Passive Acoustic Monitoring of Habitat Use by Bottlenose Dolphins in Doubtful Sound

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ABSTRACT

In the context of testing the appropriateness of current conservation management, this study used nine moored acoustic monitoring devices (T-PODs) to monitor habitat use by bottlenose dolphins in Doubtful Sound, New Zealand, and identify current critical habitats. Static acoustic monitoring offers several advantages over visual surveys, including detection of submerged animals, non-invasiveness, long-term 24 hour coverage, lower expense and reduced dependence on calm weather. T-PODs are relatively new devices however, and required investigation of their performance and limitations. T-POD frequency settings were found to significantly influence detection ability. The A/B filter settings of 50/30, 70/30 and 90/30 (kHz) were found most effective. The maximum range of bottlenose dolphin detection was measured at 1313m. Dolphin detection rate and probability both declined with distance from T-POD. The conservative nature of T-PODs was highlighted as only 47% of bottlenose dolphin groups were detected when within 500m of T-POD. The effective detection radius (EDR: range at which all groups can be assumed to be detected) was calculated to be 266m (95% CI; 222m-317m).

Detailed inspection of T-POD data files allowed identification of foraging echolocation trains, which were used to define parameters to identify 'buzzes'; a unique echolocation signal used when capturing prey. Click trains with interclick-intervals between 18-2 ms and >20clicks were defined as foraging. These foraging parameters, when tested on a new sample of T-POD data, positively identified 92% of visually identified foraging trains.

Nine separate T-POD sites within Doubtful Sound were acoustically monitored for twelve months from 1st April 2009. Foraging behaviour was not focused in particular sites, suggesting opportunistic foraging strategies are employed by the population. Foraging and encounter rates, among all T-POD sites, were significantly higher during diel phases dusk and dawn, compared to day and night. T-POD data showed that dolphin use of the fiord varies seasonally with inner fiord sites being used most in summer and autumn, and outer fiord sites in winter and spring. Seasonal dolphin presence was positively correlated with surface water temperature. Seasonal trends from this study were consistent with previous studies, highlighting Crooked Arm (site D), Hall Arm (site B) and 'The Crossing' (site E) as most critical.

Habitat use data gained in this study suggested that the current Dolphin Protection Zones, in which boat activity is voluntarily limited, do not provide adequate protection for the population. Seasonal variation in the scope of the DPZ, additional no boat zones and extensions to current DPZs are proposed for re-assessed critical areas. These modifications are seen as necessary for effective conservation management, whilst being practical for Doubtful Sound stakeholders.

Key words: Bottlenose dolphins, *Tursiops truncatus,* Fiordland, T-POD, Conservation Management, Tourism, Habitat use, Acoustic.

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CHAPTER 1

GENERAL INTRODUCTION

Static passive acoustic monitoring has become increasingly useful in studies of odontocete habitat use and behaviour, in particular when conditions are unsuitable for land-based observations or boat-based research (Teilmann et al., 2002; Carlström, 2005; Wang et al., 2005; Carstensen et al., 2006; Tougaard et al., 2006; Philpott et al., 2007; Koschinski et al., 2008; Rayment et al., 2009; Simon et al., 2010). The T-POD (www.chelonia.co.uk) is one acoustic monitoring device available to detect and log cetacean echolocation activity.

Passive acoustic monitoring, in general, offers several advantages over visual surveys, including detection of submerged animals, 24 hour monitoring, lower expense and reduced dependence on calm weather (Leaper et al., 1992; McDonald and Fox, 1999; Carstensen et al., 2006). Because the method is passive (i.e. no sound is produced), it minimizes disturbance to the subject animals, and because standardized equipment is used, observer bias is reduced (McDonald and Fox, 1999; Wang et al., 2005; Rayment et al., 2009).

Disadvantages of acoustic monitoring include potential uncertainty in species identification and abundance, limited spatial coverage of static systems, and limited knowledge of the effects that sound source levels, distance to the receiver and directionality have on detection rate (Wang et al., 2005; Tougaard et al., 2006; Rayment et al., 2009).

Although the T-POD has several limitations, its positive attributes have made it widely recognised as a very effective method for long term habitat monitoring of odontocetes (Teilmann et al., 2002; Carlström, 2005; Wang et al., 2005; Carstensen et al., 2006; Tougaard et al., 2006; Philpott et al., 2007; Koschinski et al., 2008; Rayment et al., 2009; Simon et al., 2010). This study used nine T-PODs to monitor bottlenose dolphin habitat use in Doubtful Sound, Fiordland, New Zealand, in the context of refining current conservation management.

1.1 The Study Site: Doubtful Sound, New Zealand

Doubtful Sound, Fiordland National Park, (area = 12,524km^2) is in the southwest corner of New Zealand's South Island. It is not directly accessible by road. The fiord is reached via vessel across Lake Manapouri, followed by a vehicle trip over the Wilmot Pass to the head of the Doubtful Sound complex at Deep Cove. Doubtful Sound (c. 45˚28'S, 167˚09'E) is the second longest of the 14 fiords in the National Park at 40.3km. It is made up of two main openings to the Tasman Sea; the Main Fiord and Thompson Sound. There are also four major arms extending roughly perpendicular to the Main Fiord. These are First Arm, Crooked Arm, Hall Arm and Gaer Arm (an extension of Bradshaw Sound) (Figure 1.1). Shores are characterized by near vertical, rock walls that plunge to an average depth of 200m, with the deepest basin exceeding 430m.

Fiordland is one of the wettest places on earth. It lies within the 'Roaring Forties', where strong westerly winds predominate. This exposes the area to intense, moisture-laden fronts resulting in mean annual rainfalls in Doubtful Sound of 5290mm (Stanton and Pickard, 1981). Due to the steep topography of the area and hard rock geology, little precipitation is absorbed. Peak flows of rivers and creeks coincide with peaks in rainfall resulting in extreme freshwater runoff into the fiord (Grange, 1990). Freshwater is less dense then the sea water, causing runoff to float, forming a halocline ranging to 5-10m depending on freshwater influx (Pickrill, 1987). Seasonal variation in water temperature is greatest at the surface, related to the low-salinity layer. In summer it is warmest at 18-22˚C with a sharp drop at the halocline. In winter surface temperatures occasionally fall below freezing at the ends of the arms; maximum temperatures are around 50-100m depth (Pickrill 1987; Elliott pers comns). Several studies have suggested links between seasonal changes in bottlenose dolphin distribution and surface water temperature (Hanson 1983; 1990; Wells 1986; Wells et al., 1990; Smolker et al., 1992; Wilson et al., 1997). Schneider (1999) made this link explicitly for Doubtful Sound.

1.2 The Bottlenose Dolphin

Bottlenose dolphins (*Tursiops truncatus,* Montagu) are a common focus of cetacean research. This is because they are abundant (Kenney, 1990), widely distributed (Leatherwood and Reeves 1983, Weller 1998, Schneider 1999) and they adapt reasonably well to captivity

(Townsend 1914, Caldwell and Caldwell 1972). Bottlenose dolphins occupy a very diverse range of habitats, including shallow coastal waters, deep fiords, estuaries and offshore zones beyond continental shelves (Leatherwood 1979, Scott and Chivers 1990, Williams et al., 1993), and their geographical distribution spans from the tropics, to the cool-temperate waters of both hemispheres (Shane 1980; Hammond and Thompson 1991; Wells and Scott 1994; Schneider 1999). Not surprisingly, bottlenose dolphins show wide variation in ecology, habitat use and behaviour (Schneider 1999).

Most research on bottlenose dolphins has occurred in sub-tropical coastal waters (Au, 1993). Starting in 1990, extensive research has been undertaken on the resident dolphins in the cool-temperate waters of Fiordland, New Zealand (e.g. Williams et al., 1993; Schneider, 1999; Lusseau et al., 2003; Currey et al., 2009a).

1.3 Doubtful Sound Bottlenose Dolphin Population

Williams et al. (1993) were the first to collect data on the bottlenose dolphins in Doubtful Sound. They found a resident population of around 60 bottlenose dolphins living approximately at the southern limit of the species' distribution. Schneider (1999) built on this research compiling detailed records of the population size, body proportions, seasonal movements, diving and surface behaviour. Since this time, research has been relatively continuous with regular population monitoring. Most recently, research has demonstrated a decline in the population by 34% over the past 12 years (Currey et al., 2007), and identified the demographic cause of this decline as low juvenile survival (Currey et al., 2009a). This information prompted the IWC Scientific Committee and the Department of Conservation (NZ) to request actions that would increase protection for the Doubtful Sound bottlenose dolphins.

Although there have been rare sightings of individuals from the Doubtful Sound population in other fiords, generally these dolphins remain within the fiord complex year round (Schneider 1999; Lusseau et al., 2002). Immigration and emigration are not thought to be factors in the decline of the population, however further research is required to rule this out (Currey et al., 2007). Analysis of the long term dataset (from 1990 to 2008) has shown that adult survival has not changed significantly but calf survival has approximately halved (Currey et al., 2009a). Population modelling suggests that this is the main underlying demographic cause for the decline of the population. In the absence of any significant migration into the fiord, a decline in calf survivorship has been flagged as a key factor influencing total abundance (Currey et al., 2009a).

Freshwater input from the Manapouri hydro-electric power station may be related to this decline. This project commenced operation in 1969, draining water from Lake Manapouri, through a hydroelectric station, and releasing it through a tail race in Doubtful Sound's Deep Cove. The tailrace discharge approximately tripled freshwater input into Doubtful Sound, increasing the thickness of the low-salinity layer (LSL) and altering the fiord's surface water temperature range (Gibbs, 2001). The LSL is significantly colder than underlying salt water in winter and spring because of snow melt and lower air temperatures. In summer and autumn, freshwater inputs are warmer than oceanic temperatures, increasing the LSL water temperature (Stanton and Pickard, 1981; Gibbs, 2001). The thickness of the LSL depends on the input of freshwater runoff, and in Doubtful Sound, variation in the tailrace discharge from the hydroelectric dam.

Research indicates that these factors have had significant biological impacts. Rutger and Wing (2006), for example, found fewer bivalve species and lower abundances of key primary organisms in the inner Doubtful Sound complex where the LSL is thickest (between 2m and 12m depth). Boyle et al. (2001) made shoreline community comparisons with Batham (1965), pre Manapouri hydro-dam, showing that an abundance of characteristic zone forming organisms are no longer present anywhere in the inner reaches of the fiord. From these studies it seems likely that limited tolerance to increased freshwater flow now entering Doubtful Sound, has pushed algae and invertebrate distributions further seaward.

Lusseau and Wing (2006) highlighted the importance of local productivity for the population using stable isotopes from skin samples (taken with Velcro pads). They discovered that bottlenose dolphins in Doubtful Sound rely almost entirely on local productivity sourced from macroalgal production along the shallow rock walls. Therefore the population may be vulnerable to localized environmental and ecological changes induced by increased freshwater inputs.

Impacts, if any, of increased freshwater input on the dolphin population are not yet fully understood. However these fluctuations in surface water temperature may be linked to calf survival rate halving from 0.8621 (95% CI: 0.6851–0.9473) to 0.3750 (95% CI: 0.2080–0.5782) in 2002 (Currey et al., 2009a). This is the period when a second tailrace tunnel was commissioned for the hydro station; further increasing freshwater input. Currently it is unknown whether this correlation represents causality or coincidence. Further work is underway to tease apart this and other potential impacts. What is known, however, is that cold extremes in surface water temperatures caused by increased freshwater output can add stress to calving mothers, possibly increasing probability of still born calves (Schneider, 1999). The population shows distinct seasonal changes in distribution, with colder areas avoided in winter, and calving periods confined to summer months. Both of these have been hypothesised to be driven by seasonal variation in surface water temperatures (Schneider, 1999).

Boat traffic has been found to adversely affect the behavioural budget of the population (Lusseau et al., 2003; 2006). Similar adverse effects have been found in other dolphin populations (Foote et al., 2004; Bejder et al., 2006; Wiley et al., 2008). The main source of boat activity in Doubtful Sound is tourism; making up 87% of all dolphin-boat interactions. Private and fishing charter vessels comprise 8% and 5% of interactions respectively (Lusseau 2003a). Boat interactions with bottlenose dolphins in Doubtful Sound have been shown to change the behavioural budget of the dolphins. Resting and socializing groups are most adversely affected by interactions with boats, causing a change in behavioural state, typically to travel (Lusseau et al., 2003).

Other factors possibly affecting the population include ecosystem changes due to historical commercial fishing inside the fiord complex, current commercial fishing practices outside the fiord complex, recreational fishing, climate variability, as well as disease vulnerability due to a limited gene pool (Currey et al., 2007).

1.3.1 Conservation and Management

While there are several factors potentially implicated in the population decline, there is no evidence that unequivocally establishes the involvement of any one of them. For this reason the Department of Conservation (DOC) aimed to mitigate or avoid potential effects by establishing conservational management based on available information (DOC, 2008).

In January 2008, a new management strategy was implemented. The strategy identified boating pressure as a major factor potentially causing disruption to the population. The document summarized evidence from Lusseau et al. (2002) that over 70% of boat interactions observed had violated the Marine Mammal Protection Regulations 1992 (there was no information on whether the situation in 2007 has changed from that observed by Lusseau in 1999-2002). DOC set several primary objectives:

- Increase efforts to fully identify factors contributing to the population decline without delay
- Involve all stakeholders in the protection and on-going conservation of this population
- Restrict vessel movements within Doubtful Sound
- Formally adopt and enforce the Marine Mammal Care Code
- Establish marine mammal sanctuaries to further protect this population

To achieve these objectives, DOC established a voluntary Marine Mammal Code of Management that was implemented in January, 2008. Although a voluntary Code of Management was not the highest level of protection DOC could establish, it was seen as more beneficial than legislation as it could be implemented immediately and would be more likely to have the support of the affected parties. There has been international criticism of voluntary approaches however. The IWC Scientific Committee's report (2008) states that voluntary codes of conduct have proven to be of limited value in a wide variety of locations (Scarpaci et al., 2003; Whitt and Read, 2006; Allen et al., 2007; IWC, 2008; Wiley et al., 2008). The Code of Management forms only one part of the conservation strategy. DOC will also fund monitoring, research, education and increase public awareness (DOC, 2008).

From research on the behaviour of the Doubtful Sound dolphins (Lusseau 2003b), DOC recognised that resting and socialising are critical. Based in part on analysis of "critical habitats" by Lusseau (2003a), and operator's suggestions on what would be practical, DOC established three Dolphin Protection Zones (DPZs). These extend 200m from the shore and voluntarily exclude motorised vessels from entering. If dolphins are not visible within this zone, entry is permitted (but only by the most direct route) for reasons such as viewing of shore features, access to anchorages or diving/fishing spots, or for agency management work. The DPZs are extensive (see Figure 1.1).

Figure 1.1 Map of Doubtful Sound fiord complex indicating the dolphin protection zones (DPZs) in red, established by the Department of Conservation under the voluntary Marine Mammal Code of Management January 2008.

1.3.2 Seasonal Distribution

The distribution of the Doubtful Sound population changes seasonally. They are found further up the inner arms of the fiord in summer and autumn, but are largely confined to the middle and outer fiord in winter and spring (Schneider, 1999). This is primarily due to temperature variations caused by freshwater inputs (Schneider, 1999). The dolphin population is most vulnerable in the cold winter months when energy demands are highest, particularly for pregnant and lactating mothers and calves (Lusseau, 2003a).

DOC recognized the dolphin's seasonal distribution and planned to establish protection zones that function around this. However the current 'critical' DPZs do not include a seasonal component. Furthermore, the recognition of zones as 'critical' was sourced from vessel-based observation data collected seven years ago. These data were limited to good weather, available man-hours and daylight observation. This excluded a large proportion of time when dolphins are still active. Because of this, it is important to determine if these 'critical zones' are actually being utilised by the dolphins to a greater degree than other areas of the fiord complex. In addition, current data on behaviour, distribution and seasonal habitat use would be inherently more appropriate for management goals.

As part of its risk-minimisation strategy, DOC required that boat-based research in the vicinity of the dolphins be reduced, and has set a limit of 100 hours of research time within 100 m of the dolphins. This new restriction eliminates the possibility of conducting detailed boat-based studies, and requires the development of alternative data gathering systems. Acoustic monitoring is the most promising of the alternatives, providing non-invasive, quantitative measures of dolphin habitat use day and night, for extended periods of time.

1.4 Echolocation and Acoustic Monitoring

Acoustic monitoring enables insight on habitat use and activity by utilising cetacean echolocation. Echolocation is an active sensory system that evolved independently in mammals at least twice: in bats and in toothed whales. Both emit high-frequency sounds and process returning echoes from objects in the surroundings. Echolocation is primarily used for communication, orientation and finding prey (Verfuss et al., 2009).

For echolocation purposes, bottlenose dolphins emit very short (40-70μs), high frequency (Peak frequency = 110-130 kHz) sound pulses referred to as ‘clicks’. These clicks are broadband, meaning that they contain a wide range of frequencies (3dB bandwidth = 30-60 kHz), and are emitted in trains of a few dozen to several thousand (Au, 1993). In bottlenose dolphins and most other dolphin species, the animal “waits” for the echo of the previous click before emitting the next, so the time between clicks (Interclick interval; ICI) and target distance are closely correlated. Other factors influencing the number of clicks emitted and the time intervals between clicks (ICIs) are: whether the object is of interest or not; the difficulty of detecting the object, and even the expectation of finding a specific object (Au, 1993). The behavioural state of the animal also affects click characteristics (Koschinski et al*.,* 2008).

Bottlenose dolphins have been described as extremely vocal animals (Caldwell and Caldwell, 1967; dos Santos et al*.,* 1990; Connor and Smolker, 1996). They produce a variety of vocalizations, which are typically divided into three categories, broadband echolocation pulses, narrowband whistles and broadband burst pulses (Au, 1993).

Whistles have been suggested as the major form of communication (Caldwell and Caldwell, 1965). They are narrowband, low frequency and omnidirectional. They convey information about identity, relative position and emotional state of the whistler to all members of a dolphin group (Caldwell and Caldwell, 1972). Bottlenose dolphin whistles range between 0.8-24 kHz, with peak frequencies of 3.5-14.5 kHz and source levels of 125-173 dB re 1 μPa @ 1 m (Lilly and Miller, 1961; Caldwell et al., 1990). Whistles from 3.5 to 10 kHz can be perceived by dolphins that are up to 25 km away from the whistler when seas are shallow and calm (Janik, 2000c). These attributes make whistles ideal as contact calls.

Broadband clicks appear to be primarily used for investigating the environment and capturing prey (Au, 1993), although they may have social uses also (Xitco and Roitblat, 1996). Clicks of bottlenose dolphins are among the loudest biological sounds ever recorded (up to 230 dB re 1μPa @ 1m) (Au et al., 1974). Bottlenose dolphins can control the frequency and source level of echolocation pulses. Outgoing clicks are directional with a -3 dB beam width of about 10 degrees in the vertical and horizontal plane (Au et al., 1986). Studies in captivity have shown that clicks can be used to identify targets as small as 7.6cm from distances over 110m (Au and Snyder, 1980). Burst pulses are not as well studied. Some believe their function may be social

(Gish, 1979; Overstrom, 1983; Dawson, 1991; Lammers et al*.,* 2003; Blomqvist and Amundin, 2004). Burst pulses are often described as 'yelps', 'creaks', 'squawks' and 'blasts'.

1.5 Acoustic Monitoring via T-PODs

Passive acoustic methods are increasingly used to study cetacean habitat use and behaviour. Depending on the question under investigation a wide range of techniques are available, ranging from relatively simple self-contained instruments that automatically log echolocation signals (e.g. Carstensen et al., 2006) to complex hydrophone arrays designed to track diving marine mammals in three dimensions (e.g. Miller and Dawson, 2009). Acousticians use hydrophones to record echolocation activity and infer information on abundance, distribution, behaviour and location. Acoustic methods for monitoring habitat use have become popular as they are less invasive, require fewer man-hours, provide sub-surface information and can be used in a wider range of weather conditions and at night (Philpott et al*.,* 2007).

The T-POD (www.chelonia.co.uk) is a passive acoustic monitoring device used to record cetacean echolocation activity. It is made up of a hollow, waterproof PVC cylinder with a hydrophone at one end and battery-powered hardware data-logger that detects cetacean echolocation clicks. Six separate scans are performed per minute. Scan settings can be adjusted to detect and log dolphin or porpoise echolocation at a range of frequencies. T-PODs have become widely used to investigate cetacean habitat use, distribution and behaviour (Jefferson et al*.,* 2002; Cox and Read, 2004; Leeney et al*.,* 2007; Philpott et al*.,* 2007; Koschinski et al*.,* 2008; Rayment et al*.,* 2009; Simon et al., 2010).

The T-POD records the time and duration of clicks as well as the inter-click intervals (ICI). T-POD software (v8.19) classifies click trains into four classes according to likelihood of being of cetacean origin: 'Cet Hi' and 'Cet Lo' for click trains that have a high and low probability of being from the target species. Other sounds that cannot be easily classified into trains (e.g. snapping shrimp clicks) are classified as 'Doubtful' or 'Very doubtful'. Very regular trains of pulses are classified as boat sonar (or 'fixed'). In general the T-POD classification algorithm works well, although several studies have found that it is conservative. Click trains that are known to be of cetacean origin are often classified as 'Cet lo' and 'Doubtful' (Thomsen et al*.,* 2005; Rayment et al*.,* 2009). Because of this, manual inspection of trains is sometimes necessary.

The literature describes a range of peak frequencies for bottlenose dolphins. For example, dos Santos and Almada (2004) recorded peak click frequencies of 70kHz, Finneran et al. (2005) recorded 20-120 kHz from one individual and 30-60 kHz from another, and Au (2004) recorded peak frequencies of 100-130 kHz from several animals. Peak frequencies are important for filter settings on T-PODs. Because of the inconsistency of bottlenose frequencies in the literature, it was recognized that prior knowledge of the characteristics of the sonar signals of the bottlenose dolphins of Doubtful Sound would be highly desirable, and a variety of T-POD settings should be tested. This would enable the most accurate settings to be found, maximising detection rate whilst minimising false detections.

One problem, that of discriminating among different species in the T-POD records, is not present in Doubtful Sound, as no other cetacean species are resident in the area and sightings of others have been very rare. In some cases, different species can be discriminated via comparisons of outputs from two bandpass filters in the T-POD. The only other dolphin species likely to be seen in the area, and with overlap in frequencies with the bottlenose dolphin, were Dusky dolphins (*Lagenorhynchus obscurus*) who echolocate at a peak frequencies of 80-100k Hz (Au 2004; Au and Wursig, 2004). Research on bottlenose dolphins in Doubtful Sound has been long-term (1990-present) and intensive. In this time, Dusky dolphins have been seen very rarely and only ever at the openings of the fiord. Therefore Dusky dolphins were unlikely to cause detections on the T-PODs.

Detection range of T-PODs is important for acoustic habitat monitoring. This facilitates appropriate spacing thus achieving greatest coverage and spatial representation. Further, with any automated monitoring system, it is important to know what area is monitored. Range estimates have been made for harbour porpoise (Tougaard et al., 2006), Hector's dolphin (Rayment et al*.,* 2009) and bottlenose dolphins (Philpott et al*.,* 2007). Maximum detection range for bottlenose dolphins in Shannon Estuary, Ireland, was 1246 m with 82% detection when dolphins were within 500m (Philpott et al*.,* 2007). Range and detection probability may differ within Doubtful Sound due to its unique fiord environment and potential for differences among localised populations.

The major limitation of the T-POD for habitat monitoring is that it can only detect cetaceans that are actively echolocating. Dolphins can often travel silently (without echolocating) especially in areas often used (Philpott et al*.,* 2007). Because the Doubtful Sound population is resident, silent travel is likely. It is important to investigate this limitation for long term habitat monitoring in order to quantify the conservative nature of recordings.

1.6 Study Objectives

In order assess the effectiveness of the conservation measures for the Doubtful Sound population, and to provide for their improvement, current, robust, quantitative information on the dolphins' habitat use is required. To this end, this study used an acoustic monitoring system to address the following objectives:

1. Determine the most effective T-POD settings for bottlenose dolphins in Doubtful Sound
2. Estimate approximate range of detection by the T-POD, and acoustic detection probability
3. Investigate whether behavioural states can be inferred from T-POD data, specifically foraging, and hence whether T-POD data can be used to determine whether different parts of the fiord are used for different purposes
4. Establish an acoustic monitoring system using moored T-PODs to cover representative areas of Doubtful Sound
5. Monitor the population's habitat use and distribution patterns over a 12 month period to gain insight on seasonal and spatial habitat use
6. Based on the above, propose changes to improve current conservation measures for the dolphin population

1.7 Thesis Structure

This thesis is presented as a series of manuscripts each of which will be submitted to a scientific journal. Unavoidably, this format has resulted in some repetition of content. In attempt to reduce this, I have provided a general introduction and general discussion with all references combined in a single list at the end of this thesis.

All data collection, analysis and writing was conducted by myself with the exception of temperature data used in chapter 4, which was collected and processed by Shaun Henderson, PhD candidate of Otago University.

