristics of Hector's dolphin sounds as sonar signals, and also for my investigations of possible acoustic schemes to reduce gillnet entanglement.

Based on the assumption that cetaceans get caught in gillnets because they cannot detect them, two types of acoustic modification have been proposed (e.g. Awbrey et al., 1979). The first is to make gillnets more detectable by increasing their reflectivity to sonar. The second is to mark the nets with active sound emitters, which would warn of the net's presence. Although many researchers have suggested that net entanglement is an acoustic problem, few with an active interest in bioacoustics have become involved in net entanglement research. I believe that a combined bioacoustic and behavioural outlook has much to offer in deciding which management strategies are likely to be most effective in reducing entanglement.

Certainly the entanglement of marine mammals in gillnets is a major international conservation problem. Although most captures are of dolphins and porpoises, large cetaceans are also vulnerable to entanglement (e.g. humpback whales; Lien and Merdsoy, 1979). Gillnet fisheries cause the deaths of thousands of cetaceans per annum (e.g. Jones, 1984, Harwood et al., 1984; Harwood and Hembree, 1987). Perhaps as many as 500,000 to 1,000,000 cetaceans die in gillnets each year (Leatherwood, pers. comm.). Although the impact of such mortality on the species' population structure is unknown, the sheer numbers of cetaceans killed is cause for considerable concern. Of even greater concern are the stocks and species whose small populations appear directly threatened by gillnet entanglement (e.g. Gaskin, 1984; Diamond and Hanan, 1986; Hanan et al., 1986, 1987; Read and Gaskin, 1988; Barlow, 1986; see also Chapter 6). Net entanglement appears to be a general problem that arises wherever gillnets and cetaceans coincide.

The Thesis

This thesis is divided into three sections, and is written as a series of seven self-contained research papers, each in the format of the appropriate journal. This approach has led to some overlap in content. To minimise redundancy the references are in one section at the end of the thesis.

Section I. Physical characteristics of Hector's dolphin sounds

The primary focus of this section of the thesis is to provide a thorough analysis of the acoustic repertoire of Hector's dolphin. There are four manuscripts in this section. Chapter 1 provides the first description of the high-frequency signals of Hector's dolphin. Chapter 2 provides a detailed, quantitative analysis of the Hector's dolphin's acoustic repertoire, using digital signal processing techniques and multivariate statistical methods. Chapter 3 provides a detailed description of the techniques used to accomplish this and how they were automated, and describes some further features of Hector's dolphin's sounds. Chapter 4 applies theoretical techniques used for designing technological sonar and radar systems to determine the range and velocity resolution possible with Hector's dolphin sonar sounds. The motivation for this analysis was to better understand what sorts of targets Hector's dolphin sonar signals could resolve.

Section II. Sounds and behaviour

As we have seen above, the communication systems of cetaceans are of considerable interest. The results of the quantitative analysis (Chapter 2) were used to classify Hector's dolphin sounds into "types". While making the recordings analysed in Section I above, I also noted the behaviour of the group or individual being recorded from. In Chapter 5 I explore the communicative significance of the sounds by analysing whether certain sound types are used more often in particular behavioural or biological contexts.

Section III. Gillnet entanglement and its acoustic solutions

It is now clear that Hector's dolphin has been subject to an alarming level of incidental catch in coastal gillnets (Slooten and Dawson, 1988, and In press). I believe that a full understanding of the entanglement problem, and the identification of successful solutions to it, are difficult to reach without an understanding of dolphin sonar. There are two manuscripts in this section of the thesis. Chapter 6 reports the nature and magnitude of the incidental catch of Hector's dolphins in the Pegasus Bay/Canterbury Bight area. Chapter 7 analyses the logic and prospects for success of proposals to decrease entanglement via acoustic modifications to gillnets.

The seven manuscripts are followed by a brief set of general conclusions.

The division of labour in co-authored manuscripts of this thesis

As Section I contains three co-authored manuscripts it is appropriate for me to briefly describe the collaboration that produced them. To facilitate a thorough, quantitative analysis of Hector's dolphin sounds, I sought assistance from the Department of Electrical and Electronic Engineering at this University. Much of the work of Section I has been the result of an interdisciplinary collaboration between myself and William Thorpe, who is completing a PhD in signal processing. William's expertise enabled us to achieve a far more complete and detailed analysis of Hector's dolphin sounds than I would have been capable of on my own.

The division of labour was as follows: I made all of the recordings of Hector's dolphin sounds, and made written transcripts of all of the tapes. I chose a subset of sounds which co-occurred with observed behavioural events, and I did most of the digitising of them. Based on my preliminary analysis of the sounds (Chapter 1) William and I together decided what acoustic features we would measure. William wrote programs to measure these features and automated the programs so that a subset of sounds could be batch processed overnight. I conducted all statistical analyses of the measured data. All steps of the analysis were accompanied by a great deal of consultation between us.

William and I agreed from the outset that our interdisciplinary work should be written as two manuscripts, one with a biological focus, and one focussing on the signal processing aspects, and that we would swap senior authorship between them. As the focus of the "Quantitative analysis..." manuscript (Chapter 2) was biological, I did the bulk of its writing. Conversely, the "Automated measurement..." manuscript (Chapter 3) has a far more technique-oriented focus, so William did most of its writing. I contributed ideas, provided (or revised) several sections of the manuscript, and provided the descriptive statistics and histograms. As in the analysis phases, William and I conferred often during the writing and revisions.

Prompted by the entanglement of Hector's dolphins in gillnets, one of my original aims in this study was to learn something about the resolution capabilities of Hector's dolphin sonar signals. Professor Bates (of Electrical and Electronic Engineering) suggested the ambiguity function approach to the analysis of my data. William computed the ambiguity functions, and wrote the engineering-oriented parts of the manuscript. Professor Bates contributed ideas, guidance and revisions. I provided the recordings and wrote the biological parts of the manuscript.

All other parts of this thesis are solely my own work.

Section I. Physical characteristics of Hector's dolphin sounds

Chapter 1

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The High Frequency Sounds of Free-Ranging Hector's Dolphins, *Cephalorhynchus hectori*

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ABSTRACT

Wideband recordings of the sounds of *Cephalorhynchus hectori* were made over the austral summer of 1986/87. Analysis of these sounds shows them to be low-level, high-frequency, single and double pulses that occur in sequences of very variable repetition rate. The structure of these sounds has much in common with those described from *Cephalorhynchus commersonii* and the distantly related *Phocoenoides dalli*. Like *P. dalli*, *C. hectori* is often incidentally caught in gillnets and the similarity of these two species' sonar systems suggests that this type of sonar system is poorly suited to detecting monofilament gillnets.

INTRODUCTION

Hector's dolphin, *Cephalorhynchus hectori*, is a small, coastal delphinid which occurs only in New Zealand waters (Slooten and Dawson, 1988). It is usually found in small groups within 5 n.miles (9.2km) of the shore and its total population is estimated at between 3,000 and 4,000 individuals (Dawson and Slooten, 1988).

Until recently the only sound recordings made of any of the *Cephalorhynchus* genus were those made by Watkins, Schevill and Best (1977). They recorded the sounds of four Heaviside's dolphins, *Cephalorhynchus heavisidii*, that were temporarily held in a sealed-off rock pool near Paternoster Bay, South Africa. The sounds recorded were:

> 'clicks at slow and variable repetition rates, bursts of clicks at relatively constant rate but variable frequency emphases, and pulse series at a variable but rapid enough rate to produce a tonal 'cry' sound.' Watkins *et al.* (1977, p. 316).

They found only low-level pulsed sounds with a bandwidth less than 5kHz and often less than 2kHz, with major frequency emphases at around 800Hz and secondary, non-harmonic emphases at 2–5kHz. Watkins *et al.* also noted that they had recorded some similar sounds from Commerson's dolphin, *C. commersonii*, and from a group of *C. hectori* recorded off Oaro (42°34′S, 173°30′) near Kaikoura, New Zealand. As the equipment used for these recordings had a limited bandwidth of 60Hz–10kHz, they were unable to record the high-frequency sounds made by these species. Watkins and Schevill (1980) described similar sounds from four captive *C. commersonii* held temporarily at Mystic Marinelife Aquarium (Connecticut, USA) but again the upper frequency limit of their recording equipment (100kHz) prevented recording of the high-frequency sounds.

Studies of the high-frequency sounds have been made on only two of the species in the genus *Cephalorhynchus*, *C. commersonii* (Kamminga and Wiersma, 1981, 1982; Shochi, Zbinden, Kraus, Gihr and Pilleri, 1982; Hackbarth, Awbrey and Evans, 1985; Evans, Awbrey and Hackbarth, 1988) and *C. hectori* (this study). The high-frequency pulses of *C. commersonii* were found to be low-level, narrow band, single pulses with peak energy around 124kHz, and durations of 120 to 180µs (Shochi *et al.*, 1982). Similar conclusions were reached by Kamminga and Wiersma (1982). That the results of these two groups of researchers are similar is not surprising as they made their recordings from the same group of *C. commersonii* held at the Duisburg Zoo in Germany. Evans *et al.* (1988) report that this species produces two types of pulse, single pulses and double pulses. The single pulses recorded by Evans *et al.* (1988) seem to have been of slightly higher frequency (133kHz) than those of Shochi *et al.* (1982) and Kamminga and Wiersma (1982) and the pulses appear significantly longer (350-500µs).

METHODS

Recordings were made in Akaroa Harbour (43°50'S, 172°56'), on the south coast of Banks Peninsula, New Zealand (Fig. 1). Nine hours of vocalisations were recorded from free-ranging dolphins over the summer season of 1986/87. The sounds described here were recorded from a group of three dolphins that was playing with seaweed at the water surface. These recordings were made between 0802 and 0804 on 19 November 1986 and are typical of the sounds analysed from the rest of the tapes.

The recording system comprises a *Brüel and Kjaer* 8103 hydrophone, *Brüel and Kjaer* 2635 charge amplifier and a *Racal Store* 4DS recorder, operated at 60ips (152.4cm/s). The signal/noise ratio of this recorder is in the order of 40dB and the recording system has a frequency response that is essentially flat (±3dB) from 300Hz to 150kHz. As with the equipment of Evans *et al.* (1988), the upper end of this response is limited by the *B & K* 8103 hydrophone (-10dB at 200kHz). The equipment is battery powered and all recordings were made from a 4m inflatable boat. While the tape was running, a simultaneous behavioural commentary and timing information were dictated into another channel of the recorder. The settings of the signal input amplifier on the recorder were varied (and noted in the commentary) to avoid saturation.

Before detailed analysis, the tapes were transcribed at 1/16 speed using a *Multigon Industries Uniscan* II spectrum analyser. The transcripts provide a directory of sound type, location on the tape and intensity, along with a written version of the commentary. The tapes were analysed at 1/32 speed using a *Hewlet-Packard* 3561A 100kHz Dynamic signal analyser (analysing filter bandwidth 59.678Hz) with an *HP* 7470A plotter and *Gould* OS4000 digital storage oscilloscope. Several thousand pulses have been analysed using the *Unigon* analyser and 200 of these have been analysed in detail with the *HP* signal analyser and the oscilloscope.

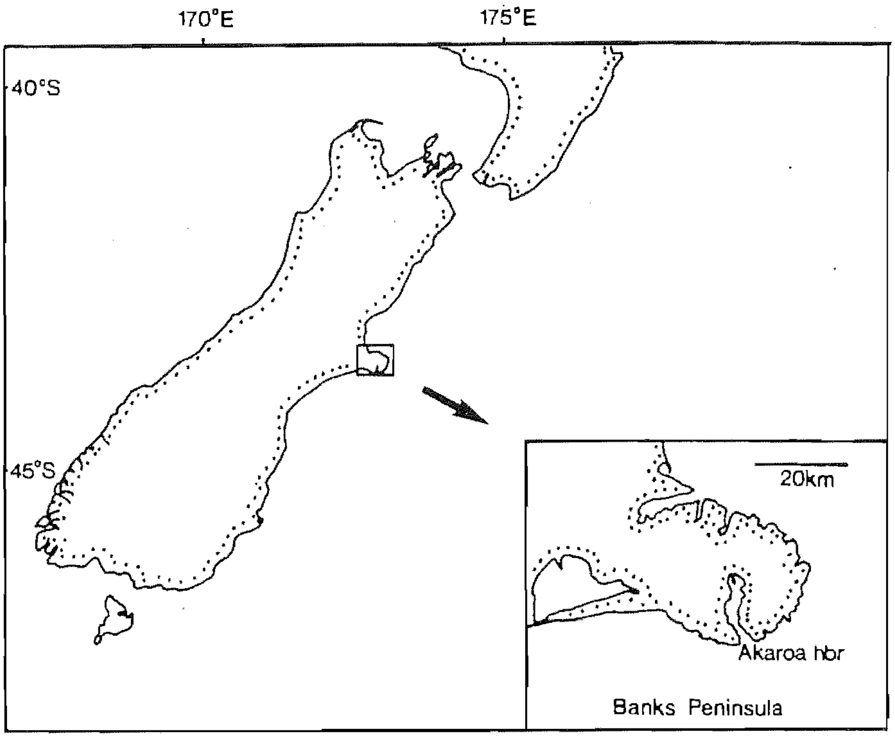

Fig. 1 Location of study site.

RESULTS

Being curious animals, Hector's dolphins are easy to approach, repeatedly coming to the boat to investigate the boat and hydrophone. They are also very vocal, so recording opportunities are frequent. The sounds are highly directional, however, and the examples reported here are from animals oriented directly at the hydrophone.

The recorded sounds are almost exclusively high-frequency pulses which, as in *C. commersonii* (Evans *et al.*, 1988), can be single or double pulses. A typical single pulse (Fig. 2) is centred around 120kHz. Of the pulses analysed in detail, the peak energy was always between 112kHz and 130kHz. Single pulses are usually less than 200µs long. The maximum sound pressure so far calculated (from a dolphin 1m from the hydrophone) was 150.7dB re 1µPA.

Double pulses (Fig. 3) occurred less frequently than single pulses. They are generally similar in their energy spectra and are approximately twice as long as single pulses, being usually less than 400µs in duration.

Both types of pulse occur in 'trains', series of pulses that can be extremely variable in length. The repetition rate of pulses within trains is also highly variable, ranging from about 2 to over 600 pulses per second, one of the highest rates recorded from a cetacean. Such high repetition rates generate the tonal 'cry' that Watkins *et al.* (1977) observed.

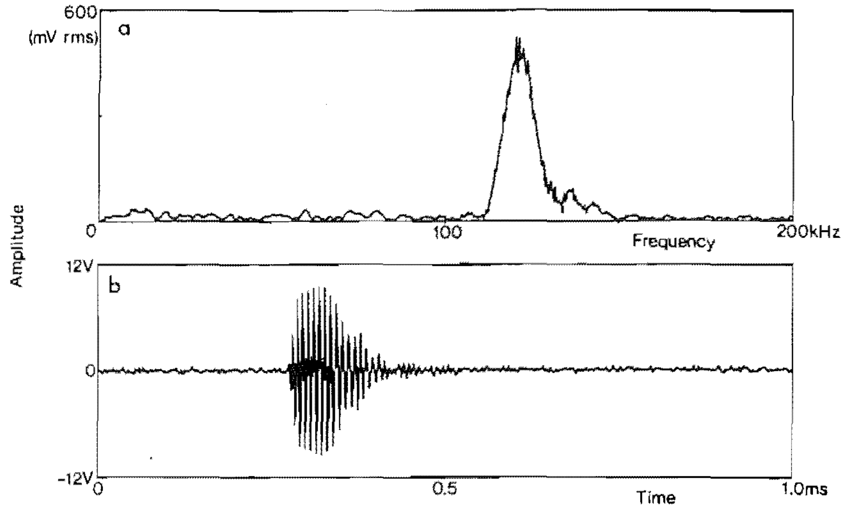

Fig. 2 Frequency spectrum (2a) and amplitude envelope (2b) of a single pulse.

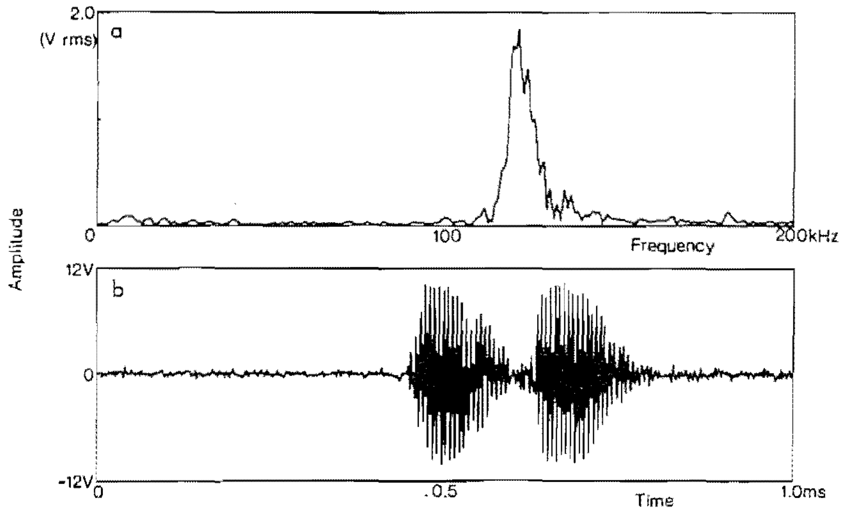

Fig. 3 Frequency spectrum (3a) and amplitude envelope (3b) of a double pulse.

DISCUSSION

While it seems certain that these high-frequency signals are used in echolocation, there is no *a priori* reason why this type of signal could not be used in intraspecific communication. Indeed the two aspects of echolocation and communication seem likely to be coupled, perhaps inseparably.

Kamminga and Wiersma (1981) showed that *Phocoena phocoena* and *Delphinapterus leucas* emit two-component sonar pulses consisting of a high-frequency and a low-frequency component. They, and Dudok van Heel (1981), suggest that the high-frequency component functions in food finding, while the low-frequency component may function in coastal navigation. Although Shochi *et al.* (1982) did find a weak low-frequency component in the clicks of *C. commersonii*, the work of Evans *et al.* (1988) and Kamminga and Wiersma (1982) indicates that the sonar pulses of *Cephalorhynchus commersonii* are single-component pulses. As in *C. hectori*, the energy within the pulses is concentrated in a narrow, high-frequency band, with almost no energy at lower frequencies. This would appear to be the basis of a sonar system tuned for fine discrimination and food-finding. Such a sonar system would be of limited value in coastal navigation, where a much lower dominant frequency, such as in the low-frequency components of *Phocoena* and *Delphinapterus*, would provide appropriate resolution and better range (Dudok van Heel, 1981). Hector's dolphins are non-migratory and individuals typically range over small areas close to the coast (Slooten and Dawson, 1988) which they probably know in great detail. In this habitat these dolphins would seem to have little need for the low-frequency navigational components.

In an evolutionary sense, the non-migratory coastal niche of this species (and probably all the *Cephalorhynchus* species) and the lack of a low-frequency navigational component in the sonar are possibly related. Although it could be that the niche of this species did not favour the evolution of a navigational component, it is equally possible that the non-migratory coastal niche was dictated by the lack of a low-frequency navigational component in the sonar system.

Double pulses similar to those emitted by *C. commersonii* were commonly recorded from *C. hectori*. In general, the double pulses are approximately twice as long as single pulses and appear to be formed by two single pulses of normal length (150–200μs), with the second pulse immediately following the first. This contrasts with the double pulses which Evans *et al.* (1988) described from *C. commersonii*, in which each pulse of the double pulse is approximately half the length of a single pulse. There are some discrepancies in the length of high-frequency pulses reported from *C. commersonii*. The single pulses described by Evans *et al.* (1988) are at least twice as long (350–500μs) as those reported by Kamminga and Wiersma (1982) and Shochi *et al.* (1982).

The annual incidental catch of Dall's porpoise, *Phocoenoides dalli*, in monofilament gillnets runs into thousands and is the best-known marine entanglement problem (e.g. Jones, 1984). Evans and Awbrey (1984) and Evans *et al.* (1988) have shown the clear similarities between the high-frequency pulses of *C. commersonii* and *P. dalli*, and suggested that these pulses appear to be well suited to finding targets on the bottom among clutter. They further suggest that monofilament gillnets might be disregarded as clutter by echo-locating dolphins and predict that entanglement in such nets is likely to be a problem for Commerson's dolphin and perhaps all of the *Cephalorhynchus* species.

Recent work has shown that Hector's dolphin is often entangled in monofilament gillnets (Slooten and Dawson, 1988; Cawthorn, 1988) and that in some areas this may give cause for concern. An understanding of the sonar system of Hector's dolphin is crucial to the development of management strategies to reduce the impact of net entanglement.

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Chapter 2. A Quantitative Analysis of the Acoustic Repertoire of Hector's Dolphin

ABSTRACT

The difficulty of obtaining accurate, repeatable measurements of the features of animal sounds has been a major handicap in the analysis of vocal repertoires. Automation of the measurement process would facilitate investigations which require the analysis of large samples of sounds. We developed an automatic, computer-based system in which digital signal processing techniques were used to measure 31 variables from digitised Hector's dolphin (Cephalorhynchus hectori) sounds. Principal component analyses of these data were used to investigate the relationships between sounds. Hector's dolphins make only a very few types of pulsed "clicks", most of which are centred around 125 kHz. None of these had an average frequency of less than 82 kHz, and the only audible sounds were made up of high-frequency clicks repeated at such high rates that the repetition rate was audible as a tonal "cry" or "squeal". In comparison to signal levels recorded from other cetaceans, all the Hector's dolphin signals were low-level; the maximum received sound pressure level was 163.2 dB (re 1µPa).

INTRODUCTION

Elucidation of the communication systems of delphinid cetaceans is of considerable interest because of the animals' large brains (e.g. Morgane et al. 1986) and complex behaviour (e.g. Conner and Norris 1982; Würsig 1986). Yet the acoustic repertoires of very few cetacean species have been analysed and described in detail. Whereas the frequencies of mysticete sounds seldom extend past the upper limit of human hearing, sounds of Odontocetes often contain ultrasonic components, which in some cases reach over 200 kHz (Norris 1969).

Many studies have described the sonar pulses and sonar performance of dolphins (e.g. Au et al. 1974, 1987; Turl et al. 1987), but few have attempted to analyse quantitatively the vocal repertoire of a dolphin species over the entire frequency range of its sounds. Also, to our knowledge, no study has attempted this with recordings gathered from free-living dolphins.

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by Stephen M. Dawson and C. William Thorpe. Submitted for publication.

Most studies of acoustic communication in Odontocetes have focussed on the signals that are audible to the human ear (e.g. Lilly and Miller, 1961a, Caldwell and Caldwell 1971; Ford and Fisher 1982). The reason for this is partly technological, as standard audio recording equipment is more readily available and much less expensive than wideband equipment. Also, many researchers seem to have assumed that the high-frequency pulses are used strictly for echolocation. Yet there is no obvious reason why high-frequency pulses could not be used in communication.

As recording of animal sounds has been limited by available equipment, so too has the analysis. In earlier studies, animal sounds were classified subjectively by human listeners (e.g. Thorpe 1966; Dreher 1966). The development of electronic instruments which produce a visual representation of the time and frequency components of sounds (e.g. the Kay sonograph, Potter 1945) allowed researchers to compare sounds pictorially. These sound spectrograms have been compared subjectively (e.g. Hultsch and Todt 1981; Marler and Peters 1981) and via measurement.

There have been several approaches to the problem of quantitatively comparing visual images of sounds. Many researchers have measured variables directly from the images (e.g. Sparling and Williams 1978; Dawson and Jenkins 1983). Others have digitised the printed image of the sounds using an overlaying grid (e.g. Miller 1979), graphics tablet (Clark 1982; Chabot 1988) or automatic image analyser (Pickstock et al. 1980). The resulting data are usually analysed using multivariate statistical methods (e.g Sparling and Williams 1978; Martindale 1980). In only the most recent studies have researchers digitised sounds directly via a computer and used digital signal processing techniques to analyse them (Goedeking 1983; Seyfarth and Cheney 1984; Clark et al. 1987; Owren and Bernacki 1988).

Hector's dolphin, the world's smallest cetacean, is restricted to the inshore coastal waters of New Zealand. Until recently this species' biology was poorly known (for review see Slooten and Dawson 1988) and had received little attention from bioacousticians. The only previous studies of Hector's dolphin sounds are those of Watkins et al. (1977) and Dawson (1988). Watkins et al. (1977) described some low-frequency "cry" sounds recorded from four Heaviside's dolphins (Cephalorhynchus heavisidii) held temporarily in a cemented-off rock pool, and noted that Hector's dolphins made similar sounds during one day of recording off Oaro (42° 34'S; 173° 30'E) near Kaikoura, New Zealand. As their equipment was incapable of recording frequencies higher than 10 kHz, high-frequency signals remained unrecorded until recently (Dawson 1988).

The present study is a quantitative analysis of the acoustic repertoire of Hector's dolphin, for which we used automated, digital measurement methods and multivariate statistical analyses. Such techniques allow the detailed examination and comparison of large numbers of sounds, and are useful tools for the biologist examining any question that requires quantitative comparison of sounds.

METHODS

Recording

Recordings were made in Akaroa Harbour (43° 50'S; 172° 56'E), and in the nearby inshore waters of the south coast of Banks Peninsula, New Zealand, over the summer seasons of 1986/87 and 1987/88. We used a Brüel and Kjær 8103 hydrophone, Brüel and Kjær 2635 charge amplifier, and a Racal Store 4DS recorder operated at a tape speed of 60 ips (152.4 cm/s) or 30 ips (76.2 cm/s). At these tape speeds, the recorder has a signal/noise ratio of 40 dB and a minimum frequency response of 300 Hz to 150 kHz (+/-3 dB). We used a Brüel and Kjær 4223 hydrophone calibrator to generate a reference level from which received sound pressure levels could be calculated.

Onto another channel of the recorder we dictated behavioural notes, timing signals, and the settings of the recorder's signal input amplifier, which varied to avoid saturation. Recordings were made in calm conditions (windspeed <10 knots) from a four-metre inflatable boat.

Analysis

We transcribed all tapes at 1/16 or 1/32 recording speed using a Multigon Industries Uniscan II spectrum analyser or Gould OS4000 digital storage oscilloscope to view the signals. Signal output was also fed to a Nagra IV-L tape-recorder operating in 'test' mode so that its calibrated modulometer could be used to read relative sound pressure levels. Transcripts provided a directory of the sounds, their location on tape, relative sound pressure level, and a written version of the commentary. During transcription, complete click trains with high pulse repetition rates (>200 Hz) were printed on the Uniscan analyser to determine pulse rate. To measure sound pressure levels, we re-examined the tapes with the highest signal levels using the oscilloscope. Replaying all tapes at the original recording speed allowed us to check for any audible sounds missed at slow replay speeds.

Using the transcripts as a guide, we chose 435 click sequences which had a high signal to noise ratio (SNR). An eight second segment of each sequence was then digitised at a tape replay speed 1/32 of the original recording speed and with a sampling rate of 20 kHz on a Vax 11/750 computer. Hence the effective sampling rate was 640 kHz and each digitised segment (record) corresponded to 0.25 s at the original recording speed. To avoid aliasing, we filtered the signals with a 48 dB/octave low-pass filter (Kemo VBF/8) with a cutoff frequency of 9 kHz, before they were digitized. Sounds were digitised with 12 bits precision (using a Digital LPA11/k D/A converter), which corresponds to a dynamic range of 72 dB. The digitised records were stored on magnetic tape.

Measurement

We measured features of the digitised sounds automatically using custom-written programs operating within a signal processing package on the Vax computer. The package (SIGPROC, developed by N. P. Briesman, C.W. Thorpe, and A. G. Elder, Electrical Engineering Department, University of Canterbury, New Zealand) currently runs only on Vax computers, and is available (for the cost of copying) to universities from the Electrical Engineering Department of Canterbury University. A detailed description of the measurement process, how we automated it, and of several other features we measured is available in Chapter 3.

Ultrasonic dolphin sounds are typically short pulses, with comparatively long periods between each subsequent signal. To calculate their properties, signals must first be separated from the intervening silent periods. We extracted each click by removing a 0.8 ms segment whenever a signal in the record exceeded a preset threshold (1/3 the maximum amplitude value of the record). This segment length (0.8 ms) was long enough to encompass all the useful features of a click, but short enough to avoid sampling overlap when click repetition rates were high. To ensure that the start of the each click was included, segments were positioned 0.05 ms before the time at which the preset threshold was first exceeded.

Any acoustic signal can be analysed with respect to its frequency components (frequency domain) or with respect to how the signal varies with time (time domain). Measurement of a signal in both domains simultaneously (e.g. by means of a spectrogram) results in compromised resolution of frequency or time measurements (Beecher 1988). To avoid this, our programs measured variables from the time and frequency domains separately.

Time Domain features

A label representing the tape number, tape side and counter index for the sound sample was recorded with each set of measurements. The number of clicks in each 0.25 s record was noted as the first variable.

From the clicks within each record, the programs calculated the average amplitude envelope (by means of an rms envelope detector) and measured variables which characterised the shape of that envelope. The programs counted and measured peaks that exceeded an arbitary threshold of 1/3 of the maximum amplitude of the envelope. For each of the four greatest peaks in the average envelope, the programs measured the amplitude of each relative to the first peak (A1, A2, A3, A4), time of occurrence of the peak since the start of the click (T1, T2, T3, T4) and how long it took the envelope to decay to an arbitary 40% of its maximum value (D1, D2, D3, D4).

Frequency Domain features

The major part of each click is generally much shorter than 0.8 ms. We used a shorter segment (0.4 ms) to calculate the spectral content of clicks because we wished to characterise the emitted click, rather than its subsequent reflections. This 0.4 ms segment was centred on the largest peak in the click envelope, and the fast Fourier transform (FFT) was used to calculate the spectrum (Brigham 1974). Only the magnitude of each spectral component was retained and in the remainder of this paper, "spectrum" refers only to the spectral magnitude.

Spectra for all clicks in a record were averaged together to give an average spectrum for each record, and, as for the time domain, the programs counted and measured any peaks >1/3 of the maximum spectral amplitude. Next we measured variables to characterise the profile of the average spectrum. For each of the four largest peaks we measured the peak frequency (PF1, PF2, PF3, PF4), amplitude (FA1, FA2, FA3, FA4), half-power bandwidth (W1, W2, W3, W4) and centre frequency (CF1, CF2, CF3, CF4). The half-power bandwidth is the width of the spectral profile at half the maximum power (magnitude^2) of that peak. The centre frequency is the frequency midpoint between the half-power points.