CHAPTER 2

OPTIMISING T-POD SETTINGS AND TESTING RANGE OF DETECTION

2.1 Introduction

Because the T-POD is a fairly new monitoring device, there are many unanswered questions about its performance and limitations in the field. One of the most prominent is its detection range for different species of odontocetes in the wild. T-POD range has mainly been assessed for the harbour porpoise *(Phocoena phocoena)*, with many studies covering a range of habitats (Cox et al*.,* 2001; Culik et al*.,* 2001; Teilmann et al*.,* 2002; Koschinski et al*.,* 2003; Carlstrom, 2005; Carstensen et al*.,* 2006; Koschinski et al*.,* 2006; Philpott et al*.,* 2007). Finless porpoise *(Neophocaena phocaenoides)*, bottlenose dolphin *(Tursiops truncates)* and Hector's dolphin (*Cephalorhynchus hectori*) have been subject to one range study each (Jefferson et al*.,* 2002; Philpott et al., 2007; Rayment et al., 2009). Philpott et al. (2007) used a land based theodolite experiment, common for assessing range, to record a maximum detection range for bottlenose dolphin of 1246 m.

Probability of detection is another aspect of T-POD performance that requires investigation. It has previously been assessed for Hector's dolphin (Rayment et al*.,* 2009) and bottlenose dolphin (Philpott et al*.,* 2007). Both studies found that probability decreased with distance from T-POD. Philpott et al. (2007) observed a detection probability of 82% when bottlenose dolphins were within 500 m of the T-POD.

Field trials are required to determine both detection range and probability because optimum spatial distributions of moorings, and the conservative extent of results, are influenced by these respectively. Additionally, since bottlenose dolphins occupy a wider range of habitats than any other odontocete (Leatherwood and Reeves 1983), and it is reasonable to expect that detection range will vary across habitats due to the differing acoustic characteristics, the trials by Philpott et al. (2007), in the Ireland's Shannon estuary, may not be applicable to bottlenose dolphins in Fiordland.

An important limitation of any passive acoustic monitoring system is missed detections due to non-echolocating cetaceans. Research has shown that dolphins are often ‘silent’ (not echolocating), especially during travel and in areas commonly used (Jones and Sayigh, 2002; dos Santos and Almada, 2004). Dos Santos and Almada (2004) found that 23% of one minute acoustic samples from bottlenose dolphins in the Sado estuary, Portugal, contained no echolocation clicks. Gannon et al. (2005) showed that bottlenose dolphins use passive listening extensively while searching for certain food types, arguing that echolocation clicks may alert prey species of their presence, thus hindering foraging success.

In addition to these inherent limitations of acoustic monitoring, the detection ability of a T-POD can be changed by the filter settings chosen by the researcher. Settings need to be species-specific due to variation in echolocation signals (Au, 1993). Bottlenose dolphins have been shown to modify their sonar signals to suit the noise environment of different habitats (Au et al., 1985), emphasising the need for matching the T-POD settings to the sonar signals used in the habitat of interest. Little research has been conducted to determine the best settings to be used for bottlenose dolphins.

T-PODs use two filters to focus on a particular point within the frequency range of the target species (Philpott et al*.*, 2007). Essentially, the “A” filter should be set at the peak of the click spectrum, while the “B” frequency should be set at a point where spectral energy is low. Because detection rates are dependent on the filter settings, it is important to match the settings to the population under study.

In a preliminary study by Elliott (2008), several alternate T-POD frequencies were quantitatively compared using multiple T-PODs moored together. Settings trialled were based on those reported by Philpott et al. (2007), and published studies of bottlenose dolphin echolocation clicks (Au, 2004; Dos Santos and Almada 2004; Finneran et al*.*, 2005; Philpott et al*.*, 2007). In addition, a wide-band recording system capable of recording frequencies up to 176 kHz, was used to measure the characteristics of the signals used by Doubtful Sound bottlenose dolphins, and hence design T-POD settings to suit (Elliott, 2008). The following settings were trialled (Table 2.1).

Table 2.1 Six different T-POD settings trialled by Elliott (2008) for the monitoring of bottlenose dolphins in Doubtful Sound, New Zealand. Only A and B filter settings were altered.

	Philpott et al. 2007	***Other***	***Settings***	***Trialled***	
Trial #	T1	T3	T4	T5	T6
A Filter (kHz)	**50**	**30**	**50**	**70**	**90**
B Filter (kHz)	**90**	**50**	**30**	**30**	**30**
Click Bandwidth	*5*	*5*	*5*	*5*	*5*
Noise adaptation	++	++	++	++	++
Sensitivity	*12*	*12*	*12*	*12*	*12*
Scan limit on # of clicks logged	*240*	*240*	*240*	*240*	*240*

Analysis showed that the T4, T5 and T6 settings were about equally effective, and were significantly more effective than the settings used by Philpott et al. (2007). T-PODs have six, ten second scans each minute, and the settings for each scan can be different. For the remainder of his study, Elliott (2008) set T-PODs to do two 10sec scans at each of the T4, T5 and T6 settings in rotation. The wideband recordings showed that the sonar clicks were broadband with maximum energy from 40 - 120 kHz, and relatively weak at 30 kHz. This explains why Philpott et al. (2007) settings were not very effective (their "B" filter was set in the strongest part of the click spectrum, it should have been set in the weakest). It also explains why the T4, T5 & T6 settings, which differ only in the "A" filter, were about equally effective (the click energy at 50-90 kHz is similar). This three setting combination is similar to the 'dolphin sweep' setting available in the T-POD software package.

This study extended the preliminary work by Elliott (2008) to determine which settings were most effective at detecting bottlenose dolphins. The influence of distance on detection rates and probability was also investigated during field trials. Furthermore it was examined whether group size, behaviour or location in the fiord channel had any effect on detection rates.

2.2 Methods

2.2.1 Frequency Setting Experiment

Multiple, factory calibrated, version 5 T-PODs were moored together at Pack Point, in Doubtful Sound (45° 23’ 442” S, 167° 06’ 047” E), a known area of high dolphin activity, with the ‘Dolphin sweep’ settings (from T-POD software) and those proposed as most effective by Elliott (2008). While not expected to be very effective, the settings used by Philpott et al. (2007), and from Simon et al. (2010) (50/70 A/B frequency) were included for comparative purposes also.

Upon retrieval, T-PODs were downloaded and click trains identified using T-POD software (v. 8.19). Numbers of echolocation clicks cannot be reliably compared due to the highly directional beam pattern and high frequency of dolphin echolocation (Au et al*.,* 1986). Because of this, trains of echolocation clicks were counted and compared over respective mooring periods, a strategy recommended by dos Santos and Almada (2004).

Trains were classed into ‘Cet Hi’, ‘Cet Lo’ and ‘Doubtful’ categories via T-POD software. It was assumed that a larger number of positively identified click trains reflected a more effective setting. A list of detection rules was applied to trains identified by T-POD algorithm because T-POD software occasionally logs false positives in all categories. These rules were as follows and apply throughout this thesis.

1. At least 10 clicks in a train
2. Detection classified by T-POD software as ‘Cet Hi’, ‘Cet Lo’ or ‘Doubtful’

All trains then investigated individually to meet points 3, 4, 5 and 6 below;

3. Click Duration: 20-500 microseconds. Most between 50-150 microseconds (Au, 1993). Durations longer than a few tens of ms appear to arise via multipath.
4. Pulse repetition frequency: smooth trend in click rate, click rate usually 10-25 clicks/sec, but up to 500 clicks/sec.
5. No accompanying noise when PRF and "all+sync" is selected in T-POD software (sometimes the software will find a train of clicks within random noise. If PRF and “all + sync” are selected, noise will appear as dots scattered about on the screen. If it is a reliable detection, the contour of the PRF will be clean (see Figure 2.1b & c). There may be some dots at the very top of the screen; this is artefact probably caused by multipath propagation).

Figure 2.1 indicates how click trains are depicted in the T-POD software and how each train can be investigated using different levels of magnification.

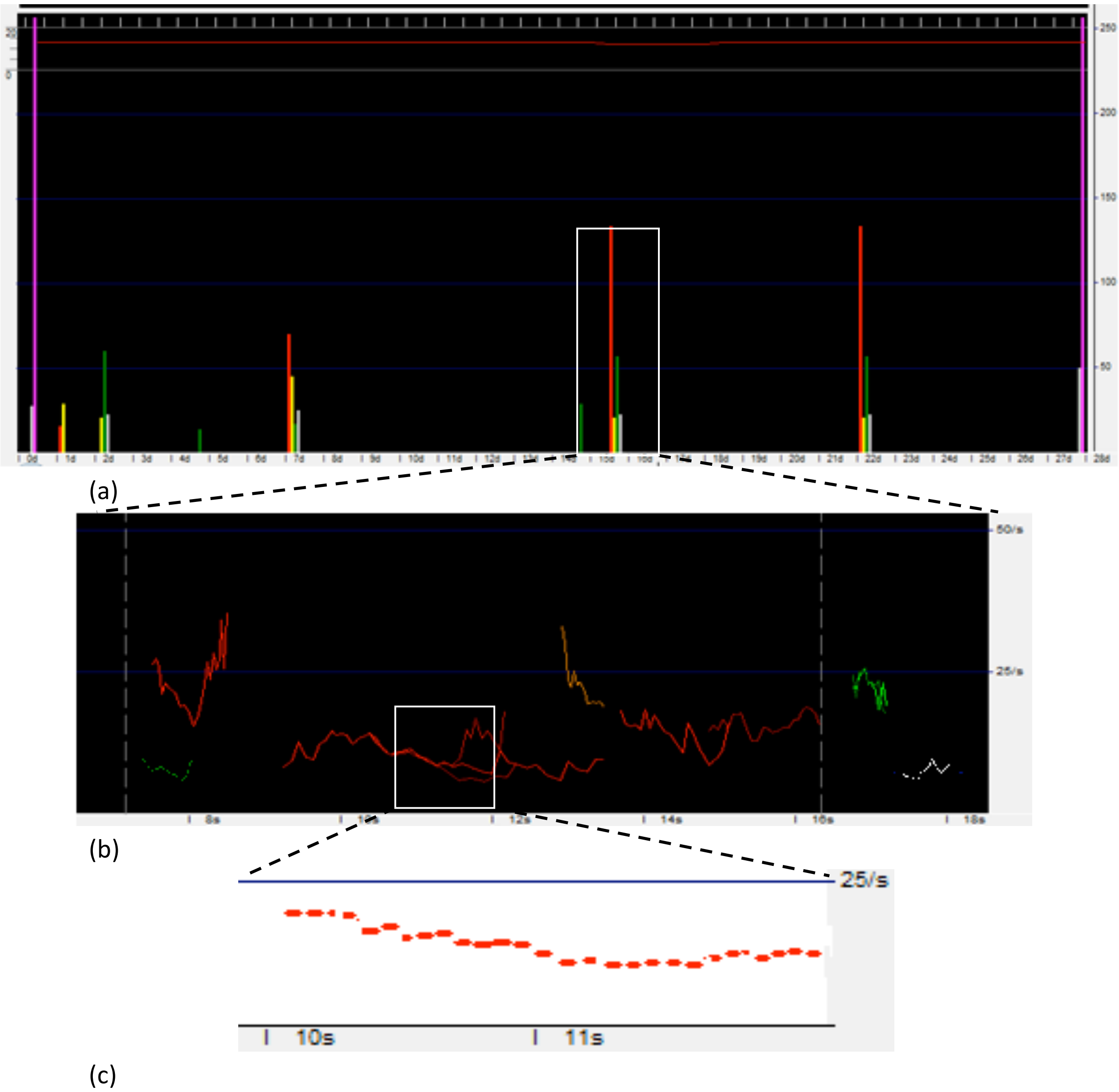


Figure 2.1 Exported results from a T-POD monitoring bottlenose dolphins in Doubtful Sound, NZ. (a) Results from 28day monitoring period. Plot shows amplitude (y-axis), time (x-axis) and classification (colour of bars) of detections. The purple detections at start and finish are the boat's echo sounder operating during deployment and collection of the T-POD. Red is a 'Cet-hi' probability detection; yellow is 'Cet-lo' probability detection; green is 'doubtful' detection; grey is 'very doubtful'. (b) Detections viewed at higher magnification showing pulse repetition frequencies (y-axis), characteristic patterns and click rates (around 25/s) of bottlenose detections over time (x-axis). (c) A single detection shown at highest magnification allowing pulse repetition frequencies (y-axis) of individual clicks in an echolocation train over time (x-axis).

2.2.2 Detection Range and Probability Experiment

The steep, inaccessible walls of the fiord made a land based theodolite methodology impossible in Doubtful Sound. The bottlenose dolphins within this fiord are often grouped very tight, moving through the fiord on predictable, direct routes. This enabled T-PODs to be deployed well in front of a moving group so distance from dolphins to T-POD can be calculated via GPS using a boat travelling parallel to the dolphins.

Dolphins were located via systematic searching of the fiord and approached to determine direction of movement and group size. Only tight groups, in which all dolphins were within 50 m of each other, were used. The boat was moved 1.5 nautical miles ahead, into the dolphins' presumed path (a distance well beyond range from Philpott et al., 2007). The boat's echo-sounder was turned off and two version 5 T-PODs were deployed (set at the Elliot (2008) settings; see Table 2.1) at 5 m depth beneath a large floating buoy. The buoy had a portable GPS taped to its upper surface. The GPS logged the position of the buoy and hence the position of T-PODs, every ten seconds.

The boat then returned to the dolphin group, approaching the leading dolphins from behind. The boat was kept abreast of the leading dolphin/s about 100 m off to the side. Distance and magnetic bearing to the leading dolphins was measured every 30 seconds (via laser-rangefinder), to enable calculation of the location of the dolphin group, until the dolphins passed the buoy, or turned around. Any influence of the directionality of the dolphins' sonar (see Au, 1993) was reduced by using only those dolphin tracks which remained within a 400m strip centred either side of the T-POD they were approaching. In some range trials, distances did not always reach zero. Group size, state of behaviour (determined using criteria from Schneider (1999), and position in the fiord channel (along fiord wall (within 100m of wall) or mid-water) were recorded.

T-POD and GPS devices (from boat and buoy) were downloaded using T-POD software (chenolia.co.uk) and Mac GPS software. Location estimates for the leading dolphins were compared with GPS data from the drifting buoy, to estimate the range from dolphins to T-PODs. Data were exported into Excel to illustrate characteristics of echolocation click trains along with date, time and respective distances. Detection train decision rules outlined above were applied. Data was grouped into distance bins of 100m.

It was identified that a detection made by the T-POD could be from an individual behind the lead dolphin/s. This meant the detection would have come from a dolphin that was further than the distance calculated using the boat/lead dolphin; thus range estimates were conservative.

To investigate the effect of distance on T-POD performance, a click train detection rate and probability of detection was calculated for each 100 m bin. Detection probability is a measure of how likely the T-POD is to detect a dolphin group given that it approaches within a certain distance of the T-POD. However, this probability can vary depending on time spent within each range. For example, a group that spends 10 minutes within 200 m of the T-POD may be more likely to be detected than a group that spends one minute within 100 m (Rayment et al*.,* 2009). To account for the effect of time on detections, a click train detection rate was calculated for distance bins. The time a group spent within a bin was calculated and referred to as a period.

Analogous to Rayment et al. (2009), the click train detection rate, Rj, for each period was calculated as:

$$Rj = Cj / Tj$$

where: Cj is the number of click trains detected in period j, Tj is the duration of period j in minutes. The values of Rj were then averaged for each distance bin. Zero values, occurring when no detections were made in a bin, were included in samples. The detection probability for each distance bin, Pi, was calculated analogous to Rayment et al. (2009) also, where:

$$Pi = Di / Ni$$

Di represents the number of periods in distance bin i with acoustic detections of dolphins, Ni is the total number of periods in distance bin i. To provide a realistic time frame for detections, only periods longer than 30 seconds were included in samples.

Detection rates were not independent of each other as autocorrelation can exist between bins with detections, recorded during the same sample. For example, a dolphin echolocating at 500m would then be more likely to echolocate at 400, 300, 200, and 100 m. To achieve independence, distances of first detection from groups approaching within 100 m of T-POD, were also plotted. Although detection rate data are not statistically independent, it was still a useful way to investigate the effect of range on T-POD detection ability.

A cubic logistic equation was fitted to the binned detection data in order to estimate an effective detection radius (EDR), analogous to an effective strip width in line transect surveys (Buckland et al., 2001; Rayment et al., 2009). The EDR was calculated as the area under the fitted curve. A parametric bootstrapping procedure was used to obtain a 95% confidence interval for the EDR.

2.3 Results

2.3.1 T-POD Settings Experiment

Two separate field trials of 50 and 24 days were made to compare 'Dolphin sweep' with Elliott (2008) settings, and Philpott et al. (2007) plus Simon et al. (2010) with Elliott (2008) settings respectively (Table 2.2). Settings derived from Elliott (2008) were significantly more effective at obtaining positive trains from bottlenose dolphins than 'Dolphin sweep' settings (Two-sample T-test, p. <0.001), and Philpott et al. (2007) and Simon et al. (2010) settings (Kruskal-Wallis, p. <0.001; Nemenyi post hoc, p. <0.001). In both field trials, Elliott (2008) settings recorded by far the highest number of detections in 'Cet hi', 'Cet low' and 'Cet doubtful'. The 'Dolphin sweep' settings appeared to be more effective than Philpott et al. (2007) and Simon et al. (2010) but they were still significantly less effective than those obtained by the Elliott (2008) settings. Elliott (2008) settings are used for the remainder of this research.

Table 2.2 Comparisons of the number of positively identified bottlenose dolphin trains collected from multiple T-PODs moored together over two separate trial periods with different settings being compared with those from Elliott (2008).

Setting	Frequencies (A/B filters)	# of days trialled	# of positively identified dolphin click trains		
			'Cet Hi'	'Cet low'	'doubtful'
'Dolphin Sweep'	50/70; 70/113; 92/130; 113/159; 130/92; 159/113	50	36	90	50
Elliott (2008)	50/30; 70/30; 90/30	50	249	325	858
Philpott *et al.* (2007)	50/90	24	1	1	0
Elliott (2008)	50/30; 70/30; 90/30	24	6	18	42
Simon *et al.* (2010)	50/70	24	2	1	3

2.3.2 Detection Range and Probability Experiment

A total of 52 range trials were made of which 23 had T-POD detections at varying distances. Acoustic detection rates decreased with increasing distance from T-POD to dolphin group (Figure 2.2). The maximum range of positive detection was 1313 m. Average range of first detection was 593 m (± SE 82 m). Variation in detection rate was highest at closer ranges. The average speed of the dolphin groups during the range trials was 1.32ms^{-1} (± SE 0.14).

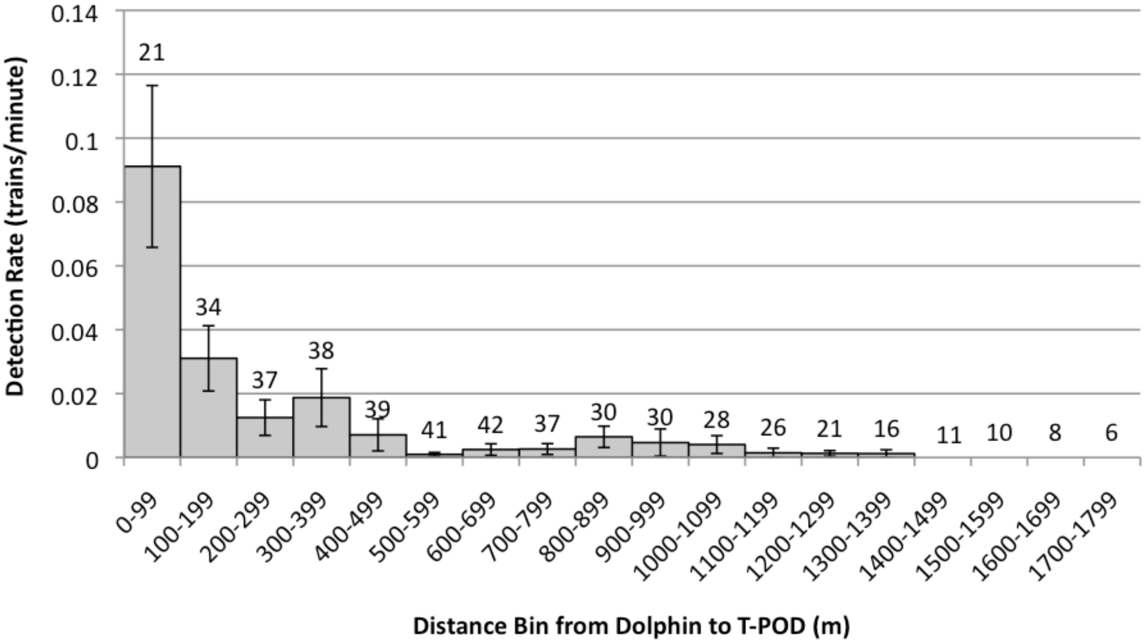


Figure 2.2 Detection rates plotted over distance from dolphin group to T-POD. Numbers above columns indicate sample size of train/minute rates averaged to get overall rate for each 100m bin. Error bars are +/- one standard error. Detection rates per bin only included samples in which dolphins were present within a bin for 30seconds or more.

Distance of first detection (Figure 2.3) is highly constrained by sample size, because only one data point is gained from each trial. It does show however that most groups were first detected at a range of 200-400m.

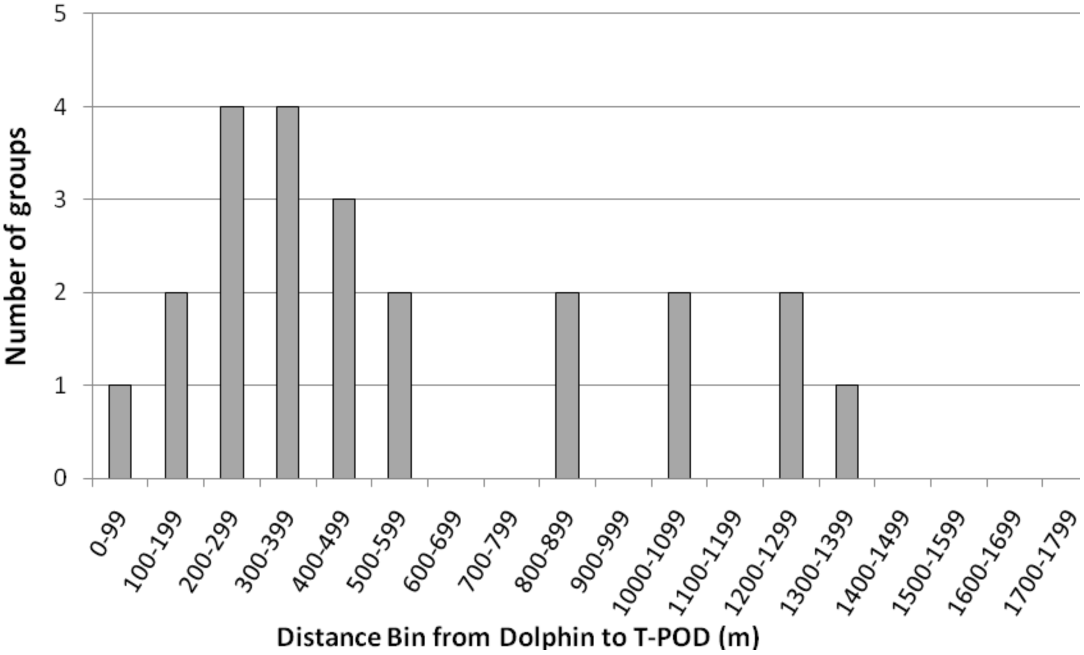


Figure 2.3 Range at first detection for groups approaching within 100m of T-POD plotted over distance from dolphin group to T-POD.

No significant differences were found between group size (Kruskal-Wallis, p. > 0.05), behaviour (Kruskal-Wallis, p. > 0.05), or channel location (Mann Whitney, p. > 0.05), with respect to detection rates (Table 2.3).

Table 2.3 Average detection rates (trains/minute) of data categorised by group size, behaviour and channel location.

	Average detection rate (trains/min)	**Sample size of detection rates averaged**
Group Size		
0-10	0.011 (±SE 0.005)	66
11-20	0.008 (±SE 0.004)	105
21-30	0.013 (±SE 0.006)	89
31+	0.018 (±SE 0.01)	33
Behaviour		
Travel	0.017 (±SE 0.005)	142
Tr/dive	0.007 (±SE 0.003)	57
Milling	0.003 (±SE 0.002)	40
Tr/social	0.006 (±SE 0.004)	28
Channel location		
Along wall	0.009 (±SE 0.004)	105
Mid-channel	0.015 (±SE 0.005)	195

Detection probability decreased with increasing distance from T-POD to dolphin group (Figure 2.4). Of the groups observed within 500m, 47% were acoustically detected. Of 52 groups observed within the 1300m maximum detection range of the T-POD, 44% were detected acoustically. Using overall time in minutes spent within 500m, 10% of minutes had positive detections. Of overall minutes spent within the 1300m range, 6% of minutes had positive detections.