We also measured average frequency (AF) by treating the positive frequencies of the spectrum as a probability distribution function, and calculating the mean (see Wiersma 1982). The resulting measurement is similar to the peak frequency, but takes into account asymmetries in the spectrum.

We visually inspected stackplots of the waveforms of each pulse within each record, and the average envelope and average spectrum of each record (see Figs 4, 5) on a Vax graphics Workstation. This, and listening to the slowed-down sequences as they were being digitised, allowed us to identify records which contained overlapping pulses from several dolphins. These were discarded, leaving 401 records for statistical analysis.

Statistical analysis

To calculate descriptive statistics from the measured variables we imported the matrix of acoustic measurements into a spreadsheet on an Apple Macintosh SE microcomputer. Principal component analyses (PCA) were conducted using the Systat statistics package (Wilkinson 1987).

Not all measured variables were included in our PCAs. Some variables were measured for descriptive purposes (no. of clicks per record, no. of peaks in frequency domain, no. of peaks in time domain, and expected frequency of each record). As very few records had four peaks in either their average amplitude envelope (12 records) or their average spectrum (8 records), we omitted these measurements from the PCAs.

We used PCA as a descriptive technique to ascertain the similarity of sounds and to describe the dolphins' acoustic repertoire. PCA is a multivariate statistical technique that transforms a set of correlated variables into a new set of uncorrelated factors (Tabachnick and Fidell 1983). A major aim of PCA is to reduce the dimensionality of the dataset and so simplify the interpretation of its structure.

We applied the Varimax rotation to allow interpretation of the resulting factors. Component loadings give a measure of how well each variable correlates with each factor, and can be used to determine what each factor represents. Comrey (1973) suggested that a factor loading in excess of 0.55 respresent a "good" correlation between a measured variable and a factor. He rated factor loadings in excess of 0.63 as "very good" and those over 0.71 as "excellent". Following Comrey, we set 0.55 as an arbitary cutoff point in our intepretations of what factors represent.

RESULTS

Description of the sounds

Our 401 records contained a total of 7661 "clicks" (Fig. 1). The number of clicks within records ranged from one to 192 (median = 8). Mean interclick interval (within records containing more than one click) ranged from 1.3 ms to 164.5 ms (median = 27.6 ms).

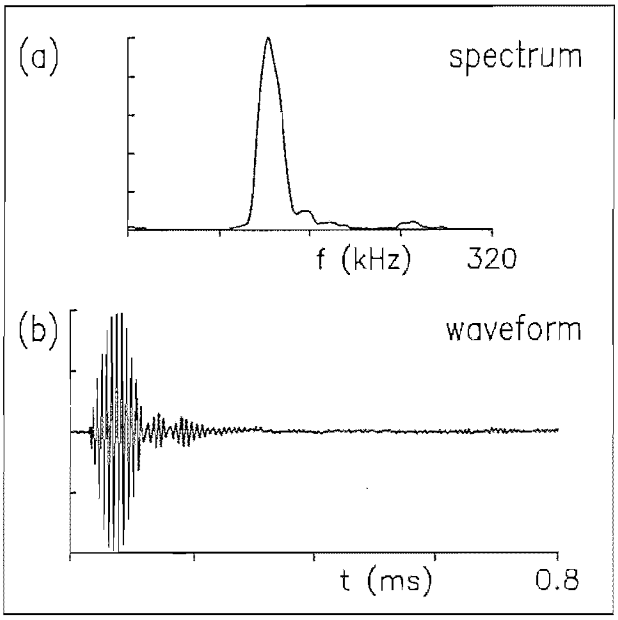

Fig. 1. Spectrum (spectral magnitude vs frequency) (a) and waveform (b) of a typical Hector's dolphin click.

Average frequency (AF) measurements showed that the digitised sounds were exclusively high-frequency (>82 kHz) "clicks". Most sounds

(92%) were in the range 115 -135 kHz and the highest average frequency of a record was 136.7 kHz (Fig. 2), while the highest freqency peak found in any record was 141.6 kHz. Records containing any frequency peaks below 100 kHz were rare (2.2%), as were records containing any frequency peaks in excess of 135 kHz (4.5%).

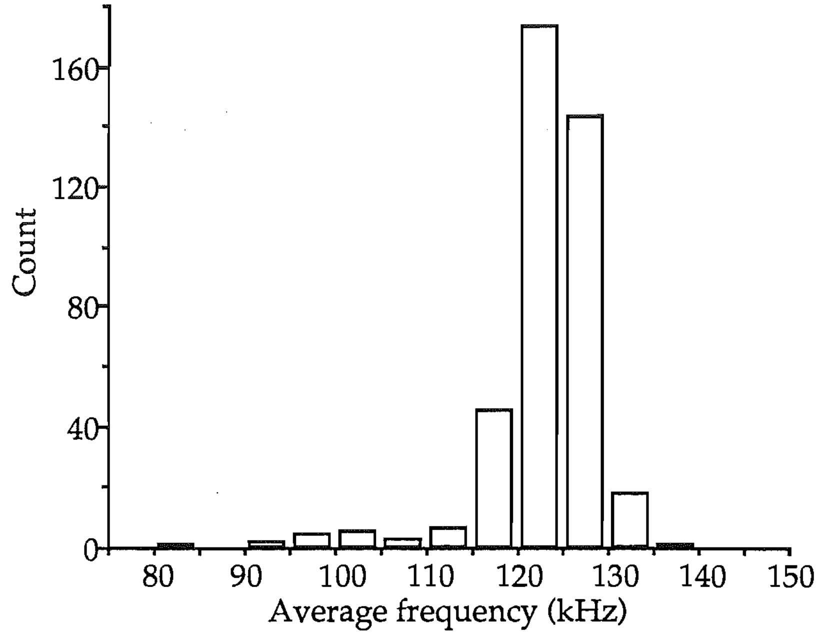

Fig. 2. Histogram of the average frequency (AF) of the 401 digitised records.

Most signals had a simple structure, with one (51.8%) or two (35.7%) peaks in the time domain. Few records contained clicks with more than two peaks in the time (12.5%), or frequency domains (8.0%). Our measurement process characterised the profile of the average amplitude envelope and of the average spectrum by measuring features of the first four peaks in these domains. Fewer than 2% of the records had more than four peaks in either of these domains.

Total pulse length (defined as the time from the start of the pulse to the time at which its last peak had decayed to 40% of its maximum value) ranged from 87.5 µs to 800 µs. This latter pulse length was the only one that our 0.8 ms window could not fully accomodate. Most pulses (96.2%) were between 100 - 600 µs long (see Fig. 3; median = 137.5 µs).

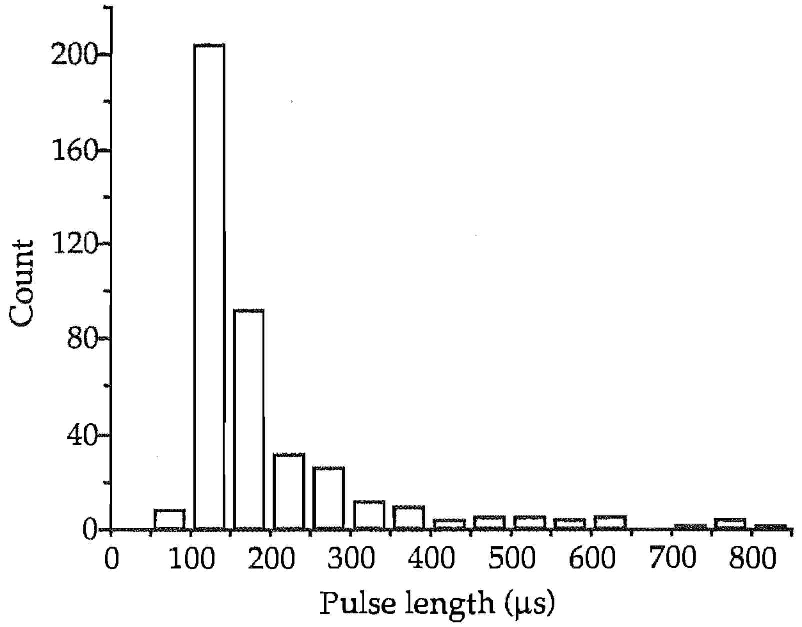

Fig. 3. Histogram of total pulse length of the 401 records.

The maximum sound pressure level received at the hydrophone was 163.2 dB (re 1 μPa). Only two click sequences were received at levels over 160 dB. Both were recorded within one minute of each other, from a group of dolphins milling around the boat while feeding at the surface on yellow-eyed mullet Aldrichetta forsteri. No precise calculation of source level is possible because we could not ascertain which individual made the sounds, but the closest dolphins were within 4 m of the hydrophone. In cases where the distance of the phonating dolphin from the hydrophone could be estimated (<5m), and the animal was oriented towards the hydrophone, source levels were typically around 150 dB (re 1 μPa at 1m).

Our tapes contained no audible sounds such as the whistles and burst-pulse sounds that have been described from bottlenose dolphins and other species (e.g. Lilly and Miller 1961a, b; Lang and Smith 1965; Caldwell and Caldwell 1971). The only audible sounds on the tapes were "squeals" made up of high-frequency pulses at extremely fast repetition rates (i.e. when 125 kHz pulses are repeated at a pulse repetition rate of 1000 Hz, a 1000 Hz tone is heard, even though the high-frequency pulses themselves are not audible to the observer). There were nine occasions on which pulse rates rose above 600 Hz, the highest pulse rate being 1149 Hz. These high pulse repetition rates generate a tonal "cry" or "squeal" very similar to the high pulse rate sounds previously recorded from Hector's dolphin and a congener, Heaviside's dolphin, by Watkins et al. (1977) and from other species (e.g.

Phocoena phocoena, Schevill et al. 1969; Neomeris phocoenoides; since renamed Neophocaena phocoenoides, Mizue et al. 1968).

Statistical analysis

PCA for the time domain

To explicitly include variables expressing the timing of the peaks relative to each other, we included the time differences between the peaks (dT21, dT31, dT32) obtained by simple subtraction (T2-T1, T3-T1, T3-T2). This was necessary because peak positions are not relevant unless referred to each other.

PCA of 11 variables from the time domain (T1, D1, A2, T2, D2, A3, T3, D3, dT21, dT31, dT32) revealed three significant factors (eigenvalue >1) accounting for 74.6% of the total variance after varimax rotation. As amplitudes were measured relative to that of the first peak, A1 was necessarily a constant (1.0) and not included in the PCA.

Factor loadings (Table I) show that factor 1 represents the amplitude and time of the third peak, and the timing of the third peak relative to the first and second peaks. Factor 2 represents characteristics of the second peak and the timing of it with respect to the first. Factor 3 represents the decay rate of the first and third peaks.

Table I. Rotated PCA Factor loadings for the time domain analysis. High correlations between variables and factors are accentuated in bold type.

variable	Factor 1	Factor 2	Factor 3
T1	-0.073	-0.041	0.456
D1	0.129	0.065	**0.725**
A2	0.240	**0.723**	0.380
T2	0.110	**0.977**	-0.015
D2	0.305	**0.642**	0.458
A3	**0.775**	0.171	0.425
T3	**0.965**	0.191	0.056
D3	-0.001	0.107	**0.703**
dT21	0.057	**0.932**	-0.168
dT31	**0.960**	0.185	-0.060
dT32	**0.936**	0.040	-0.135
Variance explained	31.98%	26.15%	16.50%

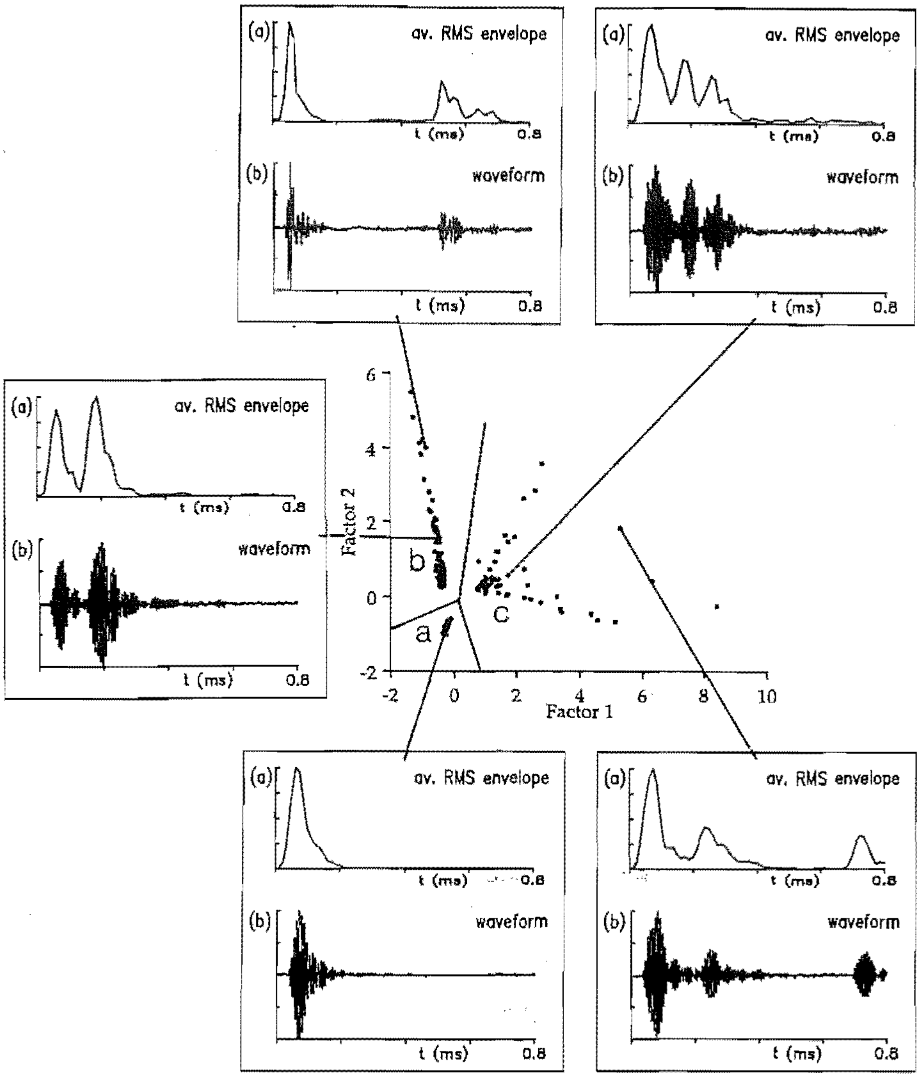

Fig. 4. A plot of the first two principal components of variables measured in the time domain. The average amplitude envelope (amplitude vs time) (a) and a typical waveform (b) are given for five example records.

In a plot of the first two factors (Fig. 4), which accounts for 58.1% of the total variance, sounds are positioned according to their number of peaks, and the relative separation of those peaks. The dense cluster of points at bottom left (region a) represents simple sounds that all have one peak in the time domain. Immediately above that group (region b) are sounds with two peaks in the time domain. These are spread along the axis of Factor 2 according to the separation of the two peaks; sounds positioned low on factor two have small time differences between their first and second peaks while those high on factor 2 have large time differences between the first two peaks. Region (c) contains sounds with three peaks in the time domain. These sounds were less common and are spread along the axis of factor 1 according to the separation of the third peak from the first and second peaks.

PCA for the frequency domain

As in the time domain PCA, we included variables expressing the frequency differences of the peaks relative to each other (dF21, dF31, dF32) obtained by subtraction (PF2-PF1, PF3-PF1, PF3-PF2).

PCA of 16 variables from the frequency domain (PF1, FA1, W1, CF1, PF2, FA2, W2, CF2, PF3, FA3, W3, CF3, dF21, dF31, dF32) revealed four factors accounting for 86.2% of the total variance after rotation.

Table II. Rotated PCA Factor loadings for the frequency domain analysis.

variable	Factor 1	Factor 2	Factor 3	Factor 4
PF1	-0.260	-0.186	**-0.878**	-0.215
FA1	0.014	-0.011	-0.136	**-0.710**
W1	0.220	0.199	-0.056	**0.791**
CF1	-0.170	0.040	**-0.960**	0.052
PF2	0.043	**0.962**	0.106	0.152
FA2	0.014	**0.808**	-0.096	-0.225
W2	0.218	**0.766**	0.140	0.441
CF2	0.068	**0.958**	0.114	0.158
PF3	**0.969**	0.075	0.170	0.072
FA3	**0.852**	0.125	-0.092	-0.125
W3	**0.862**	0.034	0.227	0.306
CF3	**0.967**	0.074	0.177	0.078
dF21	0.048	**0.644**	**0.690**	0.093
dF31	**0.657**	0.008	**0.683**	0.052
dF32	**0.854**	0.025	0.406	0.168
variance explained	31.37%	24.01%	19.97%	10.88%

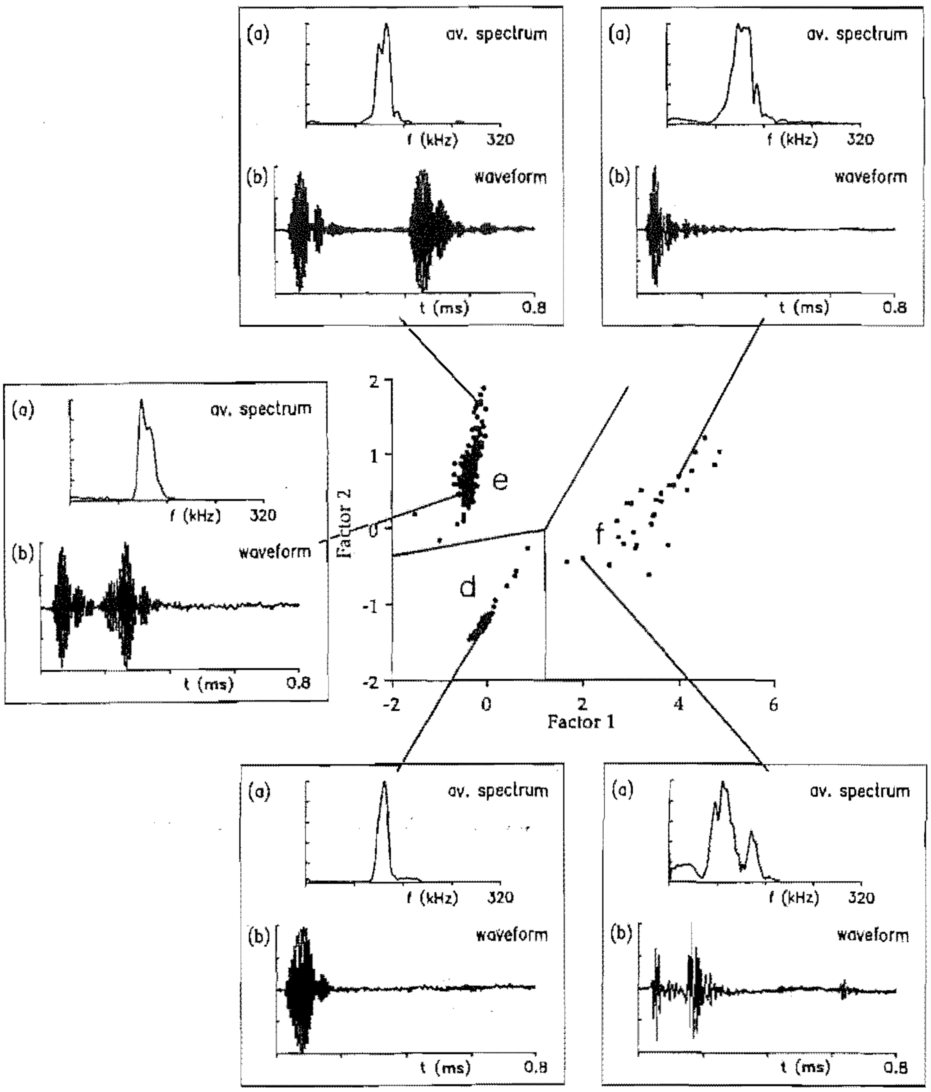

Fig. 5. A plot of the two principal components of variables measured in the frequency domain. The average spectrum (spectral magnitude vs frequency) (a) and a typical waveform (b) are given for five example records.

Factor loadings (Table II) show that factor 1 represents characteristics of the third frequency peak and the frequency difference between the third and the other two peaks. Factor 2 represents characteristics of the second peak and the frequency difference between the first and second peaks. Factor 3 represents the peak and centre frequencies of the first peak, and the frequency differences between the second peak and other two peaks. Factor 4 represents the amplitude and the width of the first frequency peak.

In a plot of the first two factors (Fig. 5), which accounts for 55.4% of the total variance, sounds are represented largely according to the number and characteristics of the frequency peaks. Sounds which have no significant second peak are grouped in a tight bunch at the lower left of the plot (region d). Above this group is a more diffuse group of points (region e) which are signals with two large frequency peaks. All signals in both these groups were narrowband. Sounds with three large frequency peaks were uncommon, and are spread along factor 1 towards to right of the plot (region f). These points represent sounds with complex, multi-peaked spectra of broader bandwidth than any of the other sounds (see Fig. 5).

DISCUSSION

Compared to signal levels recorded from other Odontocetes, all of the sounds we recorded from Hector's dolphins were low-level. Similarly low sound levels have been measured from a congeneric species, Cephalorhynchus commersonii (Awbrey, pers. comm.). Much higher levels (>218 dB) have been recorded from bottlenose dolphins (Tursiops truncatus) and beluga (Delphinapterus leucas) that were attempting to detect distant targets (Au et al. 1974, 1978, 1987). These high levels may represent the maximum bottlenose dolphins and beluga are capable of, and measurements outside the context of such long-range sonar experiments typically reveal much lower sound pressure levels (Norris and Møhl 1983).

Our principal component analyses summarise the structural differences between the many clicks we measured, and provide a way to describe and compare the sounds in a repeatable, accurate and relatively objective way. We initially attempted a PCA based on a combination of both time and frequency variables, but this resulted in so many significant factors that the variation in the signals was not reducible to the two or three dimensions necessary for visual representation. The separate PCAs of time domain and that of the frequency domain as illustrated here were successful, and arranged signals according to their number of peaks, their characteristics, and their positioning. This is intuitively satisfying, because these are obvious and easily recognisable features which have relevance in a sonar (or communication) context. Current models of cetacean perception suggest that sounds are percieved largely according to the shape of their time domain and spectral envelopes (Altes 1988; Au 1988).

Clicks consisting of one pulse immediately followed by another have been termed "double pulses" by Evans et al. (1988) and Dawson (1988). Both these studies created this category subjectively rather than via quantitative analysis of large samples of pulses. Some workers have suggested that "double pulses" are artefacts, caused by the single pulses of two dolphins overlapping, or by an echo arriving at the hydrophone after the original signal (Au, pers. comm.). While this is undoubtedly true in some cases, during transcription we found long sequences of double pulses in which the timing and the structure of the second pulse was stable relative to the first pulse, strongly implying that only one dolphin was responsible. This also argues against the hypothesis that the second pulse is an echo of the first; because our dolphins were unrestrained and moving, the delay of their echoes would change as they moved with respect to their sonar target.

In a much smaller sample of pulses examined by Dawson (1988) it appeared that "single pulses" were usually less than 200μs long and "double pulses" were approximately twice as long, being usually less than 400μs. We therefore expected to find a tight group of double pulses in the time domain analysis. However the signals with two peaks in their envelopes did not form a tight bunch, but spread out according to the separation of the second pulse from the first (see Fig. 4). Also, the histogram of total pulse length (Fig. 3) is not bimodal, which it would be if there was a standard type of double pulse. This suggests that the timing of the second pulse is as important as the prescence of the second pulse. This accords well with the observation of Au and Moore (1988) that the spacing between pulses is an important facet in dolphin acoustic perception. It also ties in with the "time separation pitch" model of Hammer and Au (1980) in which the spacing of of multiple pulses in a click echo is used to identify targets.

The ambiguity functions of Hector's dolphin clicks recorded during this study are presented in Chapter 4. They show that the signals are well suited for range resolution, but, unlike the signals of some bat species, are poorly suited to resolution of target velocity. All of the signals were doppler insensitive; none had any practical velocity resolution. If variations in pulse structure are not to provide velocity information, there are three other possibilities. Different pulse types could enable the transmission of more powerful pulses for longer range sonar (multi-pulse clicks), to enable better target recognition by altering the pulses to suit the target, or to fulfil some communicative role.

It could be argued that much of the variation we have reported here could be explained by the dolphin's orientation to the hydrophone. Work on several Odontocete species has shown that sonar pulses are not emitted equally from all parts of a dolphin's head, but are generally projected forwards in a beam, often called the "sonar field" (e.g. Au et al. 1978, 1986, 1987; Pilleri et al. 1983). Au et al. (1987) showed that the structure of a single emitted sonar pulse of a beluga varies considerably with the position in the sonar field from which the pulse was recorded, and that only those pulses that are recorded from at or near the axis of the sonar field are recorded with fidelity.

While it is possible to get a high signal to noise ratio (SNR) "off-axis", in our experience this was very rare. While recording, we noticed many times that when a dolphin turned slightly away from the hydrophone, the SNR dropped markedly. Therefore our inclusion of only very high SNR sounds in the analysis would have eliminated most "off-axis" signals, and maximised the chance of capturing undistorted signals. Furthermore, "on-axis" signals are characterised by "clean", symmetrical waveforms without abrupt phase changes, while the waveforms of signals recorded off-axis are "chaotic" (see Fig. 4 in Au et al. 1987), and of lower intensity. In each group of both the time and frequency domain analyses we have many signals whose "clean", undistorted structure indicates they were not recorded "off-axis", and that the variation in signal structure is real, not merely an artefact of orientation. This is why we have included representative waveforms in Figs 4-5.

Our digital/statistical approach to the analysis of sounds has several advantages. It is a more direct approach than the spectrographic measurements that have been used in the past, in that the computer makes the measurements directly from digitised sounds. This removes the need to "turn sounds into pictures" before measuring variables from the printed images. This is an important advantage because traditional analysis instruments (e.g. the Kay Sonagraph) may distort features of sounds by forcing variation in sounds to be displayed in only two dimensions, often with emphasis on the timing components rather than frequency. This reduced dimensionality may obscure important aspects of sounds and their information content. Also, instruments that simultaneously analyse both frequency and time force a compromise in the measurement resolution obtained from each domain (Beecher 1988). Our measurements were obtained separately from the time and frequency domains and so are not subject to this compromise.

Another advantage of the digital/statistical approach is the removal of measurement error that may be introduced by a human inconsistently measuring variables from printed images of sounds. Our methods provide a repeatable and relatively objective analysis technique, that if reapplied to the same data, always give the same answers. This is not always true of classification systems that rely on subjective judgements of similarity by a human analyst.

Disadvantages of this approach are that the investigator must decide what variables to measure, and must ensure that the system measures those variables properly. The variables to be measured should be chosen so that they characterise the sounds appropriately. We attempted to avoid problem by measuring features that describe the actual form of the signal, and will show that accurate reconstructions of the original signals are possible from the measured data used here (see Chapter 3). However, there are inevitable compromises in any system that attempts to characterise a sound with a few measurements. For example, the application of thresholds (above which a feature is measured) can occasionally cause two similar sounds to be classified differently (i.e. if one has a feature that is just over the threshold, while the other has the same feature just under the threshold).

As the investigator is "removed" from any automatic measurement process, we found it essential to check carefully the measured data and the nature of signals that make up the groups and outlying points in the statistical analysis. There is a danger that a mistake in the data acquisition or measurement process may cause the statistical analysis to produce a result indicating that the mistake was a new and different category of sound. Provided checks are made, the "digital/statistical" approach allows a more objective analysis of much larger datasets in greater detail than is possible via the labour intensive process of manually measuring variables from printed images.

Although few studies have used digital signal processing techniques to analyse animal sounds, there are already different approaches that suit different research questions. We used a variable-based comparison system, in which we chose the variables we wished to measure, then developed software to automatically measure them. If one is attempting a quantitative analysis and description of an unknown repertoire, we believe that this approach is superior, as the variables quantify familiar aspects of sounds that are easy for researchers to conceptualise, measured in their appropriate units (e.g. kHz or μs).

Using a different digital/statistical approach, Clark et al. (1987) developed an elegant system to measure the similarity of sounds, and used this to describe the process of song development in swamp sparrows. Their "sound comparative method" results in a single (ordinal) number assessing the similarity of two sounds. Series of such comparisons form a similarity table that can be analysed with multivariate statistical or graphical methods. If one is interested in questions associated with quantifying the similarity of sounds, the "sound comparative method" is an excellent approach.

Another approach uses vocal tract modeling techniques developed by electrical engineers for the analysis of human speech (Flanagan 1972). These techniques include LP (linear predictive) modeling (Markel and Gray 1976), which has been used to characterise features of vervet monkey alarm calls (Owren and Bernacki 1988). We experimented with these techniques, but adopted a measurement system based on many different variables because of the problems involved with LP analysis of such narrow-band signals (Markel & Gray 1976; see also Chapter 3).

We were surprised by the apparent simplicity of the Hector's dolphin repertoire. We recorded no audible whistles or burst pulses such as those of bottlenose dolphins, and found only a few different types of high-frequency click. Many delphinids have a relatively rich repertoire of audible signals, yet the only audible Hector's dolphin sounds are "cries" (caused by high-frequency pulses repeated at such high repetition rates that the pulse repetition rate itself becomes audible), and the lower-frequency emphases of rare broadband clicks. The apparent simplicity of the Hector's dolphin's repertoire argues against the hypothesis that these dolphins use acoustic signals as the basis of some kind of "language". If sounds are used by the dolphins to label different objects or contexts, we would have expected to find many more different types of sounds.

Most pulses within our 401 records had a very simple structure, and were consistent with the hypothesis that they are used chiefly, if not entirely, for echolocation. However it is possible that such signals could be used in communication between individuals. One intriguing possibility is that listening dolphins may be able to gather information from other dolphins' sonar echoes (See Chapter 5). Given their ability to process their own signals we would be surprised if they could not interpret (at least to some extent) the echoes resulting from another individual's use of sonar. If this is so, then the boundary between echolocation and communication is fuzzy indeed.