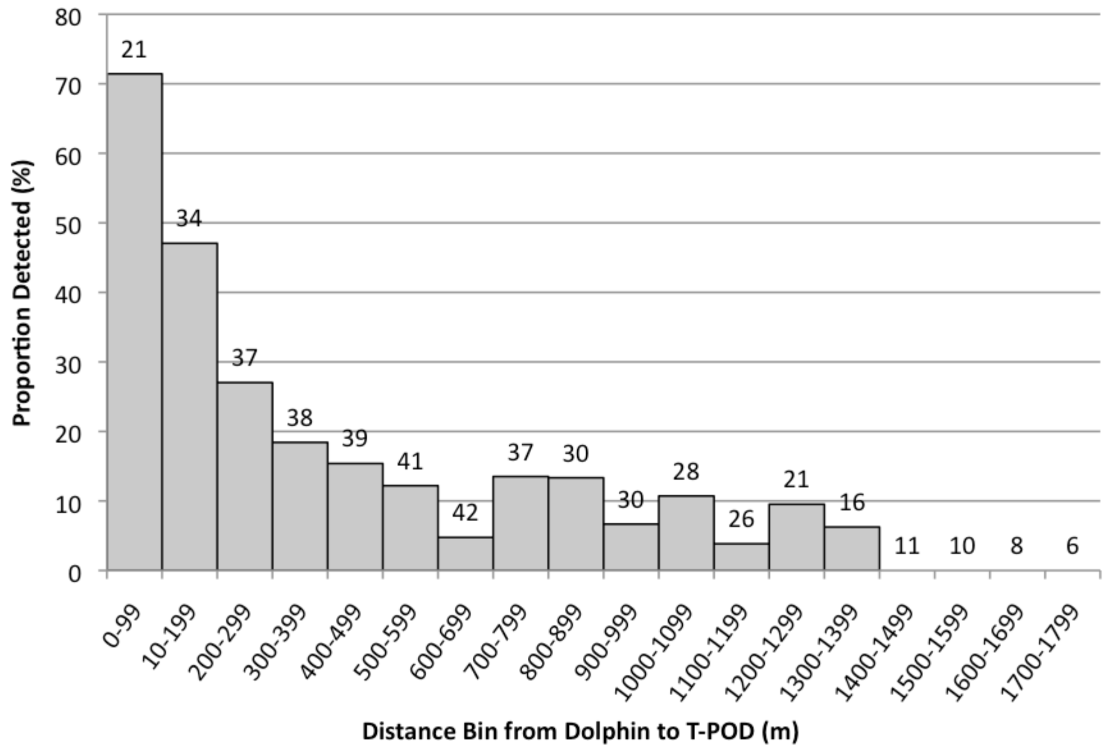


Figure 2.4 Histogram showing proportion of dolphin groups detected when entering distance bins from a total of 52 passes. Numbers above each column indicate sample size for each bin. To be included in any one distance bin, dolphins had to remain in it for >30sec.

A cubic logistic regression of the probability data was used to fit a smooth curve from which to calculate EDR (Figure 2.5). The regression equation was

$\log(p/(1-p)) = a + b*x + c*x^2 + d*x^3$, where $a = 1.609$, $b = -13.71$, $c = 16.53$, $d = -6.661$

where:

$p = 1/(1+\exp(-u))$, where $u = a + bx + cx^2 + dx^3$

Effective detection radius (EDR) was calculated from this at 266m (95% CI; 222m-317m). EDR estimates the radius of the circle within which detection probability can be assumed to be unity. In other words, detecting the groups at the distances shown in Figure 2.4 is analogous to detecting all groups out to a radius of 266m from the T-POD (Figure 2.5).

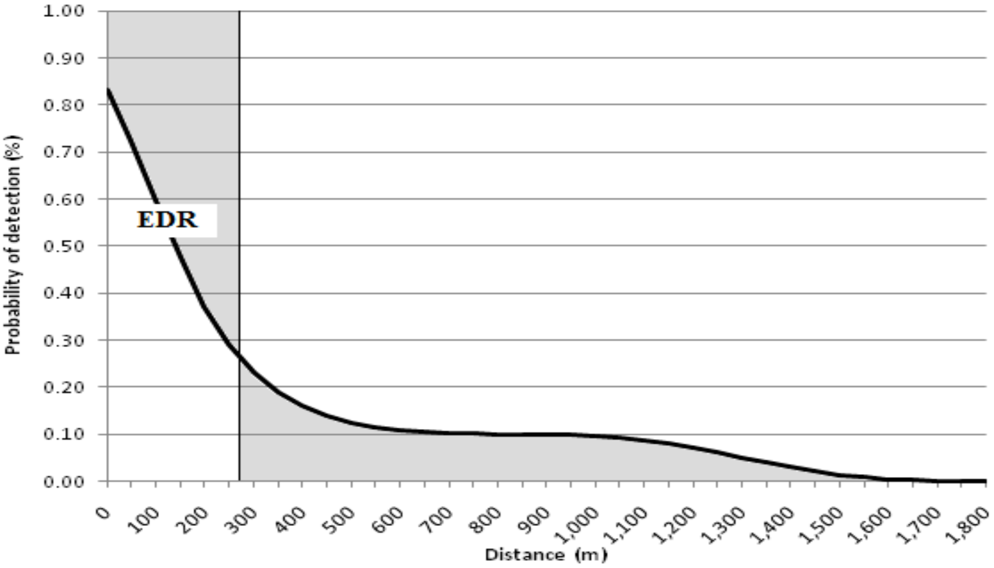


Figure 2.5 Cubic logistic regression of detection probability data enabling EDR to be calculated via integration of the area under the curve. The grey area under the curve equals the grey area above the curve where probability =1 and thus the EDR of 266m.

2.4 Discussion

2.4.1 Settings Experiment

The major point of interest gained from comparing settings in field trials was the significant difference in number of positive dolphin trains obtained using different settings. Elliott (2008) settings recorded higher numbers of trains than other settings trialled. More trains were classified as ‘Cet doubtful’ using Elliott (2008) settings, which may cause critics to believe these settings recorded more false positives, however all trains displayed in Table 2.2 were individually identified as positive detections using the detection rules outlined earlier.

Only A/B filter settings differed among trials. Click bandwidth, noise adaptation, sensitivity and scan limit were all set the same due to variability in T-POD versions used in different studies. To avoid differences in individual T-POD performance, all T-PODs were Version 5, which have standardised detection thresholds set using a calibrated sound source upon construction (Chelonia, 2006). This results in reduced variation in sensitivity (Rayment et al., 2009).

In both trials, the Elliott (2008) settings consistently made most detections. Combining the ‘Cet Hi’ and ‘Cet lo’ categories only, the Elliott (2008) settings made between 4.5 and 12 times as many detections as the others. Optimising detection rate is extremely important in habitat monitoring as the T-POD device is inherently conservative due to directionality of sonar clicks, limited range of detection and requirement of active echolocation. Despite the importance of getting the settings right, there appears to be no published quantitative comparisons of different frequency settings.

This experiment revealed that Elliott (2008) settings were the most effective of the trialled settings; however more appropriate settings may exist. Additionally, results from this project may be influenced by local variation in echolocation, sample size and behavioural state at time of sampling. The data confirm the value of trialling different settings, and if possible, making wideband recordings of the population under study. Because bottlenose dolphins can modify the frequency content of their sonar signals (Au et al., 1985), one should not assume that characteristics recorded elsewhere will necessarily apply in other populations.

2.4.2 Detection Range and Probability Experiment

As expected from the literature, detection rate and probability decreased with increasing distance between the T-POD and dolphin group. These patterns can be attributed to directionality and loss of click energy over distance (Au, 1993; Philpott et al., 2007). Echolocation clicks are focused by the melon, producing a highly directional transmission beam from the dolphin's head (Au, 1993). Within this echolocation beam, intensity decreases at increasing angles from the source and the spectral content of clicks changes. In the bottlenose dolphin, the 3-dB beamwidth is 10-11.7º with an upward angle of approximately 5º (Au et al., 1986). As a result of this directionality, echolocation clicks become more distorted at increasing distances from the centre of beam (Au, 2002). Therefore at larger ranges, a smaller proportion of clicks will be on-axis, reducing click energy available to induce detections. Click energy is also lost over distance via spreading losses and absorbtion, the latter being dramatically frequency-dependent. For example absorbtion loss at 10 kHz is about 1 dB/km, while at 100 kHz loss is 36 dB/km (calculations via Malme, 1995). The T-POD will only record clicks with energy over a certain threshold. Both of these factors reduce detection ability of the T-POD over distance.

Of 52 trials, 29 resulted in no acoustic detections. Of these 29, 14 came within 200m and five within 100 m or less of the T-POD. Only 47% of groups that came within 500m were detected, compared to 82% by Philpott et al. (2007). Of all time in minutes spent within 500m and 1300m only 10% and 6% respectively had positive detections. In addition to directionality and click energy factors discussed above, these results suggest that the dolphins in Doubtful Sound may also be echolocating less than those investigated by Philpott et al. (2007) in the Shannon Estuary, Ireland.

'Silent' behaviour (non-echolocation) has been identified through research on wild bottlenose dolphins (dos Santos and Almada, 2004). Explanation may be that bottlenose dolphins use passive listening extensively while searching for certain food types because echolocation clicks can alert prey species to the presence of dolphins, hindering foraging success (Gannon et al., 2005). Alternatively, dolphins do not need to rely on echolocation for navigation during the day as they could be familiar with a variety of features of their environment (Nowacek, 2005). For example, bathymetric features such as channel confluences or subsurface rises may provide navigational aids. Bats do not need to echolocate after becoming familiar with an area and will avoid objects that have been removed or collide with newly introduced obstacles

(Holler, 1995). Reduced echolocation for navigation would not be surprising in Doubtful Sound as the population is resident and uses common routes every day.

Studies have also shown that echolocation occurs significantly less frequently when bottlenose dolphins are travelling compared to other activities (Jones and Sayigh 2002, dos Santos and Almada 2004). Therefore another explanation for lower detection rates in this study compared to Philpott et al. (2007) is that the proportion of time spent travelling in this study was higher than that in Philpott et al. (2007); thus reducing echolocation activity. This is probable as the methodology used in this study utilised the travelling nature of the dolphins to obtain varied range distances. Wideband recordings from a hydrophone made during different behavioural states would be beneficial for assessing how echolocation rates differ with behaviour and location. However this would be confounded by directionality factors.

Results indicating the range of first detection range from groups that approached within 100m were highly constrained by sample size. The purpose of Figure 2.3 was to highlight how detection range data in Figure 2.2, while not independent, are nonetheless very informative. An apparent peak in the range at first detection data occurred within 200-400m. This may possibly be the distance at which approaching dolphins recognise the T-POD in the water column as a foreign object, and echolocate at it to determine what it is.

The maximum range of detection was 1313 m, very close to the 1246 m measured by Philpott et al. (2007). This is of interest as the two study sites are extremely different. The greater distance recorded in Doubtful Sound could be related to the long, narrow, hard rock walls of the fiords and/or the low salinity layer, which could cause increased reflection of echolocation clicks, allowing clicks to propagate further. Detections at greater distances than 1313 m were very unlikely as 35 bin samples were within 1400-1800 m distances, with no positive detections. This data combined with that from Philpott et al. (2007) suggests the maximum detection range of bottlenose dolphins with a T-POD is around 1300 m.

Tougaard et al. (2006) calculated maximum detection distance of 400 m for the harbour porpoise; Rayment et al. (2009) 431 m for Hectors dolphin and Jefferson et al. (2002) 250-350 m for finless porpoises. These are much less than distances for bottlenose dolphins. These results can be explained by the much lower source levels of harbour porpoises, Hector’s dolphin and finless porpoises, which are all quite similar (157 dB for harbour porpoise, Au et al., 1999; 163 dB for Hector's dolphin, Dawson and Thorpe, 1990; 167 dB for finless porpoise, Akamatsu et al*.,* 2001). Bottlenose dolphin source levels are much greater (220 dB4 for a dolphin echolocating on a distant target; Au, 1993). Additionally, the broadband clicks of bottlenose dolphins have much more energy at low frequencies, which suffer much less absorbtion and therefore propagate further, than the narrow-band high-frequency clicks that are characteristic of the other three species (Dawson and Thorpe, 1990; Villadsgaard et al., 2006). This enables clicks to maintain energy over longer distances, enabling T-POD detection thresholds to be met at greater ranges.

Distances in this study were conservatively measured, as they were taken from the closest dolphin/s to the T-POD, not necessarily the ones that are echolocating. The use of tight groups (all individuals within 50m of each other) for the trials would have acted to reduce inaccuracy. In no case was a group other than the target group observed. The boat based method made these trials possible; in most places the extremely steep topography would have made theodolite observation methods impractical. Also, the boat-based method made multiple trials possible within a day. Obviously, with a theodolite station one has to wait until the dolphins travel past it. The potential disadvantage of the method is that boat presence may have influenced echolocation behaviour.

Non-detection via directionality and non-echolocating dolphins are unavoidable limitations of T-PODs. Estimates of EDR are useful for determining a range where the T-POD effectively detected all dolphin groups, however, the time dolphins spend within the range of the T-POD will also affect detection probability. This explains why detection probability is less than one, even when within very close ranges. Another limitation is that the T-POD measures echolocation activity, not abundance. It is not possible to tell from a T-POD record how many dolphins were present it its vicinity.

Further investigation on the effects of group size and behaviour on T-POD detection is recommended. Furthermore, assessment of variables such as ambient weather conditions, geographic location and low salinity may be important in detection efficiency of T-PODs.

CHAPTER 3

DERIVING BEHAVIOURAL STATES FROM ACOUSTIC DATA

3.1 Introduction

Within the animal kingdom, signals and vocalisations are often correlated with the performance of specific behaviours (Lorenz, 1950); therefore it may be possible to infer certain behavioural states from recorded vocalisations. In odontocetes, specific vocalisations often occur predominantly or exclusively in certain behavioural states (Smith, 1986; Dawson, 1991; Boisseau, 2004), and this has been used to infer call function. This is a common approach used to study wild vertebrate populations (e.g. Cheney and Seyfarth, 1990).

Delphinid vocalisations have commonly been classified into three main groups; whistles (narrowband, tonal signals), clicks (broadband or narrowband pulses with rapid onset), and burst pulses (broadband trains in patterned sequences) (Au, 1993). Within this study, T-PODs recorded echolocation clicks and burst pulses (thus excluding whistles).

Echolocation in odontocetes has mainly been investigated in the context of target detection and discrimination (Au, 1993; Kastelein et al*.,* 1997). An increasing number of studies, however, have investigated correlations between behaviour and echolocation characteristics (Goodson et al*.,* 1988; Dawson, 1991; Goodson et al*.,* 1994; Miller et al*.,* 1995; Madsen et al*.,* 2002; Johnson et al*.,* 2004; Miller et al*.,* 2004; Akamatsu et al*.,* 2005; Madsen et al*.,* 2005; Johnson et al*.,* 2006; Johnson et al*.,* 2008; Jones et al*.,* 2008; Koschinski et al*.,* 2008; Verfuss et al*.,* 2005; 2009).

Dawson (1991) correlated 42 distinct behaviours with click types made by Hector's dolphin. Variations in inter-click intervals (ICIs) of harbour porpoises recorded by T-PODS have been used to distinguish among feeding, approach and communication behaviours (Koschinski et al., 2008; Verfuss et al., 2009). For bottlenose dolphins, multiple studies have found similar echolocation/behaviour correlations (Caldwell and Caldwell, 1967; dos Santos et al*.,* 1990;

Smolker et al*.,* 1993; Schultz et al*.,* 1995; Connor and Smolker, 1996; Connor et al*.,* 2000; Janik, 2000a; Boisseau, 2004). Echolocation used during foraging is the best understood.

In dolphins, ICI is governed mostly by range to a target; clicks are typically spaced apart so that the echo returns before the next click is emitted (Turl and Penner, 1989). ICIs are thus a combination of the two-way transit time plus a short lag time used to process the echo. Dolphins share this relationship with echolocating bats (Thomas et al*.,* 2004).

Verfuss et al. (2009) defined the echolocation behaviour of foraging, captive, harbour porpoises into phases very similar to those described for bats (Kalko and Schnitzler, 1998). An initial search phase (before detection of prey) is characterised by long variable click intervals that gradually decreased with distance towards a reference. Once prey is detected, the approach phase is characterised by an initial period in which click interval is reasonably constant, followed by a terminal phase ('buzz') in which click rate rapidly increases until the prey is captured. This is followed by increasing ICIs, as the animal reorients (See Figure 3.1 below; Verfuss et al. 2009).

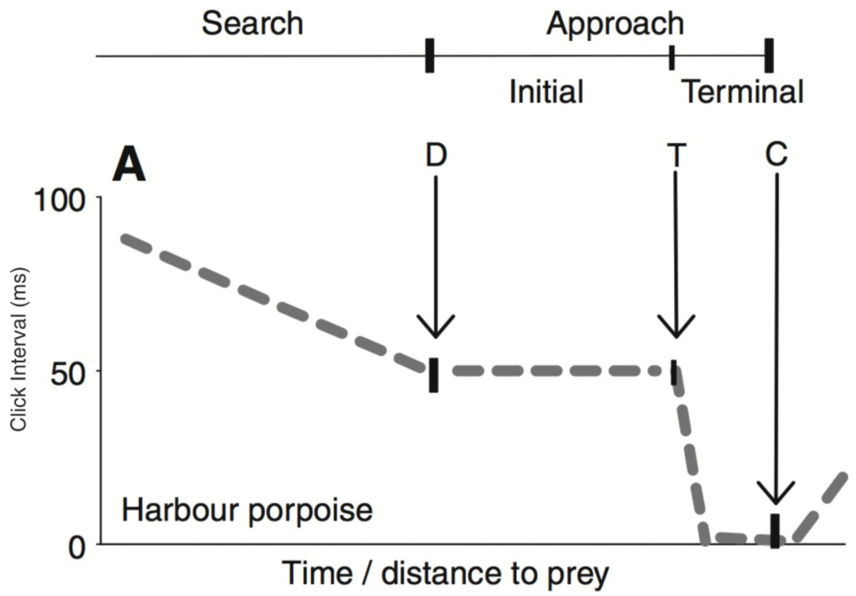


Figure 3.1 Echolocation phases of foraging harbour porpoises (from Verfuss et al*.,* 2009).

'Buzzes' have been recorded in the field for bottlenose dolphins (Goodson et al., 1988; Goodson et al*.,* 1994; Morozov et al*.,* 1972), narwhals (Miller et al*.,* 1995), beaked whales (Johnson et al*.,* 2004; Johnson et al*.,* 2008), sperm whales (Miller et al*.,* 2004), finless porpoises (Akamatsu et al., 2005), Hector's dolphins (Dawson, 1991) and Atlantic spotted dolphins (Herzing, 2004). All suggest that 'buzzes' are associated with prey capture or attempted prey capture, or close investigation of a sonar target. Several studies have demonstrated that the 'buzz' is connected with the final approach to a target (Busnel and Dziedzic, 1967; Evans and Powell, 1967; Johnson, 1967; Madsen et al., 2005; Morozov et al., 1972). Analysis of clicks made by foraging free-ranging bottlenose dolphins show very similar patterns to that illustrated above (Figure 3.1; Morozov et al., 1972). Boisseau (2004) correlated the acoustic calls of bottlenose dolphins in Doubtful Sound, New Zealand, with specific behavioural states. 'Buzz' and 'creak' calls were defined as foraging calls.

ICIs recorded by T-PODs have been used to define different acoustic behaviours of harbour porpoises. Trains were classified by Koschinski et al. (2008) as feeding when ICIs rapidly declined to less than 10ms if preceded by an initial phase with much longer intervals. The initial phase had ICIs oscillating between 30 and 70ms, in which the porpoise was presumed to be searching for prey. This was followed by a gradual decrease in ICIs over several seconds, indicating an advance on the prey item, followed by a rapid decrease of ICI from 40 to 2ms, indicating the final stage of prey capture ('buzz'). Koschinski et al. (2008) noted that T-POD software classified most 'feeding' trains as several separate trains, with different levels of confidence (i.e. Cet Hi, Cet Lo, Doubtful), perhaps due the narrow directionality of the sonar emission pattern. Koschinski et al. (2008) recommended manual searching through T-POD data for trains indicative of feeding. No similar classification scheme is available for bottlenose dolphins.

The aim of this chapter is to define bottlenose dolphin echolocation click parameters that are likely to indicate foraging behaviour, and hence allow basic behavioural interpretations to be made from T-POD data without manual searching.

3.2 Methods

Multiple T-PODs (version 5) were moored at Pack Point, in Doubtful Sound (45° 23’ 442” S, 167° 06’ 047” E); an area of high dolphin activity (pers. obs), from 01/04/09 to 09/06/09. The T-POD settings found most effective by Elliott (2008) and in Chapter 2 (Table 2.1) were used. T-POD data were downloaded and processed as described in chapter 2. Complete ‘Cet-Hi’ or ‘Cet all’ foraging trains were identified visually using descriptions of ICI patterns from Koschinski et al. (2008) and Verfuss et al. (2009). An initial search phase, approach phase and terminal phase ending with a ‘buzz’ were required (as seen in Figure 3.1). In most cases, these phases were split into separate trains by T-POD algorithm. Furthermore, the diagnostic phases were required, rather than the specific ICIs identified by Koschinski et al. (2008) and Verfuss et al. (2009), as the latter related specifically to harbour porpoises.

Complete foraging train sequences identified from T-POD data were used to develop characteristics of the terminal ‘buzz’ (which is indicative of a foraging event and distinct from click trains of other behaviours; Boisseau, 2004). This would allow buzzes to be identified in trains in which the foraging train is incomplete, or only the buzz is present.

‘Buzzes’ were defined as starting at the steepest decrease in ICI in the “approach phase” and ending when ICI increased (Figure 3.2A & B). Upper and lower ICI limits of these‘buzzes’ (terminal to capture phases, Figure 3.2A), were identified to calculate a maximum range of ICIs. These were compared and combined with estimates from the literature (Morozov et al*.*, 1972; Goodson et al*.*, 1994; Boisseau, 2004; dos Santos et al*.*, 1990; Herzing, 1996; Reyes-Zamudio, 2005) to define an ICI range indicative of a ‘buzz’. The number of clicks within a foraging train was also investigated. The lower range was identified as the minimum number of clicks required for a train to be defined as foraging.

These two criteria (ICI range indicative of a buzz, and minimum number of clicks in a buzz associated train) were combined to identify foraging trains in a further set of T-POD data, gathered at Pack Point from 09/09/09 to 27/10/09. Clicks trains were exported to EXCEL where mean ICIs were calculated as:

$$(\mathrm{TrDur} - \mathrm{TotDurClx}) / (\mathrm{NofClx} - 1)$$

where TrDur = train duration; TotDurClx= total duration of clicks in train; Nofclx = number of clicks in train. If a train's mean ICI was within parameters established, and it had greater than 20 clicks, it was classified as foraging. This classification scheme relied on the fact that complete foraging trains recorded by T-PODs are almost always split into sections due to the narrow sonar beam of a dolphin, moving on and off the T-POD axis regularly while chasing prey (Koschinski et al., 2008; pers. obs).

Maximum target range was calculated from ICI as the two-way travel time assuming a sound speed of $1500ms^{-1}$. This is maximum range as it makes no allowance for the dolphin's echo processing time.

3.3 Results

Click trains consistent with foraging events were rare in the T-POD records. Twenty-eight click trains from Pack Point 01/04/09 to 09/06/09 data showed ICI dynamics characteristic of foraging click trains (see Figure 3.2A for example).

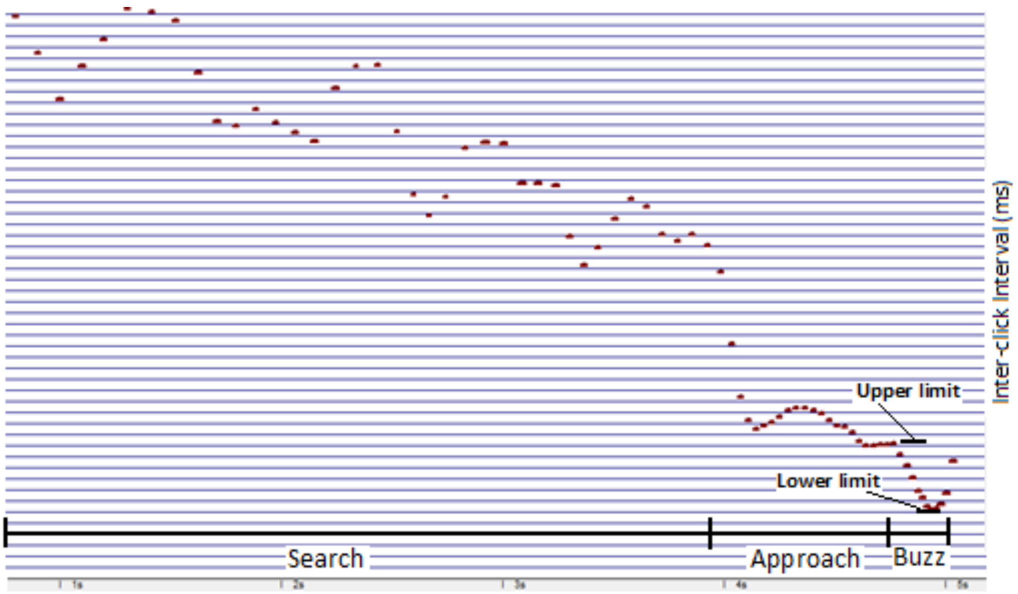


Figure 3.2A ICIs of a bottlenose dolphin echolocation click train interpreted as foraging, recorded by V5 T-POD at Pack Point in Doubtful Sound on 30/05/09.