The difficulty of quantitative analysis and comparison of animal sounds has severely handicapped studies of acoustic behaviour. Our development of objective, automatic measurement techniques has, in combination with multivariate statistical methods, facilitated a much more detailed analysis of Hector's dolphin sounds than would have been possible via previous manual methods. We believe that the development of such techniques is an important advance towards an understanding of animal signals and their significance.

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Chapter 3. Automatic measurement of descriptive features of Hector's dolphin vocalizations

Abstract

The reliable and accurate measurement of descriptive features which enable the statistical comparison of animal sounds has been a persistent problem in bioacoustics. A computer-based measurement system was developed and written in a signal processing language (SIGPROC), to analyze the acoustic repertoire of Hector's dolphins (*Cephalorhynchus hectori*). This automated system allowed us to easily measure the descriptive features from 401 samples of the dolphins' sounds. The reliability of the measurement procedure was confirmed by reconstruction of some original sounds from their measured features. The analysis revealed that Hector's dolphins make only a few types of sounds, mostly simple high-frequency and narrow-band "clicks". A few examples of wide-band clicks were found, as was a sound comprising two frequency components.

1. Introduction

One approach to the study of an animal's vocal repertoire is to extract features from representative examples of the sounds and compare them, so that the sounds may be classified. Ideally, the process of extracting and comparing features should be objective, quantitative and repeatable.

In early studies, animal sounds were described by the subjective impressions of human listeners, and classified according to the resulting set of subjective features (e.g. Dreher, 1966). However, the results so obtained are not repeatable, and the human processing that is required limits both the number of sounds that can be studied (due to fatigue and time limitations) and the types of features that can be used (to those distinguishable by human hearing).

Later studies compared sounds according to pictorial representation of their time and frequency components in the form of sound spectrograms. Many of these studies compared the spectrograms subjectively (e.g. Hultsch and Todt, 1981). Although this approach allows the use of more features than simple listening does, the other problems remain.

There have been several approaches to the problem of quantitatively comparing spectrograms. Many researchers have measured variables

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by C.W. Thorpe and S.M. Dawson. Submitted for publication.

directly from the images (e.g. Dawson and Jenkins, 1983). Others have digitised the hard copy of the sounds using an overlaying grid (e.g. Miller, 1979), graphics tablet (Clark, 1982; Chabot, 1988) or automatic image analyzer (Pickstock et al., 1980).

These approaches to quantifying sounds are laborious. Also, in an earlier study (Dawson and Jenkins, 1982) we often found it difficult to ensure consistency of manual measurements from sonograms. A few recent studies have digitised sounds directly and used digital signal processing techniques to extract features for analysis (e.g. Clark et al., 1987). Because of its removal of inconsistencies, and its ability to measure many features from large samples of sounds, this approach greatly facilitates the quantitative comparison of sounds.

In the present study, we used programs written in a high-level signal processing language to automatically measure features (both in the time and frequency domains) from 401 digitised sequences of Hector's dolphin sounds, containing 7661 individual clicks.

This paper discusses quantitative measurement of the features, and the implementation of an automatic system to measure those features. A fuller report of the other aspects of the study, including our protocols for recording the sounds, the statistical analysis and the resulting classifications, is presented in Chapter 2.

Section 2 of this paper discusses some of the problems of measuring features that adequately and realistically describe sounds. In Section 3 we present a qualitative description of the sounds themselves, together with the features that we used to describe them. We introduce our signal processing language, Sigproc, in Section 4, and in Section 5 we describe how we used it to automatically calculate and quantify features from all the sample sounds. The results obtained are briefly outlined in Section 6, and we offer some conclusions and comments on automatic feature measurement in Section 7.

2. General considerations of feature measurement schemes

For a classification of any group of items to be meaningful, the features that characterize different items in the group must be relevant in the context of those items. In some fields this is readily accomplished. In speech recognition, for example, we are able to identify what features are important for recognising words, both because of our intuitive knowledge arising from our own use of speech, and from the relative ease of experimentation to test the importance of different features. However, the problem of choosing relevant features becomes more acute in the analysis of animal sounds, because we seldom know the meaning of the sounds to the animal or the auditory and cognitive processing by which they are heard.

In such cases, probably the only reasonable approach is to use features which describe the form of the signal itself. To compare dolphin sounds we employed 43 measurements, each of which characterized a particular feature of the time or frequency representation of the signals. The appropriateness of our measurement scheme was confirmed by our use of simple reconstruction techniques to closely approximate the shape of the original pulses from the measured data.

After a set of relevant features has been chosen, the practical problem of performing the measurements remains. A signal processing package (see Section 3) allowed us to write programs to measure the chosen features. Trial runs on a subset of the data were checked to ensure that the measurement techniques were able to accommodate the variety of signals that we encountered, and the aforementioned reconstructions confirmed that the measurement programs were accurate.

It is obvious that any measurement scheme should attempt to minimise measurement errors. Although an automated measurement system avoids errors due to human inconsistencies, the "removal" of the investigator from the measurement process means that a mistake in data acquisition or measurement may not be obvious. In addition to the reconstructions, we attempted to minimise this possibility by listening to each sound as it was digitised, and by visually inspecting the processed signals on a graphics workstation.

3. Qualitative description of the sounds and their features

Sounds were recorded from free-ranging dolphins, and 401 records (each 0.25 seconds in length) were digitised at a sampling rate of 640 kHz. Details of the recording and sampling techniques can be found in Chapter 2.

Examples of the sounds that we encountered in the study are shown in Figs 1 to 3. In Fig. 1 the envelope profiles for two of the sound records are drawn. This shows that the clicks are extremely short compared with the inter-click interval. The interval between clicks varied from about 1 ms to 160 ms (median = 27 ms).

In order to examine more closely the features of the clicks, we extracted the individual clicks from each record. The waveforms of representative clicks are shown in Figs 2 and 3, together with their envelope profiles and plots of their spectra. Most of the clicks are short, narrow-band signals with a dominant frequency of approximately 120 kHz, and contained within an envelope consisting of one or more peaks spread over 100 to 600 µsec (Figs 2 and 3).

The following discussion of the descriptive features is qualitative only, and we refer readers to Appendix A for the details of our measurement procedure. For each of the features discussed here, we indicate which step in Appendix A describes its measurement.

Three general features which describe the signals are evident from Figs 1 to 3. The first feature consists of the inter-click interval, which varies widely between records, and may increase or decrease within a record (see steps 1, 2 & 3 in Appendix A).

The second feature is the envelope profile of each click. This can be affected by echoes and multipath distortion and must be examined with caution. However, by averaging the envelope profile for each click in a record, the effects of echoes are minimised, since they vary with time and hence tend to cancel out. The shape of the envelope profile is described by quantifying the amplitude, width (or decay time) and position of each of the individual peaks (step 4).

The third feature describes the frequency components of the signal. As stated above, most of the signals were narrow-band. A simple way to characterize such signals is by their dominant frequency and half-power bandwidth. Signals having a more complicated spectral shape (see Fig. 3) were characterized by measuring the amplitude, frequency and width of several of the larger peaks in the spectrum (steps 5, 6 & 8).

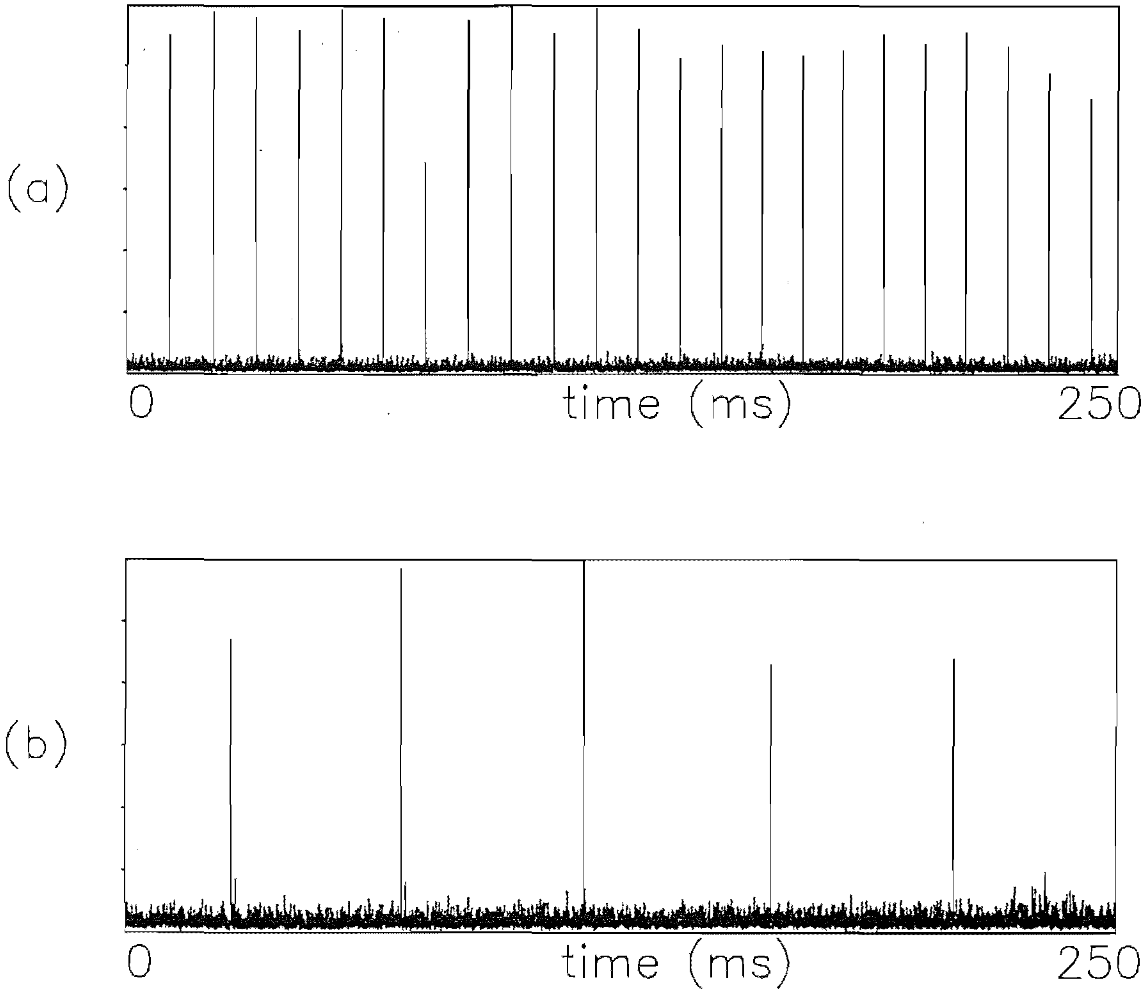

Figure 1. Envelope profiles for 0.25 second long sonar pulse trains. **a**: 10 ms and **b**: 50 ms inter-click interval. The y axes of Figs 1-5 and 9-10 are linear, but uncalibrated, as the amplifier used during digitizing was uncalibrated.

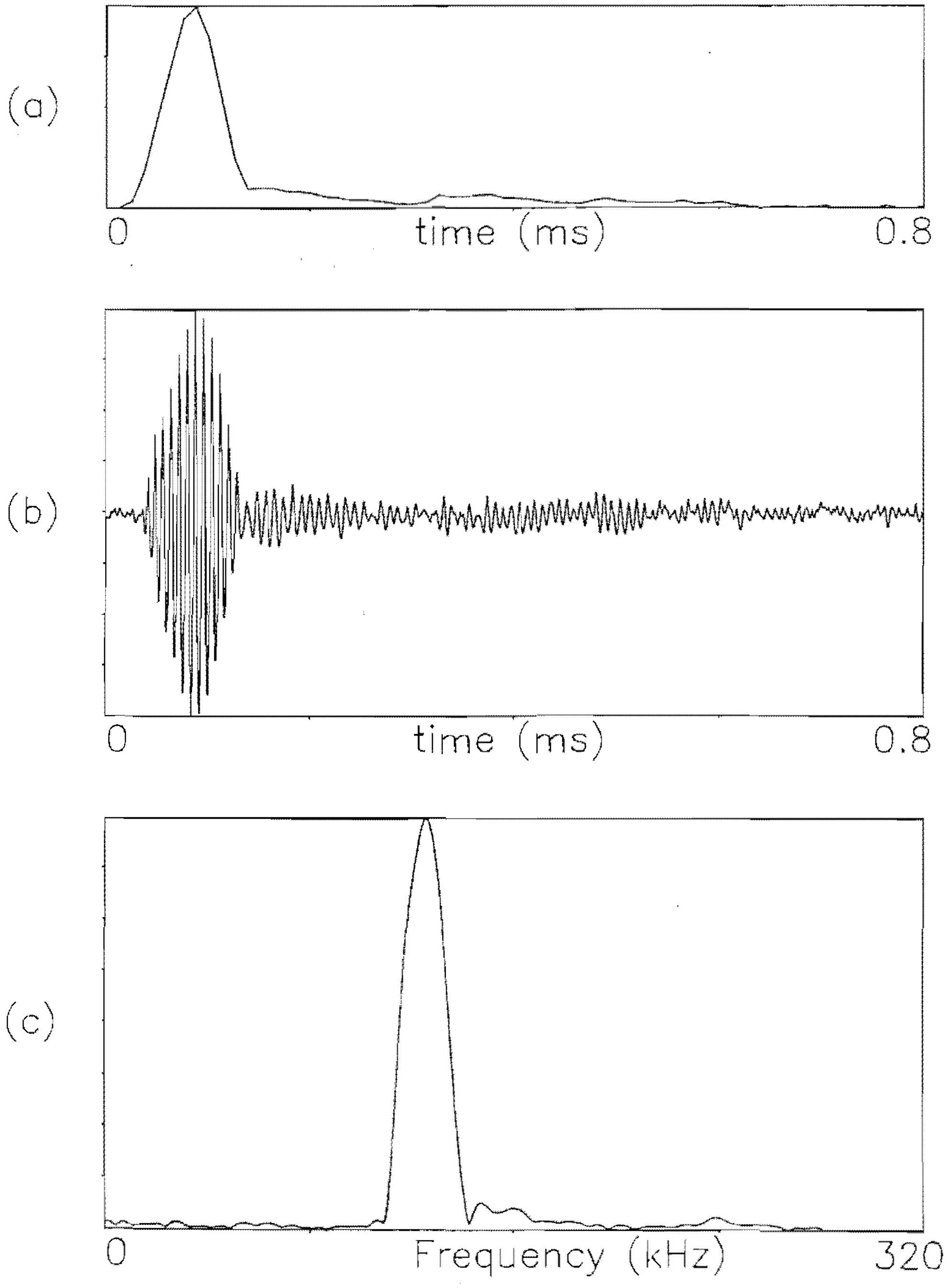

Figure 2 **a**: Average envelope profile, **b**: click waveform and **c**: average spectrum for a narrowband click with a single pulse in the time domain.

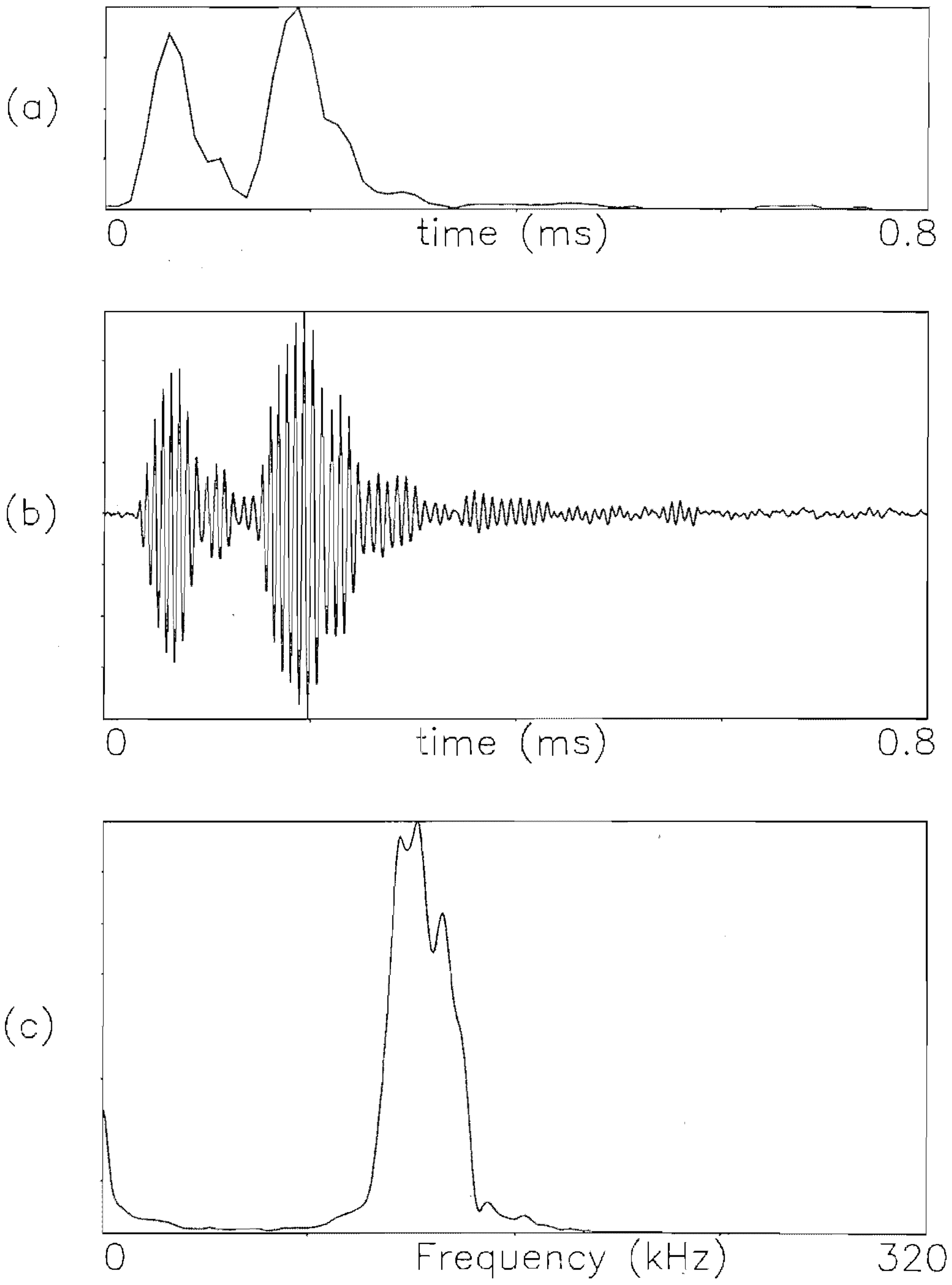

Figure 3 a: Average envelope profile, b: click waveform and c: average spectrum for a click with a double pulse in the time domain.

3.1. Reconstructing the pulses from the measurements

In order to show that the measured features characterize the signal, we reconstructed the signals shown in Figs 2 and 3, and these are shown in Figs 4 and 5 respectively.

The reconstruction of the pulses from the measured data comprised two separate stages. Firstly, synthetic spectral and time domain envelope records were reconstructed from the measured data values, and then these were used to generate the reconstructed pulse.

The spectral magnitude was reconstructed from the frequencies, amplitudes and half-power width measurements by overlaying a gaussian shaped pulse, having the appropriate height and width, for each of the measured peaks. In a similar manner, the time domain envelope was reconstructed by overlaying a pulse, consisting of a gaussian combined with an exponential decay, for each of the measured peaks.

We deliberately kept our reconstruction techniques as simple as possible. More sophisticated shapes could have been used to achieve a closer match to the original signals, but as shown by the reconstructed pulses (Figs 4a,b and 5a,b), the simple shapes were successful in approximating the shape of the original pulses, hence achieving our aim of demonstrating the validity of our features in representing the signals.

Reconstructing the time signal from the spectral magnitude and time domain envelope is one of a class of problems termed "phase retrieval" (Bates, 1986) which arise because the phase must be recovered from the magnitude measurements in order to uniquely determine the actual signal. However, if the form of the signal is suitably constrained, there are well-established methods of uniquely determining the phase from the magnitude only (Burge et al., 1976). Knowledge of both the spectral and time domain magnitudes is one such constraint, allowing us to reconstruct the signal by applying a simple iterative algorithm (Gerchberg, 1972).

The reconstruction algorithm comprises the following steps, repeated until the error reaches a sufficiently low value.

The iterations start with a random phase for $\tilde{\phi}^{0}(f)$.

1. The estimate of the frequency domain signal $\tilde{S}^{i}(t)$ is formed from the input spectral magnitude $|S(f)|$ and the previous phase estimate $\tilde{\phi}^{i-1}(f)$:

$$\hat{S}^{i}(f) = |S(f)|\, exp\,(j2\pi\, \tilde{\phi}^{i-1}(f))$$

2. The new estimate of the time-signal $\hat{s}^{i}(t)$ is calculated by means of the inverse Fourier transform (F^{-1}):

$$\tilde{s}^{i}(t) = F^{-1}\{\hat{S}^{i}(f)\}$$

3. The time domain estimate is constrained to have the same envelope as the input envelope $R(t)$:

$$\tilde{s}^{i}(t) = \hat{s}^{i}(t)R(t)/(R_{\hat{s}^{i}}(t) + \psi)$$

where $R_{\hat{s}^{i}}(t)$ is the envelope of $\hat{s}^{i}(t)$ and ψ is a small constant (= 0.001) to avoid division by zero.

4. The estimate of the frequency-domain signal $\tilde{S}^{i}(f)$ is formed from $\tilde{s}^{i}(t)$ by means of the Fourier transform (F):

$$\tilde{S}^{i}(f) = F\{\tilde{s}^{i}(t)\}$$

5. The error is calculated from the average difference between $|\tilde{S}^{i}(f)|$, the magnitude of $\tilde{S}^{i}(f)$, and $|S(f)|$.

6. The phase $\tilde{\phi}^{i}(f)$ of $\tilde{S}^{i}(f)$ is used for the next iteration:

When the error reaches a sufficiently low value (0.2 was used), the current time domain estimate $\tilde{s}^{i}(t)$ is determined to be the output time domain signal. In all the examples that were reconstructed, this procedure converged and a reasonable estimate of the time domain signal was found within 10 iterations (see Figs 4c and 5c).

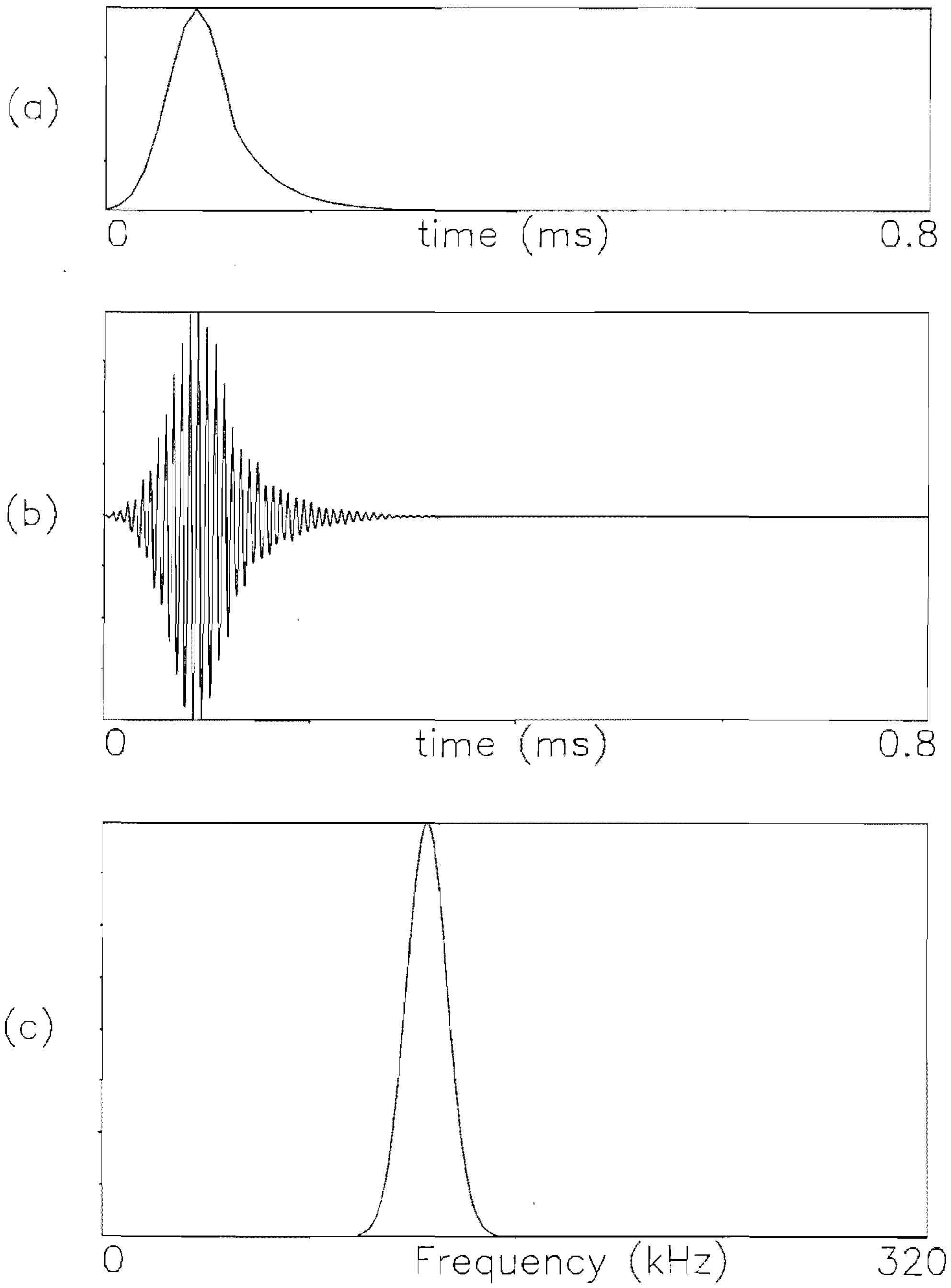

Figure 4 **a**: Average envelope profile, **b**: click waveform and **c**: average spectrum of the reconstruction of the click shown in Fig. 2.

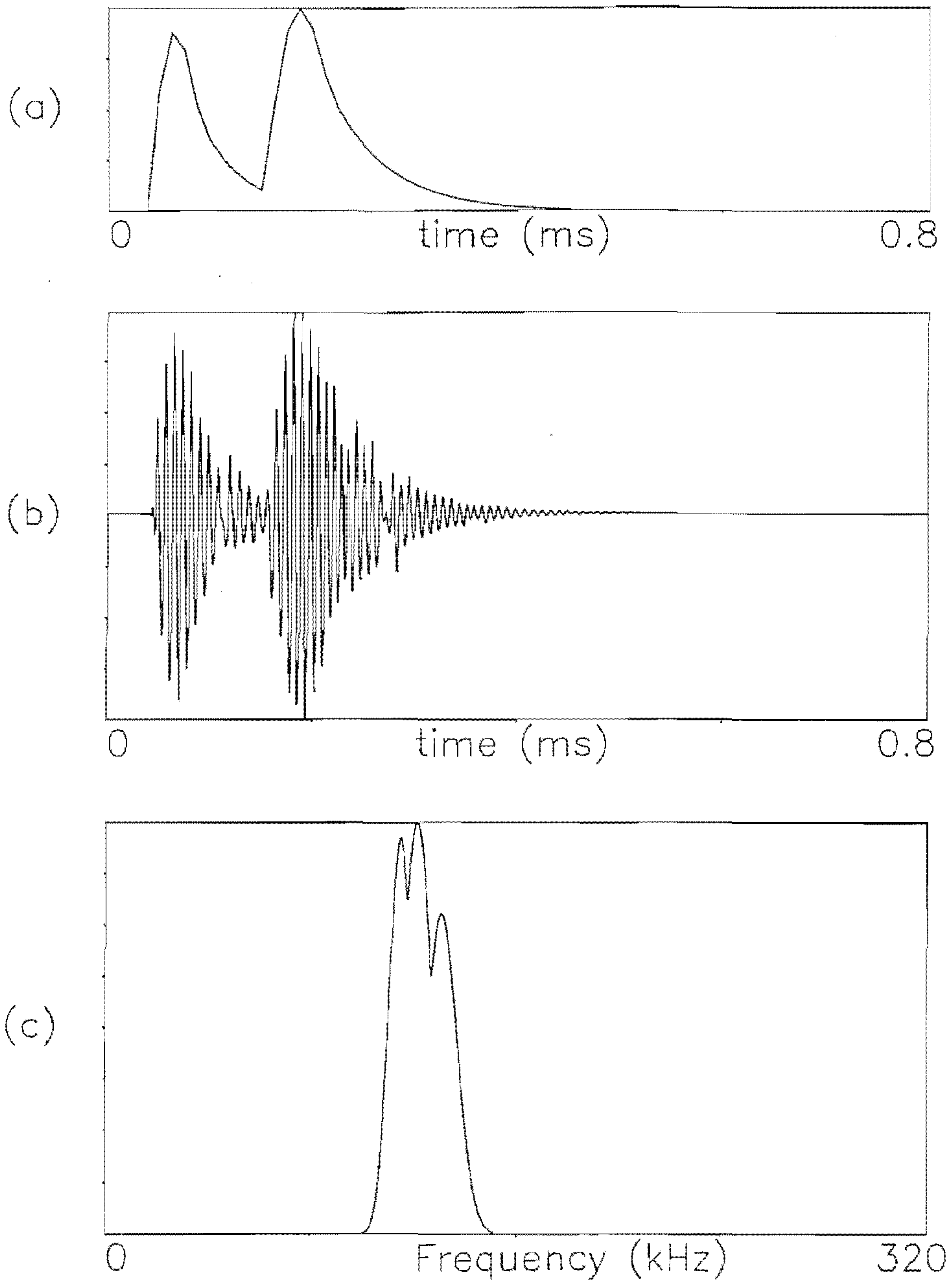

Figure 5 **a**: Average envelope profile, **b**: click waveform and **c**: average spectrum of the reconstruction of the click shown in Fig. 3.

3.2 Additional and alternative features

In addition to determining the dominant frequency of the sounds by means of the average peak frequency in the spectrum of each click (see steps 6 & 9), two other methods of characterizing the dominant frequency were employed.

We measured the period of oscillation for each click (zero-crossing rate), which gives an estimate of the dominant frequency in the click without the need to perform a Fourier transform (step 11).

The spectra of the signals was also characterized by calculating the mean frequency and its standard deviation (corresponding to its bandwidth) (Wiersma, 1982) from the average spectrum of each record, using statistical formulae (step 9).

The length of the pulse can be similarly characterized by calculating the standard deviation of the energy envelope of the signal (step 10). From the time duration and bandwidth measurements, we obtained the time--bandwidth product (step 11). This is a measure of the information in a signal (Gabor, 1946), and has been calculated for the sonar signals of a few dolphins and porpoises (Wiersma, 1982).

As an alternative to characterizing a signal by measuring its time and frequency components, a set of linear prediction coefficients (LPCs) can be calculated from the signal (Markel and Gray, 1976). These coefficients model the behaviour of the signal in that they allow one to predict the upcoming value of the signal from its previous values. LPC analysis is often used in speech analysis, and has also been applied to primate vocalizations (Owren and Bernacki, 1988). However, in our initial attempts to apply LPC analysis to Hector's dolphin sonar clicks, two significant problems emerged. Firstly, the matrices involved in the calculations were often effectively singular (Markel and Gray, 1976). Secondly, the coefficients calculated from "similar-looking" clicks were often very different. These problems appear to arise from the narrow-band nature of the signals, which causes the resulting minimisation matrix to become ill-conditioned (see Markel and Gray, 1976). Because of these computational problems, we decided against using the LPCs as features, despite their attraction as simple descriptors of the spectral shape of the signal.

4. Sigproc, a Signal processing language

The Sigproc signal processing language was developed at the University of Canterbury Electrical & Electronic Engineering Department by postgraduate students in order to facilitate their research into speech processing techniques. It consists of a suite of signal processing routines together with an interpreted programming language allowing easy use of the routines, both interactively and by means of command level programs. Sigproc is available to universities from the Dept. of Electrical and Electronic Engineering, University of Canterbury, N.Z., for the cost of copying, handling and postage.

The programming language is based on the VAX/VMS Digital Command Language (DCL), both to ease its implementation on our VAX computers, and to minimise the extra learning required by users (who are assumed to already have some familiarity with VAX DCL concepts). Programming constructs are implemented to facilitate the writing of high level programs, and include the IF-ELSE-END conditional statement, REPEAT-UNTIL and FOR-NEXT loops, subroutines and variables (which may hold string or numeric data).

Signals in Sigproc are held in buffers which are referred to by name, and may be of any size (subject to virtual memory limitations). The signal processing operations are accessed by means of commands, such as FFT, or RMS, with command parameters specifying the input and output buffers. Signals (buffers) can be acquired and replayed via an Analog-to-Digital (A/D) and Digital-to-Analog (D/A) interface on the VAX. They may also be stored in files, and plotted on various display and hard-copy devices.

Examples of Sigproc programs (Appendix B) illustrate how relatively complicated signal processing operations can be implemented by means of straightforward programs. The major drawback of a Sigproc program compared to an equivalent program written in a compiled language is that it is usually slower. For most applications this disadvantage is outweighed by the advantages of fast program development time, the ability to use the same programming language interactively, and its high-level signal processing constructs. If more processing speed is required, it is relatively straightforward to write the routine in a compiled language and add it to Sigproc.

Sigproc consists of a "core" program, which contains the command interpreter and a basic set of operations, together with a number of separately compiled and linked modules which contain the signal processing routines. This structure means that a new routine can be added to Sigproc in a separate module, without affecting the rest of the program. In this way, the speed of a compiled language (usually Fortran) can be easily employed, together with the convenience of using it within the Sigproc environment.

5. Automatic feature measurement procedure

Automatic implementation of the feature measurement process required the programs to be capable of processing the entire range of sound records. The programs were written in a modular fashion, and the processed signals (prior to the actual measurement of features) were saved on magnetic tape. If any part of the measurement procedure was later found to require modification, it was a simple matter to perform that measurement again on the processed signals.

After each set of variables was measured, they were written out as a text file, together with a label denoting the original tape and tape counter number that the corresponding signal was from. These labels allowed us to integrate the matrix of measured variables into an already existing database (on a Macintosh SE micro-computer) listing the behavoural contexts of each recording.

The labels also enabled us to keep track of all the measured data. This was important due to the sheer volume of data (401 raw data records of 300 kBytes each). The processing was performed in batches of about 60 records each, with the rest of the data stored on magnetic tape. To avoid having to re-process the raw data if we needed to adjust some of the analysis parameters, we stored the extracted clicks, average time envelope and spectral magnitude records and the record of inter-click intervals separately from the raw data. This data compression (effectively removing the gaps between the clicks) allowed us to store the data for all records in about 20 MBytes.

The measurement process comprised a series of steps, each of which transformed the signal in some way or measured a particular feature. Each step in the procedure was programmed as a separate Sigproc command file (see 10 for an example), although common types of measurements, such as that of the peak amplitude and width (part of both step 7 and step 8), employed the same "subroutine" command file. The details of the steps are described in 9. The numbers denoting each variable have a T or F prefix denoting whether the variable was measured from the time or frequency domain. Extra variables, which combine time and frequency domain measurements, are denoted by a prefix E (E47 - E48).

Each part of the measurement process was refined by means of trials on a sub-set of the data. This was found to be necessary because of the detailed specification required, both of how the features were to be measured, and of how to deal with the signals that deviated from the "norm".

6. Summary of results obtained

The 401 records that were analyzed contained 7661 "clicks", with the average interval between clicks in a record (T3) ranging from 1.3 ms to 164 ms (median = 27.6 ms). The average frequency of the clicks (F44) ranged from 82 kHz to 135 kHz (median = 124.2 kHz). Most of the records had clicks with one (52%) or two (36%) peaks in their energy envelope (T8), and 92% had one or two peaks in their spectrum (F21) (see Chapter 2).

Principal component analyses (PCA) on the time domain features, the frequency domain features, and on features from both domains indicated three major groupings of sound type. The groups broadly classified pulses according to whether they had 1, 2 or more than 2 pulses in their spectra or amplitude envelopes (see Chapter 2).

To further investigate the characteristics of the signals, we calculated the click duration and bandwidth, together with the time-bandwidth product, using the statistical approach described in step 9 (appendix A). Histograms of pulse lengths and bandwidths (Figs 6 and 7) illustrate the short and narrow-band nature of most of the pulses. The few that are very wide-band and/or long-duration are generally "noisy" signals, including one with a low-frequency component (see the discussion later this Section). Noise served to increase the standard-deviation measurement in both the time and frequency domains. We reduced the effect of noise and echoes on the time duration measurement by setting everything in the average signal envelope that was below a certain threshold to zero before calculating the variation (see steps 9 and 10).

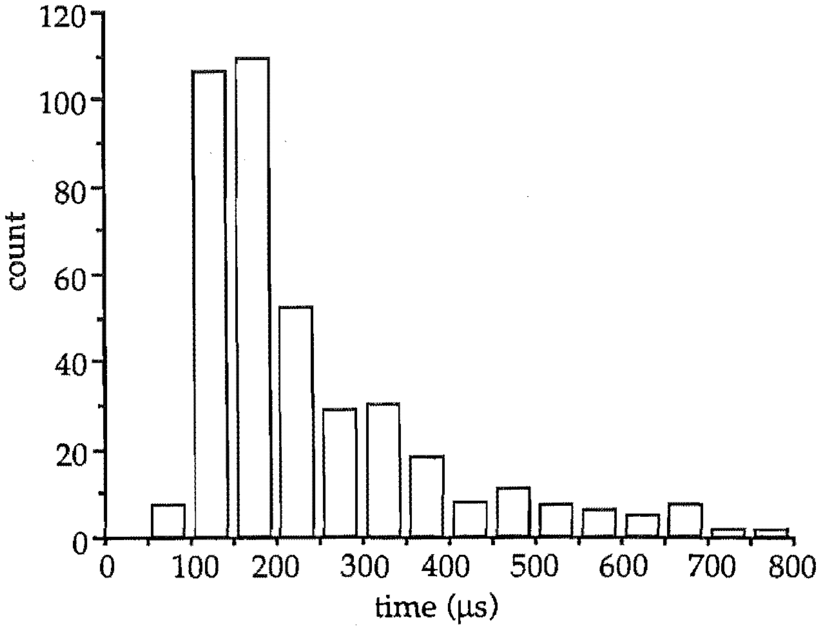

Figure 6. Time durations of the dolphin pulses. The time duration is calculated as described in step 10 (appendix A).

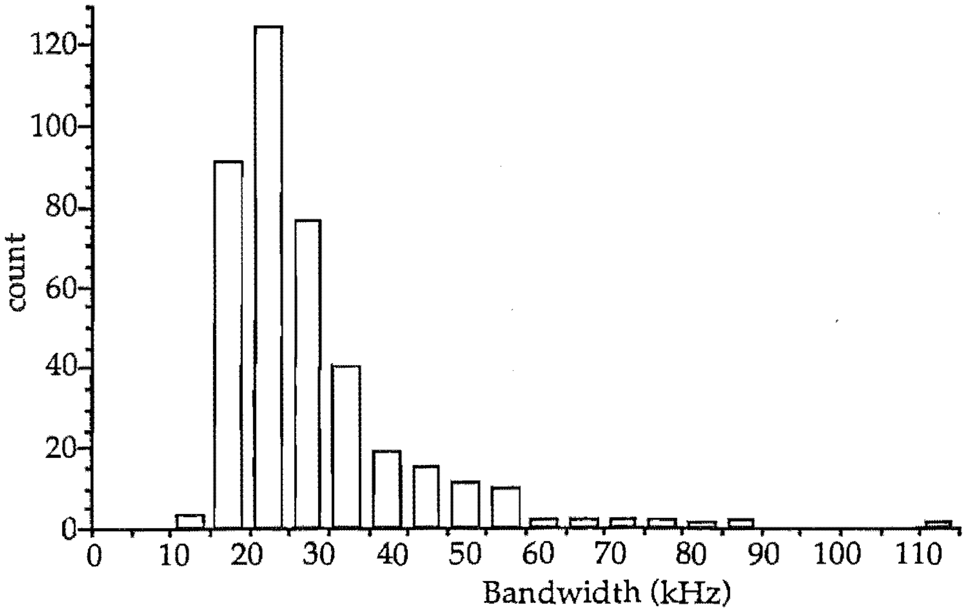

Figure 7. Spectral bandwidths of the dolphin pulses (half power width of the largest spectral peak).

The time--bandwidth product gives a measure of how "complicated" a signal is. Gabor (1946) showed that there is a minimum value that indicates the "simplest" type of signal. Because of the way that we calculated it, the minimum value for these signals was unity. While most of the signals have a near-minimum time-bandwidth product, some values are considerably larger (Fig 8). The values are much greater than those obtained by Wiersma (1982) for various other odontocete sonar signals, which were all between 1.1 and 1.5, suggesting that Hector's dolphin sonar signals are more "complicated" than the ones that Wiersma studied. However, as above, the ones with very large values generally consisted of noisy signals.

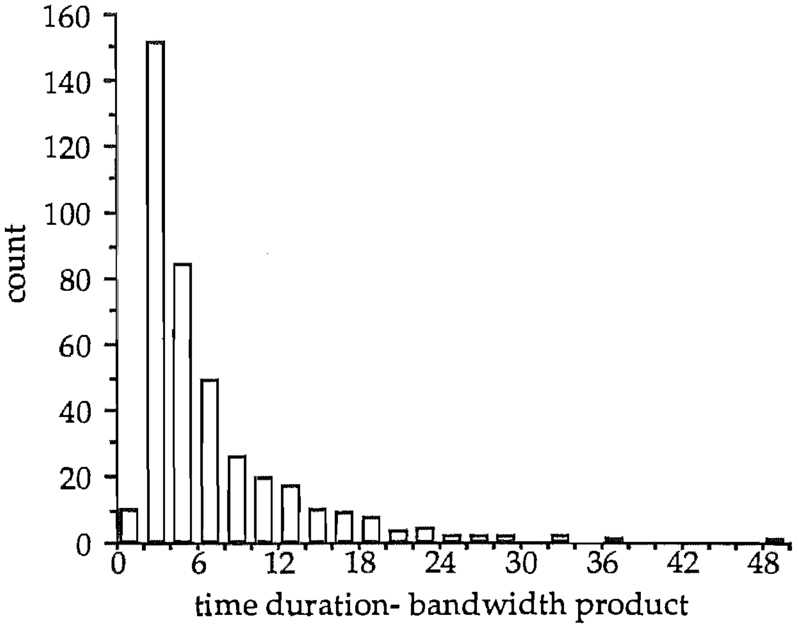

Figure 8. Time-bandwidth product of the pulses. The time duration and bandwidth of each pulse was determined by calculating the standard deviation of the time domain energy profile and power spectrum respectively.

The difference between our time--bandwidth results and those of Wiersma suggest that the sonar pulses of Hector's dolphins are quite different from those of the cetaceans that he studied. Most of the difference, however, probably arises from different measuring techniques. Wiersma measures the features from only the portion of the signal that he assumes is attributable to the sound "source", ignoring the effects of echoes inside the dolphin's head. Using this technique, it is not suprising that Wiersma obtained near-minimum values for time--bandwidth product. We think that the measurements should include the entire signal as emitted by the dolphin, since this is what the dolphin actually uses for its echo-location (Kamminga and Wiersma, 1981). We reduced the effect of noise by measuring only those pulses that exceeded a threshold of 1/3 of the maximum amplitude of the record, and the effect of external echoes by restricting our measurements of individual clicks to an 800 µs window. However, it is apparent that the statistical approach to measuring bandwidth and time duration is not appropriate when the signal consists of several components or peaks, or is corrupted with significant amounts of noise.

To study the effect of measuring a feature using different techniques, we measured the dominant frequency component of the clicks in three different ways. The first (F22) was by measuring the peak frequency for each click in a record and averaging over all the clicks in the record. The second technique was to measure the mean frequency from the average spectrum (F44). Finally, for each click, we measured the zero-crossing rate, and found the average of these for all the clicks in the record (F41). These measurements were highly correlated ($r > 0.733$, $p < 0.001$). However, there were 22 records in which the measurements differed by more than 10 kHz between the three methods. Closer examination of these records revealed that they were generally noisier than the other records, with some of them exhibiting significant amounts of low-frequency noise. They also tended to have relatively wide bandwidths with several peaks, which means that a simple measurement of the dominant frequency component is not adequate to represent the spectral content.

One of the wide-band records consisted of a click containing two distinct frequency components, at 5.8 kHz and 122 kHz (Fig. 9). Separating the two components by means of filtering shows that the high-frequency part is similar to the other high-frequency signals that we recorded (Fig. 10c). The two parts are clearly not independent, since the production of the high-frequency component severely affects the low-frequency component (Fig. 10a). No other records contained low-frequency (<50 kHz) peaks greater than 1/3 of the maximum peak in the spectral magnitude.

7. Conclusions and discussion of salient points

Our method of automatic feature measurement allowed us to analyze in detail 401 1/4 s records of Hector's dolphin click trains, containing 7661

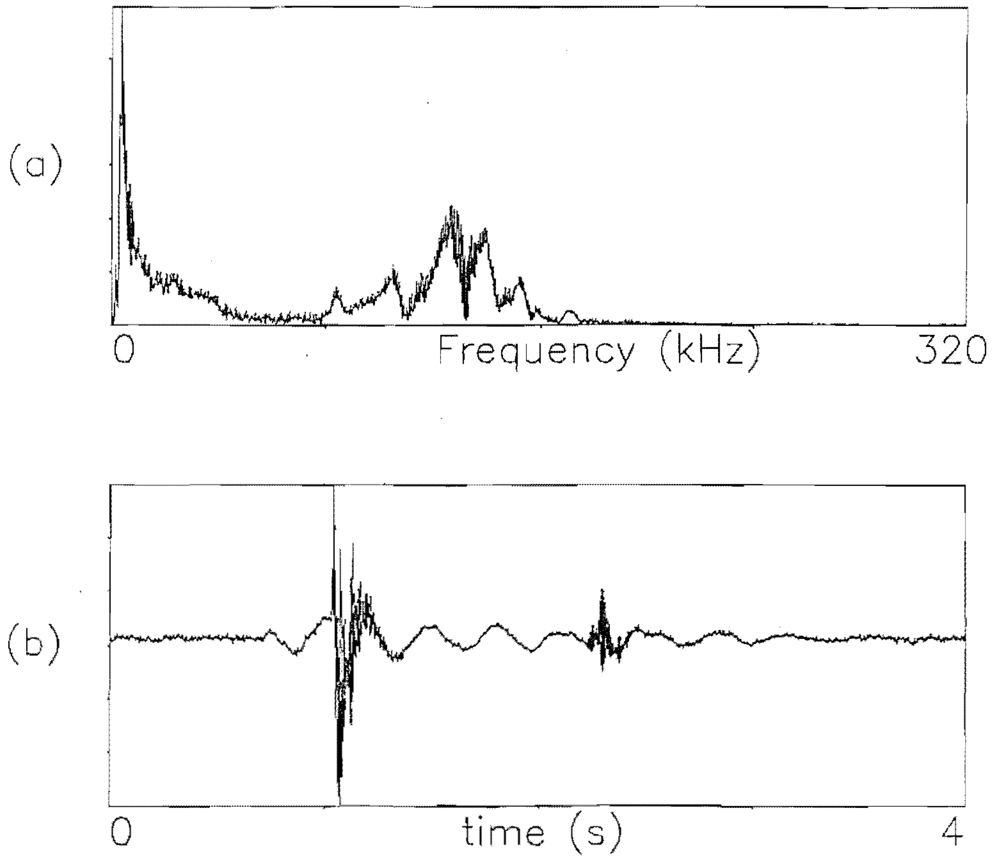

Figure 9 a: Example of a click with distinct high- and low-frequency components, together with b: its corresponding spectrum.

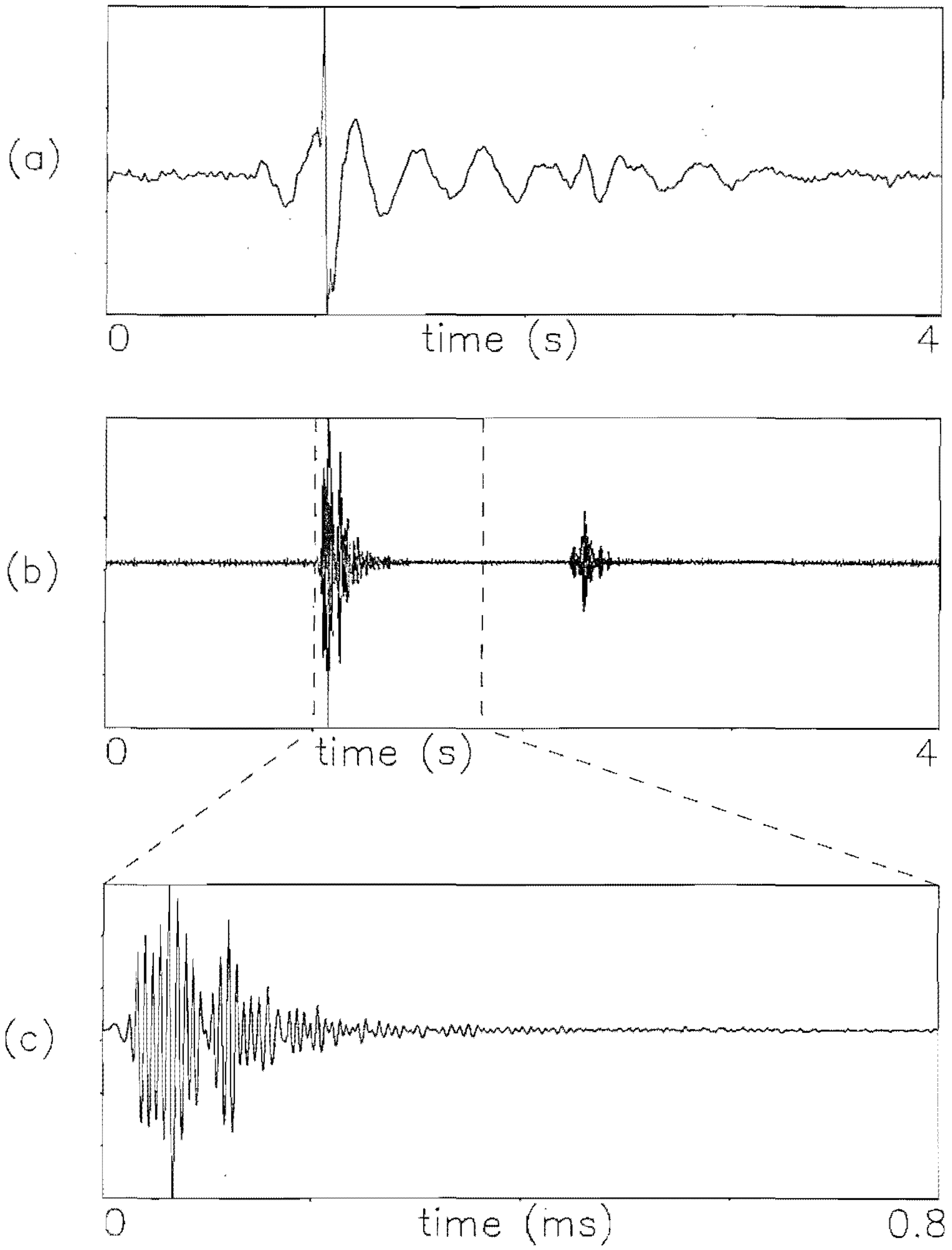

Figure 10 **a**: Low-frequency component, **b**: high-frequency component and **c**: expanded high-frequency component of the click of Fig. 9.

clicks. Using basic operations in a signal processing language, we measured 44 variables from each record, and hence characterized them according to various features. Without the aid of these computer-based measurements, and especially the ability to perform them automatically, this analysis would have been prohibitively labour intensive.

One of the problems involved with an automated measurement procedure is that the researcher does not measure the features directly. In manual methods of measurement (such as measuring variables from a sonogram using a ruler, graphics tablet etc.) it is relatively easy to determine which features should be measured, and when a particular sound should be discarded because it has been severely corrupted by noise. However, for an automatic measurement procedure to be successful, all the steps involved in the measurement process, and the rules for discarding records, must be stated explicitly, and in such a way that they encompass all the expected variations. We found that achieving these goals required a considerable amount of testing on trial subsets of the data. Although this development process took some time, it resulted in a procedure that was able to process all the data records in an identical manner.

Although we did not delve deeply into the process of reconstructing the signals from the measured features, we believe this is an exciting concept in feature measurement schemes. Accurate reconstruction confirms that the measurements characterize the signal. This is important because the choice of which particular features to measure is arbitrary, and can influence the results obtained. In some situations, the choice of features is determined by the importance of the features in the particular context of the signal. For example, in the analysis of human speech, we know that features such as formant frequencies carry important linguistic information, while the pitch frequency carries much less linguistic information (at least in the English language; Lieberman and Blumstein, 1988). Because of our lack of knowledge of what features of the sounds were important to the dolphins (apart from our knowledge of the features important to sonar signals in general), we had to rely on features that described the actual form of the signal. Our reconstructions confirmed both that the features that we chose to measure were sufficient to describe the signal, and that our measurement technique was correct. Hence we believe that confirming the validity of features in this way is a useful approach that could be fruitfully applied in other acoustical studies.

Measuring some of the variables in different ways also enabled us to check the validity of our measurements. Our three ways of measuring the dominant frequency produced data that were highly correlated. Cases in which the three measures differed widely were signals whose spectra could not be adequately described by a single factor, either because of noise on the signal, or because the signal contained several frequency components.

Our studies have revealed that the vocal repertoire of Hector's dolphins is remarkably simple, consisting almost entirely of short, narrow-band, high-frequency clicks (see also Chapter 2). This is what one would expect if the pulses are used for simple echo-location purposes. In addition, almost all of the signals had a near-minimum time--bandwidth product (60% had values < 5), indicating again their simplicity (Fig. 8). The few that were different had time--bandwidth products ranging up to about 50 (but only 22 records had values greater than 20, see Fig. 8). The interpretation of these exceptions is made difficult because of their scarcity in the dataset, and because of our lack of precise knowledge of what they are used for. Three possibilities suggest themselves as explanations for the more "complicated" signals. Firstly, they could be artefacts caused by noise, multipath distortion or measurement errors. However, as noted in Chapter 2, the high signal to noise ratio and clean waveforms of many examples indicates this is not the case. Secondly, they could be a different type of sonar signal, for use in different type of target situations (see Chapter 4). Thirdly, they could be signals for use in communication (see Chapter 5).

The relative scarcity of the "complicated" sounds in the entire sample may not indicate low importance, since we would expect most of the sounds recorded to be for the purpose of sonar. High-frequency cetacean sonar signals are highly directional (Au et al., 1986), and so the strongest signals are recorded when the phonating dolphin is orientated towards the hydrophone. This situation is likely to have occurred most often when they were using sonar to examine it.

One of the records was different from the others in that it contained a low-frequency component in addition to the normal high-frequency one (Figs 9 and 10). This type of LF-HF signal has been observed in the sounds of other species of odontocetes (e.g. *Phocoena phocoena* and *Delphinapterus leucas* by Kamminga and Wiersma, 1981). However the significance of these low-frequency components is unclear to us. One possibility is that they are used for long-range or navigation purposes. Hector's dolphins appear to reside in small areas over long periods (Slooten and Dawson, 1988, and In press), implying that they know that habitat in detail. Hector's dolphins would appear to need navigational signals only occasionally, which would help explain the scarcity of combined LF-HF clicks in our dataset.

8 Acknowledgements

We are grateful for the help and advice given us by many people, especially Richard Bates, Andrew Elder, Richard Fright and Peter Gough for the engineering aspects of the study, and Elisabeth Slooten for help in the field. The field work for this study would not have been possible without support from the N.Z. Lottery Board, Greenpeace International, NZ Department of Conservation, World Wide Fund for Nature (NZ), Project Jonah (NZ) Inc., Cetacean Society International, Pacific Whale Foundation, IBM (NZ) Ltd, Anthoni Computer Automations, NZ Underwater Association, and Neill Cropper and Co. Brüel & Kjær, Reid Technology, Tech Rentals, Racal Electronics and Tait Electronics kindly lent equipment for various phases of this project. CWT is grateful for the support of a NZ University Grants Committee postgraduate scholarship.

Appendix A. Details of the measurement procedure

The measurement process for each sound record comprised the following sequence of steps. The values specified for the various thresholds and other parameters are those which we found produced reasonable measurements for the sound records in the trial datasets.

1. The energy envelope (RMS) of the 0.25 second record was calculated. This was accomplished by dividing the sound record into overlapping segments, each of length 32 samples, and spaced at every 8 samples. A Hanning window (Harris, 1978) was applied to each segment and the RMS value calculated. This value was deemed to represent the amplitude of the sound envelope at the instant corresponding to the sample at the centre of the segment. Hence the envelope record contained 1/8th the number of samples as did the sound record.

2. Each click in the record was extracted by means of an iterative procedure that examined the envelope to determine the positions of the clicks. In each iteration, the time at which the envelope amplitude next (after the end of the previous click) exceeded a trigger value (which we set to equal 1/3 the maximum amplitude in the entire record) was found. A 0.8 ms segment was then extracted from both the envelope and the sound records, starting 0.05 ms before the trigger time to ensure that the segment encompassed the start of the click. The number of clicks found in each record was denoted by variable T2.

3. The trigger-time for each click was saved in a time-buffer, and the difference between each was measured to give the intervals between the clicks. The average (T3), variance (T4), maximum (T5) and minimum (T6) of the click intervals was calculated. The differences between successive click intervals was calculated to measure any trend in the intervals, and the average of this trend denoted as variable T7.

4. The average of all the click envelopes within the record was calculated, and variables measured which characterized its shape. These consisted of the position, amplitudes and decay-times of the peaks in the envelope. We measured these by locating all the peaks and troughs in the signal and placing them in a list, and, in an iterative loop, a: finding the largest (or next largest) peak; b: measuring its amplitude, position and decay time (how long the envelope took to decay to 40% of the peak value); and c: removing it from the list of peaks. We did this until we had found all the peaks that were greater than 1/3 the amplitude of the largest one. The number of such peaks was denoted by variable T8, and the 3 measurements for each of the four largest peaks became variables T9-T20 (four sets of three variables). If there were fewer than four peaks, the variables corresponding to the remaining peaks were set to zero.

5. For each of the clicks in the record, the frequency spectrum was calculated by means of the fast Fourier transform (FFT). So that the spectrum characterized the spectral content of the click itself, and not the surrounding noise and echoes, we calculated the FFT on a segment of 0.4 ms, centered on the largest peak in the click envelope. Using a short segment such as this also meant that the calculated spectrum was

smoother, and so it was easier to measure features from it. However, it also reduces the resolution in the frequency domain , and with a length of 0.4ms, the frequency resolution becomes 2.5 kHz. The signal was multiplied by a Blackman-Harris window to reduce leakage in the frequency domain (Harris, 1978) and zero-extended to a length of 4096 samples before performing the FFT calculation in order to increase the precision with which features in the frequency domain could be measured (with 4096 samples the precision = 156 Hz). This precision is the accuracy with which the features are measured, while the resolution mentioned above is the minimum spacing for two features to be resolved. We calculated the squared magnitude of the spectrum (the power spectrum), and used it for all our measurements.

6. From the spectrum of each click, we found the frequency having the greatest amplitude. The average (F22), variance (F23) and trend (F24) of this frequency was calculated over all the clicks in the record.

7. The dominant frequency of each click was also determined by measuring the period of oscillation within the click. This was accomplished by counting the number of zero-crossings in the click (during the period of time that the amplitude of the click was greater than 1/3 of its maximum) and the length of time in which they occurred. We increased the accuracy of measuring the time of the zero-crossings by increasing the sampling rate of the click by a factor of 10 (we inserted 9 zero-valued samples between each sample, and then interpolated between the original samples by smoothing with an ideal filter having a cutoff frequency of half the original sampling rate). From the zero-crossing rate for each click, we calculated the average (F41), variance (F42) and trend (F43) over all the clicks in the record.

8. The spectra for all the clicks in a record were averaged together, to produce an average click spectrum for the record. The number of peaks greater than 1/3 of the maximum were found (F21). For each peak (up to a maximum of 4), we measured its frequency, amplitude and half-power width (the width between the points on either side of the peak where the magnitude of the power spectrum falls to half of its value at the peak). We also measured the centre frequency (between the half power points) as this is generally different from the peak frequency (due

to the non-symmetric form of the spectrum). The resulting 4 sets of 4 variables are labelled (F25) to (F40) respectively and, as in step 4, if the number of peaks is less than 4, the remaining variables were scored as zero.