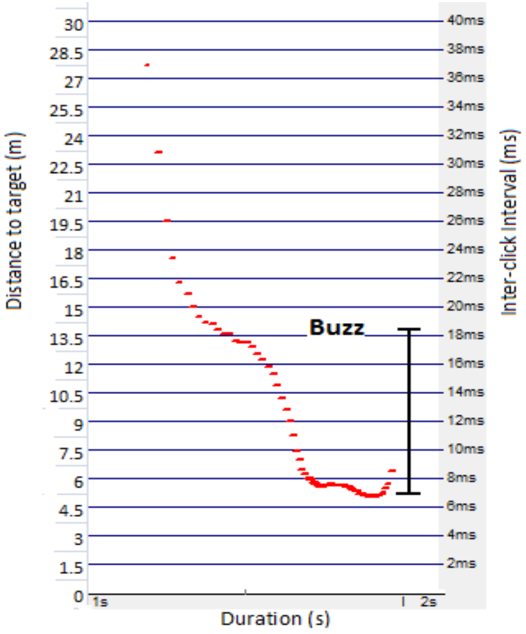


Figure 3.2B Example 'Buzz' at higher resolution. Maximum distance to the target is calculated from ICI as the two-way travel time assuming a sound velocity of 1500m/s.

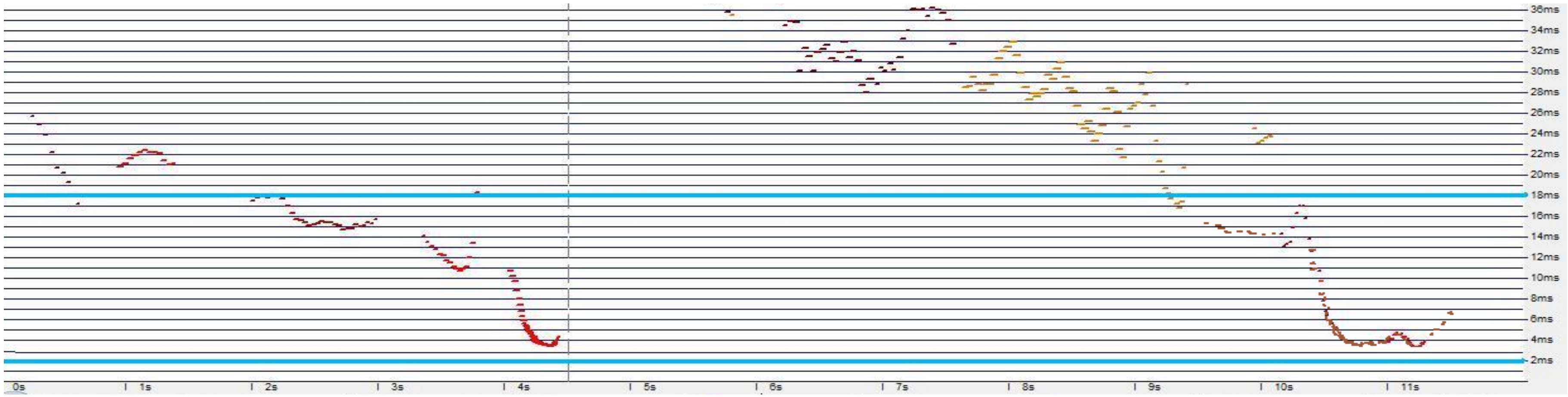
Of the 28 foraging trains visually identified, buzz ICIs ranged from 18 ms (upper limit) to 3 ms (lower limit). Equivalent maximum target distances for this ICI range for a 'buzz' are 13.5 to 1.5 m (Table 3.1).

The average number of clicks within the 28 visually identified foraging trains was 62 (SE = 4: range = 20-134; Table 3.1). Trains identified as foraging trains had significantly more clicks than trains not identified as foraging (Two sample t-test, p. <0.05).

Table 3.1 ICI (ms) and distance equivalents (m) for 'buzz' calls derived from the literature and 28 foraging trains identified in bottlenose dolphin T-POD data sourced from Pack Point 01/04/09 to 09/06/09, Doubtful Sound, NZ.

Source	Buzz ICI range (ms)	Distance equivalent (m)	# clicks in associated train
This study			
Upper limit:	18	13.5m	20-134
Lower limit:	3	1.5m	
Boisseau (2004):	5.9 - 1.9	4.4 - 1.4	
Herzing (1996):	5.0 - 2.0	3.75 - 1.5	

The combination of Boisseau (2004), Herzing (1996) and this studies 'buzz' ICI ranges, resulted in a finalised ICI range of 2 - 18 ms to define a 'buzz'. The minimum number of clicks required in a probable foraging train was 20. After inspection of T-POD (V5) data gathered at Pack Point from 09/09/09 to 27/10/09, 36 probable foraging trains were identified visually. When the established 'buzz' ICI and minimum click number parameters were applied to the same data set, 33 out of the 36 visually identified trains probable of foraging, were within the 'buzz' parameters defined above. Fifteen examples of these are depicted in Figure 3.3 (A-E). In most cases, an initial search phase was detected before ICIs rapidly declined to within 'buzz' parameters, indicating the capture or attempted capture of a prey item. In all but one case, these events were recorded as separate trains by the T-POD, enabling the buzz sections mean ICI to be correctly identified by ICI parameters. In the single case (G.1), the entire foraging event was recorded as a single train by the T-POD, from search, through approach and terminal buzz. This is a very rare event, due to directionality factors (Koschinski et al., 2008). This caused the mean ICI of the train to be outside the established ICI range, even though the buzz section was within, resulting in a false negative. G.2 depicts another false negative whereby only the 'buzz', or a section of it, was recorded by the T-POD, most probably due to directionality of the dolphins sonar emission beam. In this case fewer than 20 clicks were within the established buzz parameters, again resulting in a false negative. Figure 3.3 (F) indicates false positive ‘buzzes’, whereby >20 clicks within parameters were detected however visual inspection reveals click patterns unlike those of a buzz.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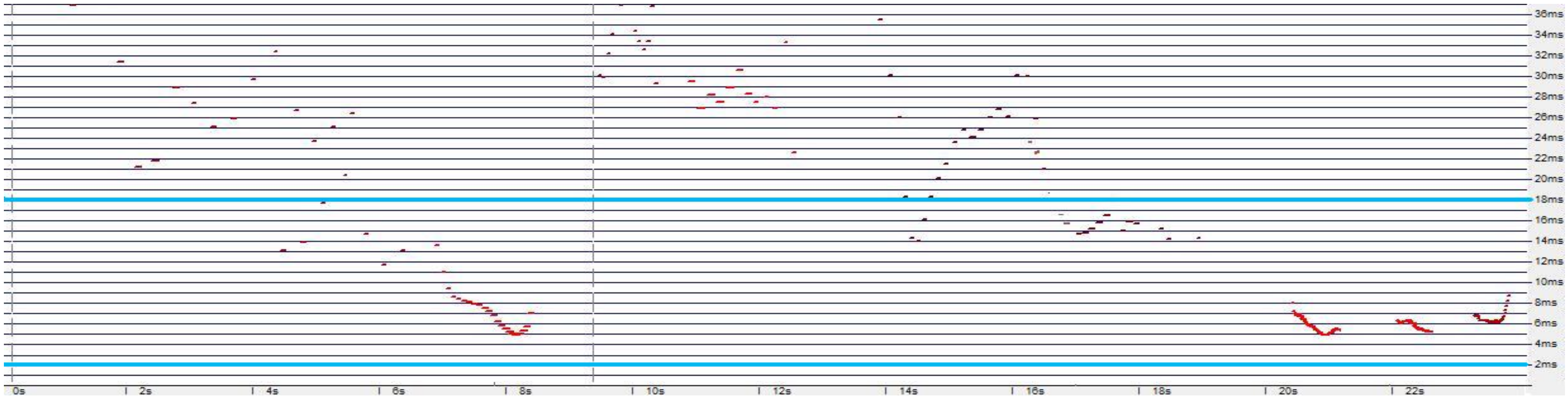
(A)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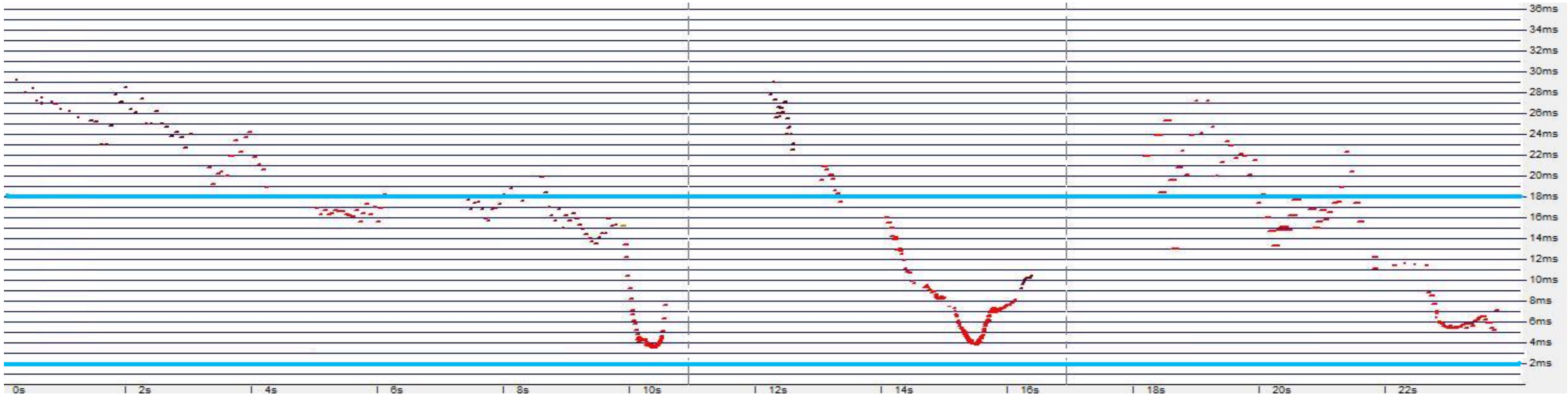
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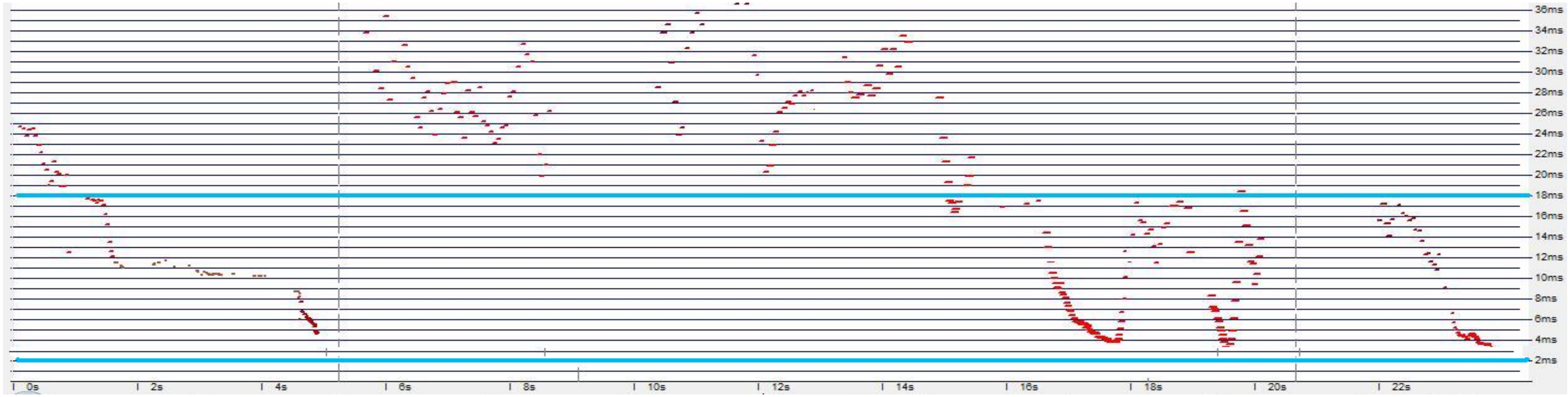
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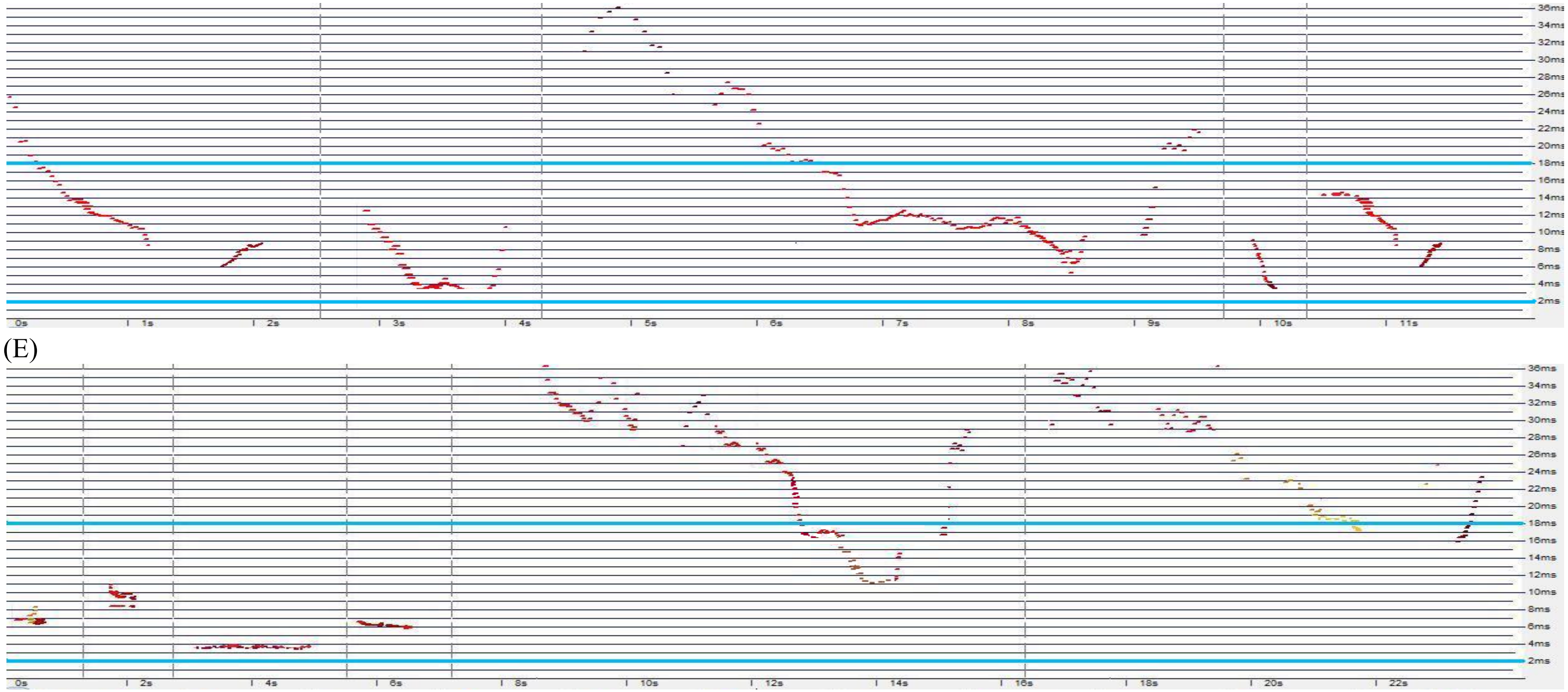
(D)



(E)

(F) (G.1) (G.2)

Figure 3.3 (A) – (E) depict 15 examples of the 33 / 36 positively identified foraging trains from the Pack Point period 09/09/09 to 27/10/09 using ICI ‘buzz’ parameters (blue lines) and >20 clicks rule. Each red/brown/yellow dot represents a click. (F) four examples of potential false positives. (G.1 & 2) are examples of false negatives from Pack Point data. (G.1) a foraging train that has a ‘buzz’ within ICI parameters but not classified as foraging as the train’s mean ICI is outside of the ICI parameters. (G.2) a buzz appears to have occurred but the sonar emission beam from the dolphin has potentially gone off T-POD axis resulting in <20 clicks detected within buzz parameters.

3.4 Discussion

Visual inspection of foraging trains and the literature, show that the ‘buzz’ is the most reliably identifiable part of a foraging echolocation train. ICIs of other, non-foraging echolocation click trains from bottlenose dolphins, as defined by Herzing (1996) and Boisseau (2004), show no overlap in ICI with the range described for a ‘buzz’ in this study. This unique aspect of the buzz enables foraging trains to be segregated from other trains. Further confidence is added to this categorisation by a rule requiring a minimum number of clicks. The number of clicks within a train is generally thought to reflect the difficulty of the echolocation task and its duration (Au, 1993). A more difficult task requires more information, thus more clicks. A simple target such as a wall or obstacle would require few clicks to identify. Pursuing a fish however, would require a dolphin to obtain as much information as possible. It can do this by increasing its click rate. Distance to an object also determines click rate (Turl and Penner, 1989). Bottlenose dolphins can distinguish small objects at great distances, for example a 7.62 cm sphere at a range of 113 m (Au, 1993). Therefore sonar investigation does not necessarily require close ranges. However a dolphin must approach a fish to a range of zero to catch it. This reduction in range during feeding is reflected by declining ICIs. The maximum target ranges implied by ICI parameters are within what is expected of foraging. Although non-foraging calls with such low ICIs are possible, the dynamics of the foraging click train appears to be reliably distinctive.

For the reasons above, it is assumed that a click train having at least 20 clicks within the ICI ranges outlined in this chapter would be more likely a foraging call than an alternative. These train parameters seem appropriate given the low level of misclassification (8.3%) resulting from their application to a separate set of T-POD data from the later monitoring period. It therefore seems possible to identify foraging behaviour in acoustic T-POD data. This is valuable as it allows inferences about areas important for foraging. This is a simple first step in classifying behavioural states via acoustic data.

It needs to be noted, however, that false negatives and false positives can occur using these parameters, as seen in figure 3.3 (F), (G.1) and (G.2). False positives (Figure 3.3F) can occur via noise unrelated to dolphin echolocation. False negatives can occur as Figure 3.3 (G.1), where a foraging event has occurred but is not recognised as the entire click train was recorded in full by the T-POD. Koschinski et al. (2008) noted that T-POD software classified most ‘feeding’ trains as several separate trains. Because of this, it was seen in most cases that the ‘buzz’ section of a foraging train was classified as separate to the approach and search phases. False negatives can also occur as Figure 3.3 (G.2), whereby a foraging train has been detected by the T-POD however the ‘buzz’ section was not recorded, most likely due to the sonar beam moving off the T-POD’s axis.

Although the foraging parameters within this study can be subject to error, the purpose of this chapter was to allow potential foraging events to be identified within T-POD data in order to allow comparisons between sites, seasons and diel phases. Because of this, conservative or non-conservative aspects of the parameters do not significantly influence results as all T-PODs are exposed to the same criteria.

CHAPTER 4

ACOUSTIC HABITAT MONITORING OF BOTTLENOSE DOLPHINS IN DOUBTFUL SOUND

4.1 Introduction

Previous research in Doubtful Sound has suggested that habitat use of the bottlenose dolphin population changes seasonally. Boat based, daytime observations, identified that the population inhabits the inner arms of the fiord in summer and autumn, while being largely confined to the middle and outer fiord in winter and spring (Schneider, 1999). It is suggested this is primarily due to temperature variations caused by freshwater inputs (Schneider, 1999; Currey et al., 2003). Current, quantitative data on distribution and behaviour would be extremely valuable for conservation management of this population.

Acoustic monitoring is a very useful method for investigating cetacean habitat use and distribution. Acousticians use hydrophones to 'listen' to cetacean echolocation activity to infer information on abundance, distribution, behaviour and location. This technique has become very popular as it is less invasive, requires fewer man hours, provides sub-surface information and can be executed in poor weather and at night (Philpott et al., 2007).

The T-POD is a passive acoustic monitoring device used to record cetacean echolocation activity (Philpott et al., 2007). The ability of T-PODs to acoustically record cetaceans passively and around the clock, makes them an excellent tool for long term monitoring. T-PODs have been used in several recent studies to provide data on habitat use over periods from weeks to years (Jefferson et al., 2002; Cox and Read, 2004; Leeney et al., 2007; Philpott et al., 2007; Koschinski et al., 2008, Rayment et al., 2009; Simon et al., 2010).

This study used nine T-PODs moored throughout Doubtful Sound to assess dolphin distribution patterns and habitat use over a 12 month period.

The principal research questions investigated:

- What were annual distribution patterns?

- Were seasonal patterns apparent?

- Was surface water temperature correlated with dolphin distribution?

- Did foraging behaviour differ spatially and/or temporally?

- Did diel patterns exist?

4.2 Methods

Nine T-PODs (versions 3, 4 and 5) were moored throughout Doubtful Sound in specific areas to gain optimum spatial coverage of the fiord (see Figure 4.1). Prior research assisted in choosing appropriate mooring sites to ensure areas inside and outside DPZs were monitored (Schneider, 1999; Lusseau, 2003a; Boisseau, 2004).

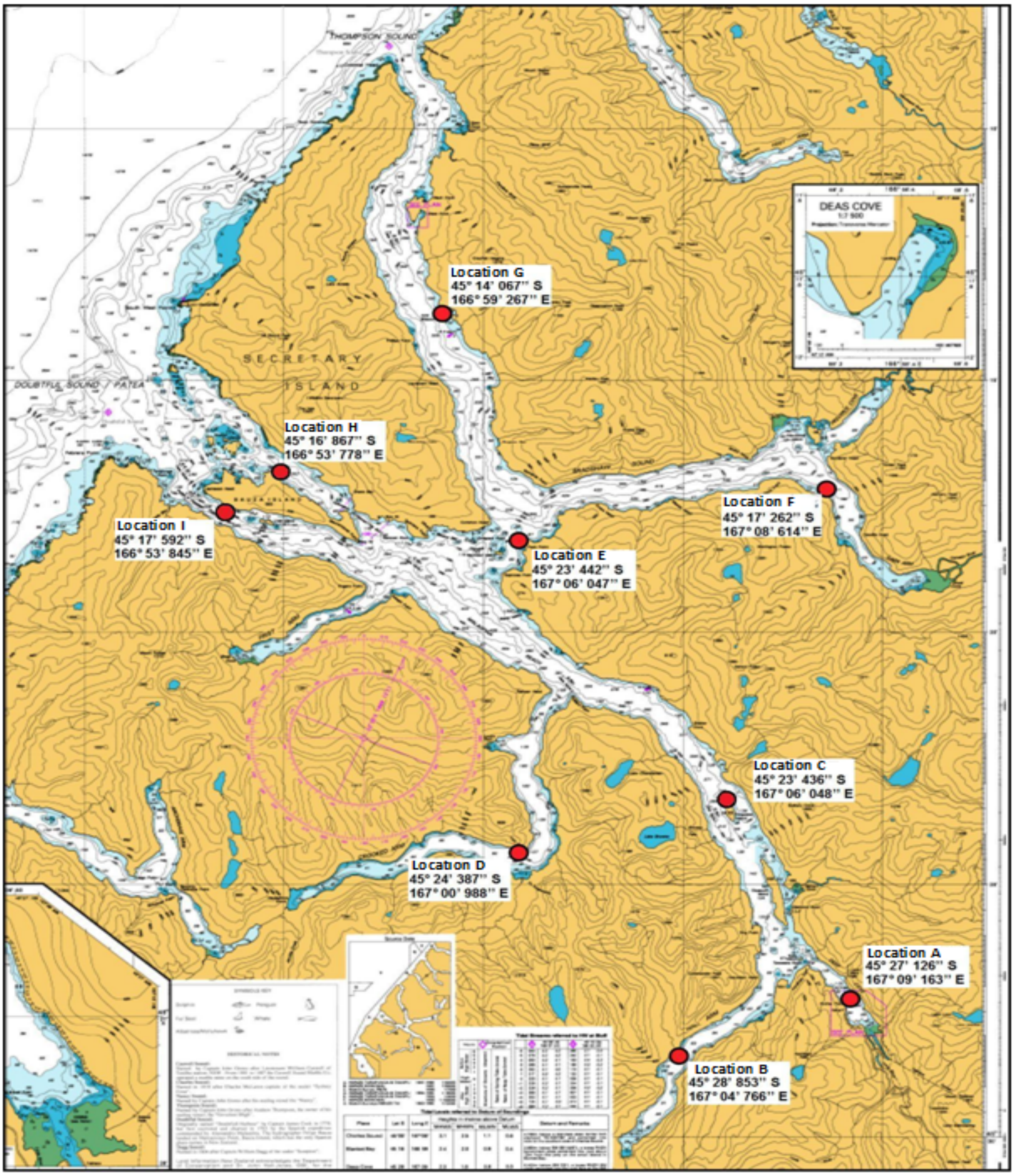


Figure 4.1 Map of Doubtful Sound, Fiordland, New Zealand, indicating alphabetical locations of nine T-PODs and their respective latitude and longitude.