9. We next characterized the average click spectrum by considering the power spectrum as a probability function, calculating its mean frequency (F44) and variance (F45). The bandwidth (F46) is obtained by multiplying the square root of (F45) by 2 (Wiersma, 1982).

10. From the average RMS envelope (from step 4) we calculated the click time duration. Only the first 0.4 ms of the envelope signal was used, and all values less than 0.1 times the greatest RMS value were set to zero. These measures were taken because otherwise noise or subsequent reflections in the signal produced unrealistically large results. The RMS envelope was squared to give the signal energy distribution, before calculating the standard deviation of the signal energy (from its mean time position). This is slightly different than the method used by Wiersma (1982) who calculated the standard deviation from the actual time signal rather than the envelope. However, identical reults are obtained. We multiplied the standard deviation by a constant equal to 2π (Wiersma, 1982) to give the time duration of the average click (E47).

11. The time--bandwidth product (E48) is obtained simply by multiplying variable (F46) by (E47).

Appendix B. Examples of Sigproc programs

In order to demonstrate the types of signal processing that Sigproc can easily perform, we include two examples of Sigproc command-language programs.

The first example demonstrates the ease with which flexibility can be built into Sigproc programs. Its purpose is to calculate the FFT of the input signal, but by means of global symbols, which are initialised in the main program, the details of the operation can easily be changed. The example also shows the use of symbols as both numerical and string variables, and the usefulness of "lexical functions" (beginning with b$) which provide information about buffers. This example was used in the measurement process, to calculate the spectrum of each click.

The lines that begin with a '!' are comment lines, P1 and P2 refer to the parameters given when the sub-program was called from the top-level program, vis

```
@ dol_FFT signal_buff FFT_buff
```

All commands, qualifiers and lexical functions can be abbreviated to the least unambiguous size, although in this example they have been given more fully to aid understanding.

```
! DOL_FFT.CND - calculate the FFT of the input signal P1,
!
! Parameters : P1 - buffer with the input signal
! P2 - Name of the output FFT buffer
!
! Need symbols FFTWIN - window or not
! FFTWINTYPE - type of window (hanning, 3_term Blackman, etc)
! FFTSIZE - size of the FFT in samples


! Find the size of the input buffer - length * sampling frequency
define FFTsi "'blength('p1')' * 'b$x_sampling_freq('p1')'"
! Need to add one on because first sample is labeled 0
define FFTsi "'FFTsi' + 1"

if 'FFTwin' "=" "YES"
! Window the input data with the desired window
generate/size='FFTsi'/window='FFTwintype' -
/sampling='b$x_samp('p1')' FFT_win
arith/mult=FFT_win sig 'p1'
delete FFT_win
else
copy sig 'p1'
end
```

```
! Zero-extend if this is what is wanted
if 'FFTsize' ">" 'FFTsi'
! Create the extra zero-valued samples
def extend "'FFTsize' - 'FFTsi'"
set mess/noinfo
gen/siz='extend'/samp=1 extend
set mess/info
! Calculate the centre of the zero-buffer
def exthalf "'extend'/2"
set bu/en='exthalf' extend
set bu/x='b$x_samp(sig)' extend
! Insert the input signal into the middle of the zeros
insert sig extend
del sig
set bu/st/en extend
rename sig extend
end


! Now calculate the FFT - need to specify the size
! and spacing
FFT FFT sig/siz='FFTsize'/spac=10000
del sig
! Only want the positive frequencies, so get rid of the rest
def half "'bx_samp('p1')'/2"
set bu/en='half' FFT
copy 'p2' FFT
del FFT
```

The second example demonstrates how signal-processing operations can be easily implemented by means of the basic Sigproc commands. This program resamples the input buffer by the specified amount, and interpolates between the data-points by ideal filtering (step 7 in 9). It would be called from another program by a command such as the following:

```
@ dol_interpolate time_buffer 10
```

```
! DOL_INTERPOLATE.CND
! Resample the signal and interpolate the data
! - for smoothing curves when plotting or similar.
! Parameters: P1 - the name of the buffer to resample
! - Returns the interpolated data in the same buffer
! P2 - the factor to resample by


! Calculate the nyquist freq. - for sinc interpolation
def nyquistfreq "'bx$_samp('p1')'/2"
! Resample it
resamp/interpolate/factor='p2' interp_buff 'p1'
del 'p1'
! Generate the low-pass filter to interpolate with
gen/size=128/samp='b$x(interp_buff)'/filt=low/freq='nyquistfreq' filt
! Good idea to window it - Blackman 3-term window
generate/si=128/samp='b$x(interp_buff)'/win=3_term win
arit/mul=win filtwin filt
! Perform the filtering convolve/convolution_data=filtwin 'p1' interp_buff
! Tidy up
delete interp_buff,win,filt,filtwin
```

Chapter 4. Intrinsic echolocation capability of Hector's dolphin, *Cephalorhynchus hectori*

Abstract

A sonar system's echo-location capabilities can be inferred from the ambiguity distribution (defined here in terms of the conventional ambiguity function) of each of its transmitted signals. We analyze several records of sounds emitted by Hector's dolphin. The computed ambiguity distributions indicate that the sonar clicks of Hector's dolphins should be capable of resolving the ranges of targets as close together as 2 cm, but target velocities cannot be resolved to any useful degree from a single echo.

1. Introduction

As part of a comprehensive study (Slooten and Dawson 1988) of Hector's dolphin (*Cephalorhynchus hectori*), which is only found in the coastal waters of New Zealand, we recorded many sounds emitted by free-ranging individuals (Chapters 1 & 2). Interpreting these sounds as sonar signals allows us to assess the ability of Hector's dolphin to localise prey and underwater obstacles.

Unlike some other echolocating mammals, such as a few species of bats (e.g. *Rhinolophus ferrumequinum* which employs CF-FM sonar signals; Schnitzler 1968), and some other odontocetes (e.g. *Phocoena phocoena* which has a dual-component sonar signal, Kamminga and Wiersma 1981), Hector's dolphins emit sounds of comparatively narrow (3 dB) bandwidth (typically 15% of the frequency of the spectral peak-see Section 3 below). Consequently, we can invoke standard radar signal processing theory (Skolnik 1970) for assessing the dolphin's echo-location capabilities. The narrowness of the bandwidth, and the small time-bandwidth product of each of the recorded sounds permits us to (Cook and Bernfield 1967):

(i) Invoke a readily computable analytic signal representation $\psi(t)$ of the sound expressed as

$$\psi(t) = u(t)\ exp(i2\pi f_0 t) \qquad (1)$$

where $i = \sqrt{-1}$, f_0 is the carrier frequency (defined in (iii) below) of the sound, and $u(t)$ is the waveform (i.e. the modulation on the carrier) of the sound.

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by C.W. Thorpe, R.H.T. Bates and S.M. Dawson. Submitted for publication.

(ii) Construct $\psi(t)$ by, first, computing the spectrum (i.e. the temporal Fourier transform) $S(f)$ of the sound, then defining

$$\begin{aligned}\Psi(f) &= 0 \quad \text{for } f < 0 \\ &= S(f) \quad \text{for } f \geq 0,\end{aligned} \tag{2}$$

and finally taking $\psi(t)$ to be the inverse Fourier transform of $\Psi(f)$.

(iii) Take $u(t)$ to be the inverse Fourier transform of $\Psi(f\text{-}f_0)$, with f_0 defined as the mean value of $|\Psi(f)|$:

$$f_0 = \int_0^{\infty} f|\Psi(f)|df \tag{3}$$

(iv) Assume that the intrinsic localization capability (from an echo-location point of view) of the sound is characterized by the conventional signal response function (often called the ambiguity function)

$$\chi(\tau,\phi) = \int_{-\infty}^{\infty} u^*(t)\; u(t+\tau)\; exp(-i2\pi\phi t)dt \tag{4}$$

where τ and ϕ represent the usual incremental delay (equivalent to target range) and doppler (equivalent to target velocity) variables.

It is appropriate to call

$$A(\tau,\phi) = |\chi(\tau,\phi)/\chi(0,0)|^2 \tag{5}$$

the ambiguity density of the sonar sound whose analytic signal representation is $\psi(t)$. The ambiguity density sets the fundamental limit on the sound's ability to distinguish by echo-location between two targets of equal strength (i.e. equal reflectivity) separated by τ and ϕ in delay and doppler respectively (Woodward 1953). It is important to remember that all waveforms possess the same "total ambiguity" because

$$\int_{-\infty}^{\infty}\int_{-\infty}^{\infty} A\,(\tau,\phi\,)d\tau\, d\phi \equiv 1 \qquad (6)$$

Section 2 of this paper describes our implementation of the above processing steps, and in Section 3 we present some ambiguity diagrams (our terminology for plots of ambiguity distributions) obtained from Hector's dolphin sounds. We conclude in Section 4 by discussing the capabilities of the dolphin's sonar system that are implied by our results.

2. Recording and Processing of the Sounds

The procedures by which the dolphin sounds were recorded and digitized are presented in Chapter 2. A sample of 7661 clicks was digitally analyzed and classified according to various features of the waveforms and spectra by Dawson and Thorpe (Chapters 2 & 3). Here we present ambiguity diagrams for a few typical clicks, chosen from the click types encountered.

The sounds (recorded as described in Chapter 2) were digitised at a sampling rate of 640 kHz, and all the processing implied in Section 1 was performed on a digital computer. Segments of 0.8 ms duration, encompassing a single sonar click, were processed as described in Steps (ii & iii) of Section 1 with the fast Fourier transform (FFT) algorithm (Bates and McDonnell 1986) used to implement the (discrete) Fourier transform.

The signal response function $\chi(\tau,\phi)$ was calculated by evaluating $u^*(t)u(t+\tau)$ for discrete incremental delays $\tau = \tau_n$ and then employing the FFT to generate $\chi(\tau_n,\phi)$ for each value of the integer n defined by $\tau_{n,} = n\Delta\tau$ within the range $-\tau_{max} < \tau_n < \tau_{max}$, where τ_{max} is the maximum desired temporal delay and $\Delta\tau$ is the required temporal resolution. Both $\Delta\tau$ and τ_{max} were calculated using the usual radar range equation (Skolnik 1970) from the range resolution Δr and the maximum range r_{max} respectively that we deemed to be sufficient to reveal relevant details in each ambiguity diagram. For the results reported in Section 3 we set $\Delta r = 5$ mm and $r_{max} = 200$ mm.

The spacing $\Delta\phi$ of adjacent values of ϕ, at which $\chi(\tau,\phi)$ is evaluated, need be no less than the reciprocal of the effective duration of $u^*(t)u(t+\tau)$. In order to display more clearly the detail revealed in our ambiguity diagrams and to ensure that the number of temporal samples of $u^*(t)u(t+\tau)$ is a power of 2 (necessary to implement the FFT algorithm available to us), we added samples of zero amplitude (this is a standard procedure called zero-padding) to $u^*(t)u(t+\tau)$ to make its actual duration up to an order of magnitude longer than its effective duration. Consequently, $\Delta\phi$ was always somewhat less than both $1/T$ and the value, corresponding to a velocity resolution of 4 m/s, which we deemed adequate to reveal relevant details in the ambiguity diagrams.

Note that the ambiguity diagrams displayed in Figs 1 - 3 are plotted as functions of incremental range r and velocity v, rather than delay τ and Doppler frequency ϕ.

Even though target velocities exceeding 10 m/s are probably of little concern to Hector's dolphin, we plot all the detail (out to values of $|\phi|$ corresponding to velocities of 100 m/s) revealed in our computed ambiguity diagrams, in order to display the complete structure of each diagram.

3. Results

The sounds that we recorded were all high-frequency "clicks" with peak frequencies ranging from 82 kHz to 135 kHz (median = 124.2 kHz). The 3 dB bandwidths ranged from 7 kHz to 56 kHz (median = 20 kHz) with the relative bandwidths ranging from 6% to 55% (median = 16%). Only 2% of the records had relative bandwidths greater than 25%, and those that did exhibited relatively high levels of noise. The lengths of the clicks ranged from 80 µs to 800 µs (median = 138 µs; see Chapters 1 - 3). Of the 7661 clicks analysed by Dawson and Thorpe (Chapter 2), three typical examples are shown in Figs 1a, 2a and 3a. The "clean" waveforms of these clicks strongly suggest that they were not distorted by off-axis recording, or multipath propagation.

Figs 1b,c 2b,c and 3b,c depict the ambiguity diagrams of the clicks shown in Figs 1a, 2a and 3a respectively. We present contour plots and relief maps of the ambiguity diagrams in order to display as clearly as possible the full structure of each diagram. Note that the relief maps reveal more detail. Since our reason for including the contour plots is to make it easier to interpret the relief maps, we consider a comparatively coarse contour spacing to be adequate. Figs 1b and 1c show an ambiguity diagram exhibiting

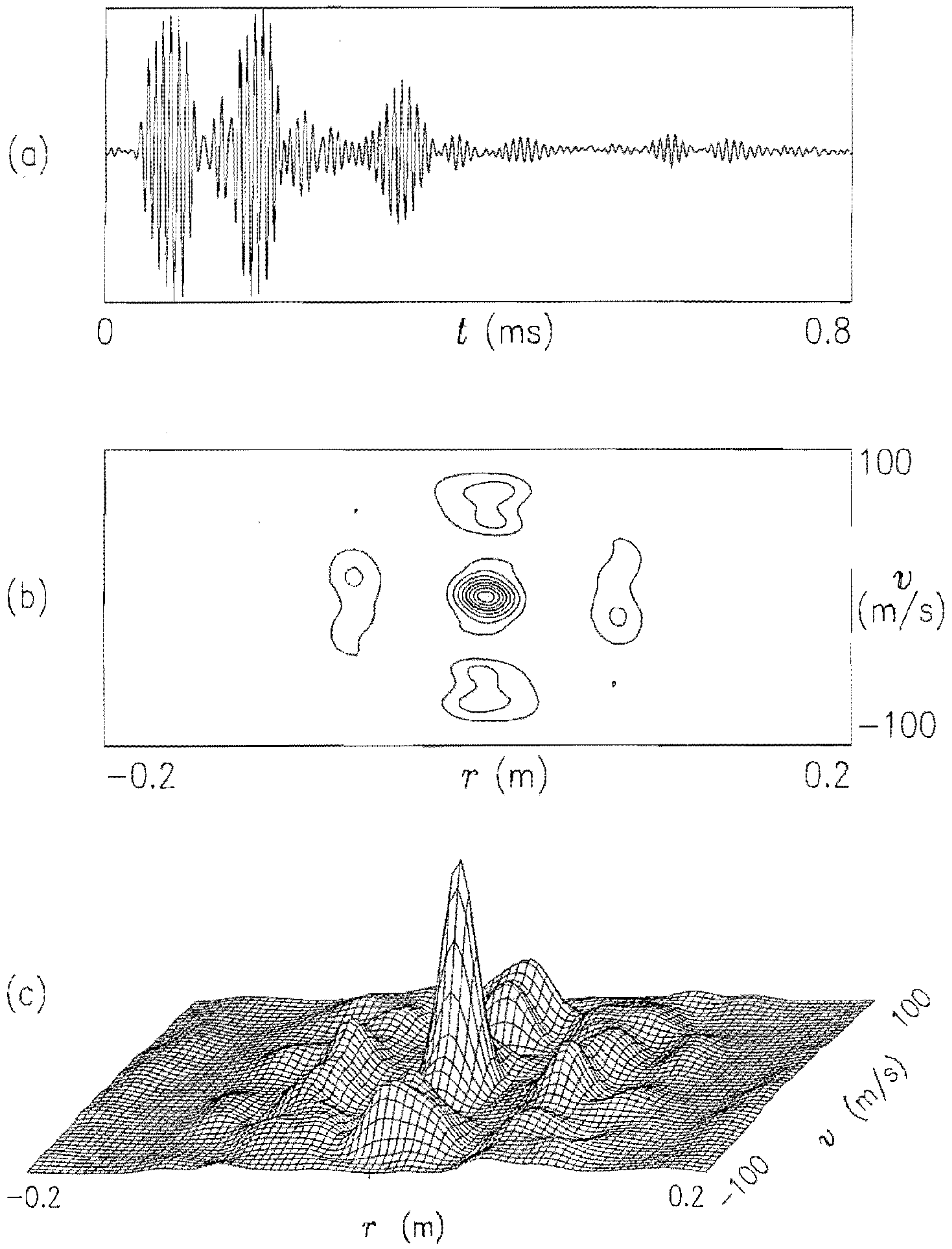

Figure 1 (a) Example of a sonar click exhibiting several distinct peaks and its ambiguity diagram: (b) contour plot, (c) relief map

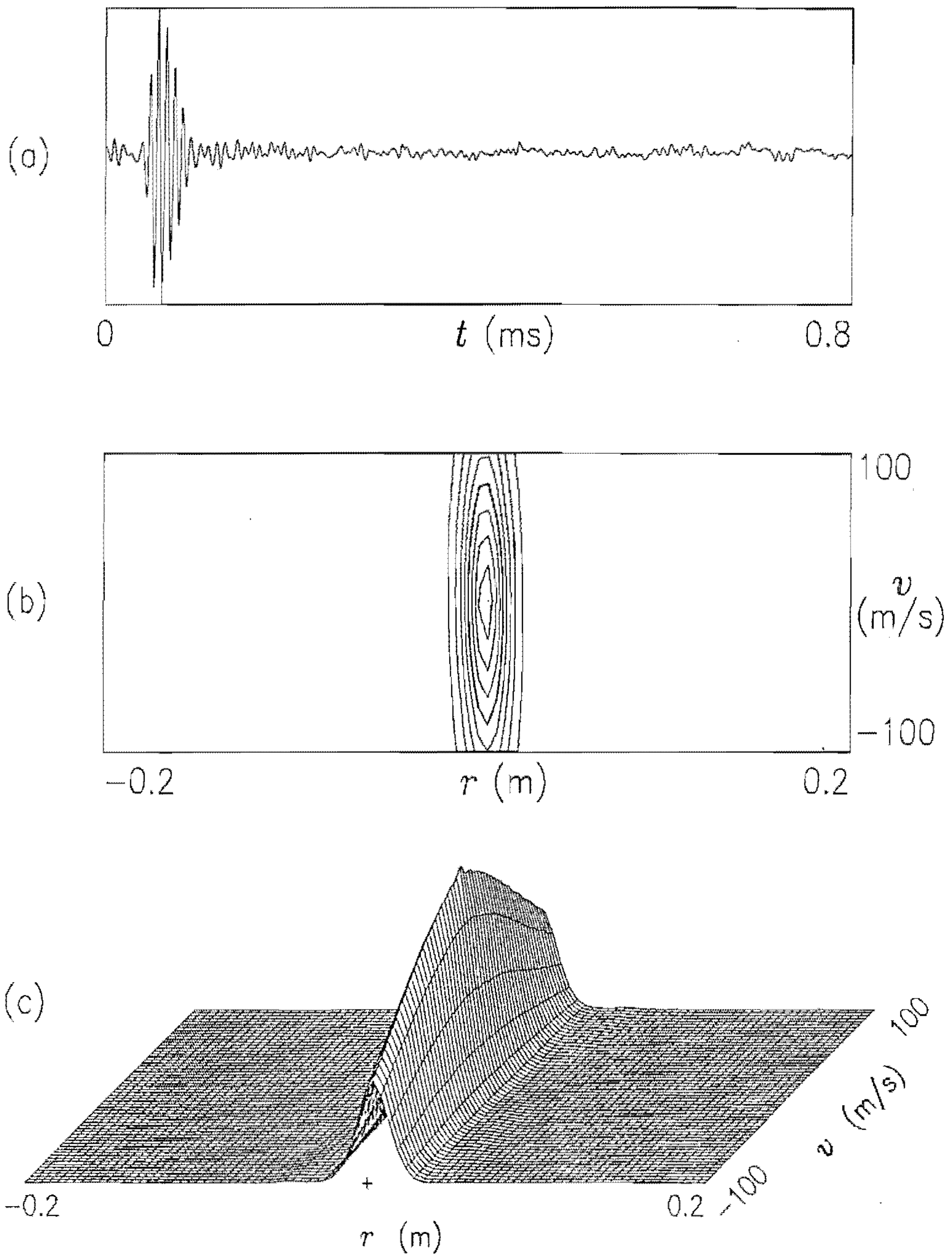

Figure 2 (a) Example of a short sonar click and its ambiguity diagram: (b) contour plot, (c) relief map

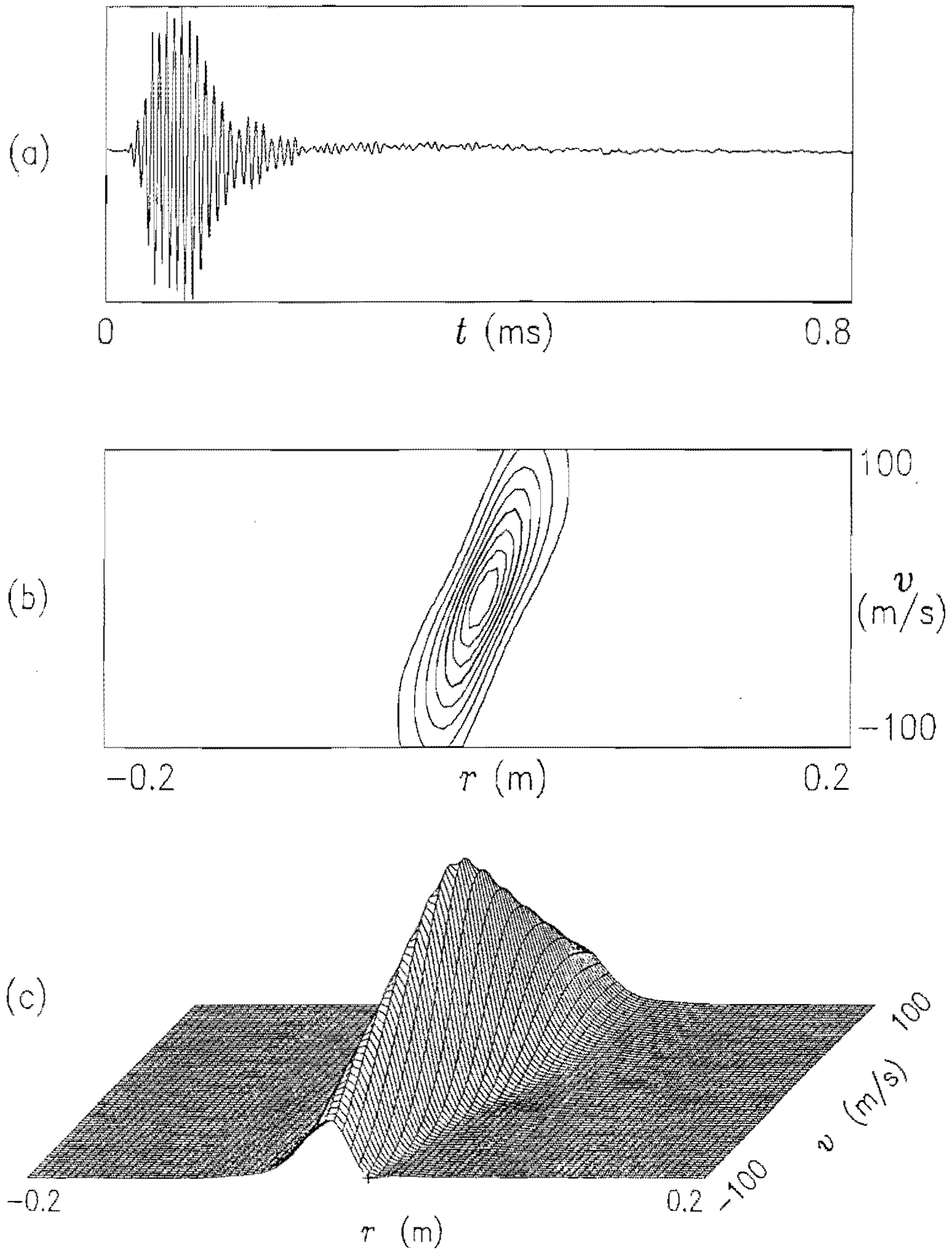

Figure 3 (a) Example of a sonar click exhibiting a small frequency sweep and its ambiguity diagram: (b) contour plot, (c) relief map.

several major peaks, which occur along the velocity and range axes, with only a little ambiguity density off these axes. The main peak has a width (measured from its center to where it falls to half of its peak value) of 2 cm along the range axis and 20 m/s along the velocity axis. The other lobes all have peak amplitudes which are less than half the value of the main peak. The click used for this ambiguity diagram could resolve velocity differences down to 20 m/s and range differences greater than 2 cm. However, Hector's dolphins have a maximum swimming speed of about 10 m/s (Slooten and Dawson 1988) and so seem unlikely to have much use for such coarse velocity resolution.

The ambiguity diagram shown in Figs 2b and 2c consists almost entirely of a narrow ridge (in range) extending beyond 50 m/s along the velocity axis, with negligible ambiguity density more than 1 cm (in range) from this axis. A sonar system employing the click shown in Fig 2a would have negligible ability to resolve velocity differences and can be described as doppler insensitive. The range ambiguity of 2 cm is essentially the same as that for the click shown in Fig 1a.

Figs 3b and 3c show an ambiguity diagram that again consists of a single narrow ridge, but which is angled with respect to the velocity axis, due to a slight frequency sweep within the click. The extent of this sweep implies that the velocities of targets are resolvable if their differences exceed about 70 m/s, which is far too coarse a resolution to be of practical assistance to the dolphins in detecting real targets whose velocities seldom exceed 10 m/s. However, it may be useful in that it enables the dolphin to emit a click longer than that shown in Fig 2a (for example), thereby significantly increasing the energy in the transmitted sound while retaining a similar range resolving ability. In our experience, clicks similar to that displayed in Fig 3a are much more common than clicks like those shown in Figs 1a and 2a.

4. Discussion and Conclusions

Hector's dolphins, utilising the types of sounds examined in Section 3, should be capable of resolving targets down to 2 cm apart. This accuracy is achieved at the expense of velocity resolution, which is never better than 20 m/s. It is extremely doubtful if any prey hunted by Hector's dolphin are capable of swimming at 20 m/s (39 knots), implying that the velocity resolution of the sonar clicks is not useful for foraging. Many of the sounds indicate a slight frequency sweep, but this appears insufficient to improve velocity resolution to any useful degree.

Compared to the sonar sounds emitted by bats, those of Hector's dolphin are relatively simple. Most are short (<400 µs), narrowband clicks centered around 124 kHz (Dawson 1988; see also Chapters 2 & 3). As we have shown, these sounds are suited to resolving the ranges of targets rather than their velocities. Many bats emit compound signals allowing the simultaneous resolution of target range and velocity differences. For example, the medium-sized, insectivorous bat *Rhinolophus ferrumequinum* employs signals with a long (about 50 ms) constant frequency (CF) component of about 85 kHz followed immediately by a short (about 5 ms) frequency-modulated (FM) component which sweeps down to approximately 65 kHz. Doppler shifts in the returning CF component allow precise determination of the target velocity, while the echoes of the FM component provide information about the target's range and other characteristics (Schnitzler 1968; Simmons 1973; Schuller et al. 1974).

The ambiguity diagrams of sonar sounds emitted by marine mammals have been calculated for only a few species (e.g. *Phocoena phocoena* and *Delphinus delphis*, Dziedzic 1978). They mainly consist of narrow ridges aligned along the velocity axis (Dziedzic 1978; Dziedzic et al. 1977), which tend to be broader along the range axis than those of Hector's dolphins. However, Dziedzic appears to have recorded the sounds with equipment having a restrictive upper frequency response (30 kHz). More recent studies have cast doubt on the validity of the low-frequency (about 2 kHz) signals obtained in this way (Kamminga and Wiersma 1981).

In a review of echolocation by marine mammals, Evans (1973) found that their sonar clicks are generally short and broadband, with peak frequencies ranging from about 15 to 80 kHz, and with energy often extending up to 150-200 kHz. However, most of the recording equipment used in the early 1970s and before was inadequate to record to the transient nature of the sounds, which seems to have influenced the results obtained (Diercks et al. 1973; Watkins 1974). More recent studies (e.g. Kamminga and Wiersma 1981, who used wide-band recording equipment) of the sounds of *Phocoena phocoena* and other cetaceans indicate that their sonar signals usually consist of a high-frequency, narrow-band click at about 120 kHz, with some also exhibiting a low-frequency component at about 20 kHz. The high-frequency clicks appear to be similar to those we observed from Hector's dolphins. However, to our knowledge, no ambiguity diagrams for such sounds have been published.

Hector's dolphins seem primarily concerned with resolving the ranges of targets, and single sounds possess no useful doppler resolving capability. This probably stems from the high speed of sound in water, which results in small doppler shifts for the range of target velocities. However, the apparent lack of velocity resolution applies only to a single click, and in no way inhibits the dolphin from inferring velocities of targets from changes in their ranges over several clicks.

5. Acknowledgements

Financial and equipment support for the field recording phase of this project was provided by New Zealand Lottery Board, Greenpeace International, World Wide Fund for Nature (N.Z.), Project Jonah (N.Z.) Inc., Cetacean Society International, IBM (N.Z.) Ltd., Brüel and Kjær, Reid Technology, Tech Rentals, Racal Electronics, Neptune Aquasuits and Tait Electronics Ltd. William Thorpe is grateful for the support of a N.Z. University Grants Committee Postgraduate Scholarship.

Section II. Sounds and behaviour

Chapter 5. Behavioural and Social Contexts of Hector's dolphin Vocalisations

Abstract

Hector's dolphins (*Cephalorhynchus hectori*) have a simple vocal repertoire, consisting almost entirely of ultrasonic clicks. They produce no whistles, and very few audible sounds. To examine acoustic communication in this species I analysed the relationship between click types and behaviour. Hector's dolphin clicks do not appear to be used solely in echo-location. The proportion of complex click types is greater in large groups, and in "surface active" behaviour states, suggesting that these sounds have social significance. High pulse rate sounds, in which the repetition rate of ultrasonic clicks is audible as a "cry", are most strongly associated with aerial behaviours. I suggest that dolphins may have evolved the ability to gather information from the echoes of each other's sonar pulses. This may reduce the need for a large number of vocal signals, and may explain the apparent simplicity of the acoustic repertoires of some odontocetes.