Each mooring consisted of a concrete filled car tyre with a secondary danforth anchor attached via chain to ensure the mooring did not slide down the slope. Rope attached to the tyre was held vertical by a small buoy at 6m below the water's surface. Subsurface buoys were used to reduce visual impact and to reduce the likelihood of tampering. The T-POD was clipped onto a carabineer (stainless steel lifeline clip) so it floated hydrophone element uppermost, at 5m (Figure 4.2). TPODs were serviced via diving at 6-8 week intervals.

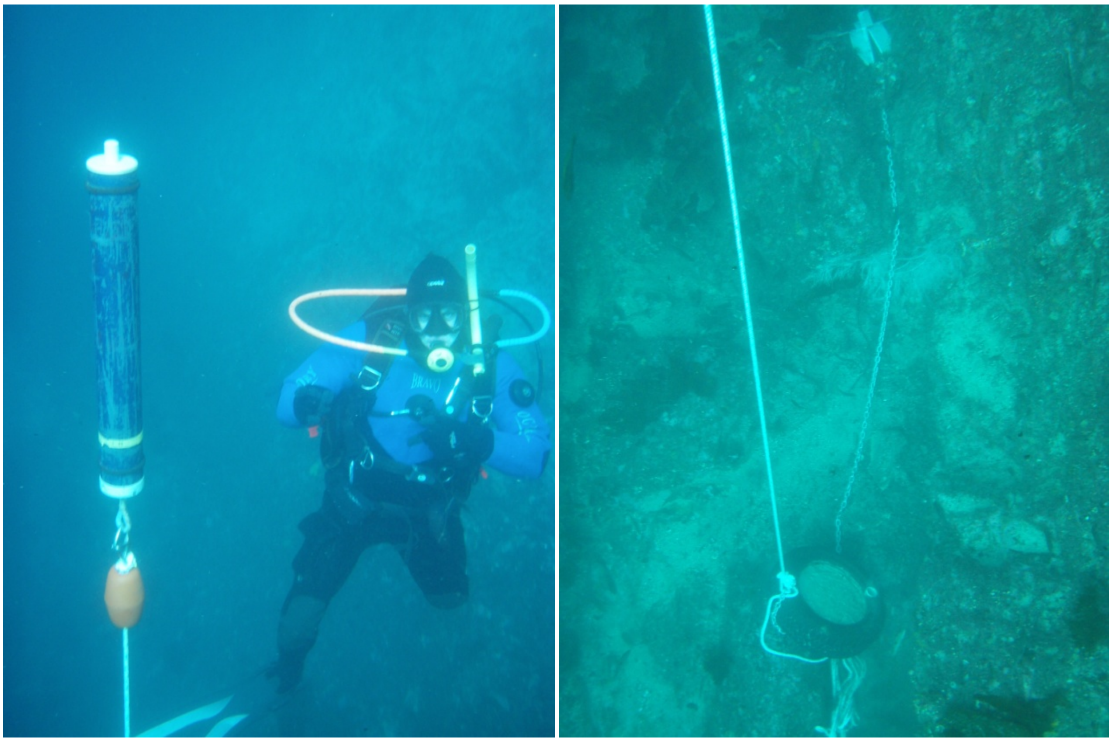


Figure 4.2 Mooring and attachment of T-PODs used in Doubtful Sound, New Zealan**d.**

Each T-POD had identical settings determined from chapter 2 (Elliott, 2008; Table 2.1). T-PODs were deployed from April 1st, 2009 for 12 months. T-PODs were downloaded using the T-POD programme v.8.19. Once downloaded, T-PODs were filled with fresh batteries and re-deployed the next day with the same settings. All T-POD data were exported to EXCEL and subjected to the decision rules outlined in chapter 2. Detections that did not meet the rules were deleted.

4.2.1 Seasonal Distribution

T-POD data were grouped into seasonal periods as defined by previous studies within Doubtful Sound (Schneider, 1999; Boisseau, 2004) to maintain consistency and because these seasonal periods are relative to the dolphins, based on seasonal changes in water temperature. Seasonal definitions:

Summer: 1 January- 31 March
Autumn: 1 April – 30 June
Winter: 1 July – 30 September
Spring: 1 October – 31 December

The number of detection positive days (DPDs) were calculated from T-POD data for each seasonal period at each site. A DPD was defined as any day with one or more positive detections. DPDs from each site were divided by the number of days monitored at each site, standardising missed days due to instrument failure and/or data processing days.

Because some areas received multiple visits per day, detection positive minutes (DPMs) were also calculated. This measure is commonly used in T-POD habitat monitoring studies because it provides a measure of the length of time dolphins are in the vicinity of the T-POD. A DPM was any one minute interval that included one or more positive detections. DPM per day were calculated and averaged over each seasonal period.

Seasonal Distribution and Surface Water Temperature

Dolphin presence data (DPM/day) were compared with surface water temperatures obtained by Shaun Henderson (PhD candidate, Otago University, 2010) in the course of his fieldwork. Mean surface water temperatures for each season, for each site, were derived from data measured with a RBR XR-420CT recorder, which continuously measured temperature and salinity to three decimal places in real time during photo identification trips over the same period as this study.

4.2.2 Foraging Patterns

Decision rules based on the characteristics of foraging trains, as identified in chapter 3, were applied to T-POD data, categorising trains as foraging or other. The number of foraging trains and percentage of foraging trains (number foraging/all trains), were calculated for each day monitored and averaged over seasonal periods for each site.

4.2.3 Diel Patterns

Annual data sets of bottlenose dolphin detections from each location were categorized by a custom written EXCEL macro into four diel phases (dawn, day, dusk and night), using civil twilight (from www.timeanddate.com) and sun-state tables (from Royal Astronomical Society of New Zealand: www.rasnz.org.nz/SRSStimes.htm). Definitions of diel periods were adapted from Carlstrom (2005) and Todd et al. (2009); dawn was defined to begin at the onset of civil twilight (when the sun was six degrees below the horizon). The duration of dawn was calculated as twice the time between the beginning of civil twilight and sunrise. This total period was centred on sunrise (see Figure 4.3). Dusk was analogous, ending at the end of civil twilight and lasting twice the duration of the time between sunset and end of civil twilight, with this total period being centred on sunset (see Figure 4.3). The effects of the lunar cycle were not considered.

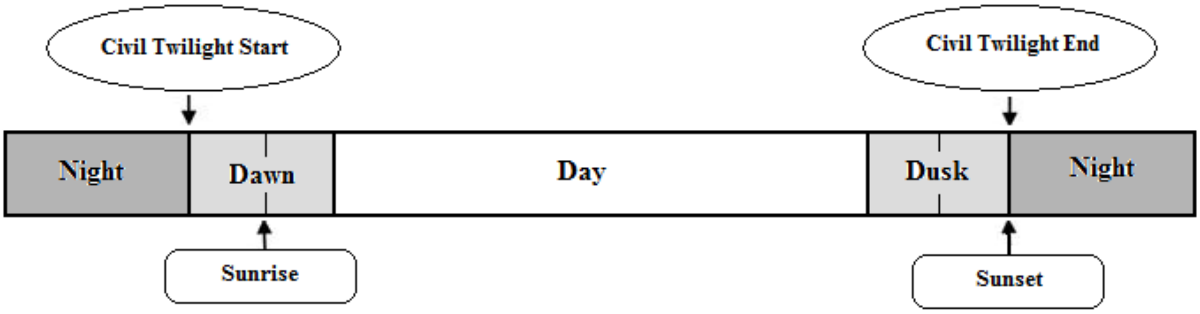


Figure 4.3 A graphical representation of the classification of diel phases based on civil twilight and sunrise/set times.

For each site, within each diel phase, annual averages of mean ICI (ms), DPM/hour and foraging trains/hour were calculated using daily data. DPM and foraging rates per hour were calculated by dividing DPM or number of foraging trains, from each diel period of each day, by the duration of the given diel period. Because day, night and civil twilight periods vary with season, average monthly durations of each diel period were used in calculations. Only days when dolphins were present within each site were used in data sets because no information on diel pattern is contained within a day without dolphin presence. Trains were classified as foraging using criteria set out in chapter 3.

4.2.4 Statistics

At each T-POD site, annual/seasonal data and foraging data sets were dominated by zero values resulting in highly skewed distributions. To avoid bias, non-parametric Kruskal-Wallis tests adjusted for tied ranks were used to determine whether differences existed between sites and seasonal periods. A non-parametric Tukey-type post-hoc test referred to as the Nemenyi non-parametric test for multiple comparisons (Zar, 1999), was used to identify individual sites and seasons that differed significantly from the others.

Diel data were not skewed, as zero value days were not included. Data sets from each site had to have at least ten values within each diel phase to be included. One-way ANOVA and Tukey’s post hoc tests were applied to determine whether significant differences were present between diel phases and each parameter measured.

One-way ANOVA and Tukey’s post hoc tests were applied to surface water temperature data, with Pearson’s correlation coefficient used to test for correlation between surface water temperature and dolphin presence (DPM/day).

4.3 Results

Data from all nine T-PODs were successfully recovered during the study period resulting in a total of 76,104 out of a possible 78,840 hours (one year x nine T-PODs) of acoustic monitoring. The monitoring time that was missed (4%) was due to T-POD malfunction or delayed re-deployment due to bad weather.

4.3.1 Seasonal Distribution

Sites compared within each season

Dolphin presence, expressed by mean DPM/Day, varied significantly among sites within each season (for all seasons: Kruskal-Wallis, p. <0.001). In autumn, site E had significantly more dolphin presence than any other site (Nemenyi, p. <0.001) followed by sites C and F with significantly higher presence than other sites except E (Nemenyi, p. <0.05). Site I had the lowest mean DPM/Day. Similar trends were found in winter, although mean DPM/Day values were generally lower than in autumn. In spring, distribution patterns were very similar to winter and autumn, however values increased from those in winter, primarily site D. Site E once again had the highest mean DPM/Day in spring (Nemenyi, p. <0.001), with sites D and H both being significantly higher than remaining sites (Nemenyi, p. <0.05). Site I was again the lowest. In summer, patterns in habitat use varied most compared to the other seasons. Site D expressed the highest mean DPM/Day value (Nemenyi, p. <0.001). Site B was also seen to increase in summer, joining sites E and F as significantly higher from remaining sites (Nemenyi, p. <0.05) (Figure 4.4).

Over the twelve month monitoring period, dolphin presence was highest at site E, however in summer, sites D and to a lesser extent site B, were often used. In general, echolocation detection was highest in summer and autumn compared to lowest activity in winter then spring (Figure 4.4).

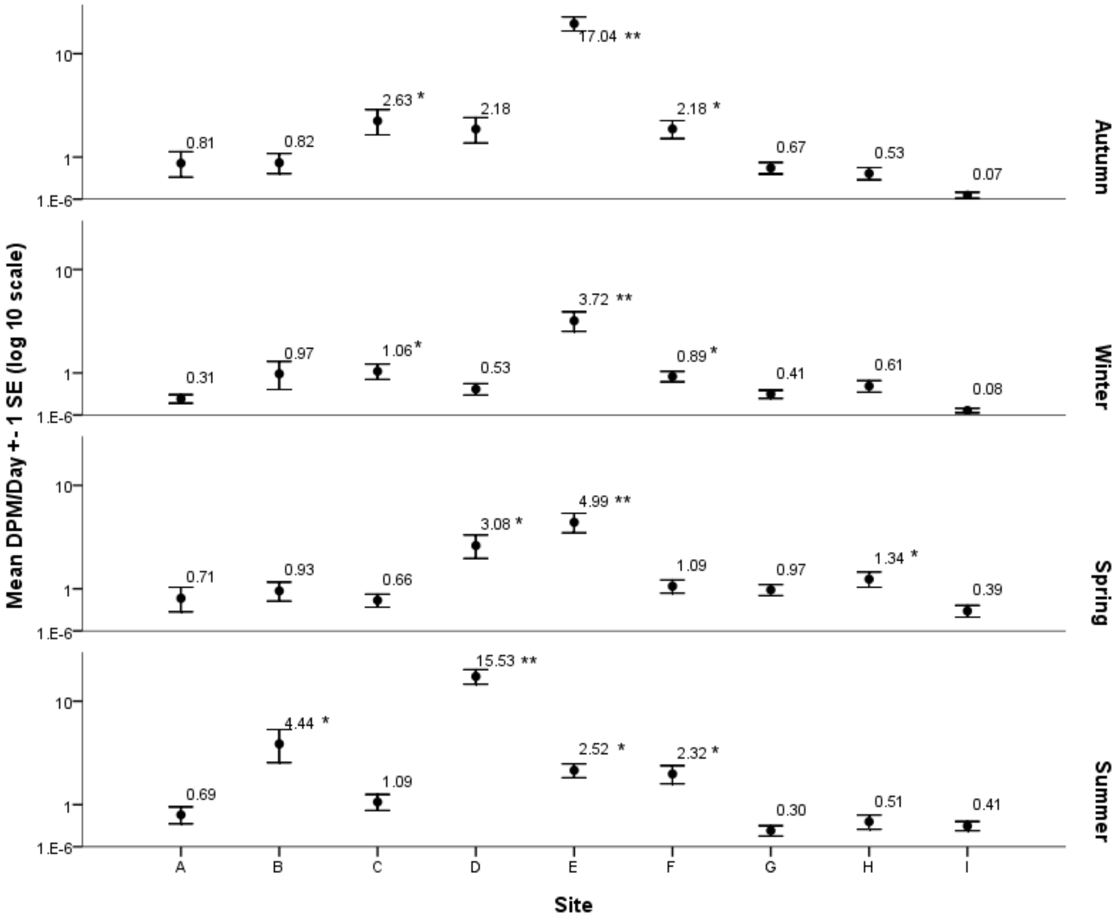


Figure 4.4 Dolphin presence represented by mean DPM/Day for each site within each seasonal period to show seasonal variation among sites. Value labels are shown. ** indicates significantly different from all others (p. <0.05). * indicates data point/s significantly different from others except other * data points (p. <0.05). Error bars are +/- 1SE. A log axis was used to better illustrate variation in data. Note that the statistical tests used ranked data, not means, as plotted here.

Seasons compared within each site

Seasonal variation in mean DPM/Day was apparent within some sites (Kruskal-Wallis, sites B, C, G, I: p. <0.05; sites D, E, H: p. <0.001). Site A and F showed no significant seasonal variation in dolphin presence. Site B had similar presence values through autumn, winter and spring, however in summer, mean DPM/Day was significantly higher (Nemenyi, p. <0.05). Autumn in site C had significantly more dolphin presence than other seasons (Nemenyi, p. <0.05). Site D recorded lowest dolphin presence during winter, with summer having the highest mean DPM/Day (Nemenyi, p. <0.001). Autumn and spring in site D both had significantly higher presence than winter (Nemenyi, p. <0.05), but significantly lower than summer. Site E recorded significantly higher mean DPM/Day in autumn than any other season (Nemenyi, p. <0.001). Site G and H had significantly higher mean DPM/Day in spring than other seasons (Nemenyi, p. <0.05). Site I had highest mean DPM/Day in summer (Nemenyi, p. <0.05) (Figure 4.5).

Overall, the lowest mean DPM/Day values in the inner fiord sites (A, B, C and D) were mostly centred on the winter and spring months; highest values in summer and autumn. The most outer fiord sites (G and H) had highest dolphin presence during spring, while I was in summer closely followed by spring (Figure 4.5).

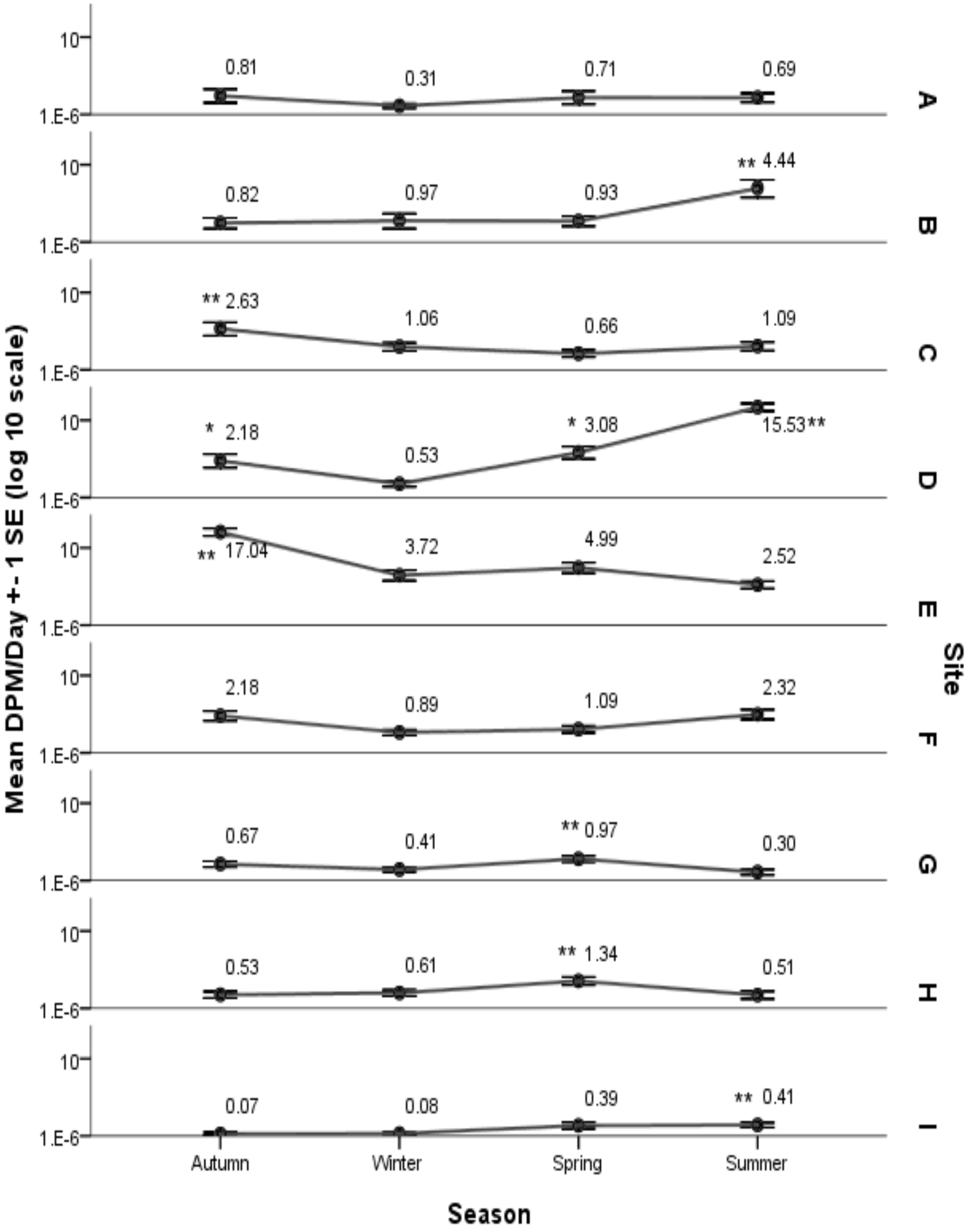


Figure 4.5 Dolphin presence represented by mean DPM/day, graphed for each season within each site to show seasonal variation within sites. Data point labels represent mean DPM/Day. ** indicates data point significantly different from all others (p. <0.05). * indicates data point/s significantly different from others except other * data points (p. <0.05). Error bars are +/- 1SE. A log axis was used to better illustrate variation in data. Note; statistical tests used ranked data not raw data means as presented in graph.

Seasonal Distribution and Surface Water Temperature

Across all sites, mean surface water temperature differed significantly across seasons (all sites: One-way ANOVA, p. <0.001). In most sites, temperatures dropped from autumn to winter, remained low in spring, and then increased with the onset of summer (Figure 4.6).

Inner fiord sites (A, B, C, and D) varied more in surface water temperature than outer fiord sites, with means ranging from 5.5°C – 16.5°C. Variation was predominantly driven through sites D and B (Figure 4.6). Dolphin presence (DPM/day) within all inner fiord sites was positively correlated with surface water temperature (Pearson's correlation, p. <0.01) (see Table 4.1).

Outer fiord sites experienced smaller temperature variation, with means ranging from 10.3 °C – 15.7 °C (Figure 4.6). Dolphin presence (DPM/day) in all outer fiord sites (E, F, G, H and I) was not correlated with surface water temperature (Pearson's correlation, p. >0.05) (see Table 4.1). Applying a sequential Bonferroni correction (Rice, 1989) to these results indicates that the correlations are highly significant for sites A, B & D at a table wide p.=0.05 level.

In most cases, dolphin presence (DPD/Days monitored) was highest in outer fiord sites when it was lowest in inner fiord sites; occurring predominantly in winter and spring; with the opposite occurring during summer and autumn. Autumn in site E and G, and summer in site F and I, were exceptions to this trend (Figure 4.6).

Table 4.1 Pearson's correlation co-efficient (r) results for comparisons between surface water temperature and dolphin DPM/day. Sample size is comprised of days when both temperature data (obtained via vessel based photo identification trips) and dolphin presence data (DPM/day) were recorded on the same day, during the annual study period for each T-POD location.

SITE	A	B	C	D	E	F	G	H	I
Pearson's (r)	0.742	0.669	0.530	0.773	0.366	0.096	-0.283	-0.120	0.107
p. value	0.002	0.003	0.009	<0.001	0.103	0.822	0.400	0.636	0.715
Sample size	14	17	23	23	21	8	11	18	14

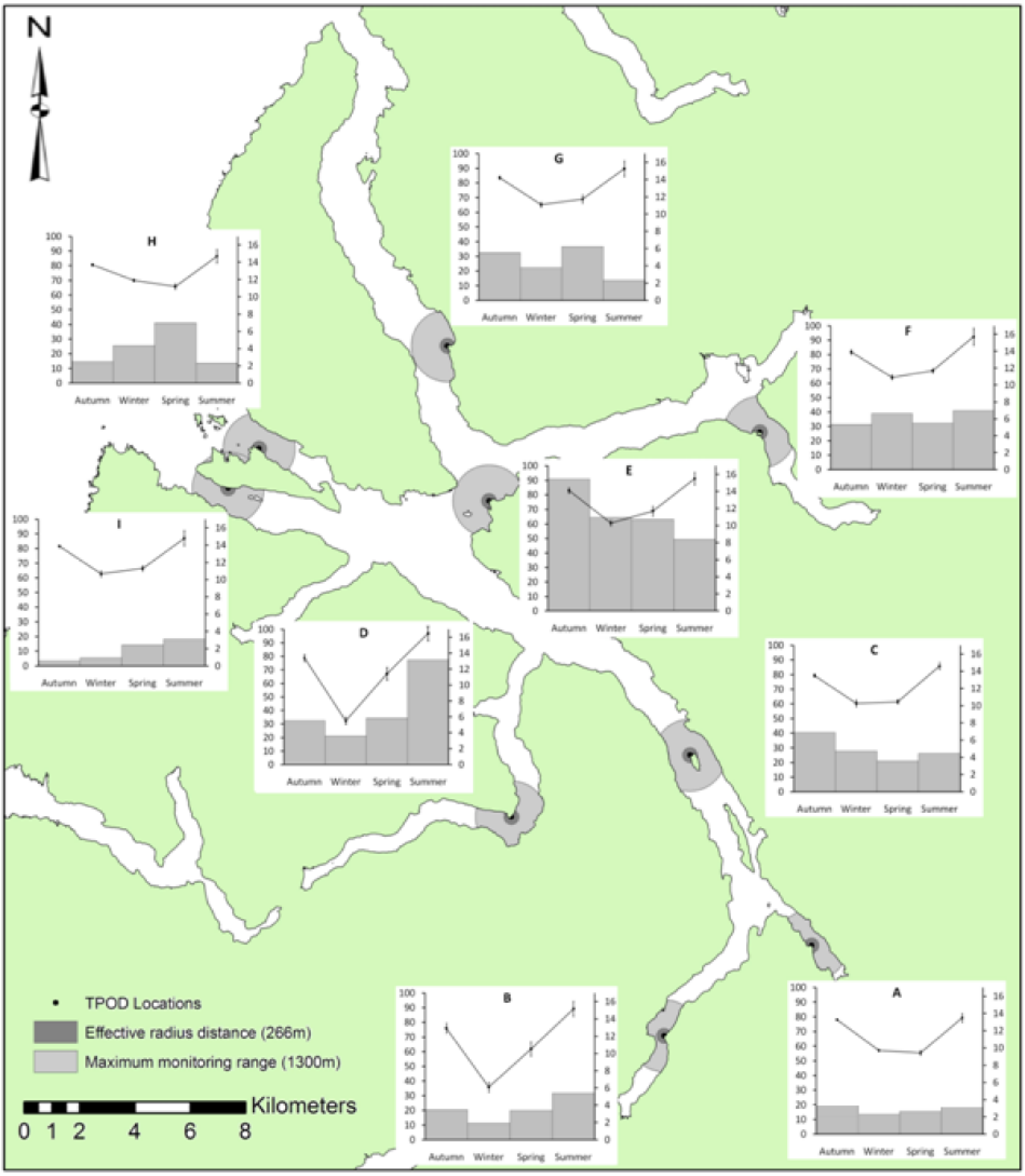


Figure 4.6 Mean dolphin presence (Bars = DPD/Days monitored [%]; Left hand Y-axis) compared with water temperature (Lines = mean surface water temperature [°C]; right hand Y-axis) at each T-POD location during seasonal periods. Monitoring range of T-PODs is expressed by differing shades of grey as described in map key. Temperature data have error bars of +/-1 SE.

Seasonal mean water temperatures shown in Figure 4.7 indicate the trend of mild autumns, followed by significant temperature declines with the onset of winter, especially through inner fiord sites. During spring, temperatures increased but were still coldest within inner fiord sites. In summer, temperatures rapidly increased to reach highest values.

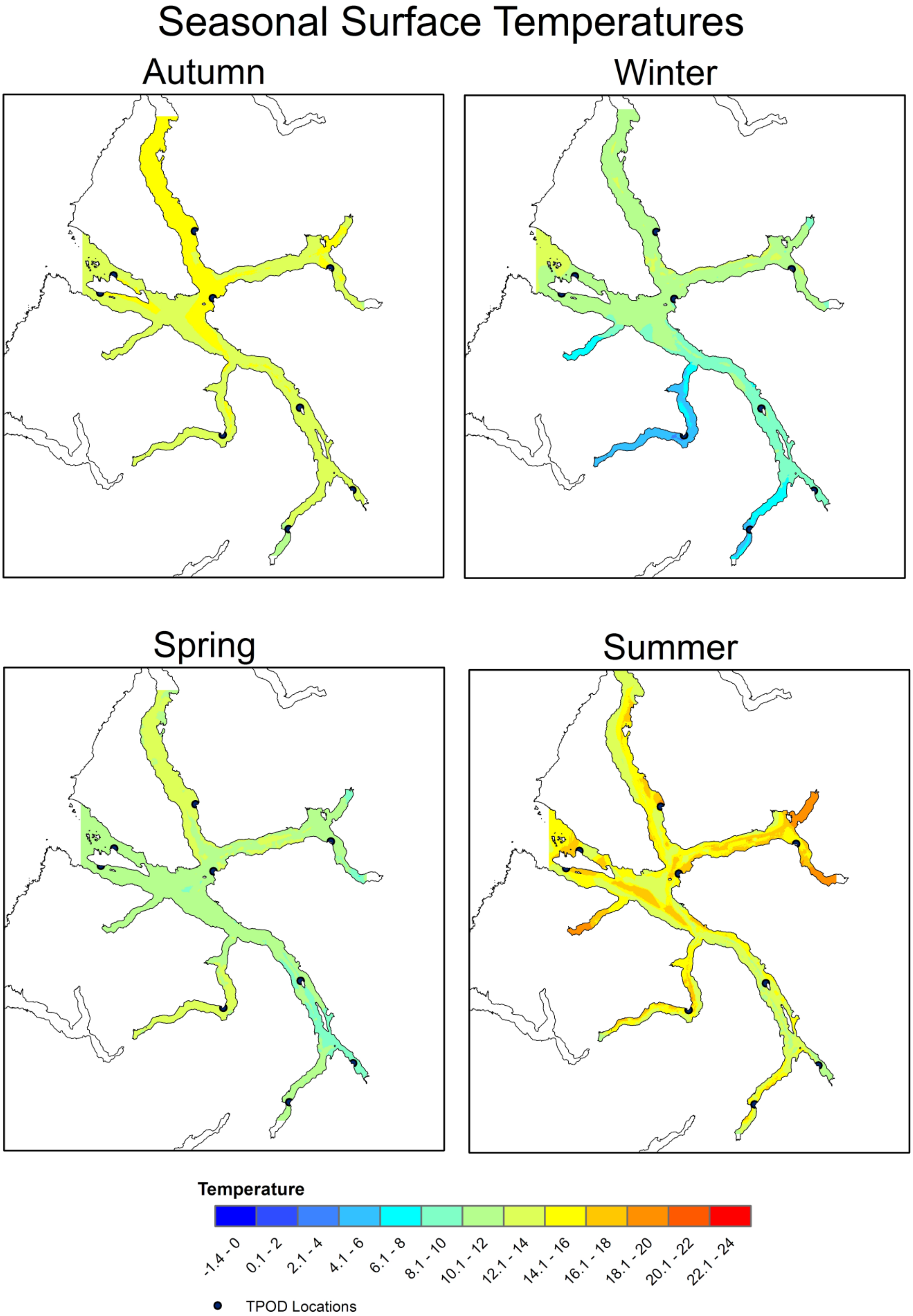


Figure 4.7 Graphical displays of seasonal mean surface water temperatures throughout Doubtful Sound, courtesy of Shaun Henderson, PhD candidate, University of Otago, 2010.

4.3.2 Foraging Patterns

Significant seasonal differences in mean number of foraging trains per day (FTD) were apparent within all sites except A, G, and I (Kruskal-Wallis, p. <0.05). The largest variation was seen in sites D and E, which showed virtually opposite trends. Site D recorded highest FTD in summer (Nemenyi, p. <0.001), followed by spring (Nemenyi, p. <0.05), with lowest in winter. Site E recorded highest FTD in autumn (Nemenyi, p. <0.001) followed by spring (Nemenyi, p. <0.05), with lowest in summer. Site B was highest in summer (Nemenyi, p. <0.001) (Figure 4.8).

Overall, the number of FTD in the inner fiord sites increased in summer through autumn, decreasing through winter and spring. Outer fiord sites were more varied but generally had highest FTD in autumn, spring and in some cases winter (Figure 4.8).

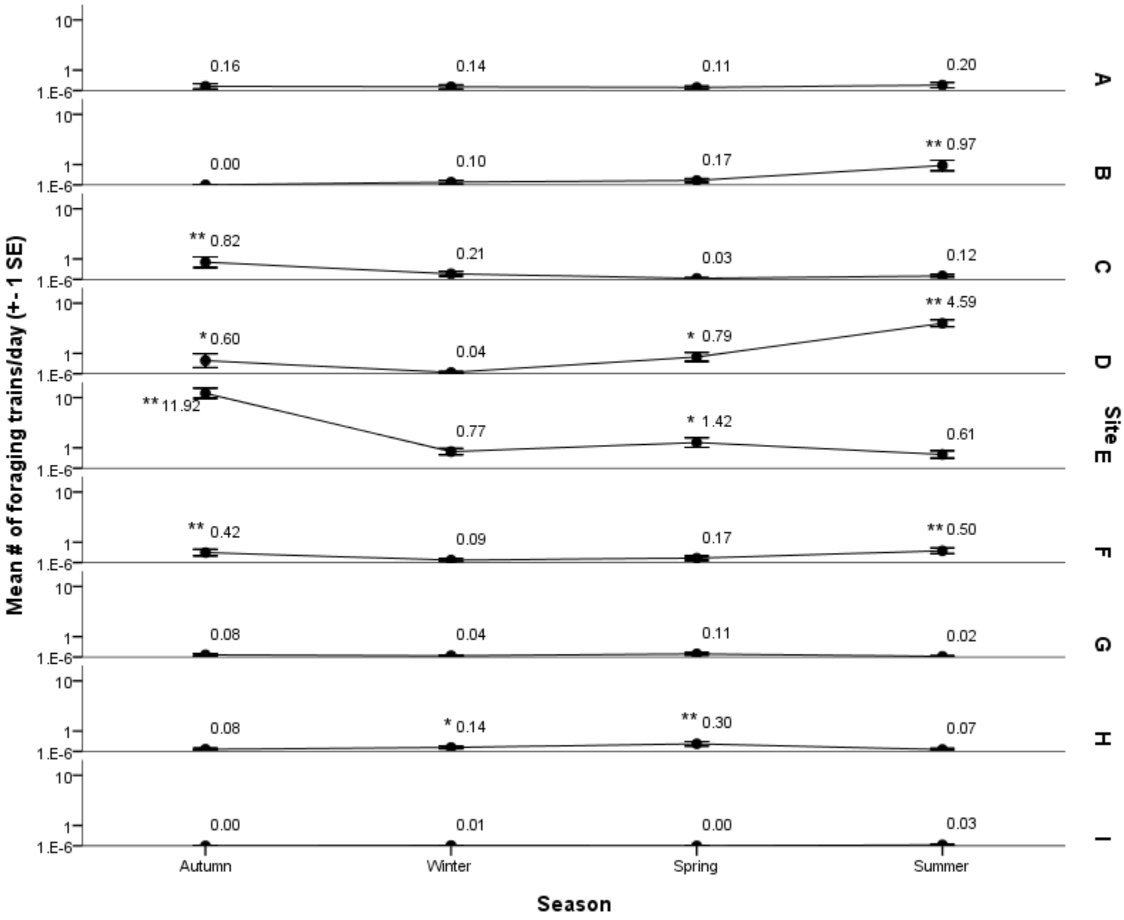


Figure 4.8 Dolphin foraging, represented by mean number of FTD graphed by season for each site to show seasonal variation within sites. Data point labels represent mean number of FTD. ** indicates data point significantly different from others (p. <0.05). * indicates data point/s significantly different from others except other * data points (p. <0.05). Error bars are +/- 1SE. A log axis was used to better illustrate variation in data. Note; statistical tests used ranked data not raw data means.

Significant seasonal differences are seen in the mean percentage of trains that were classified as foraging (per day) within all sites except site A and G (Kruskal-Wallis, p. <0.05). Inner fiord sites (B, C and D) showed increased foraging from spring to summer. Outer fiord sites (E, F, H and I) varied more with site E receiving the highest mean foraging percentage in autumn (Nemenyi, p. <0.001), while F and I were in summer (Nemenyi, p. <0.001), and H in both winter and spring (Nemenyi, p. <0.001) (Figure 4.9).

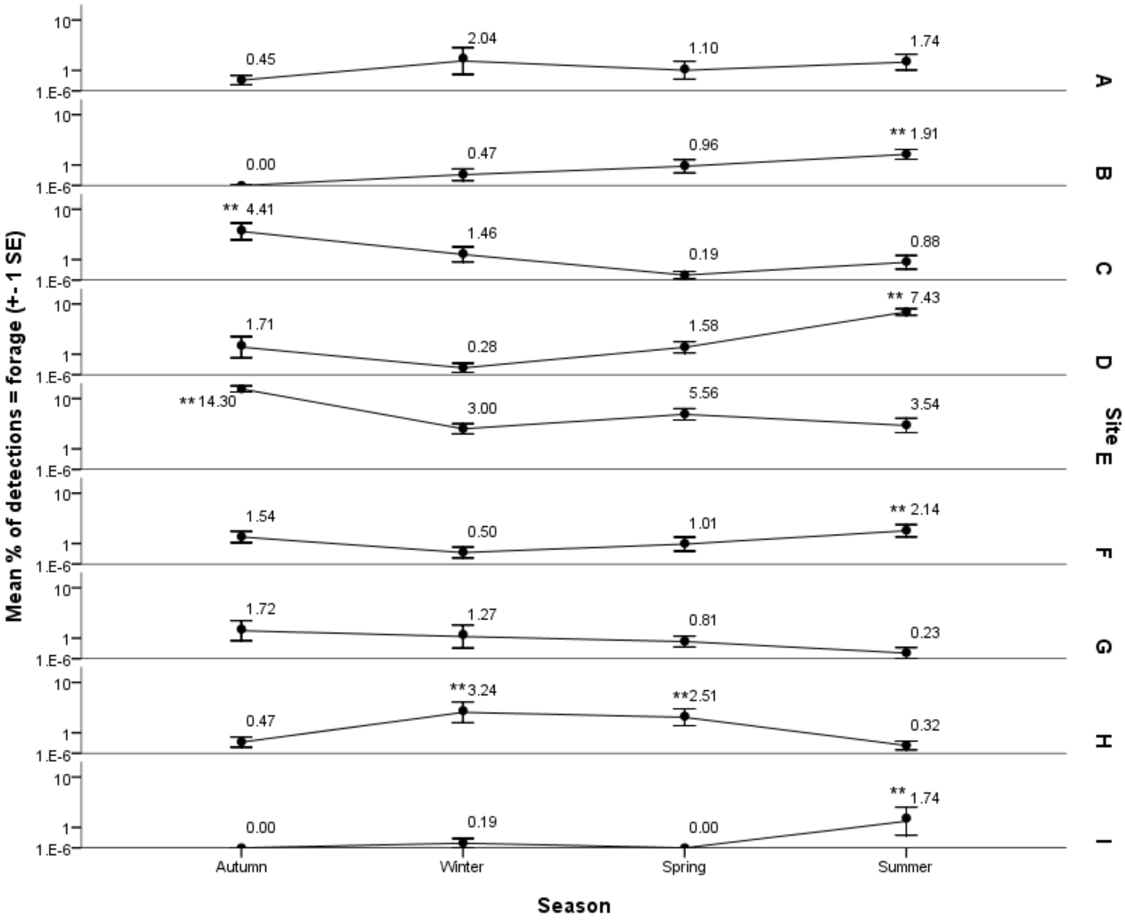


Figure 4.9 Dolphin foraging, represented by mean % of trains being foraging/day, graphed for each site across seasons to show seasonal variation within sites. Data point labels represent mean % of trains being foraging/Day. ** indicates data point significantly different from others (p. <0.05). Error bars are +/- 1 SE. A log axis was used to better illustrate variation in data. Note; statistical tests used ranked data not raw data means as presented in graph.

The proportion of trains classified as foraging trains differed across sites within each seasonal period (all seasons: Kruskal-Wallis, p. <0.001). In autumn, winter and spring, site E received significantly higher percentages (Nemenyi, p. <0.001). No other significant differences among sites were apparent in these three seasons. In summer, site D had the significantly highest foraging train percentage (Nemenyi, p. <0.001). Other sites were not significantly different from each other (Figure 4.10).

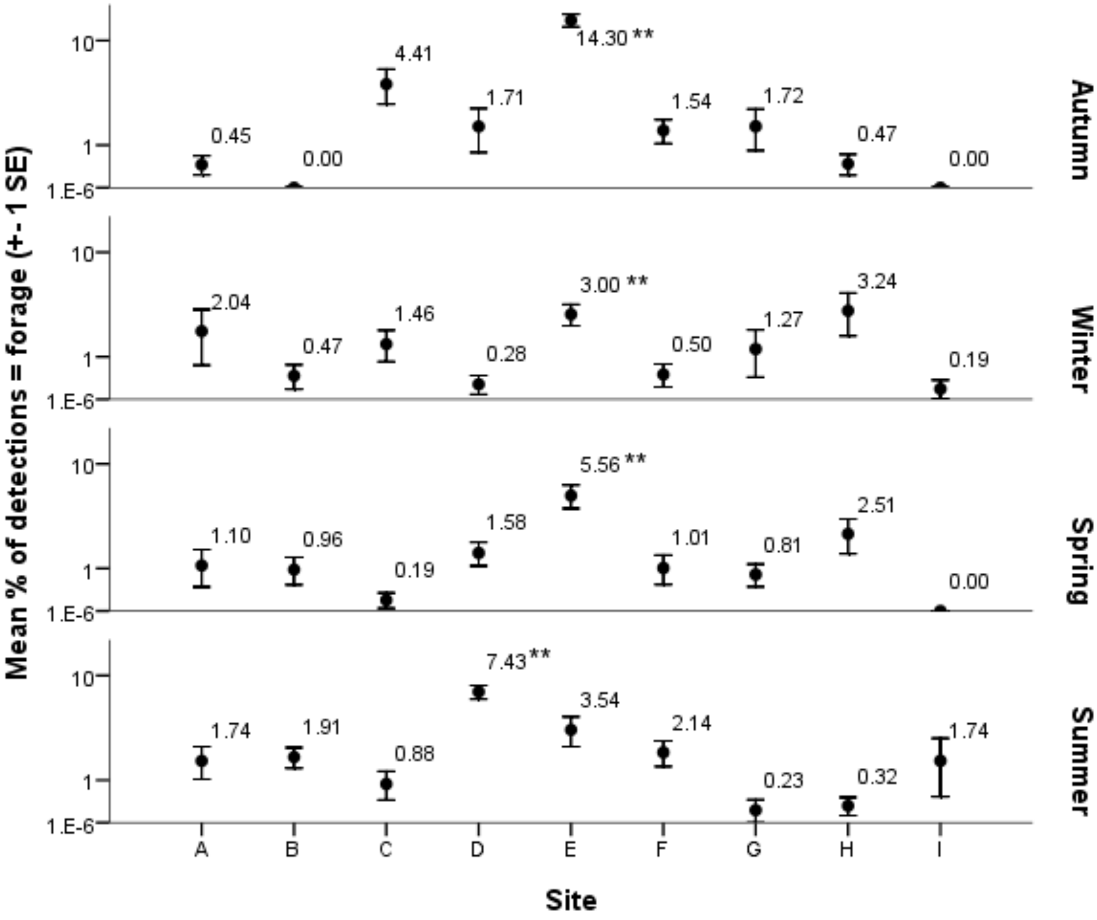


Figure 4.10 Dolphin foraging, represented by mean % of trains being foraging/day, graphed for each season across sites to show seasonal site preference for foraging. Data point labels represent mean % of trains being foraging /Day. ** indicates data point significantly different from all others (p. <0.05). Error bars are +/- 1 SE. A log axis was used to better illustrate variation in data. Note; statistical tests used ranked data not raw data means as presented in graph.

The mean number of foraging trains per day varied significantly between sites within each season (all seasons: Kruskal-Wallis, p. <0.001). Site E received significantly more foraging trains per day on average, than any other site during autumn, winter and spring (Nemenyi, p. <0.001). Site D received the second highest number of foraging trains in spring (Nemenyi, p. <0.05), increasing in summer to be significantly higher than all other sites (Nemenyi, p. <0.001). No significant variation was found between any other sites over seasonal periods (Figure 4.11).

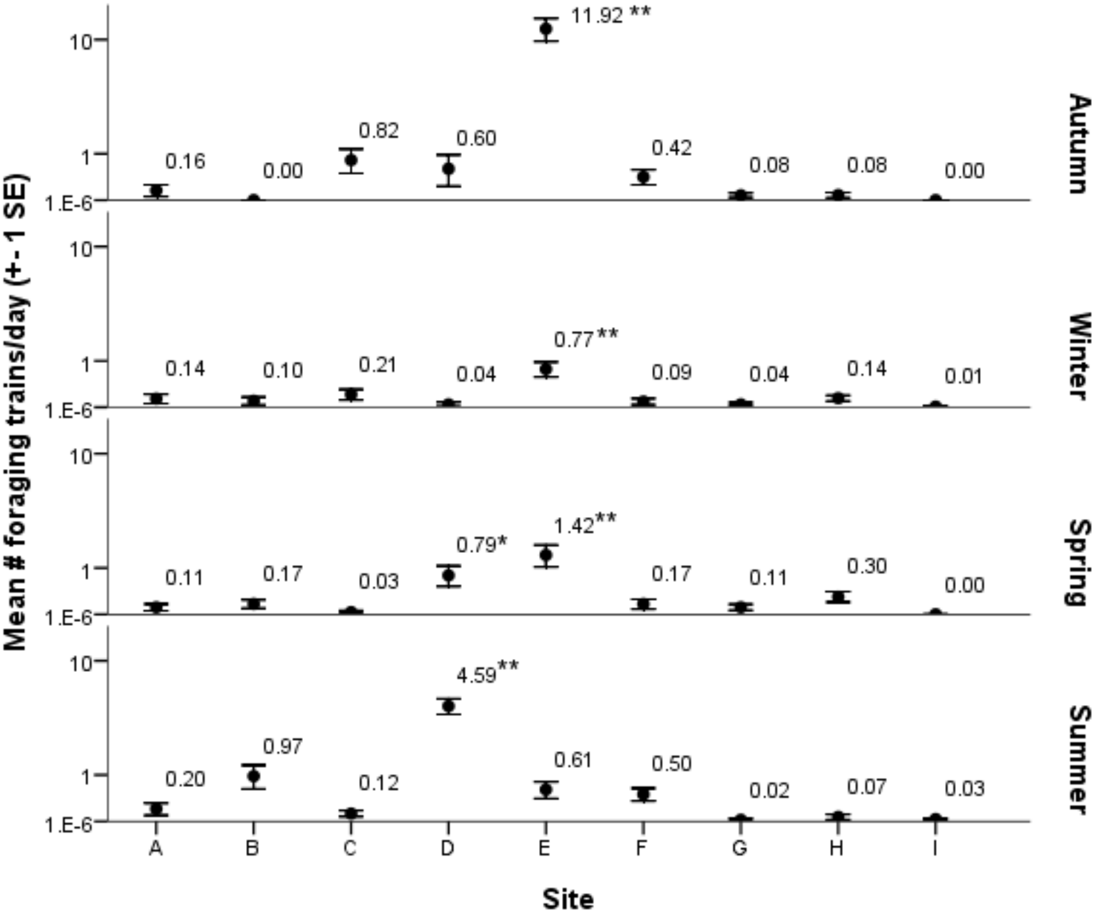


Figure 4.11 Dolphin foraging, represented by mean # of foraging trains/day is graphed for each season across all sites to show seasonal site preference for foraging. Data point labels represent mean # foraging trains/Day. ** indicates data point significantly different from all others (p. <0.05). * indicates data point/s significantly different from others except other * data points (p. <0.05). Error bars are +/- 1 SE. A log axis was used to better illustrate variation in data. Note; statistical tests used ranked data not raw data means as presented in graph.

4.3.3 Diel Patterns

Significant diel variation in average mean ICI (ms) was apparent within all sites except site A (One-way ANOVA, p. <0.05), however no common trend was shared. Sites A, B and C had no detections during dusk, and site I had no dawn detections. Sites B, D, E and H, all had significantly higher mean ICI during night phases (Tukey's post Hoc, p. <0.05). Sites F and G recorded highest mean ICI during dusk (Tukey's post Hoc, p. <0.05). The range of mean ICI among all sites was 40-110 ms (Figure 4.12).

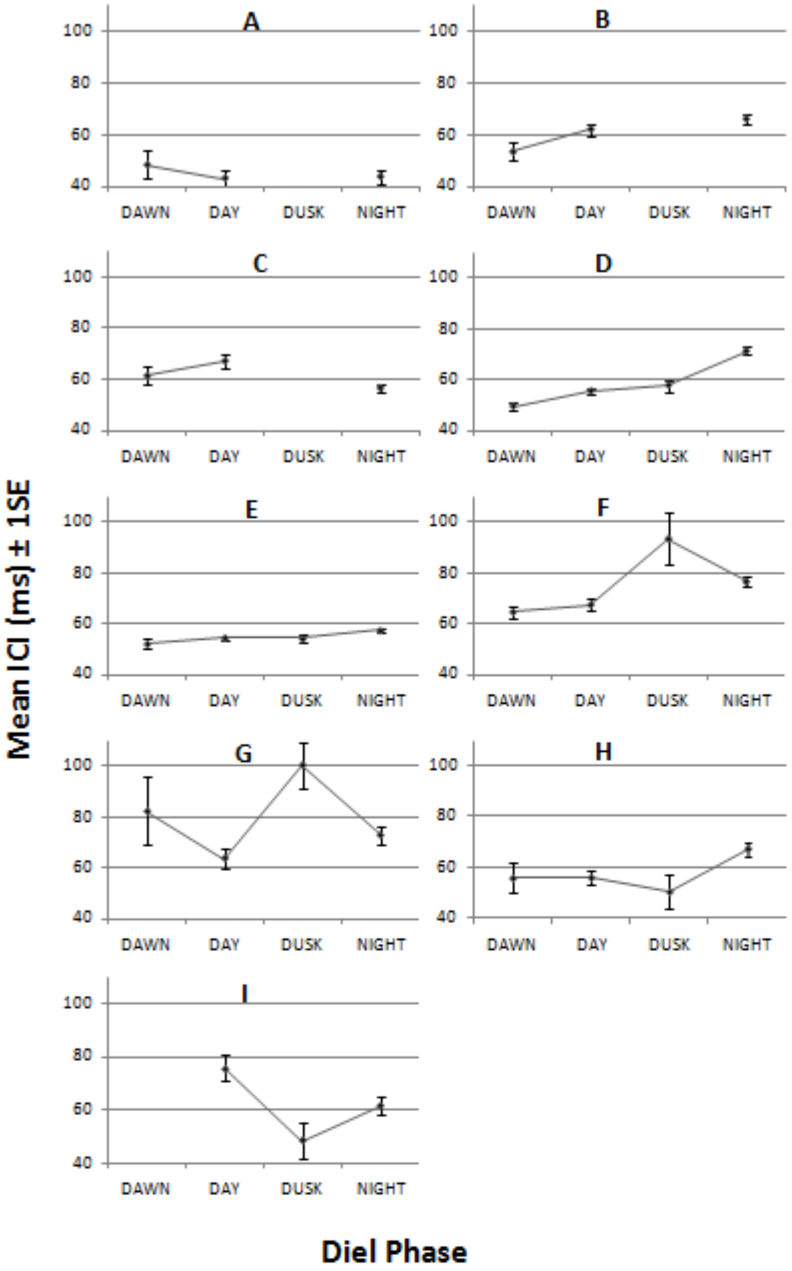


Figure 4.12 Average mean ICI (ms) of bottlenose dolphin echolocation trains recorded during each diel phase, calculated using annual data from each T-POD site.