Introduction

Studies of vocal communication in odontocetes have focussed almost exclusively on sounds that are audible to humans (especially whistles; see Caldwell and Caldwell, 1977) and easily recordable using standard taperecorders (e.g. Lang and Smith, 1965; Sjare and Smith, 1986b; Weilgart and Whitehead, In press). Although several authors suggest that click sounds may be used in communication (e.g. Lang and Smith, 1965; Watkins, 1980), "there has been little follow-up on the idea" (Herman and Tavolga, 1980, p. 164). The demonstrated use of clicks in sophisticated echo-location by odontocetes (e.g. Norris, 1969) seems to have led to an implicit assumption that clicks are used primarily, if not solely, in echo-location (e.g. Popper, 1980; Morris, 1986).

Hector's dolphin has an unusual vocal repertoire. Most delphinid cetaceans produce unpulsed, frequency modulated or unmodulated, pure tones usually between 5 to 15 kHz, which are referred to as whistles (Herman and Tavolga, 1980). Hector's dolphins do not whistle, and they make very few other audible sounds. Their most common audible sounds, which sound like a "cry" or "squeal", are caused by high frequency clicks repeated at such high repetition rates that the rate itself, rather than the individual clicks, is audible (see Watkins et al., 1977). Additionally, their typically narrowband click sounds (see Chapters 1 & 2) are unlike the broadband clicks of most other delphinids (Norris, 1969).

Several lines of evidence suggest that Hector's dolphins use their clicks in echo-location. (a) Other dolphins and porpoises use clicks in echo-location experiments (e.g. Norris, 1969, Evans, 1973). (b) The structure of Hector's dolphin signals is such that they would provide good range resolution in sonar (see Chapter 4). (c) In this study, lone Hector's dolphins were often seen inspecting the hydrophone visually, and click trains were usually recorded on these occasions. It is unknown whether any cetaceans use clicks to communicate.

Since Hector's dolphins lack the rich audible repertoire of other delphinids it seems likely that, if they communicate vocally, they do so using their high-frequency clicks. Likewise sperm whales, and some other non-whistling odontocetes, have no vocal signals other than clicks (Watkins, 1980; Herman and Tavolga, 1980).

Generally, it is assumed that the meaning of vocalisations can be interpreted from the behavioural context in which they occur (e.g. Tyack, 1981; Clark, 1983; Sjare and Smith, 1986b; Weilgart and Whitehead, In press). In this study I investigate whether Hector's dolphin clicks, which are almost certainly used in sonar, are also used in communication.

Methods

I made wide-band sound recordings of free-ranging Hector's dolphins in Akaroa Harbour (43° 50'S; 172° 56'E), and in the nearby waters of the south coast of Banks Peninsula, New Zealand, over the summer seasons of 1986/87 and 1987/88. Recording methods and equipment are described in Chapter 2. The equipment had a minimum frequency response of 300 Hz to 150 kHz +/- 3 dB. All recordings were made from a drifting 3.9 m inflatable boat in calm sea conditions (windspeed <10 knots).

Onto the commentary channel of the recorder I noted the occurrence of 40 behaviour events. I also noted "behavioural state" as one of nine subjective

TABLE 1. Behaviour events recorded

Code	Behaviour
AS	ACTIVE SURFACE (rapid surface, with spray)
BA	BELLY AWAY (from another dolphin)
BB	BLOW BUBBLES
BC	BODY CONTACT (not forceful)
BI	BITE (another dolphin)
BP	BELLY PRESENT
CH	CHASING
CO	CHIN-OUT (chin poked vertically out of water)
DE	DEFECATE
DI	DISPLACEMENT
EO	EYE-OUT (a surfacing roll high enough to show the eye)
ES	ECHELON SWIMMING
HF	HORIZONTAL FLEX (flexing body while stationary at surface)
HJ	HORIZONTAL JUMP
HT	HITTING WITH TAIL
LA	SWIMMING LINE ABREAST
LO	LOBTAIL (forcefully slap tailflukes on water surface)
OM	OPEN MOUTH DISPLAY
PN	POUNCE (forceful mounting-like contact between ventral surface of one dolphin and the lateral or dorsal surface of another)
PO	PENIS OUT
SF	SIDE FLOP (jump landing on side; in sequence analysis as NJ - noisy jump)
SP	SPYHOP
SS	SWIMMING ON SIDE
SU	SURF
TF	THROAT FLOP (partial jump splashing down on throat region; in sequence analysis as NJ - noisy jump)
TO	TAIL OUT (tailflukes lifted clear of water)
TS	TAILSPLASH
UD	UPSIDE DOWN SWIMMING
UL	UPSIDE DOWN LOBTAIL
VJ	VERTICAL JUMP
WE	PLAYING WITH WEED
CP	COPULATION (intromission observed)
PC	POSSIBLE COPULATION (intromission probable, but not observed)
FE	OBSERVED FEEDING, OR CHASING FISH
AP	APPROACH TO HYDROPHONE (<3m, oriented directly at it)
CA	CLOSE APPROACH TO HYDROPHONE (<1m, oriented directly at it)
VCA	VERY CLOSE APP TO HYDROPHONE (<0.5m, oriented directly at it)
ML	MILLING (constant direction changes while at surface)
BG	BEAK TO GENTIAL CONTACT
PA	PASS (pass hydrophone, not oriented at it)

categories which were broadly indicative of group activity (for similar approach see Sjare and Smith, 1986b; Weilgart and Whitehead, In press). I have lumped applicable states into two categories (see Appendix A), "long-diving" (which is thought to represent midwater or bottom feeding) and "surface active" (group remains mostly at surface, very active; jumps, lobtails and contact behaviours frequently seen), and have contrasted the usage of sound types between these two categories. The behaviour events recorded are given in Table 1. To examine whether certain types of sounds were used primarily when dolphins were investigating the hydrophone, I also coded three categories of approach to the hydrophone.

Sounds that occurred within 10 s of behavioural events were digitised and analysed by Dawson and Thorpe (see Chapter 2). Principal component analyses of the similarity of these sounds, which indicated three groups of sounds according to their timing characteristics, and three groups according to their frequency characteristics, are used to classify sounds into types (Figs 1 & 2).

In a detailed study of Hector's dolphin behaviour, Slooten (a) recorded the occurrence of behavioural events and used sequence analysis as a quantitative method of classifying them into five categories (Fig. 3). I used her categories to define a "behavioural context" for each of my sample of behaviour events. Because some behaviour events I scored (e.g. approaches to the hydrophone) were not included in Slooten's sequence analysis (see Table 1 & Fig. 3) "Behavioural state" (which was recorded for each behaviour event) has a larger sample size than "behavioural context". Please note that my terms "behavioural state", and "behavioural context" (defined above) are not synonymous.

Results and discussion

1. Sounds, general behaviour and behavioural context

If sounds have a social function, one might expect a different ratio of usage when dolphins are in large groups (>10 indivs; n = 61) vs small groups (1-5 indivs; n = 153). There was a significant difference in the usage of frequency domain sound types ($\chi^2 = 12.7$; 2df; p. < 0.005; 3*2 contingency table), with more complex multipeaked sounds but fewer two peaked sounds used in

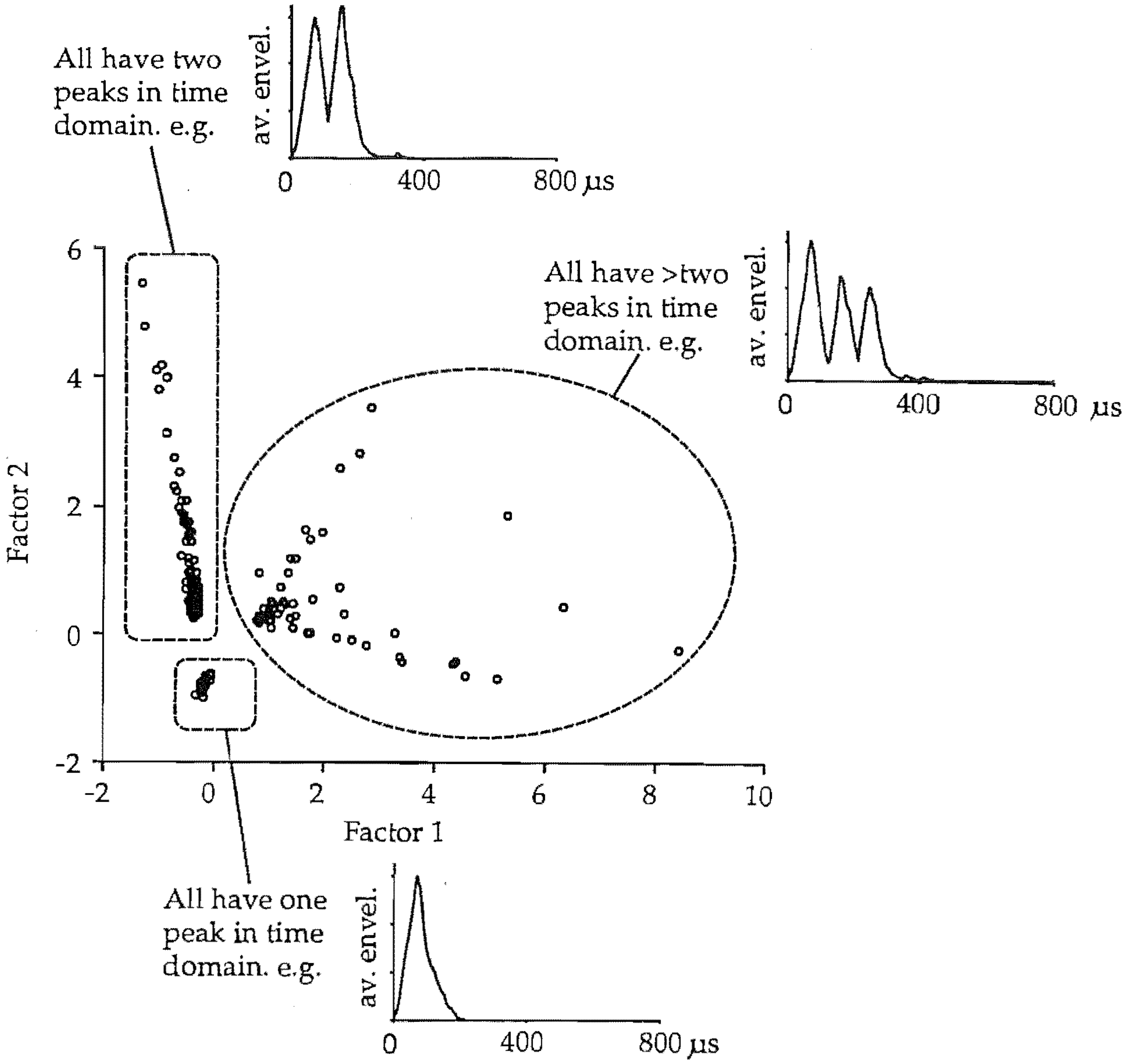

Fig. 1. The structure of Hector's dolphin sounds, grouped according to their similarity in the time domain (redrawn from Chapter 2). The average time domain envelope is given for a typical click in each group.

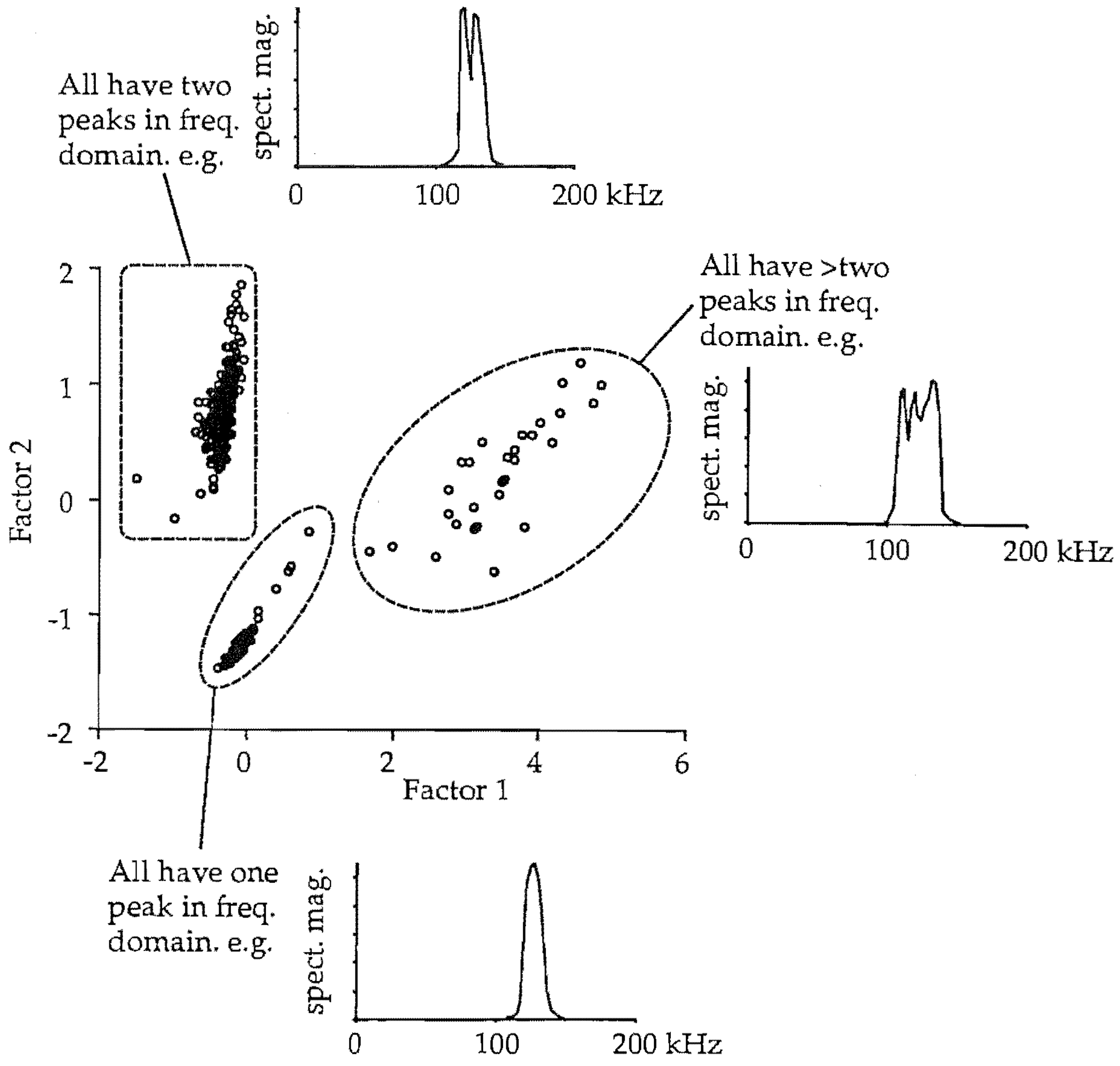

Fig. 2. The structure of Hector's dolphin sounds, grouped according to their similarity in the frequency domain (redrawn from Chapter 2). The spectrum (spectral magnitude) is given for a typical click in each group.

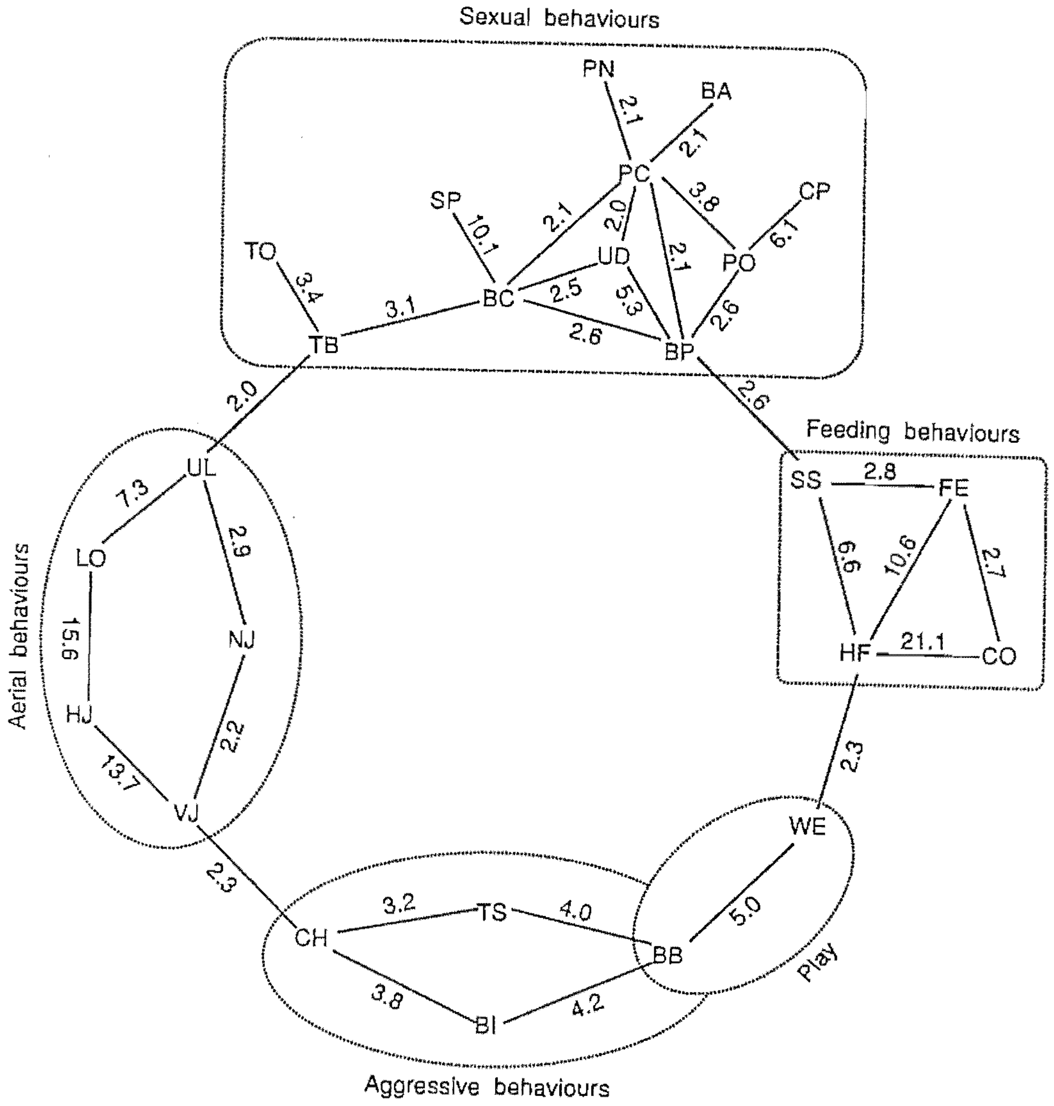

Fig. 3. Behaviour sequence diagram for one minute interval between preceding and following behaviours. The numbers (z scores; Bakeman and Gottman, 1986) indicate the strength of the association between behaviours. Reproduced with permission from Slooten (a).

large groups. No significant difference was found in the time domain (χ^2 = 0.28; 2df; p. >0.10).

Additionally, one might expect different click types in different group activities. Usage of click types between "long-diving" (n = 91) and "surface active" (n = 162) behavioural states was not significantly different in either frequency (χ^2 = 4.20; 2df; p. > 0.10) or time (χ^2 = 0.97; 2df; p. > 0.10) domains. Likewise, no significant difference was found in the ratio of usage of click types between "sexual" and "feeding" or "feeding" and "aerial" behavioural contexts as defined by Slooten's sequence analysis (Fig. 3).

2. Are specific sounds used in sonar contexts?

Dolphins would frequently directly approach the hydrophone and appear to inspect it both visually and acoustically. Signals recorded at these times were almost certainly used to examine the hydrophone (i.e. sonar), rather than to communicate with other dolphins. To examine whether Hector's dolphins preferentially use certain click types in sonar contexts, I compared the ratio of sound type usage between close approaches (direct approaches < 1 m from hydrophone; n = 35) and non-approaches (all non-approaching behaviours recorded; n = 182). The comparison was non-significant with respect to both time (χ^2 = 2.21; 2df; p. > 0.10) and frequency domain (χ^2 = 0.757; 2df; p. > 0.10) click types.

3. Incorporating criteria for peak separation

One potential problem with the classification given in Figure 1 is that current models of click perception by dolphins stress that the separation of time domain peaks within a click is possibly as important as the number of peaks (see Chapter 2; Hammer and Au, 1980; Au and Moore, 1988). Signals are spread along the axes of the time domain PCA plot (Fig. 1) according to the separation of the peaks. To incorporate a criterion of peak separation into a reclassification of peak number, each subsequent peak was counted only if it occurred later than twice the decay time of the previous peak. The decay time is the time that a peak takes to decay to 40% of its maximum value. This criterion resulted in a classification with 321 (80.1%) single pulses, 72 (17.9%) double pulses, and 8 (2.0%)triple pulses.

The proportion of single, double and triple pulses was significantly different between "long-diving" (n = 91) and "surface active" (n = 162) behavioural states ($\chi^2 = 6.381$; 2df; p. < 0.05). The principal difference was that there were approximately twice as many double pulses recorded in "surface active" as in "long-diving" behaviour states.

The proportion of single, double and triple pulses did not differ significantly between sexual (n = 23) and feeding (n = 34) behavioural contexts ($\chi^2 = 1.121$; 2df; p. > 0.10). The comparison of click usage between aerial (n = 16) and feeding (n = 34) contexts was also non-significant ($\chi^2 = 3.349$; 2df; p. > 0.10).

3. How important is click rate?

It is possible that the dynamics of click rate are important, and that increasing or decreasing click rates carry social meaning. If the signals are used strictly for sonar, one would expect click rates to increase as the distance to the target decreases (i.e. the time between clicks should be approximately proportional to the range of the target; Watkins, 1980). Usually clicks are emitted at a rate such that outgoing signals do not overlap with returning echoes (Turl and Penner, 1989).

I could determine the distance between the phonating dolphin and its sonar target only in cases where the dolphin appeared to be investigating the hydrophone. Hence I can only address the importance of click rate indirectly, by determining whether increasing or decreasing click rates occur more commonly in certain contexts. The incidence of increasing, static and decreasing click rates was not significantly different between "surface active" (n = 91) and "long-diving" (n = 162) behaviour states ($\chi^2 = 1.13$; 2df; p. > 0.10). Nor was it different between feeding and sexual behaviour contexts ($\chi^2 = 3.883$; 2df; p. > 0.10), or between feeding and aerial contexts ($\chi^2 = 0.603$; 2df; p. > 0.10).

Echolocating animals typically increase their click rate as they approach a target (Watkins, 1980). If Hector's dolphins use in their clicks principally for sonar, increasing click rates should be more common during close approaches to the hydrophone than in other situations. Increasing click rates were recorded more often in close approaches to the hydrophone (n = 35) than in non-approaching behaviours (n = 182), but their ratios of increasing, decreasing, and static click rates were not significantly different ($\chi^2 = 3.99$; 2df; p. > 0.10).

4. Are high pulse rates social or investigative?

Clicks emitted at high repetition rates generate a frequency equal to the repetition rate (Watkins et al., 1977), which in Hector's dolphin is audible as a "cry". Here a cry is defined as having a pulse repetition rate of >200 Hz.

If cries are social signals, they might be expected to occur more commonly in certain behavioural contexts. The incidence of "cry" sounds (per dolphin) was significantly greater in aerial and aggressive behaviour contexts than in feeding (Fig. 4). A sequential Bonferroni adjustment (Rice, 1989) to the probabilities in Fig. 4 indicated that the feeding/aerial difference is significant at the "tablewide" $p < 0.05$ level.

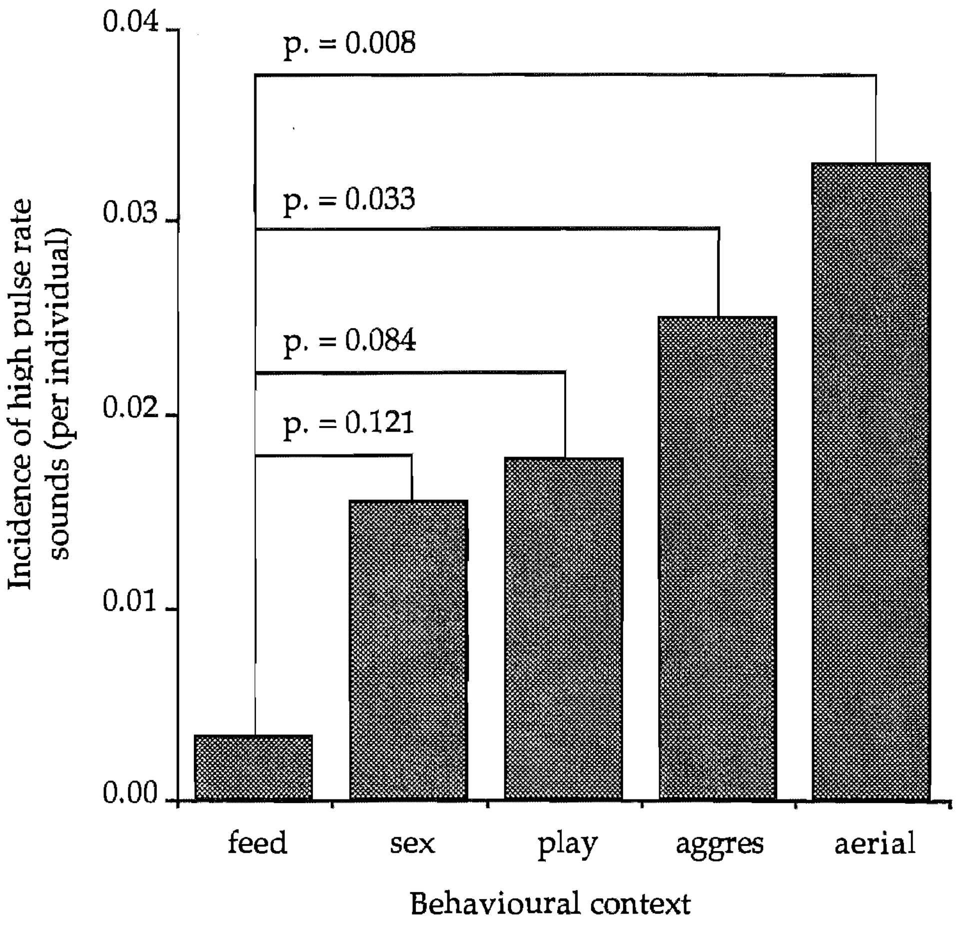

Fig. 4. Incidence of cry sounds (pulse repetition rate >200 Hz) in different behavioural contexts. Probabilities indicate the significance of pairwise

comparisons between feeding and other behavioural contexts [test of proportions, Neter et al., 1988. pp. 414-416].

I also examined the incidence of cries between "surface active" and "long-diving" behaviour states. High repetition rate sounds were significantly more common in "surface active" behaviour states ($\chi^2 = 5.26$; 1df; $p. < 0.025$; [test via 2*2 contingency table]). However, "surface active" groups typically contain more dolphins than "long-diving" groups, and the occurrence of "cry" sounds (per dolphin) was not significantly different between these two behaviour states ($z = 0.68$; $p. = 0.49$ [test of proportions, Neter et al., 1988. pp. 414-416]). Similarly, "cry" sounds are recorded more often in large groups (>10; n=61) than in small ones (≤5; n=153) ($\chi^2 = 19.75$; 1df; $p. < 0.001$), but the rate of "cry" sounds (per dolphin) was not significantly different ($z = 0.32$; $p. = 0.75$).

An alternative explanation for high pulse rates, which is based on their use in sonar, rather than communication, is that dolphins may use them to gather fine detail when investigating targets at close range. If high pulse rates are simply a function of distance to the hydrophone (closer to target implies faster rate) more "cries" should be recorded in close approaches (<1 m) to the hydrophone than in non-approaches. Paradoxically for this hypothesis, more cries were recorded in non-approaches (all non-approaching behaviours; n = 182) than during close approaches (n = 35) but the comparison was not significant ($\chi^2 = 3.75$; 1df; $0.05 > p. < 0.10$).

5. Conclusions

The nature of recording high frequency sounds imposes severe constraints on the amount of data that can be gathered and analysed. High tape speeds require a large amount of tape, and to easily hear the recorded sounds the tape must be slowed by a factor of 16. This makes even the most preliminary analyses extremely time-consuming. Despite these difficulties, this study shows a relationship between the behaviour of Hector's dolphins and their use of clicks that is not fully explicable by the hypothesis that the clicks are used only in sonar. The proportion of complex sounds (in frequency and time; respectively) is greater in large groups, and in "surface active" behaviour states, suggesting that these sounds have social significance. No one type of signal was preferred when dolphins appeared to be echo-locating.

Whether click rate is increasing, decreasing or static does not appear to be socially important, but high pulse rate sounds ("cries") are used much more often in aerial and aggressive behaviour contexts than in feeding contexts. This is a particularly interesting result, as aerial behaviours appear to indicate excitement. Dziedzic and DeBuffrenil (1989) reported that "cry" sounds were "always recorded when the emitting animal was in a situation of stress" (p. 450), because their newly captured Commerson's dolphins made these sounds when they ran into the mesh of their cage. My analysis suggests that cries are indicative of excitement, and may have a positive or negative connotation, depending on the context in which they are emitted.

While there is a general relationship between sounds and behaviour, Hector's dolphins do not seem to have signals that are used solely in any particular behavioural context. Whatever acoustic communication system they have, it is not one of simple labels for different behavioural contexts or activities. The analysis above shows that Hector's dolphins use more complex clicks in large groups and in "surface active" behaviour states, and that cries are associated strongly with behaviours suggestive of high motivational state. This is perhaps not as much as might be expected in the acoustic communication system of dolphins, which have large brains (Morgane et al., 1986) and complex behaviour (Würsig, 1986, Conner and Norris, 1982). It is appropriate here to briefly discuss some other possibilities for acoustic communication.

The hypothesis that dolphins base their acoustic communication on whistles (e.g. Herman and Tavolga, 1980; Morris, 1986) is not convincing, as it implies that non-whistling cetaceans do not communicate acoustically. Herman and Tavolga (1980) suggested that whistling odontocetes are large school, communal foraging species and that non-whistler species are more solitary. However, this relationship is far from perfect as the social and ecological differences between whistlers and non-whistlers are not so great as to expect such a fundamental difference.

It is possible that the timing of clicks contains social significance. The timing of sperm whale clicks is thought to communicate the identity of the phonating whale, and perhaps other social information as well (Watkins and Schevill, 1977; Watkins, 1980). Investigating the timing of high frequency clicks over entire click trains was beyond the scope of this study. It would be helpful if such a study could control for the sonar function of the clicks as well, by ensuring that the investigator has some knowledge of the presence and positions of sonar targets.