Significant diel differences in mean DPM/hr were present within all sites except I (One-way ANOVA, p. <0.05). Sites A, B and C recorded no detections during dusk, and site I recorded none during dusk or dawn. Ignoring diel phases with no data, sites A-H all recorded significantly highest mean DPM/hr during dawn and/or dusk, when compared to day or night (Tukey's post hoc, p. <0.05). All sites showed no significant difference in mean DPM/hr during day or night (Tukey's post hoc, p. >0.05). Only sites D and E had significant differences between dawn and dusk, both recording higher DPM/hr means during dusk (Tukey's post hoc, p. <0.05) (Figure 4.13).

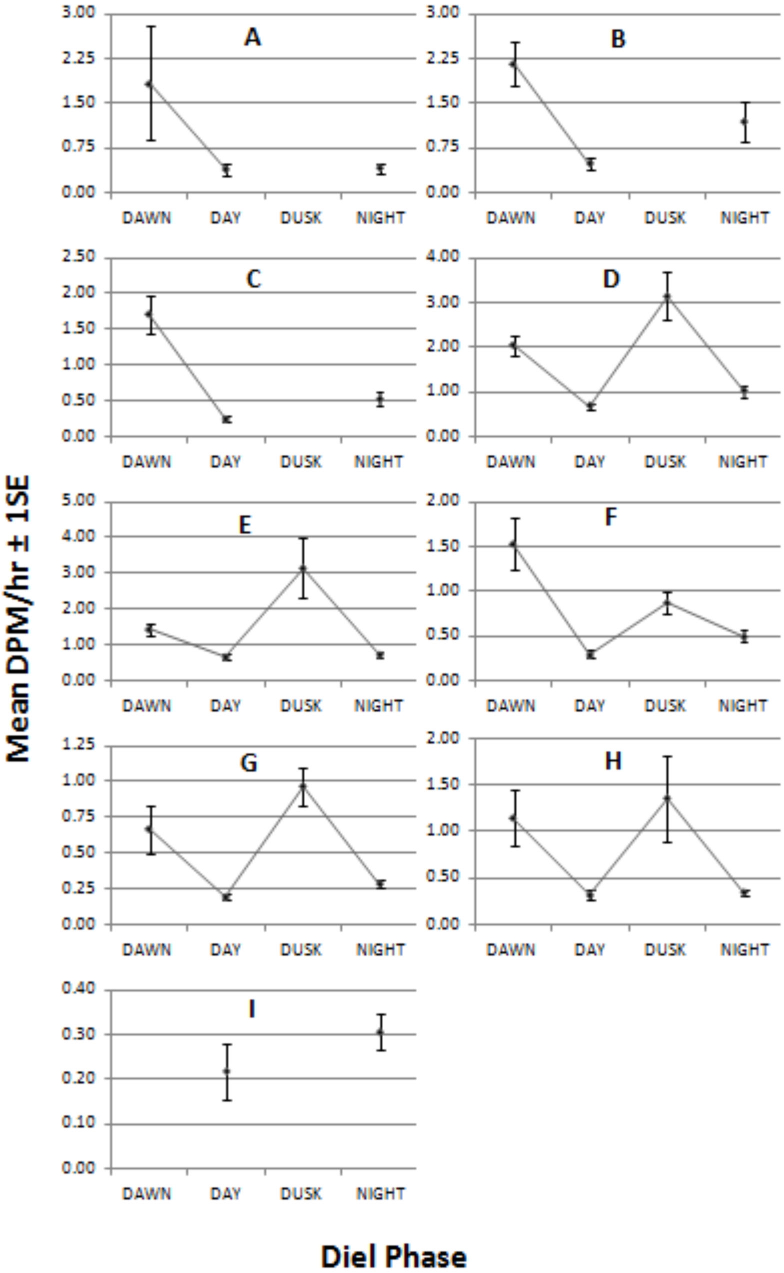


Figure 4.13 Mean bottlenose dolphin DPM/hr recorded during each diel phase, calculated using annual data from each T-POD site.

Significant diel differences in mean number of foraging trains/hr were present within all sites except I (One-way ANOVA, p. <0.01). All sites recorded similar diel trends in mean number of foraging trains/hour. Sites A, B, C, F, G and I had gaps in the data due to insufficient sample sizes, however data recorded from these sites showed similar trends to sites D, E, and H, where significantly more foraging activity occurred during dawn and dusk than during day and night (Tukey's post Hoc, p. <0.01). Within all sites (with possible diel comparisons), no significant difference was observed between day and night nor was there between dawn and dusk (Tukey's post Hoc, p. <0.01) (Figure 4.14).

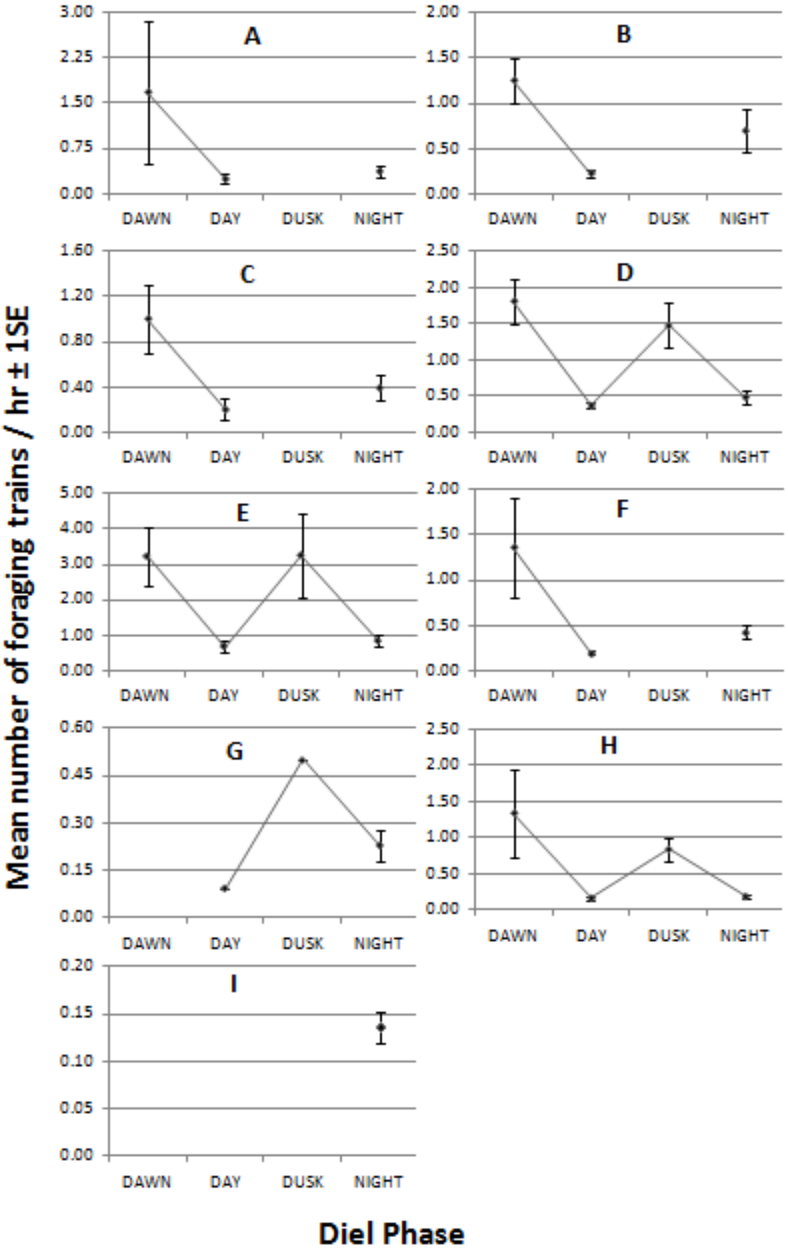


Figure 4.14 Mean number of bottlenose dolphin foraging trains/hr recorded during each diel phase, calculated using annual data from each T-POD site.

4.4 Discussion

One of the most prominent results from the twelve months of habitat monitoring in Doubtful Sound was that the number of detection positive minutes per day was in general very low. In most sites, a significant portion of days monitored had no detections at all. This is not surprising given that the fiord area is large relative to the small dolphin population, and T-POD detections are highly conservative, for several reasons outlined in chapter 2. The collection of many zero values do not detract from the quality of the data, nor its comparability among sites as all T-PODs were constrained by the same variables. Therefore the comparisons among sites remain valid. Lumping data into larger time units would have reduced the number zero values, however the larger the unit, the greater the risk is of losing sight of a potentially important pattern. Because of this, deciding on an appropriate unit was important.

Blew et al. (2006) discuss how parameter choice is important and depends on research questions and the intensity of habitat use in the study site. Different time units from days to minutes, give different information about echolocation activity. Detection positive days (DPD) were described by Blew et al. (2006) as a coarse unit, which provides information about utilisation of low density areas. It answers the question of how many days are porpoises/dolphins present in an area. Blew et al. (2006) suggest this unit as useful for describing seasonal attendance patterns in areas with low densities. In high density areas where porpoises/dolphins are present nearly every day, Blew et al. (2006) recommended higher resolutions of detection positive hours (DPH) or detection positive minutes (DPM). These units allow investigation of the kind of activity within an area. For example, high DPH in combination with a low DPM may indicate a high turnover rate with short duration of stay. In contrast, a low DPH in combination with a high DPM may describe a longer duration of stay and a low turnover rate.

Given the suggestions from Blew et al. (2006), it seems appropriate that both DPD and DPM units were used to describe habitat use in this study. However, what determined the prevalence of zero values in this study was the unit chosen to divide detection values by. In all cases, detection values were divided by day (DPM/day, DPD/days monitored) because a day is a non-arbitrary sampling unit encompassing a complete light and temperature cycle. It is also a “natural” choice because you would expect dolphin presence to vary day to day. In order to achieve fewer zero values, the denominator needs to be increased, for example DPM/week, and this choice becomes increasingly arbitrary. DPM/day illustrates multiple visits in a day whilst also being a unit commonly used throughout T-POD literature; however in low density areas, such as Doubtful Sound, zero values were high. DPD/days monitored did not reduce this problem; however it resulted in simple probabilities of dolphins being in an area each day.

From this study, it is recommended that time units be chosen considering the suggestions above. Further work on turnover rates calculated from DPH compared with DPM, as suggested by Blew et al. (2006), would be very interesting. This would only be possible in high density areas however, therefore work on low density parameters is also recommended.

4.4.1 Seasonal Distribution

Figures 4.4 and 4.5 expressing DPM/day data indicated that dolphin habitat uses varied seasonally within sites and among sites. Sites with most prominent within-site seasonal variation were E, D and B respectively. Dolphin presence was focussed predominantly in site E during autumn, winter and spring, however in summer, site D and to a lesser extent site B, obtained highest presence values.

Significantly higher mean detection rates received in site E were not surprising as the site forms a crossroads between all arms of the fiord. Because of this, the dolphins pass site E every time they travel to a different fiord arm. Several different interpretations could be made given this result. One could argue that results for site E are biased due to location at a crossroads and on a headland. This provides a larger water area being monitored. Alternatively, site E may have receive more detections because the dolphins were not just passing through (represented solely by high DPDs), but were residing for long durations (high DPMs); this emphasising high utilisation of this area and thus its importance. High dolphin presence shifted from site E to sites D and B during summer. This may be related to seasonal water temperatures and calving periods.

Detection of echolocation trains, in general, was highest in summer and autumn and lowest in winter followed by spring. Other studies have found seasonal echolocation trends, each having different explanations (Bräger, 1993; Alford, 2006; Bond, 2006; Baulch, 2007). Increased echolocation observed during summer and autumn could be attributed to increased socialising and breeding behaviour related to calving periods (Schneider, 1999). Coldest water temperatures during spring and winter (Schneider, 1999; Henderson, unpub. data) may enforce energy conservation, whereby unnecessary behaviour involving echolocation is avoided. Links between dolphin echolocation behaviour and seasonal migration of prey species have been made (Lamb, 2004). The dolphins may simply spend more time in the middle of the fiord than at the edges in winter (increasing directionality influence). Summer and autumn have highest turbidity levels via daytime sea breezes, possibly resulting in an increased reliance on echolocation.

Another relevant trend in seasonal variation (or lack thereof) was within site A. Site A, in Deep cove, recorded very low dolphin presence throughout the entire year, with no significant difference found between seasons. Site A is in very close vicinity to the docking area of all boats in Doubtful Sound therefore has the highest boat traffic. Low dolphin presence may suggest that the dolphins avoid areas of intense boat traffic. Alternatively, site A may not be a high value habitat.

Seasonal Distribution and Surface Water Temperature

Comparisons between dolphin presence and temperature data showed significant positive correlations within inner fiord sites, however no significant correlations in outer fiord sites. These correlation results could be due to the differences in seasonal temperature variation between inner and outer fiord sites.

Across all sites, mean seasonal surface water temperature dropped from autumn to winter, through spring, and then increased with the onset of summer. However inner fiord sites (A, B, C, and D) expressed larger variation in surface water temperature than outer fiord sites; with sites D and B having greatest variation, ranging from 5.5 – 16.5 °C. It is worth noting that these are mean temperature ranges. In places like Crooked Arm (site D), in the summer, temperatures were observed to fluctuate between 22 °C and 13 °C in a matter if hours with heavy rain, or 3 to 4 °C over the course of a sunny day. Likewise in winter in Crooked Arm (site D), on snowy days or days of snow melt, surface temperatures dropped to 1 °C (Elliott, pers obs), and surface ice has been recorded in Crooked Arm in the past (Schneider, 1999). This gives an actual temperature range of 1°C – 22 °C in site D in the year of this study. Observations of such extreme ranges in surface water temperature were not observed in outer fiord sites.

The temperature maps and plots do show how inner fiord sites experienced larger temperature ranges than outer sites, however they tend to blur out extremes, even with standard errors plotted. The reasoning for this is that data sets for each season, at each site, were limited by the number of photo identification trips made (source of temperature data). If temperature data were recorded more often, and preferably at the T-PODs depth (avoiding surface variation), extremes would be better represented.

The reason for greater variation in surface water temperature at inner fiord sites is that they receive highest inputs of snow melt, combined with minimal water currents, resulting in little displacement of cold freshwater. Also, the upper parts of these areas are shallow, and therefore lose heat more quickly on cold days. In addition, freshwater drained from Lake Manapouri, through the hydro-dam, predominantly flows out of Deep cove, into Hall Arm and Crooked Arm (sites B and D respectively), where it is retained via prevailing winds pushing up the main fiord channel (Gibbs et al., 2000; Gibbs, 2001). The combination of these factors results in lower surface water temperatures during winter and spring at inner fiord sites, with extremes specifically in sites B and D.

Outer fiord sites experienced much less variation in surface water temperature, with means ranging from only 10.3 C – 15.7 C. This is due to minimal effect of snow melt and freshwater discharge from Manapouri hydro-dam at these sites (Gibbs et al., 2000; Gibbs, 2001) as well as the close proximity of the more stable marine environment, reducing daily and seasonal temperature variation. The higher temperatures of outer waters appear to be more desirable during winter and spring as seen by increased dolphin presence in these sites.

The correlation between an increase of dolphin presence within inner fiord sites and increased surface water temperatures in summer and autumn is also explained by freshwater inputs. As in winter and spring, freshwater drained from Lake Manapouri flows as described earlier by Gibbs et al. (2000) and Gibbs (2001). However in autumn and summer, freshwater inputs are significantly warmer than seawater (Pickrill, 1987). This increases the inner fiord surface water temperatures.

The observed shift in dolphin presence in summer occurred in conjunction with the birth of 6 calves (observed during photo identification trips and T-POD download trips, Elliott, pers. obs.). This has been noted before (Schneider 1999; Haase and Schneider 2001; Currey, 2008) and is thought to be due to the need to reduce thermal stress on small calves. It is also possible in such long-lived, complex animals that sites D and B have some cultural value (e.g. for feeding/teaching) and/or offer better safety from predators.

The most significant finding from these results is the fact that the habitat use of the bottlenose population changes seasonally. Sites D and B are of greatest importance during summer months due to increased water temperatures and calves being born and reared. Tourism is also most frequent within sites D and B during this summer period however. Tourist boats and kayak tours focus their routes up Hall Arm (site B) as far as the Narrows (half way up the arm) and Crooked Arm as far as Turn point (site D, T-POD location), making multiple trips per day. DPZs are present within both of these arms; however this protection may not be enough for the population during these periods.

4.4.2 Foraging Patterns

Foraging rates derived from T-POD data appeared very low. Similar results were found by Alford (2006), when click train parameters were applied to define foraging behaviour in T-POD data. It is clear that T-PODs are very conservative (Philpott et al., 2007) and foraging is just one of several behaviours involving echolocation. Furthermore, factors such as directionality of echolocation signals (Au 1993) and non-echolocation, influence whether dolphin presence is detected. Foraging dolphins focus directly on the prey target, rather than scanning the surroundings (e.g. Verfuss et al., 2009); thus increasing the likelihood of missing the T-POD with its echolocation beam. Additionally, dolphins may reduce echolocation when foraging to avoid alerting prey species (Gannon et al., 2005).

The foraging parameters defined in this study may have also contributed to conservative identification of foraging trains. In defence of these parameters however, was the field test completed in chapter 3, in which the parameters positively identified 33 out of 36 visually identified foraging trains. Even if foraging detections were conservative, it should not inhibit comparisons between sites for foraging importance. This is because it is not the actual figure that is important for each site, but how that figure compares to other sites, as all would be constrained by the same conservative elements.

Differentiation between the percentage of trains classified as foraging and the number of foraging trains is important. The percentage of trains defined as foraging is a relative unit, indicating the proportion of echolocation activity used for foraging. The number of foraging trains is an absolute measure of foraging activity. Interestingly, in Doubtful Sound, among most sites, the percentage of foraging trains and number of trains both seem to be governed by overall echolocation activity. This is seen by the similarity of trends between foraging and presence (DPM/day) figures; larger presence values resulted in larger foraging values. This correlation suggests that the amount of foraging activity recorded is governed by the time spent within a site and not the site itself. This implies that the dolphins are not selecting specific sites for foraging; instead they are foraging opportunistically as they move through the fiord, "grazing" on available prey. This may reflect the fiord's characteristically low productivity (Wing et al., 2001; 2003) and sparse fish resources. If there were areas within the fiord of high prey abundance, it would be expected that foraging percentages would be much higher in specific areas. It is possible that such sites exist but were outside of T-POD monitoring areas. However, given the fact that all T-POD sites show the similar trend of a foraging/presence correlation, it appears likely that foraging is opportunistic. This theory is supported by Lusseau and Wing (2006), who used stable-isotope analysis to determine diet and feeding strategies employed by the Doubtful Sound bottlenose dolphins. Lusseau and Wing (2006) describe this population as opportunistically predating on benthic macrofauna along the rocky walls, as well as deep basin animals. Other studies support the view that bottlenose dolphins are in general, opportunistic predators with diets reflecting available food resources (e.g. Cockroft and Ross 1990, Corkeron et al., 1990).

4.4.3 Diel Patterns

No common diel trend in mean ICI was present between the nine different sites. This was a similar result to Philpott et al. (2007). Some significant differences were found within certain sites, however. Sites B, D, E and H all had highest mean ICIs during night periods. This result differs from several similar studies on cetaceans, which found ICIs to be lowest during night periods (Lamb, 2004; Alford, 2006; Todd et al., 2009). These studies suggest that during night periods, lower ICIs were required by cetaceans to obtain sufficient information about the environment for spatial orientation and foraging, due to the absence of light. On the contrary, Carlstrom (2005) suggests that higher ICIs at night, as found in this study, may reflect animals exploring their environment at greater distances than they do by day. Given the different explanations, it is possible to see how studies have found differing diel trends in

ICIs. Results are suggested to vary with habitat use, activity state, and/or geographical location (Jones and Sayigh, 2002). The literature reflects this variation in diel ICI patterns, describing them as highly variable between locations and species (Bräger, 1993; Evans, 1997; Baines et al., 2000; Gregory and Rowden, 2001; Alford 2006).

Significant diel trends common to all nine T-POD sites were observed in this study for both foraging (mean foraging trains/hr) and encounter rates (mean DPM/hr). Both were significantly higher during dawn and dusk, compared to day and night. Diel trends in foraging and encounter rates are present in the literature; however variation in the specific diel phase/s is large. For example, Gregory and Rowden (2001) recorded highest bottlenose dolphin encounters and foraging events in Cardigan Bay, Wales, during morning periods. In the same area several years later, Alford (2006) recorded highest bottlenose foraging and encounter rates during night periods. Interestingly, most studies investigating diel foraging and/or encounter trends, observed significant differences between diel phases. Many suggest that diel patterns are related to the availability and diurnal activity of prey (Saayman, 1973; Fre´on et al., 1996; Amano et al., 1998; Ohizumi et al., 2000; Freeman et al., 2004; Carlstrom, 2005; Alford, 2006; Todd et al., 2009).

Given the above hypothesis, and results found in this study, it is possible that prey species of the Doubtful Sound bottlenose dolphins are most prevalent during dusk and dawn. Lusseau and Wing (2006) suggest that dolphin feeding was concentrated on shallow rocky reefs with occasional visits to deep basins and seasonal consumption of schooling pelagic fishes and squid. These food sources could be more prevalent or accessible at dusk and dawn, possibly in relation to vertically migrating zooplankton, and associated predators (Lampert, 1989; Hays et al., 1998). Todd et al. (2009) found that porpoise diel behaviour was related to that of their prey, sandeels, who by day feed in open water, and by night, rest or avoid predators by burrowing into the sediment. As suggested above, the diel activity of fish prey, in this case sandeels, was governed by the diel movements of zooplankton (Freeman et al., 2004). Herring, another cetacean prey, also exhibit diel vertical-migration behaviour, coming to the surface at night, dispersing and swimming more slowly (Blaxter and Holliday, 1969). Diel trends in porpoise echolocation at dawn and dusk were suggested to occur in response to these differences in schooling dynamics (Fre´on et al., 1996; Todd et al., 2009).

Detailed investigation of the prey preferences of Doubtful Sound bottlenose dolphins and the diel activity of their prey are beyond the scope of this project. What is needed to advance this topic is the means to study prey species and their behaviour, in detail.

CHAPTER 5

GENERAL DISCUSSION

Despite long term research on differing aspects of the Doubtful Sound bottlenose dolphin population, recent, quantitative data on habitat distribution was required to assess their current conservation management. This study provided such data using a static acoustic monitoring system comprised of T-PODs moored throughout the fiord complex. Several aims were initially proposed:

1. Assess detection abilities of T-PODs for bottlenose dolphins in Doubtful Sound
2. Investigate whether foraging behaviour can be inferred from T-POD data
3. Apply the above to establish an acoustic monitoring system in Doubtful Sound to assess the population's habitat use and distribution patterns over a 12 month period to gain insight on seasonal, diel and spatial habitat use
4. Use findings to identify critical areas and relate these to current conservation
5. If required, propose changes to improve current conservation measures for the dolphin population

5.1 T-POD Performance in Detecting Bottlenose Dolphins of Doubtful Sound

Overall, the T-PODs performed well at monitoring habitat use of bottlenose dolphins in Doubtful Sound; however detection rates were low. Nevertheless, it is expected that echolocation rates differ between locations and populations based on behaviour, foraging strategies, habitat use and potentially group size. T-POD settings were also found to have significant influence on quality and quantity of positive dolphin detections.

This study was the first to quantitatively compare T-POD settings used previously in the literature with alternatives based on wideband recordings of the dolphins themselves (Elliott, 2008). Settings based on the latter were far superior, as suggested by the number of positive detections recorded.

The maximum T-POD monitoring range for bottlenose detection was relatively large; however as few detections were made at these distances, I do not recommend that spatial monitoring be based on maximum distance. Instead the effective detection radius (ERD: 266m, 95% CI 222m-317m) should be used for interpreting these results. Given this, it is evident that an individual T-POD monitors a relatively small area (0.22 km^2). A disadvantage of a small monitoring area is that site choice for moorings is very important and should be determined using prior knowledge of the population's distribution and in the context of research questions. Researchers must ensure that site choice does not bias results. A small monitoring radius is an advantage in that results are spatially specific and can be attributed to a precise area. This can allow quantitative comparisons between sites to be made.

Results suggested the T-PODs have several advantages over alternative methods of monitoring habitat use by bottlenose dolphins. A key advantage is that T-PODs “listen” continuously, allowing dolphin presence to be monitored 24 hours a day and in poor weather conditions. T-PODs are silent, and cannot reasonably be argued to change dolphin behaviour. They require minimal maintenance and labour. T-PODs can be set up to discriminate among species and with appropriate decision rules, false positive and false negative detections can be minimised. Acoustic monitoring via T-PODs is extremely affordable when compared with other methodologies used to assess long term habitat use. The technology is imperfect, however. A key problem stems from the echolocation behaviour of the animals themselves; unless they are echolocating, they will not be detected. For this reason further research on missed encounters, assessing just how conservative the data really are, would also be invaluable.

5.2 Inference of Foraging Behaviour from T-POD Data

Foraging events were able to be identified in T-POD data using ICI parameters derived from a combination of those in the literature with those identified in this study. Confidence was added to ICI parameters via a minimum click number required in trains. Effectiveness of parameters was tested with strong results using T-POD data collected in Doubtful Sound.

Parameters were constrained by the assumption that complete foraging sequences, involving search, approach and terminal buzz phases, are split into separate trains in T-POD recordings due to directionality factors involved with dolphins having a narrow sonar emission beam. This assumption was supported by observations within this study and Koschinski et al. (2008).