An "eavesdropping" hypothesis for dolphin communication

There is another possibility for communication, which relies more on dolphins "eavesdropping" on others rather than actively transmitting signals to each other. Wood and Evans (1980) elegantly demonstrated that bottlenose dolphins can gather precise information by listening to environmental sounds. They instrumented the head of a blindfolded bottlenose dolphin with seven broadband contact hydrophones and fed their output to a wideband taperecorder. The dolphin repeatedly chased and caught a live fish without emitting sonar pulses, apparently by listening to the sounds of the fish swimming. This suggests that dolphins can gather similar information about members of their own groups, by listening to their swimming noises.

Although the emission of dolphin clicks is usually highly directional (see Chapter 2 for discussion of this) they are likely to be audible to others nearby. Fenton (1980) suggested that this is one of the "mixed blessings" of echo-location in bats, as they might be able to localise food by listening to the "feeding buzzes" of others, and that territorial species might detect intruders from their phonations. Playback experiments have shown that some bat species are attracted to the echo-location calls of conspecifics and sympatric species (Barclay, 1982; Leonard and Fenton, 1984). Concentrations of echo-location calls may serve as cues indicating the presence of food, and eavesdropping bats might enhance their prey detection range by up to 50 times over that possible using their own signals (Barclay, 1982). Likewise, dolphins may find food by listening to others foraging (Caldwell and Caldwell, 1977).

Additionally, it is quite possible that dolphins can not only detect, but interpret the echoes of each others' sonars. Two of the four models currently used in bionic sonar development (simple energy detection in a bandpass filter; energy detection with a bank of filters of constant "sharpness" [constant Q]) do not require knowledge of the outgoing signal other than its bandwidth (Johnson, 1988). There is evidence that dolphins may use a system similar to energy detection with a bank of constant Q filters (Johnson, 1988). As most Hector's dolphin clicks are of very similar (and narrow) bandwidth, an effective "eavesdropping" system could assume the normal bandwidth, and interpret incoming click echoes accordingly.

If, in addition to gathering information from environmental sounds, it is also possible for dolphins to interpret each other's sonar echoes, then each dolphin has access to information about approximately where nearby dolphins are and what ensonifying. Such eavesdropping ability would render unnecessary many of the signals used in more active communication. Signals about activities, and positions (e.g contact calls), may be unnecessary. Simple signals signifying motivational state (such as "cry" sounds), together with active sonar, and the ability to process each other's sonar echoes, might easily form the basis of a communication system to match the apparently sophisticated and flexible behaviour (e.g. Würsig, 1986, Connor and Norris, 1982) of delphinids.

Several authors have attempted the difficult task of defining communication (see Altman, 1967, for an excellent review). The eavesdropping system above, if it exists, would require a reappraisal of Griffin's (1977) suggestion "that echo-location does not properly fall within any reasonable definition of communication behaviour" (p.252). It would also challenge concepts of communication which stress that signalling must be intentional (see also Hailman, 1977), and those which imply, or state explicitly, that the signals used should have been moulded by natural selection for that purpose (Wilson, 1985; Dawkins and Krebs, 1978, 1984). Altman's (1967) statement, that "social communication is a process by which the behaviour of an individual affects the behaviour of others" is more accommodating. While the transfer of information in my "eavesdropping" hypothesis is not necessarily intentional, it is mutualistic in the sense that the flow of information is not always one way (see Marler, 1977). When the listening dolphin uses its sonar system, others get the chance to "eavesdrop" on it. While the *mechanisms* of echo-location may have evolved to fulfil the *function* of food finding and orientation, it may be that unintentional communication is an *effect* (sensu Williams, 1966) of having a receiver system tuned to process sonar echoes.

Acknowledgements

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Appendix A: Behaviour states, as recorded in the field and as lumped in the analysis

Behaviour states:

as recorded in the field	*as lumped for analysis*
Long diving with bouts of active surfacing	LONG DIVING
Long diving	
Long diving and approaching regularly	
Travelling	
Surface behaviour	
Surface behaviour and approaching regularly	
Surface behaviour and seen chasing fish	
Surface active	SURFACE ACTIVE
Frantic	

Section III. Gillnet entanglement and its acoustic solutions

Chapter 6. Incidental catch of Hector's dolphins in inshore gillnets

Abstract

The major aim of this study was to quantify the magnitude and dynamics of the incidental catch of Hector's dolphins (Cephalorhynchus hectori) in gillnets set in the Pegasus Bay and Canterbury Bight area. During a 4-year period (1984 - 1988) at least 230 Hector's dolphins were killed in groundfish gillnets by commercial and amateur fishers. Approximately 91% of entanglements occurred during November to February. Seasonality of catch corresponds closely to increased commercial gillnetting inshore in spring and summer. Most entanglements (89%) occurred within four nautical miles (7.4 km) of the shore, and most (86%) were caught in water less than 20 m deep. Surveys show that the dolphin's summer inshore movement coincides with high levels of inshore gillnetting by amateur fishers. The age-frequency of net-caught dolphins suggests that young animals are particularly vulnerable to entanglement.

Introduction

Entanglement of marine mammals in gillnets appears to be a problem which arises wherever marine mammals and substantial gillnetting effort occur in the same area (for review see O'Hara et al. 1986). For some gillnet fisheries, such as the North Pacific Japanese drift gillnet fishery for salmon, the annual incidental catch of marine mammals (mostly Dall's porpoises, Phocoenoides dalli) reaches into thousands (Jones, 1984). Similarly large incidental catches of cetaceans occurred in the Taiwanese drift gillnet fishery in northern Australian waters (Harwood et al. 1984; Harwood and Hembree, 1987). Groundfish gillnets (nets anchored on the bottom) are also responsible for entangling large numbers of cetaceans, and some populations appear to be directly threatened by such catches (e.g. Phocoena phocoena, Gaskin, 1984, Diamond and Hanan, 1986, Hanan et al. 1986, 1987, Read and Gaskin, 1988; Phocoena sinus, Barlow, 1986).

Hector's dolphin is a small (max. TL 1.44 m, n = 60), coastal delphinid which is restricted to the inshore coastal waters of New Zealand. Baker (1978) suggested that the species' inshore distribution made it particularly vulnerable to incidental capture in fishing gear. However, at that time it appeared that the small number of reported entanglements gave no

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immediate cause for alarm (Baker, 1978). He later reported that 18 incidental captures had been recorded since 1973 (Baker 1984).

During 1984/85 I interviewed many commercial fishers for information on the distribution of Hector's dolphins (Dawson and Slooten 1988). Many reported catching dolphins in gillnets, and it became clear that many more dolphins were caught than was previously believed. The Pegasus Bay and Canterbury Bight area (Fig. 1) probably has the highest incidental catch of Hector's dolphin (Slooten and Dawson, 1988) because inshore gillnetting and locally abundant Hector's dolphins combine to an extent not seen elsewhere. The major aim of this study was to quantify the magnitude and dynamics of the incidental catch of Hector's dolphins in this area.

This work would not have been possible without the co-operation of the commercial fishermen. I am particularly grateful to Craig Hill, Malcolm Tubbs, Tim Sintes, Bob Beggs and Ron Smith. I am grateful to Elisabeth Slooten for help in the field and to Joe Waas, Robert Jackson, Elisabeth Slooten, Doyle Hanan and Cheri Recchia for comments on the manuscript. Financial and equipment support was provided for the study by Greenpeace International, the New Zealand Lottery Board, Project Jonah (NZ) Inc., Cetacean Society International, World Wide Fund for Nature (N.Z.), N.Z. Department of Conservation, Pacific Whale Foundation, IBM (NZ) Ltd, Neptune Aquasuits, Oceans Society (NZ), Hutchwilco, Anthoni Computer Automations, Tait Electronics, N.Z. Underwater Association, and Neill Cropper and Co.

The Pegasus Bay and Canterbury Bight gillnet fishery

Commercial fishery

An intensive gillnet fishery has existed in the Pegasus Bay and Canterbury Bight area (fig 1) since the mid 1970s (Massey and Francis, 1988). Primary target species were two elasmobranch fish, rig (Mustelus lenticulatus) and Elephant fish (Callorhynchus milli). School shark (Galeorhinus australis) and moki (Latridopsis ciliaris) were also targeted. Recent restrictions (1986) on the allowable catch of these fish have caused fishers to target spiky dogfish (Squalus acanthias), kahawai (Arripis trutta), and ling (Genypterus blacodes). The shift to dogfish has increased gillnetting effort in winter (Ministry of Agriculture and Fisheries, unpub. data). Nets are usually set in the afternoon or evening and emptied the next morning to be reset as soon as emptied. Nets are not returned to port unless the fisher anticipates not fishing for >2 days.

Nets are usually made of nylon monofilament. Stretched mesh size is typically between 150-215 mm but can be up to 230 mm for school shark. Nets are 60 to 1,000 m long and individual fishers set up to 6,000 m of net. "Rig" nets are the most commonly used, and are made of nylon monofilament of 0.7-0.9 mm diameter, having a mesh size of 164-178 mm. They are 10-20 meshes deep, and are set on the bottom and anchored at each end.

The Amateur Fishery

Gillnetting is a popular recreational fishing method in the large harbors and bays of Banks Peninsula during the summer holiday season (December - February). Most amateur gillnetting is carried out in shallow water over mudflats for flounder (Rhombosolea sp.), or over rocky ground close to the shoreline (typically less than 60 m) for reef fish such as moki and butterfish (Odax pullus) (Slooten and Dawson 1988). Minimum legal mesh sizes are 115 mm for moki, 108 mm for butterfish, and 100 mm for flatfish. Nets used by amateur fishers are required to be no more than 60 m long. The majority of amateur fishers set their nets to fish overnight.

METHODS

From November 1984 to October 1987 commercial gillnetters who were actively fishing in the Pegasus Bay and Canterbury Bight were interviewed informally several times each season to gather information about the nature and magnitude of the incidental catch of Hectors dolphin, and to encourage them to bring incidentally killed dolphins in for examination. As the extent of the problem became apparent, these interviews were formalized, and all commercial gillnetters were interviewed monthly during the October 1987 to March 1988 summer. Fishers were asked standard questions including their net type and its mesh size, amount of net used, fish species targeted, major catch species, whether dolphins had been seen, number of dolphins caught, the location and depth of such captures, and what species of fish were caught in the same net. There were too many amateur fishers to interview. A subsample who knew of the research reported their

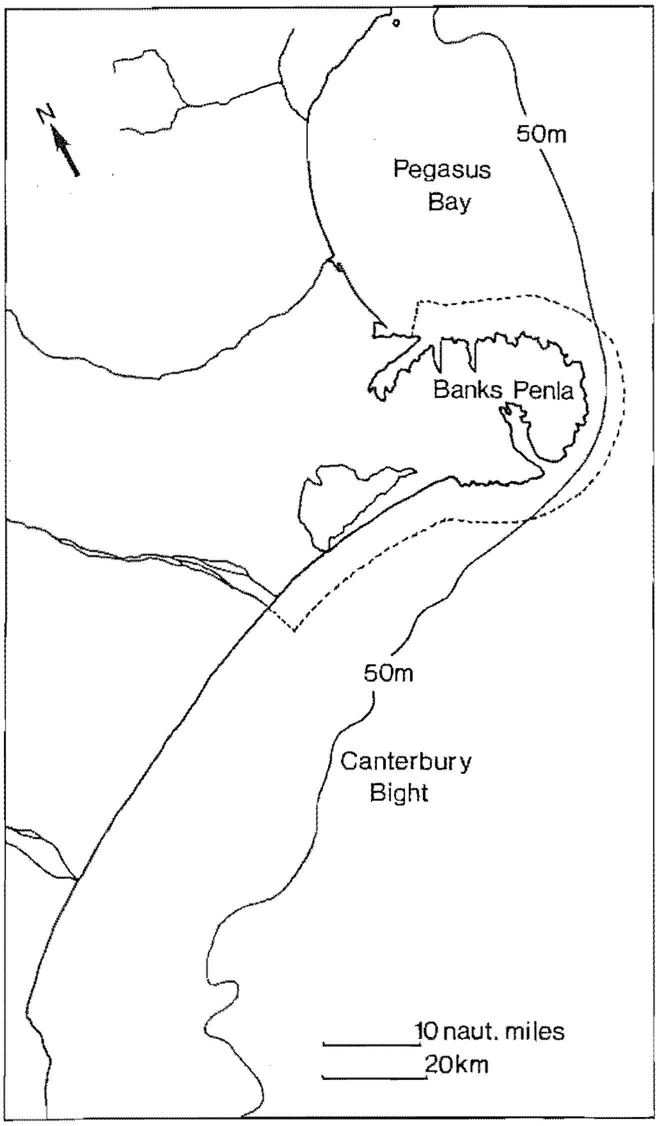

Fig. 1. Map of Pegasus Bay/Canterbury Bight. The dotted line indicates the boundaries of the Marine Mammal Sanctuary, and the 50m depth contour is shown.

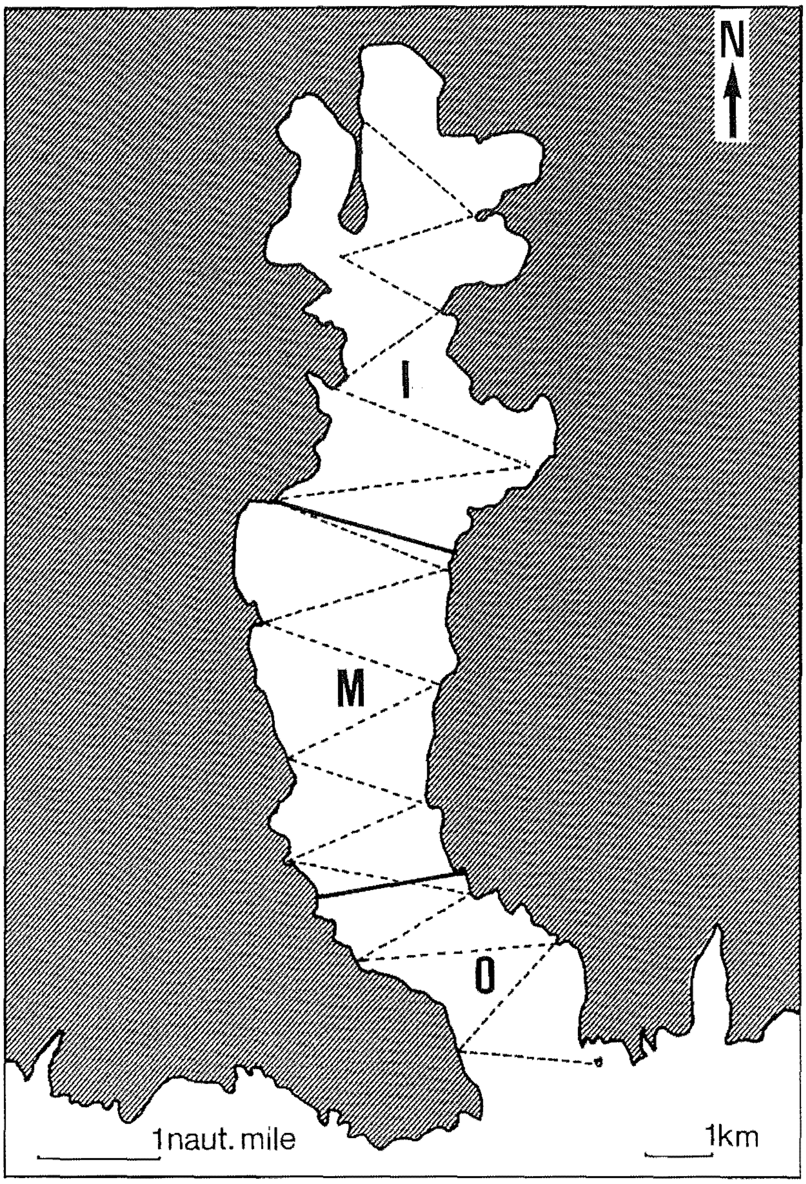

Fig. 2. Map of Akaroa Harbour showing the standardized "zig-zag" survey path, and the arbitary boundaries of the inner (I), middle (M) and outer (O) harbour categories used in the surveys.

entanglements, and were asked the same questions as the commercial fishers.

Unfortunately it did not prove possible to quantify the geographical distribution of fishing effort on a fine enough scale to be useful. Fishers did not usually record these details. In official data from the Ministry of Agriculture and Fisheries, location of effort, when recorded, is according to coarse "Fisheries Management Areas", two of which encompass the entire study area. Aerial surveys of net distribution (Read and Gaskin, 1988) were beyond the means of this study.

Dead dolphins were collected from fishers who reported catches to us via Marine VHF radio. Dead Hector's dolphins are often washed ashore and include those that died of natural causes and those that were drowned in nets and were discarded at sea. All carcasses were examined, and dissected if reasonably fresh. Gillnet entanglement often results in characteristic cuts and indentations in the dolphin's snout, dorsal fin, flippers and tailflukes. Only where such marks were obvious and fresh was the cause of death recorded as net entanglement. Net-marked carcasses found floating or beachcast well inside a large harbor, far from any commercial gillnetting activity (>10 naut. miles [18.5 km]) were recorded as resulting from entanglement in amateur fishers' nets.

Boat surveys of Akaroa Harbour were conducted From May 1986 to January 1989 to determine seasonal trends in dolphin abundance throughout the harbor. I attempted to complete one survey of the inner harbor during each month of field time (21 surveys) and one survey of the middle and outer harbor each week (56 surveys; see Fig 2 for area boundaries). Surveys were conducted using two observers, one looking each side of a 3.9 m inflatable boat powered by a 25 or 30 hp outboard motor. A standard "zig-zag" path was followed each time, referenced to conspicuous landmarks (see Fig 2). Survey speed was kept between 10 to 12 knots. When dolphins were sighted the boat was stopped and a count made of the dolphins nearby. Distinctive individuals were photographed before continuing on the survey.

From November 1987 to April 1988 the number of gillnets set in the inner harbor was counted on each survey. These counts were restricted to the inner harbor as no other fishing method using buoys at the surface is routinely used there. Elsewhere in the harbor bouys are used to mark lobster pots and, infrequently, longlines. Amateur gillnets are required to be buoyed at each end and the buoys marked with the owner's name. Each pair of buoys seen away from mooring areas was counted as one gillnet. Commercial fishers do not fish this area.

To protect Hector's dolphin from entanglement, in December 1988 the Department of Conservation created a Marine Mammal Sanctuary in Banks Peninsula waters (see Fig. 1) in which gillnetting was restricted (see Management Implications below). Legal problems with the implementation of the sanctuary resulted in widespread confusion among fishers as to whether they could legally set their nets. Hence net counts were not made in the 1988/89 field season.

RESULTS

In 1987/88 five vessels were regularly gillnetting in the Pegasus Bay/Canterbury Bight area. Only one of these five fishers used gillnets year-round, all others used some other method for part of the year. Only in November and December did all five fishers use gillnets. The total amount of net set (all fishers combined) increased from 5,350 m in October to 14,500 m in November, and remained fairly constant until February when it dropped to 7,350 m. Only 2-3 of these fishers gillnet over winter when the total amount of net set is usually 4,000-6,000 m. The amount of net set varied widely among fishers (350-6,000 m).

During the monthly interview period (October 1987 to March 1988) these fishers reported catching approximately 18 Hector's dolphins (see Table 1). All fishers reported that entangled dolphins rarely do significant damage to nets. Dolphins were caught while fishers were targeting for rig, elephant fish, school shark and dogfish (16 dolphins) and kahawai (2 dolphins). Fish caught in the same nets as the dolphins were predominantly rig, elephant fish, dogfish, school shark, kahawai, moki, flounder and sole.

Magnitude of Entanglement

The numbers of dolphins killed in commercial and amateur gillnets in the Pegasus Bay and Canterbury Bight area (Fig. 1) are given in Table 1. These data comprise only reported catches and a few net-marked carcasses found drifting or beachcast. Where fishers reported the number of dolphins they caught as a range (e.g. 12-15 dolphins), the lower figure was used. The unknown net category contains dolphins that bore clear net marks, but for which we could not be certain whether commercial or amateur fishers were responsible.

Table 1. Known incidental mortality of Hector's dolphins in gillnets in Pegasus Bay/Canterbury Bight.

	1984/85	1985/86	1986/87	1987/88
Commercial net	58	92	32	18
Amateur net	4	3	9	8
unknown net			3	3
Total	62	95	44	29

Seven commercial fishers reported catching dolphins in their gillnets between 1984-88. Only one commercial gillnetter reported catching no dolphins over this period. Two commercial gillnetters commented that over some periods (e.g. the length of the time they were fishing inshore for rig and elephant fish, (about 12-15 weeks) they typically caught one or more dolphins per week. Three fishers commented that to catch two in the same net was not unusual. In December 1985 one fisher reported that he had caught an average of one dolphin per day for the previous two weeks while gillnetting for rig and school shark. In September 1985 one fisher reported that he had caught 5-6 dolphins in one net set off Le Bons Bay, one of the eastern bays of Banks Peninsula. The maximum number of dolphins caught by a commercial fisher in any one year was 44, caught during the 1985/86 season. This was an exceptionally high catch, all other fishers caught less than 20 dolphins per year.

Seasonality of Entanglement

Reliable data on the month of entanglement are available for 45 dolphins which were passed in for dissection (from Nov. 1984 to Jan. 1989), or caught in the six-month period of monthly interviews (Fig. 3). Twenty-five of these were caught by commercial fishers, 13 by amateurs, and we found 7 fresh net-marked carcasses for which we could not determine whether a commercial or amateur fisher was responsible. A spring-summer peak of entanglement is obvious with almost 91% of entanglements occurring during November to February. The seasonality of dolphin catches by commercial fishers was significantly correlated with the number of days fished per month by commercial fishers ($p.<0.01$; effort data from Ministry of Agriculture and Fisheries).

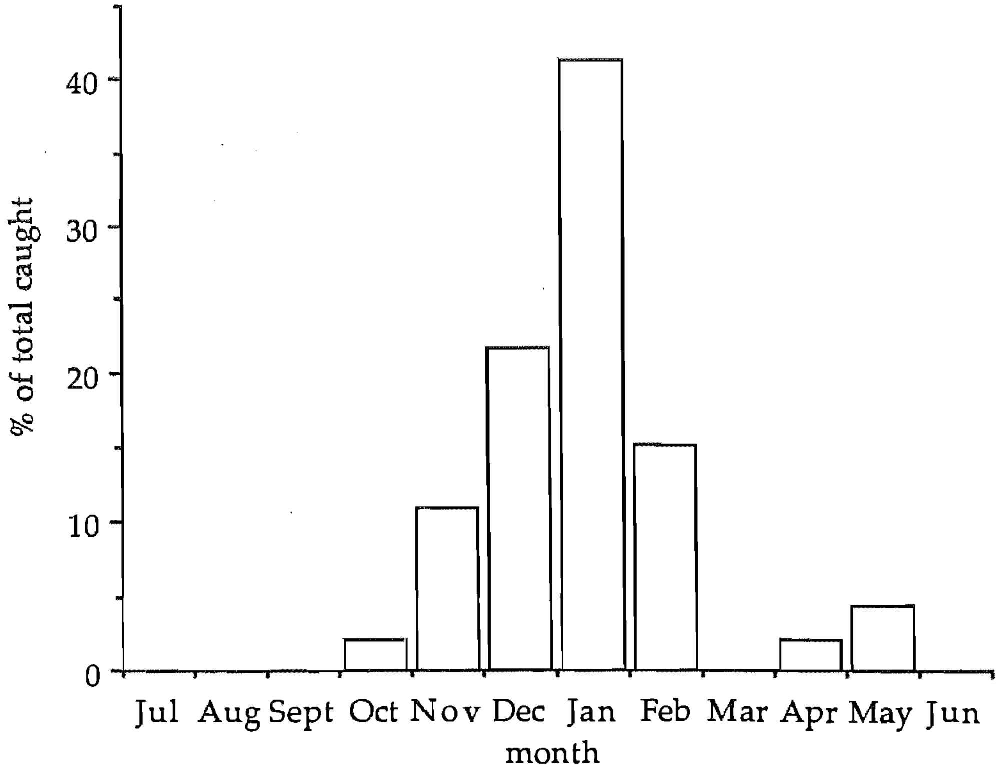

Fig. 3. Seasonality of entanglement in commercial and amateur gillnets (n=45)

All entanglements by amateur fishers occurred during December to February inclusive, the time at which most New Zealanders take their summer holidays. However, the number of dolphins caught by amateur fishers was not significantly correlated with the number of nets counted in the inner harbor ($0.10<p.>0.05$). This is because the peak in amateur netting precedes the peak in dolphin abundance in the inner harbor. During the December peak in amateur netting few dolphins were present in the inner harbor (Fig. 4). Most amateur entanglements occurred in January (8 of the 13 in the sample) when netting effort was still high (but had declined from the

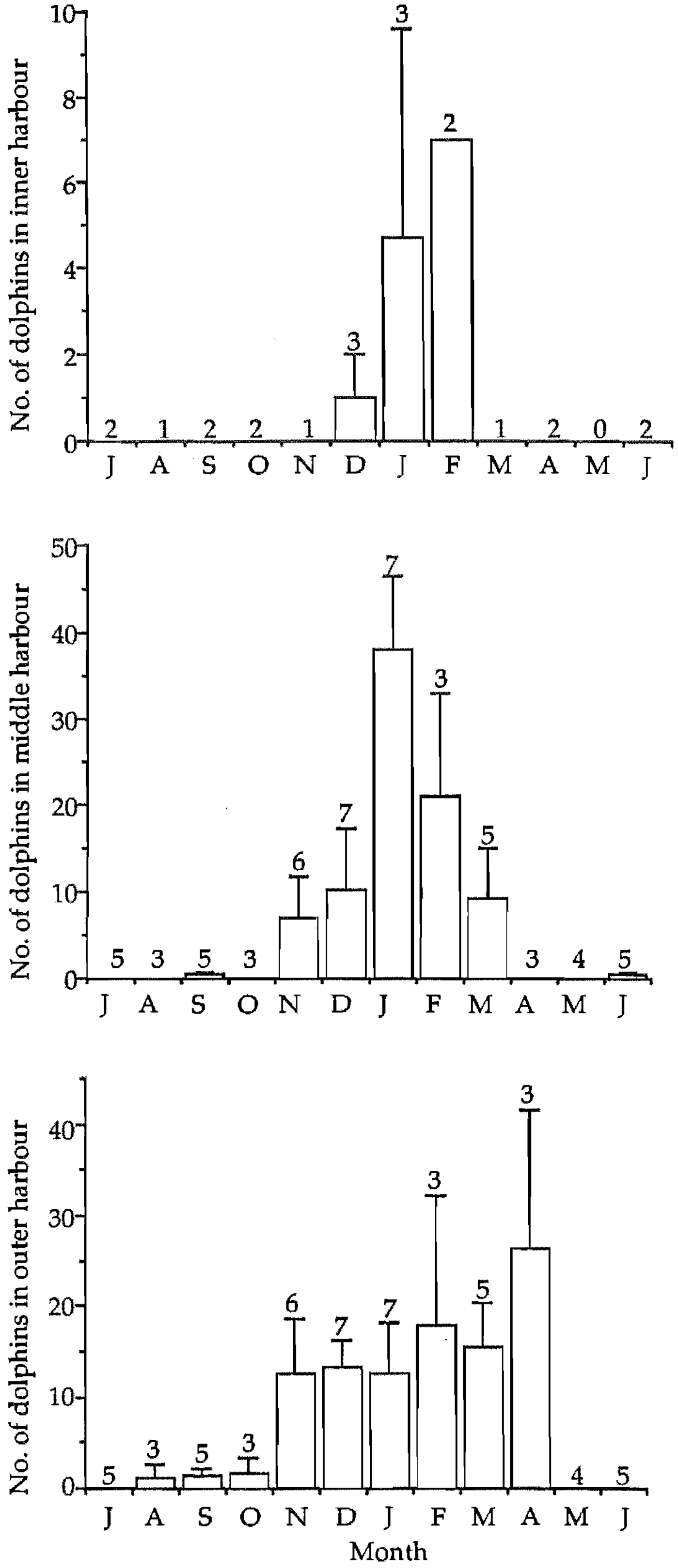

Fig. 4. Seasonal changes in the distribution of dolphins within Akaroa Harbour (areas defined in Fig. 2.). The histograms give the monthly means of the number of dolphins seen. Error bars are standard errors and the numbers above each bar give the sample size of surveys for that month.

previous month), and more dolphins were present in inner harbor waters (Fig. 4).

Offshore Distance and Depths of Entanglements

Fishers reported the offshore distance and depths for 36 entanglements. Most entanglements (89%) occurred within four nautical miles (7.4 km) of the shore, and in water less that 20 m deep (86%). The deepest entanglement occurred in a commercial net at 46 m. All amateur entanglements occurred within the first nautical mile from shore, and of the 12 for which capture location could be pin-pointed, nine were caught within the first 50 m offshore. All amateur entanglements occurred in water less than 16 m deep (range 2 - 16 m).

Dolphin distribution within Akaroa Harbour

Fifty-six surveys of the middle and outer harbor and 21 surveys of the inner harbor were completed. Dolphins are present in the outer harbor for most of the year, but are seen in the middle harbor mostly during the summer (see Fig. 4). This seasonal inshore movement was even more apparent in the data from the inner harbor, where dolphins were seen only during the months of high summer.

It is unusual for dolphins to be absent from the harbor in summer. Of the 28 surveys of the middle and outer harbor during November to March, there were only two surveys on which dolphins were not seen.

Counts of Amateur Gillnets

During the 1987/88 summer, the mean number of gillnets counted in the inner harbor was 22.5 (+/- 10.2 S.E.). Amateur gillnetting reached high levels at the peak of the summer holiday season in December (66 nets) and February (39 nets). The minimum number of nets (2) was counted in November, before the beginning of the holiday season. These data, in combination with those from the harbor surveys (Fig. 4), show the coincidence between high gillnetting effort in the inner harbor and the presence of dolphins there in high summer.

Age and Sex of Carcasses Retrieved

Sixty dead Hector's dolphins were examined. Their ages are available from toluidine blue stained thin-sections of teeth (Slooten, [b]). Forty three dolphins had died in gillnets, four had been caught in trawl nets, one had been entangled in the buoyline from a rock lobster trap, and 12 had died of unknown causes. The sex ratio was not significantly different from 1:1 in the total sample (33 females, 27 males), or in the gillnetted sample (23 females, 20 males).

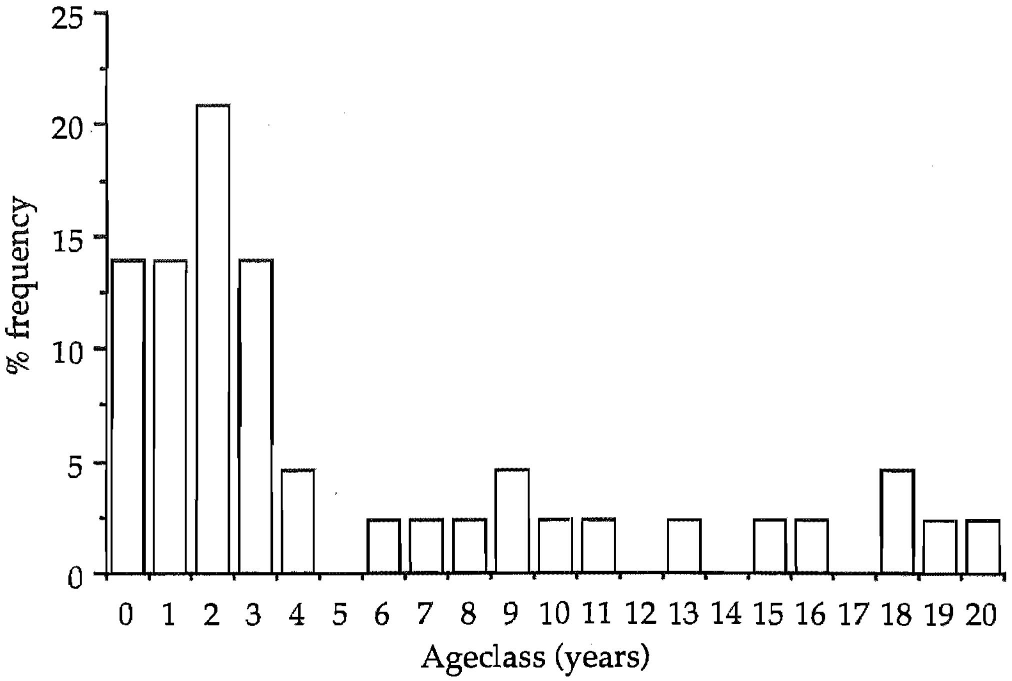

Fig. 5. Age frequency of gillnet-caught dolphins (n=43)

The age distribution of dolphins caught in gillnets (Fig. 5) suggests an over-representation of young dolphins (3 years and younger). As minimum calving interval is two years (Slooten and Dawson, 1988; Slooten, [c]), the six dolphins in the 0+ year class should have been accompanied by at least 12 mature females (>7 years). There were only four mature females in this sample, hence it could not reflect the age distribution of the population. This strongly suggests that young dolphins are especially susceptible to entanglement in gillnets.

DISCUSSION

At least 230 dolphins were caught in commercial and amateur gillnets from June 1984 to June 1988 in the Pegasus Bay and Canterbury Bight area (Table 1). As some catches are not reported, the true number of dolphins incidentally caught in gillnets must be higher, perhaps considerably so. Over the summer of 1984/85 Dawson and Slooten (1988) surveyed Hector's dolphin abundance around New Zealand. They estimated that approximately 740 Hector's dolphins were present in the Pegasus Bay and Canterbury Bight area at the time of the survey. The known level of entanglement in this area over 1984-1988 exceeds 30% of the number of dolphins estimated present in 1984.

Although no firm data are available from before this study, fishers' anecdotes suggest that entanglement rates were high since the mid 1970's. The larger number of gillnetting vessels working before the study (see Massey, 1984) supports this suggestion. Two fishers who have since abandoned gillnetting reported killing 12 and 16 dolphins in their nets in the 1982/83 summer.

The data in Table 1 indicate that commercial entanglements reached their peak in the 1985/86 season and have declined since. The primary reason for this decline appears to be the introduction of fish quotas in October 1986. The total allowable catches for rig, elephant fish and school shark were reduced by 82.5%, 65%, and 65% respectively from the catches of the previous year. This resulted in a shift by fishers towards targeting species such as dogfish, ling, and kahawai (MAF, unpub. data). Only one fisher specialized in catching kahawai. Dogfish and ling are predominantly caught in gillnets set further offshore than are rig and elephant fish, so fishers have tended to fish further offshore. This apparent shift in the distribution of fishing effort is believed to be the major reason for the reduced bycatch of Hector's dolphin in the 1987/88 season.

The data of Table 1 imply that the number of dolphins caught by amateur gillnetters was low from 1984-86 and rose during 1986-88. The Ministry of Agriculture and Fisheries estimates that several thousand amateur fishers occasionally use gillnets in this area (Coakley, pers. comm.). An increase in reporting rate as amateur fishers became aware of the study is the most likely explanation for their apparent increase in catch. In many cases amateur fishers were not aware that entanglements should be reported, and others were reluctant to report their entanglements to a government agency.

Slooten ([c], [d]) studied the reproductive biology of the 60 dolphins we examined, and determined their ages from tooth sections (Slooten, [b]). Females bear their first calf at 7-9 years, and the maximum age of any female in the sample was 19 years (Slooten, [b], [c],). Field observations of photographically identified females indicate that calving interval is 2-3 years (Slooten, [c]). Using these parameters as input values in Leslie matrix population models, Slooten and Lad (in prep) have shown that population growth rates are likely to be 1.8% or less. Based on what they considered to be unrealistically optimistic estimates of survivorship their model gave a maximum possible growth rate of 4.4% (Slooten and Lad, in prep). Even using the 4.4% population growth estimate, the Pegasus Bay and Canterbury Bight population would have to have been in excess of 2159 to cope with the 1985/86 catch without population decline. The figure is almost three times that found in the 1984/85 survey. Using the more likely 1.8% growth rate results in a required population of some 5278 dolphins to avoid population decline in this year. This latter figure is well in excess of the estimated total population of Hector's dolphin. (Dawson and Slooten, 1988).

Most dolphins are caught within four naut. miles of the shore (89%), and in water less than 20 m deep (86%). These data reflect a combination of the dolphins' distribution, and the distribution of gillnetting effort. Thus it is possible for dolphins to be caught in areas where they are seldom seen (e.g. beyond five naut. miles from shore), but where high gillnetting effort occurs. Unfortunately the lack of data on distribution of fishing effort precludes an analysis of areas or depths of high entanglement risk. Most dolphins caught by amateur gillnetters were caught within 50m of the shore. This is the zone in which most amateurs set their nets.

An inshore/offshore seasonal movement appears to be a general feature of the biology of Hector' dolphin. Summer offshore transects showed that on average almost half of the animals (45.5%) that were found within 5 naut. miles of the shore were present within the first 800 m. In winter this figure decreased to 21% (Dawson and Slooten, 1988). The inshore movement of dolphins coincides in time and space with commercial inshore gillnetting effort, particularly that for rig and elephant fish, which are typically fished in shallow, close inshore waters, sometimes just beyond the surf zone. This is precisely the zone in which Hector's dolphin are most common. Gillnetting effort for rig and elephant fish reaches its peak at the time when Hector's dolphins are calving, and calves are often caught in fisher's nets. The summer inshore movement of dolphins also coincides with the holiday season and its associated amateur gillnetting.

The age frequency of gillnet-caught dolphins suggests that young dolphins are especially susceptible to entanglement. An interesting feature of this sample is that the 2+ age-class appears especially vulnerable, more so than either the 0+ or 1+ age-classes. Field observations show that Hector's dolphin calves typically stay in close contact with their mothers for the first two years of life. From the third year they are much more independent and are sometimes seen in groups of subadults with no adults present (Slooten and Dawson, unpub. data). While with their mothers, young dolphins are with an experienced adult, who is likely to be more aware of the environmental dangers. Also, it is improbable that calves are born with a fully functioning sonar system, and sonar ability is likely to be at least partly learned. Older individuals are not only more experienced with respect to environmental dangers, but are likely to make fewer mistakes with their sonar systems.

There seems little doubt that gillnet entanglement constituted a serious threat to the Hector's dolphins of Pegasus Bay and Canterbury Bight over the years of the study. Continued reduction in the number of Hector's dolphins killed in gillnets is essential for this species long-term existence in Pegasus Bay and Canterbury Bight waters.

Conservation Management of Hector's Dolphin

In response to the entanglement data above, that of Slooten ([b], [c]) and Slooten and Lad (in prep), and after an extended period of public consultation, New Zealand's Department of Conservation has created a 1170 km^2 Marine Mammal Sanctuary (see Fig. 1) under section 22 of the Marine Mammal Protection Act (1978). A sanctuary was considered necessary to reduce current levels of entanglement and to provide protection for the dolphins from any future increases in inshore gillnetting effort. Within it commercial gillnetting is prohibited year-round, and amateur gillnetting is prohibited over the months of November to February. Amateur gillnetting is allowed outside this period subject to restrictions governing where and how nets may be used. A continuing research programme is underway focussing on determining trends in dolphin abundance, stock identity and discreteness, and refining estimates of mortality and determining its causes through long-term photo-identification and continued carcass retrieval and dissection.

Chapter 7. Modifying Gillnets to Reduce Entanglement of Cetaceans

Abstract

To reduce the number of cetaceans caught incidentally in gillnets, two forms of acoustic modifications have previously been proposed. These modifications seek to make gillnets more obvious to cetaceans so they can avoid them, and include making gillnets more reflective to cetacean sonar, and placing active sound emitters in the nets. I discuss the relationship between sonar and net entanglement, and address the assumptions and logic of net modification strategies. I argue that neither strategy is likely to be effective, and that reductions in the number of cetaceans killed in gillnets are best achieved through the closure of specific areas to gillnetting.

Introduction

The incidental capture of cetaceans in fishing gear is a geographically widespread and severe problem. Although most captures are of dolphins and porpoises, large cetaceans are also vulnerable to entanglement (e.g. Humpback whales; Lien and Merdsoy, 1979). Gillnet fisheries cause the deaths of thousands of cetaceans per annum (e.g. Jones 1984, Harwood et al. 1984; Harwood and Hembree, 1987). Forty thousand or more cetaceans are killed annually in gillnets set in the coastal waters of Sri Lanka (Leatherwood and Alling, 1985). It appears that a worldwide total of between 500,000 to 1,000,000 cetaceans die in gillnets each year (Leatherwood, pers comm.) Although the impact of such mortality on the species' population structures is unknown, the sheer number of cetaceans killed is cause for considerable concern. Of even greater concern are the stocks and species whose small populations appear directly threatened by gillnet entanglement (e.g. Gaskin, 1984; Diamond and Hanan, 1986; Hanan et al. 1986, 1987; Read and Gaskin, 1988; Barlow, 1986; see also Chapter 6).

In response to this problem, several proposals have been designed to reduce the impact of gillnet entanglement. Many are based on the concept of modifying gillnets so that cetaceans can detect and hence avoid them. The purpose of this contribution is to briefly discuss this concept and suggest a more promising alternative.

Submitted for publication.

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Sonar and net entanglement

The detectability of an object to sonar depends on several factors, principally its density (compared to that of the surrounding medium), size and orientation to the sound source, and the frequency of the ensonifying pulses. Gillnets are generally made from nylon monofilament. Because this material is almost the same density as water it gives a poor sonar echo (e.g. Pence, 1986). Prompted by this observation, many authors have assumed or suggested that entanglement occurs because the animals' sonar cannot detect the net (e.g. Awbrey et al. 1979; Gaskin, 1984; Hatakeyama, 1986a; Hembree and Harwood, 1987; Jefferson, 1987).

Dubrovskiy (cited in Evans et al. 1988) showed that Harbor porpoise can detect nylon filaments of 0.1 mm diameter. Yet that species is often entangled in gillnets made of nylon several times that diameter (0.8 mm, Gaskin, pers. comm.). Similarly, bottlenose dolphins are occasionally entangled in shark nets of coarse 3mm multifilament braid (Peddemors et al. in press). Knots between meshes of a gillnet are more easily detectable than unknotted nylon line (Pence 1986) and enhance the net's detectability. Furthermore, the floats suspending the top of a groundfish gillnet are filled with air, and should be easily detected by even a crude sonar system (see also Awbrey et al. 1979).

These observations suggest that dolphins and porpoises become entangled not because their sonar system cannot detect the nets, but because they make mistakes which sometimes result in entanglement. Two explanations can account for such mistakes: (A) When using sonar, cetaceans probably have a search image of what they expect to encounter, and may not perceive non-target objects (e.g. a foraging dolphin may disregard echoes from a net as being from non-prey, and hence become entangled (Evans et al. 1988)); (B) cetaceans do not always use their sonar, and at these times are unaware of a net's presence.

Dolphins and porpoises may make much more use of "passive sonar" i.e. listening, than the literature would lead one to believe. While gathering recordings of the high-frequency sounds of free-ranging Hector's dolphins (Dawson, 1988, see also Chapters 2-5) it became clear that dolphins were not always emitting sonar pulses. Lone dolphins often approached the boat, swimming directly toward the hydrophone. In turbid water conditions I expected the dolphins to rely heavily on their sonar, as poor water visibility restricts the usefulness of vision. Yet even under these conditions the dolphins were often silent as they approached.

Wood and Evans (1980) provided strong experimental evidence that dolphins do not constantly need to interrogate their environment with sonar pulses in order to orient with respect to complex stimuli. To record the signals made by a dolphin while chasing fish, they instrumented the head of a blindfolded bottlenose dolphin with seven broadband contact hydrophones, and fed their output to a wideband tape-recorder. The dolphin repeatedly chased and caught a live fish without emitting echolocation signals (Wood and Evans, 1980), apparently by listening to the sounds of the fish swimming. Such a "passive sonar" sense would be useful as dolphins may have energetic constraints on constant sonar emission.

Only objects that make a noise can be detected by "passive sonar". Acoustic vibrations caused by water movement could reveal the position of rocks and other solid obstacles to a "passive sonar" system. Flexible structures, however, such as a gillnets, are likely to be silent or very nearly so, and not obvious to a listening dolphin.

Individual Hector's dolphins appear to reside in small areas for long periods of time (Slooten and Dawson, 1988, and in press), implying that they almost certainly know that habitat in great detail and have no need to constantly echolocate to find out where they are. A gillnet set in this environment may constitute an unexpected hazard. To maximize their fishing efficiency monofilament gillnets are designed to be difficult to see, and, because Hector's dolphins are typically found in murky water (Dawson and Slooten 1988), a gillnet would be visible only at close range. Hence the species' eyesight is also unlikely to provide early warning of a gillnet's presence.

Reducing Entanglement Through Net Modifications

Acoustic reflectors

It is often suggested that a solution to net entanglement lies in making the nets more obvious to dolphin sonar (e.g. Awbrey et al. 1979). As discussed above, it would not matter how acoustically reflective a net was if the dolphins were not making sonar pulses when they encountered it.

Designing modifications that are practical is not easy, and several have proved operationally unusable. For example, netting braid incorporating a double strand of 0.16 mm diameter stainless steel braid became too brittle to safely handle (Peddemors et al. in press), and 6 mm airfilled plastic tubing looped through the net at intervals was compressed by the net hauler and filled with water (Hembree and Harwood, 1987).

Once a practical modification is found, assessing its effectiveness is also difficult. Although many cetaceans are caught in gillnets, the catch per unit effort (CPUE) is low, meaning that net modifications have to be trialed on a large scale (and hence the experiments need to be well funded) to produce results suitable for statistical evaluation (see Hembree and Harwood, 1987; Peddemors et al. in press). Because of the low CPUE, several studies have resulted in too few entanglements to allow statistical comparison between modified and unmodified nets (e.g. Hasegawa et al. 1987; Peddemors et al. in press).

After finding that captive, blindfolded, bottlenose dolphins reacted strongly to 4 mm chrome-plated nickel bead chain, Hembree and Harwood (1987) modified drift gillnets with this material. In their 1984 trials, alternating half and full-length pieces of bead chain were woven vertically into the net every 8 m. During the next season the chain was woven into the mesh as nine 3 m diagonals per 15 x 15 m net panel. A total of 94 dolphins were entangled during the trials, and in neither season did the net modifications significantly reduce the number of dolphins caught. The 1985 trials produced the unexpected result that the modified nets caught more dolphins than the control nets (Hembree and Harwood, 1987).

While many net modification experiments are inconclusive at best, the thorough and well-designed trials of Hembree and Harwood (1987) strongly suggest that making nets more acoustically reflective is ineffective in reducing entanglement

Sound Emitters

Another strategy is to place active sound emitters in the nets to warn of the net's presence. This approach has not yet proved practical or indisputably effective. To be most effective, emitters should produce loud sounds within the dolphins' hearing range, preferably at the frequencies at which dolphin hearing is most sensitive.

Many practical problems exist in the design, construction and deployment of sound emitters. Electronic devices need to be regularly recharged (e.g. Hatakeyama, 1987) and would be expensive to deploy and maintain (Awbrey et al. 1979). As high-frequency sounds attenuate quickly in water many emitters would be need to be spaced throughout the net (Awbrey et al. 1979). Metal devices, whether electronic or not, are vulnerable to corrosion (see Peddemors et al. in press). According to Awbrey et al. "The cost and complications of active devices would preclude their proper use and maintenance." (1979, p. 36). Further, if fishers believe that the devices are reducing catches, they are likely to stop, or modify, their use of them (Gaskin, 1984). Without the massive cost of an observer program a resource management agency could not ensure that fishers use the devices as intended.

Studies undertaken to determine whether sound emitters reduce entanglement have been inconclusive, and have so far failed to demonstrate better than a marginal reduction in entanglement rates, if any (e.g. Hatakeyama, 1986b, 1987, 1988; Peddemors et al. in press.).

In response to such inconclusive results the gillnetting industry could easily argue that because one type of modification was not successful, experimenters should try another. This could bring about a protracted sequence of tests, and therefore entanglements, that are unnecessary because, as argued here, such net modifications per se seem unlikely to achieve the necessary reductions. In areas where particular stocks have been heavily impacted (e.g Canterbury Bight and Pegasus Bay Hectors' dolphins) they may be unable to withstand the losses required to demonstrate whether a particular modification is effective.

What is known about odontocete behavior suggests that such modifications would be unlikely to work. The emitter's signal has to be recognized as a warning. It is inappropriate to argue that putting warning devices on the nets is akin to marking dangerous corners with road signs, because humans already know what the road signs mean before they reach the danger. The concept of a "warning" requires a learned behavior, yet the danger posed by nets is likely to be apparent only to those dolphins which have experienced them and survived. Only the survivors can learn to be more vigilant.

Odontocete behavior is sophisticated and highly flexible (Connor and Norris, 1982, Würsig, 1986). Thus, if the danger of the nets were not understood and associated with the warning signal, cetaceans would be expected to quickly habituate to the signal (Gaskin, 1984). Given the curiosity some cetaceans show towards new features in their environment, it is equally possible that the new (warning) sound will attract them towards the danger (see also Peddemors et al. in press), rather than warn of it.

Another problem is that in some cases marine mammals appear to feed directly on fish caught in gillnets, or on the scavengers of gillnetted fish. In Canadian waters, hagfish are abundant scavengers of gillnet-caught fish. These scavengers are commonly found in the stomachs of gillnet-caught harbor porpoises, which appear to be attracted to the nets by the presence of their scavenger prey (Gaskin, pers. comm.). In any situation in which marine mammals are directly feeding on fish in gillnets, or their scavengers, attaching an acoustic warning device to the net could have the effect of "ringing the dinner bell".

Management Implications

Making gillnets more acoustically reflective and placing warning devices in them are unlikely to achieve better than marginal reductions in the entanglement rate of dolphins and porpoises. Certainly, these two options show little promise of bringing about the dramatic reductions in entanglement rates that are required by Hector's dolphins (see Chapter 6) and several other species. The arguments above strongly support the view that the management strategy most likely to achieve effective protection of cetacean populations from gillnet entanglement is the closure of specific areas to gillnetting (Gaskin, 1984, Perrin, pers. comm.).

The location and size of such closures should be decided on the basis of distribution of the cetaceans concerned (in time, space and depth) and the extent of the entanglement problem. Detailed data on the location of fishing effort, if available, can help identify which areas should be protected through an analysis of entanglement rates among areas. However, management decisions should not be based solely on such data. Ideally, wildlife management should not merely react to problems, but should also anticipate (as far as is possible) future trends. Management strategies must take into account that fishing is an extremely dynamic industry, and that the location and amount of fishing effort often change markedly between seasons. For this reason areas subject to low fishing effort may warrant inclusion into an area closure if they support significant marine mammal populations that would be at risk if gillnet fishing effort increased.

Conclusions

This study was novel in several ways. It was the first study of the high-frequency sounds of Hector's dolphins, and (to my knowledge) the first study of the sounds and behaviour of free-ranging dolphins using wideband recording equipment. In addition, digital signal processing techniques were used to automatically measure features of the sounds. This provided a level of objectivity and consistency of measurement far beyond what is possible with manual measurement methods, and enabled a more detailed analysis of a larger dataset than would have been easily possible via manual methods.

The first aim of this study was to provide a thorough, quantitative analysis of the acoustic repertoire of Hector's dolphin. Preliminary analyses (Chapter 1) suggested that the Hector's dolphin vocal repertoire was unexpectedly simple, consisting, almost exclusively, of high-frequency clicks. Of the several thousand clicks analysed in detail (Chapter 2), most were narrowband, centred around 124 kHz, and had a comparatively simple structure. Very similar signals have been recorded from Commerson's dolphins (Kamminga and Wiersma, 1982; Shochi et al., 1982; Evans et al., 1988), which suggests that such signals are characteristic of the genus *Cephalorhynchus*.

The narrow band nature of Hector's dolphin clicks is in marked contrast to those of many other delphinids (Evans, 1973), as is the almost complete absence of audible signals in the Hector's dolphin repertoire. This latter feature is especially striking on listening to other delphinids (e.g. Dusky dolphins *Lagenorhynchus obscurus*; Bottlenose dolphins *Tursiops truncatus*; pers. obs) which produce a cacophony of audible sounds including frequent whistles and burst pulses. Hector's dolphin does not appear to whistle, and produces only two types of audible sounds, both of which are uncommon. The first, and most common of the two, is made up of high-frequency clicks emitted at such high repetition rates that the repetition rate was audible as a tonal "cry" or "squeal". The second type of audible sound comprises rare broadband clicks.

To facilitate detailed description and comparison of click characteristics, I worked closely with an electronic engineer (William Thorpe) to develop an automated, computer-based, system that could measure many features of each of several thousand digitised clicks (see Chapter 3). Such an automated system has many advantages over previous methods of quantifying features of sounds. It removed inaccuracies and inconsistencies that can be introduced by manual measurement of sonagrams (e.g. Sparling and Williams, 1978; Dawson and Jenkins, 1982), and enabled the analysis of a much larger sample of sounds than would have been possible via manual methods. I analysed the similarity of clicks via multivariate analyses of the automatically measured data. These analyses revealed different categories of high-frequency clicks, each of which contained many clicks of high signal to noise ratio and with clean, undistorted waveforms, confirming that the differences among click types were real, not artefacts caused by off-axis recording or multipath distortion. The different categories also made sense in terms of sonar theory (see Chapter 4) and accorded well with current models of how dolphins process sonar sounds (e.g. Au and Moore, 1988).

One of my aims in this study was to better understand the sorts of targets that Hector's dolphin sonar signals could resolve. This was achieved by employing techniques used by engineers to design radar and sonar pulses. For any simple sonar signal, the needs of determining target range and velocity are in opposition. Short, broadband pulses are best for determining target range, but are insensitive to the doppler effect and cannot provide target velocity information. Long, constant frequency pulses are best for determining target velocity, but are poor for resolving range. Analysing typical examples of Hector's dolphin clicks as sonar signals showed them to be well suited to resolving target range, but poor for determining target velocity. Different types of clicks had differing degrees of velocity resolution, but none had velocity resolution that would be useful in tracking targets such as prey items. Using these types of clicks, information about target velocity is accessible to the dolphin only from the trend of range measurements during a sequence of clicks. While different click types do not improve the resolution of the velocity of "real-world" targets, it is possible they are used to enable better target recognition, or that the more complex, multi-pulse, clicks enable the dolphin to transmit a more powerful signal for longer range.

In addition to their use in sonar, clicks may also have a role in communication (Watkins, 1980). Despite this rather obvious possibility there appears to have been no detailed study of high frequency cetacean clicks and the contexts in which they occur. Using wide-band recordings of Hector's dolphins sounds I examined the contexts in which different click types were made (see Chapter 5). Hector's dolphins did not appear to use clicks solely as sonar signals. Complex clicks appeared to have some social significance. Clicks with more complex spectra were used more often in large groups than in small ones, and double pulses (in the time domain) were used more often in "surface active" groups than "long-diving" ones. High repetition rate sounds ("cries") were much more commonly associated with aerial behaviours than with feeding, and may indicate excitement. While there is a general association of certain sounds with specific behaviours, it was clear that Hector's dolphins do not use simple acoustic labels which correlate with different activities.

Previous literature on communication and echolocation in bats and cetaceans has implied a dichotomy between the two processes, with neither having much relevance to the other (e.g. Griffin, 1977). However, more recent studies of bats have shown that they are attracted to playbacks of the echolocation signals of conspecifics and sympatric species (Barclay, 1982; Leonard and Fenton, 1984). According to Barclay (1982) listening bats are attracted because concentrations of echolocation calls may signify the presence of food. It seems likely that dolphins may do likewise.

In addition, dolphins may be able to not only detect, but interpret the echoes of each others' sonars. In two of the four current models used in the development of bionic sonar, echoes can be interpreted without detailed knowledge of the outgoing pulses, other than their bandwidth (Johnson, 1988). As the vast majority of Hector's dolphin clicks analysed in this study were of very similar bandwidth, a listening dolphin might be able to assume the normal bandwidth, and interpret incoming echoes from the sonar systems of nearby conspecifics accordingly, thus learning of their activities and positions. Such an eavesdropping ability might render unnecessary many of the signals used in more active communication. I suggest that the dichotomy between echo-location and communication is likely to prove false, and that the evolution of an echolocation system may give rise to an effective communication system as an effect.

Acoustic factors are commonly thought to be important in the widespread phenomenon of gillnet entanglement of cetaceans. To explore the nature and extent of gillnet entanglement of Hector's dolphin, I studied the Pegasus Bay/Canterbury Bight gillnet fishery (see Chapter 6). Over the four years of the study, 230 Hector's dolphins were reported killed in gillnets. Most dolphins (89%) were caught within four miles of the shore, and over the summer months of November to February (91%). Such an entanglement rate appeared to be far beyond the reproductive capacity of the dolphin population in the area. Although entanglement problems are far greater in other areas in terms of the sheer numbers of animals killed (e.g. Dall's porpoise *Phocoenoides dalli* in the North Pacific Salmon driftnet fishery; Jones, 1984), the small population size and limited distribution of Hector's dolphin (Dawson and Slooten, 1988) heightens the impact of recent levels of entanglement. In response to these studies, and those by Slooten (b, c, d, Slooten & Lad; submitted for publication) the Department of Conservation established a 1170km^2 Marine Mammal Sanctuary around Banks Peninsula in which commercial gillnetting is illegal, and amateur gillnetting is permitted only in non-summer months, and subject to stringent regulations.

I explored the acoustic aspects of gillnet entanglement in an analysis of proposals to reduce entanglement by modifying gillnets (see Chapter 7). Based on the assumption that entanglement occurs because the dolphin's (or porpoise's) sonar cannot detect gillnets (e.g. Awbrey et al., 1979; Gaskin, 1984; Hatakeyama, 1986a; Hembree and Harwood, 1987; Jefferson, 1987), two types of acoustic modification have been proposed (e.g. Awbrey et al., 1979). The first is to make gillnets more detectable by increasing their reflectivity to sonar. The second is to mark the nets with active sound emitters, which would warn of the net's presence. I show that neither strategy has proved effective in field trials, and that several assumptions of these proposals are challenged by knowledge of the general behaviour of dolphins, and of their acoustic behaviour.

That making nets more reflective to dolphin sonar has been ineffective in reducing entanglement can be explained by two factors. Dolphins do not always use their sonar, and when silent they cannot detect a gillnet, whether it is acoustically reflective or not. Also, when foraging they probably have a search image of what they expect to encounter, and may not perceive non-target objects. Foraging dolphins may disregard echoes from nets as being non-prey, and hence become entangled (Evans et al. 1988).

Similarly, marking nets with sound emitters has proven ineffective. Designing emitters that are practical in use has been difficult (Awbrey et al., 1979; Hatakeyama, 1987; Peddemors et al., in press). To work, the emitter's signal has to be recognised as a "warning", a concept which requires a learned behavior. Yet the danger posed by gillnets is likely to be apparent only to those dolphins which have experienced them and survived. Death by entanglement on ignoring the warning sound is a very severe, but ineffective, form of negative reinforcement, as only the survivors can learn to be more vigilant. The flexibility of dolphin behaviour (Connor and Norris, 1982, Würsig, 1986) suggests that if the danger of the nets was not clearly understood and associated with the warning signal, cetaceans would be expected to quickly habituate to the signal (Gaskin, 1984). Given the curiosity some cetaceans show towards new features in their environment, it is equally possible that the new (warning) sound will attract them towards the danger (see also Peddemors et al, in press), rather than warn of it.

Another problem that has received little attention in the literature is that some marine mammals appear to be attracted to gillnets to feed on caught fish, or on their scavengers. Harbour porpoises (*Phocoena phocoena*) in Canadian waters appear to be attracted to nets to feed on scavenging hagfish (Gaskin, pers. comm.). In any situation in which marine mammals are attracted to gillnets by the presence of food, the attachment of acoustic warning devices to nets seems likely to have the effect of "ringing the dinner bell".

These observations and arguments show that gillnet entanglement is not primarily an acoustic problem, and that acoustic modifications to gillnets are unlikely to substantially reduce entanglement of cetaceans because of logical and practical difficulties with the modification concepts. Certainly, the modifications show little promise of bringing about the dramatic reductions in entanglement rates that are required by Hector's dolphins (see Chapter 6) and several other species. Based on these results, I argue that the best management strategy for the reduction of gillnet entanglement is the closure of specific areas to gillnetting.

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