The defined foraging parameters allowed inference of foraging behaviour in T-POD data without manual/visual inspection required/recommended by Koschinski et al. (2008). This is very useful for large data sets and monitoring periods. ICI parameters may be location/population specific, whereby Doubtful Sound bottlenose dolphins may express 'buzzes' at different ICI than other populations. Because of this, further research on foraging click characteristics is recommended.

Theory behind the development of these parameters could be applied to other cetacean species and/or populations. Parameters could also be applied to other acoustic monitoring devices, given they have the ability to calculate mean ICIs and number of clicks. Caution should be taken with regard to differences in detection algorithms used in instruments to calculate click characteristics.

5.3 Establishment of the Monitoring System

Assessment of detection range assisted with the effective spatial distribution of T-PODs throughout Doubtful Sound. Assessment of T-POD settings increased the ability of T-PODs to detect the bottlenose dolphins of Doubtful Sound. Assessment of detection probability gave context to results, improving interpretation of trends and values.

Twelve months of successful monitoring was recorded at all nine sites. A hypothetical comparison between the running costs of vessel-based observations that would provide an equivalent data set to this, emphasises the cost-effectiveness of static acoustic monitoring via T-PODs. One-time costs include materials for nine moorings ($400) and the resource consent to put them in place ($1050). One-time costs for T-PODs and boat can be ignored as they are investments. To obtain 6 weeks of T-POD data from the nine sites, $200[1] petrol (for 5m, 60 hp vessel travelling to all sites) was required to recover and redeploy T-PODs at all sites.

Nine T-PODs use approximately $300 in D-cell batteries each 6-8 weeks. Accommodation for two is required for two days every six weeks ($100). Excluding one-time costs, running costs amount to about $800 for a six week T-POD deployment. To monitor the entire fiord system via vessel observations would cost at least the same $200 petrol price daily. In addition a minimum crew of two is needed, and they must be accommodated at Deep Cove ($25 each per night). For a 6 week T-POD deployment this would cost about $10, 800. While it is certainly true that boat observations can provide much more detailed data (but in daylight hours only), the cost is more than an order of magnitude greater. Also boat observation hours within close proximity to cetaceans are limited in most cases.

The first complete diel data set of Doubtful Sound bottlenose dolphins was gathered in this study. The first complete annual presence and foraging data sets were also acquired. These data are also a strong baseline from which to identify future trends.

5.4 Habitat Distribution and Trends

Clear patterns of seasonal habitat use were recorded within Doubtful Sound. Limited data on surface water temperature were available, but this should improve via a collaborative data-sharing agreement with Meridian Energy (Dawson, pers. comm.). Meridian's extensive data on water temperature, flow and depth is likely to prove important to better understand the influence of temperature, especially on calves and mothers. Comparative research with neighbouring fiords (e.g Dusky Sound), where human influence is minimal, will provide a control population which will be crucial in understanding indirect anthropogenic effects in Doubtful Sound.

No specific areas of Doubtful Sound were found to be specifically important for foraging. Foraging appeared to occur opportunistically throughout the fiord. Further research is

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[1] At prices in Doubtful Sound, which are approximately 50% more than pump prices in any New Zealand city or town.

required to determine whether this is a strategy preferred by the dolphins, or if it is forced upon them due to low productivity levels. Investigation of the influence of freshwater input on fiord productivity would assist this understanding, as would comparative research in other fiords as mentioned above.

Further research on source productivity and food web analysis would improve understanding of important prey species. Identification of such species could determine whether prey behaviours influence diel foraging and encounter trends observed in this study. Knowledge on specific prey species and distribution would enable specific areas of Doubtful Sound identified.

It is essential that critical areas such as foraging sites, along with resting, socialising and calf rearing sites, are identified as soon as possible and protected from anthropogenic impacts. Results from current and previous research indicate that these actions are imperative (Currey et al., 2007; Currey, 2008; Currey et al., 2009).

5.5 Conclusions and Recommendations for Future Management

Research undertaken in the Doubtful Sound has identified that the resident population of bottlenose dolphins is in such steep decline that it could face extinction by 2050 (Currey et al., 2009a & b). The decline is one of the steepest recorded for a dolphin population that is not exposed to direct or indirect takes from fishing. Being the agency legally responsible for the protection of marine mammals in New Zealand, the Department of Conservation (DOC) formulated a threat management discussion paper (Williams, 2007) to combine all information on threats, mitigation and options to ensure the protection of the dolphin population.

Research summarised in Williams (2007) identified that bottlenose dolphins were found within Doubtful Sound year-round, but utilised different parts of the fiord at different times of the year. Crooked Arm, Gaer Arm and Bradshaw Sound were identified as preferred areas for resting and socialising (Lusseau, 2003b; Boisseau, 2004). Seasonal changes in distribution were identified with winter months spent in the outer parts of the fiord and summer months in the upper fiords of Crooked and Hall Arm (Schneider, 1999; Lusseau and Slooten, 2002).

Few sightings were made in outer regions of Doubtful Sound and Thompson Sound (Lusseau and Slooten, 2002). Schneider (1999) visually, and Boisseau (2004) acoustically, identified foraging hotspots in Crooked Arm, Hall Arm, Espinosa/Pack Point and areas near the open ocean (possibly related to increased productivity/prey).

From the discussion paper (Williams, 2007), several conservation options were proposed. Proposals were discussed with stakeholders of Doubtful Sound to determine what was appropriate for the protection of the population whilst being practical for stakeholders. Through a submission process, DOC established a voluntary Marine Mammal Code of Management implemented in January, 2008, establishing the DPZs (DOC, 2008). Although clearly not a high level of protection, voluntary measures were preferred over legislation as they could be implemented immediately and have the support of the affected parties.

This study suggests that current DPZs do not adequately cover several key areas nor do they appropriately cater for seasonal changes in habitat use. No assessment of the DPZs has been undertaken since their establishment in 2008.

Given the value of this unique population of dolphins, published knowledge, and possible threats from vessel interactions and freshwater input, precautionary measures need to be taken to reduce/mitigate negative effects. A direct influence of freshwater input from Manapouri hydro-dam is not easily identifiable at present, but is under study. Threats from vessel interactions are better understood however, therefore these should be of immediate focus for mitigation.

It is not feasible to reduce the threat from boat interactions to zero in all areas. Compromise between protection required and practical use of the fiord by stakeholders, is seen as necessary to achieve effective conservation management (Williams, 2007). As noted earlier, DOC proposed several, seasonal, no boat zones to be established for the protection of critical areas identified by the literature and from this, DOC (2008) established the DPZs which are currently in place.

This study suggests that modifications to DPZs are needed. These are listed below and depicted in Figure 5.1. They incorporate the current DPZs as well as aspects of protection zones proposed by Williams (2007).

Firstly, I suggest establishment of a no boat zone within upper Crooked Arm (site D) from 1st December to 31st March, as seen in Figure 5.1. Total protection of upper Crooked Arm would create a sanctuary for calves and mothers during the summer. The protection period begins one month prior to this study's summer season definition as photo identification trips during

2009 and 2010 (Shaun Henderson, PhD candidate, Otago University), as well as monthly T-POD data from this study (rather than seasonal), identified the 'inner fiord migration', specifically to Crooked Arm, to commence in December.

Secondly, I suggest that the DPZ linking Crooked and Hall Arm should remain year round, as with all other DPZs. No added protection is recommended for Hall Arm (site B) in summer as T-POD DPM/day data indicated that residency time within Hall Arm was minimal compared to that within Crooked Arm (site D). Observations from photo identification trips (2009-2010) also support this trend (Henderson, pers. comm.). Furthermore, the upper reaches of Hall Arm are used by Real Journeys (the major tour boat operators) as well as other operators for unique attractions. The minimal conservation value gained by a no boat zone versus resulting conflict with stakeholders is therefore not justified. Furthermore the upper reach of Hall Arm ('the narrows') is already a five knot boat zone as all boating water is within 200m of the shore.

Thirdly, I suggest that the DPZ around site E should be extended as depicted in Figure 5.1, with current DPZ rules applying; this zone is similar to that proposed by Williams (2007). Results from this study showed the significance of this area; when utilised the least (summer) dolphins were still present on 50% of days. During autumn, habitat use increased to 93%. An increase in this zone would provide a broader area of limited boat activity with minimal inconvenience to skippers.

Results from this study support the suggestion by Williams (2007) of Gaer Arm being critical, year round. However, even though dolphins were present between 30 and 40% of days throughout the entire year at site F (start of Gaer Arm), photo identification trips (2009-2010) rarely found dolphins in the upper reaches of Gaer Arm (Henderson, pers. comm.). Most time was spent milling in Precipice Cove (site F). Furthermore, Real Journey's overnight tour boat (the Fiordland Navigator), along with a few other charter boats, moor in this area. Considering the minimal use of the upper parts of Gaer Arm, it seems unnecessary to make it a no boat as proposed by Williams (2007). Current DPZ protection from site E to F is seen to be sufficient.

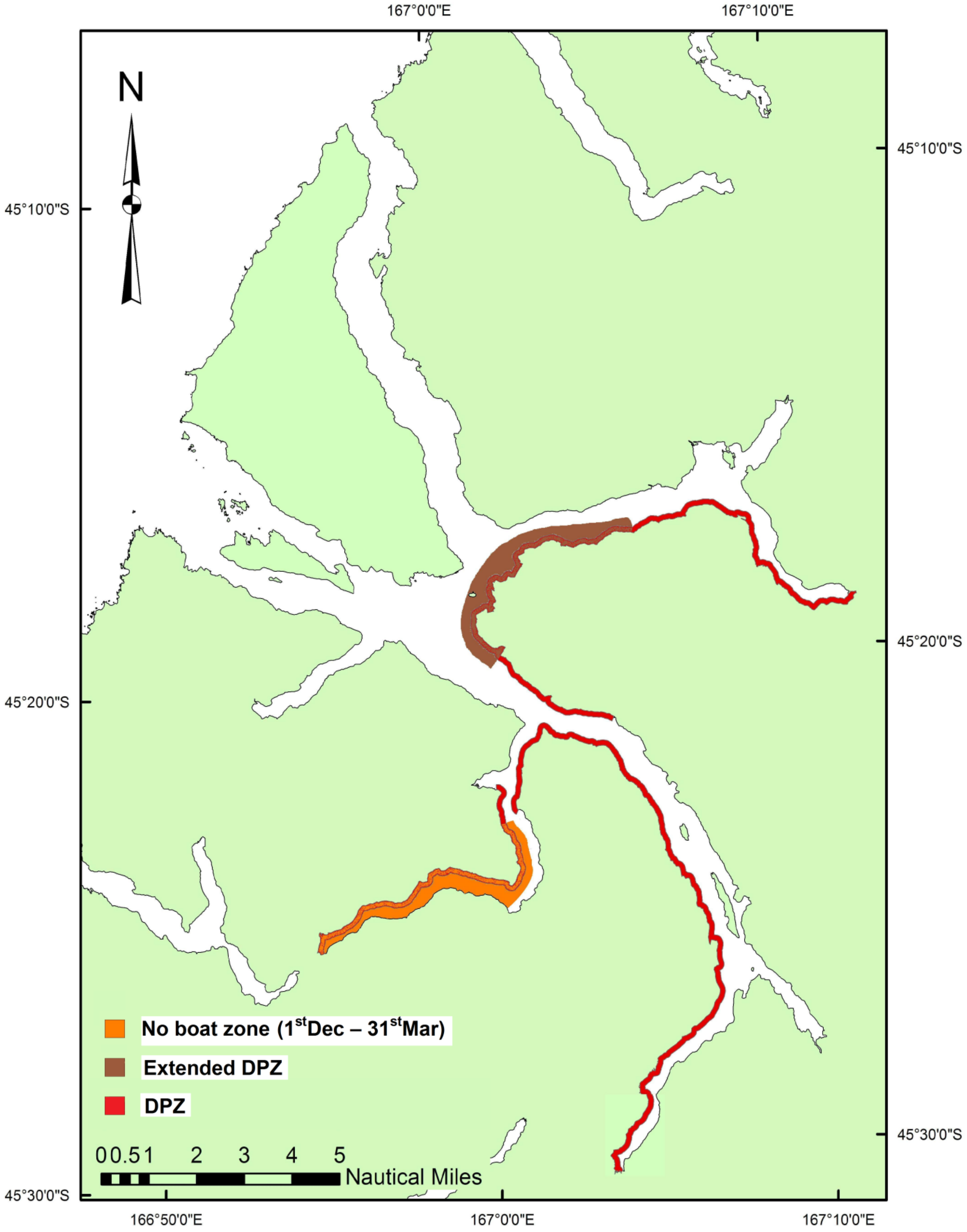

Figure 5.1 Proposed modifications to current DPZs in Doubtful Sound based on previous research and results from this study.

5.6 Further T-POD-related Research Recommended in Doubtful Sound

From this study, habitat distribution has been thoroughly investigated; primarily diel, seasonal and behavioural patterns. With more time, several additional aspects of the dolphin habitat use could have been researched. The following is a list of ideas for future research in conjunction with the T-POD monitoring programme in Doubtful Sound.

- Assess areas for residency using turnover rates via comparisons of DPM, DPH and DPD
- Using the nine moored T-PODs, detection times, and average travel speeds (derived from range experiment, chapter 2), determine whether the dolphins have routine “routes” on diel and/or seasonal scales. During trips into Doubtful Sound, personal observations suggest dolphins do have predictable routes. Quantifying these would be beneficial for assessing critical areas, especially with relation to resting, socialising and feeding behaviours
- Incorporation of more detailed water temperature data would give greater insight on temperature thresholds for the population. Three different sources exist; sharing of Meridian data, calibrating V5 T-POD’s internal temperature sensor enabling *in situ* recordings and establishment of external temperature devices at each T-POD site
- Investigation of tidal influence on habitat use, specifically diel and foraging trends.
- Further research on important prey species of the dolphins, specifically diel trends and distribution, would assist in defining important habitats, based on foraging potential, and would help explain habitat use.
- Investigate whether habitat use changes as tourism, hydro-dam developments and general anthropogenic influences change over time, thus allowing conservation management to be adapted appropriately.
- Lastly, incorporation of the newly developed digital T-POD from Chelonia Ltd, the C-POD, into habitat monitoring, and side by side T-POD/C-POD calibration in the field. Cheloni.co.uk lists several advantages the C-POD has over T-PODs:

    - Very low rate of false positives
    - Ability to log broadband clicks of dolphins without flooding the memory
    - Greater potential for discrimination among species

- Frequency range extended to 20-160 kHz, thus logging all odontocetes (except sperm whales).
- Lower power requirement enables 4 months running time on 8 alkaline D-cells.
- Removable Secure Digital (SD) memory used for storage allows large data volumes, and easy field servicing as no computer required for downloading
- Very few user-controlled settings are required so that comparable data can be captured in different studies
- Tight standardisation ensures trends over time can be more easily identified

REFERENCES

Akamatsu, T., Wang, D., Wang, K. and Naito, Y. 2005. Biosonar behaviour of free ranging porpoises. *Proc. Biol. Sci*. 272: 797-801.

Akamatsu, T., Wang, D., Wang, K. and Wei, Z. 2001. Comparison between visual and passive acoustic detection of finless porpoises in the Yangtze River, China. *J. Acoust. Soc. Am*. 109(4): 1723-1727.

Alford, L. 2006. The occurrence and foraging activity of bottlenose dolphins and harbour porpoises in Cardigan Bay SAC, Wales. MSc. Thesis. Marine Biology. The University of Wales, Bangor.

Allen, S., Smith, H., Wapels, K. and Harcourt, R. 2007. The voluntary code of conduct for dolphin watching in Port Stephens, Australia: is self-regulation an effective management tool? *Journal of cetacean research management.* 9(2): 159-166.

Amano, M., Yoshioka, M., Kuramochi, T. and Mori, K. 1998. Diurnal feeding by Dall's porpoise, Phocoenoides dalli. *Marine Mammal Science*. 14: 130–135.

Au, W.W.L. 1993. *The Sonar of Dolphins*. Springer-Verlag, New York, NY.

Au, W.W.L. 2002. Echolocation. In W.F, Perrin., J.G.M, Thewissen. And B, Wursig. (eds) *Encyclopaedia of Marine Mammals*. Academic Press, San Diego. 359-367.

Au, W.W.L. 2004. Echolocation Signals of Wild Dolphins. *Acoustical Physics.* 50: 454*–462.*

Au, W.W.L. and Snyder, K. J. 1980. Long-range target detection in open waters by an echolocating Atlantic bottlenose dolphin. *J. Acoust. Soc. Am.* 56: 1280–1290.

Au, W.W.L. and Wursig, B. 2004. Echolocation signals of dusky dolphins (*Lagenorhynchus obscurus*) in Kaikoura, New Zealand. *Acoustical Society of America*. 115: 2307-2313.

Au, W.W.L., Carder, C.A., Penner, R.H. and Scronce, B.L. 1985. Demonstration of adaptation in beluga whale echolocation signals. *J. Acoust. Soc. Am.* 77: 726–730.

Au, W.W.L., Floyd, R.W., Penner, R.H. and Murchison, A.E. 1974. Measurement of echolocation signals of the Atlantic bottlenose dolphin in open waters. J*ournal of the Acoustical Society of America*. 56: 1280-1290.

Au, W.W.L., Kastelein, R.R., Rippe, T. and Schooneman, N.M. 1999. Transmission beam pattern and echolocation signals of a harbor porpoise. *Journal of the Acoustical Society of America.* 106: 3699-3705.

Au, W.W.L., Moore, P.W.B. and Pawloski, D. 1986. Echolocation transmitting beam of the Atlantic Bottlenose dolphin. *J. Acoust. Soc. Am.* 80(2): 668-691.

Baines M.E., Evans P.G.H. and Shepherd B. 2000. *Bottlenose dolphins in Cardigan Bay, West Wales*. . Report to EU INTERREG & Countryside Council for Wales. Sea Watch Foundation, Oxford. 35pp.

Batham, E. J. 1965. Rocky shore ecology of a southern New Zealand fiord. *Transactions of the Royal Society of blew Zealand, Zoology.* 6*:* 215-227.

Baulch, S. 2007. Fine-scale spatio-temporal variation and habitat partitioning in bottlenose dolphins and harbour porpoises. MSc. Thesis. University of York.

Bejder, L., Samuels, A., Whitehead, H., Gales, N., Mann, J., Connor, R.C., Heithaus, M.R., Watson-Capps, J.J., Flaherty, C. and Krützen, M. 2006. Decline in relative abundance of bottlenose dolphins exposed to long-term disturbance. *Conserv Biol.* 20:1791–1798.

Blaxter, J. H. S. and Holliday, F. G. 1969. The behaviour and physiology of herring and other clupeids. *Advances in Marine Biology.* 1: 261–393.

Blew, J., Diederichs, A., Grünkorn, T., Hoffmann, M. and Nehls, G. 2006. Status Report. *Investigations of the bird collision risk and the responses of harbour porpoises in the offshore wind farms Horns Rev, North Sea, and Nysted, Baltic Sea, in Denmark.* Supported by the German Federal Ministry of Environment, Nature Conservation and Nuclear Safety.

Blomqvist, C. and Amundin, M. 2004. An Acoustic Tag for Recording Directional Pulsed Ultrasounds Aimed at Free-Swimming Bottlenose Dolphins (*Tursiops truncatus*) by Conspecifics. *Aquatic Mammals*. 30(3): 345-356.

Boisseau, O. J. 2004. The acoustic behaviour of resident bottlenose dolphins in Fiordland, PhD. Thesis. New Zealand. Department of Marine Science. Dunedin, New Zealand, University of Otago.

Bond, S. 2006. The use of T-PODs to identify echolocation behaviour in bottlenose dolphins (*Tursiops truncatus*) in New Quay Bay, Wales. MSc. Thesis. School of Biological Sciences, University of Wales, Bangor.

Boyle, M.C., Jillett, J. B. and Mladenov, P. V. 2001. Intertidal communities in Doubtful Sound, New Zealand: changes over time. *N. Z. J. Mar. Freshw. Res.* 35: 663–73.

Brager, S. 1993. Diurnal and seasonal behaviour patterns of bottlenose dolphins (*Tursiops Truncatus*). *Marine Mammal Science.* 9: 434–438.

Buckland S.T., Anderson D.R., Burnham K.P., Laake J.L., Borchers D.L. and Thomas L. 2001. *Introduction to distance sampling*. New York: Oxford University Press Inc.

Busnel, R.G. and Dziedzic, A. 1967. Resultants metrologiques experimentaux del'echolocation chez le *Phocaena phocaena* et leur comparaison avec ceux de certaines chauves-souris. In R.G. Busnel (eds). *Animal Sonar System, Biology and Bionics*. 307-356.

Caldwell, D.K. and Caldwell, M.C. 1965. Individualised whistle contours in bottlenose dolphins (*Tursiops truncatus*). -*Nature* (Lond). 207: 434-435.

Caldwell, D.K. and Caldwell, M.C. 1967. Intraspecific transfer of information via the pulsed sound in captive odontocete cetaceans. In: R. G. Busnel (eds). *Les systemes sonars animaux, biologie et bionique. Laboratoire de Physiologie Acoustique, Jouy-en-Josas*, France. 879-936.

Caldwell, D.K. and Caldwell, M.C. 1972. Behaviour of marine mammals. In S.H. Ridgway (eds). *Mammals of the Sea, Biology and Medicine*. Charles Thomas Publ., Springfield, Illinois. 419-465, 812.

Caldwell, M.C., Caldwell, D.K. and Tyack, P.L. 1990. Review of the signature whistle hypothesis for the Atlantic bottlenose dolphin. In S. Leatherwood and R.R. Reeves (eds). *The Bottlenose Dolphin*. Academic Press, San Diego, CA. 199-234.

Carlström, J. 2005. Diel variation in echolocation behaviour of wild harbor porpoises. *Marine Mammal Science*. 21: 1–12.

Carstensen J., Henriksen O.D. and Teilman J. 2006. Impacts of offshore wind farm construction on harbour porpoises, acoustic monitoring of echolocation activity using porpoise detectors (T-PODs). *Marine Ecology Progress Series.* 321: 295–308.

Chelonia. 2006. T-POD help file. Available at www.chelonia.co.uk/tpod_downloads.htm.

Cheney, D. and Seyfarth, R. 1990. *How monkeys see the world: Inside the mind of another species.* University of Chicago Press. Chicago.

Cockroft, V.G. and Ross, G.J.B. 1990. Food and feeding of the Indian Ocean bottlenose dolphin off southern Natal, South Africa. In S. Leatherwood and R.R. Reeves (eds). *The bottlenose dolphin*. Academic Press, San Diego, CA, p 309–323.

Connor, R .C. and Smolker, R. A. 1996. ‘Pop’ goes the dolphin: A vocalization male botttlenose dolphins produce during courtships. *Behaviour.* 133:643-662.

Connor, R., Wells, R., Mann, J. and Read, A.J. 2000. The bottlenose dolphin. Social relationships in fission-fusion society. In J. Mann., R. Connor., P.L.Tyack. and H. Whitehead.

(Eds). *Cetacean societies: Field studies of dolphins and whales*. Chicago: University of Chicago Press. 91-126.

Corkeron, P.J., Bryden, M.M. and Hedstrom, K.E. 1990. Feeding by bottlenose dolphins in association with trawling operations in Moreton Bay, Australia. In: S. Leatherwood. And R.R Reeves (eds). *The bottlenose dolphin*. Academic Press, San Diego, CA. 329–337.

Cox, T. M. and Read, A. J. 2004. Echolocation behavior of harbor porpoises *Phocoena phocoena* around chemically enhanced gill nets. *Marine Ecology Progress Series.* 279: 275 282.

Cox, T. M., Read, A. J. Solow, A. and Tregenza, N. 2001. Will harbour porpoises *(Phocoena phocoena)* habituate to pingers? *Journal of Cetacean Research and Management* 3:231-86.

Culik, B.M., Koschinski, S., Tregenza, N. and Ellis, G.M. 2001. Reactions of harbour porpoises Phocoena phocoena and herring Clupea harengus to acoustic alarms. *Marine Ecology Progress Series.* 211:255-260.

Currey, R.J.C., Dawson, S.M. and Slooten, E. 2007. New abundance estimates suggest Doubtful Sound bottlenose dolphins are declining. *Pacific Conserv. Biol.* 13: 265-73.

Currey, R.J.C., Dawson, S.M. and Slooten, E. 2009b. An approach for regional threat assessment under IUCN Red List criteria that is robust to uncertainty: The Fiordland bottlenose dolphins are critically endangered. *Biological Conservation.* 142: 1570-1579.

Currey, RJ.C., Dawson, S.M., Slooten, E., Lusseau, D.L., Boisseau, O., Schneider, K. Haase, P. and Williams, J.A. 2009a. Survival rates for a declining population of bottlenose dolphins in Doubtful Sound, New Zealand: an information theoretic approach to assessing the role of human impacts. *Aquatic Conservation.* 19:658-670.

Currey, R.J.C., Rowe, L.E., Dawson, S.M. and Slooten, E. 2008. Abundance and demography of bottlenose dolphins in Dusky Sound, New Zealand, inferred from dorsal fin photographs. *New Zealand Journal of Marine and Freshwater Research.* 42: 439-449.

Dawson, S.M. 1991. Clicks and communication: the behavioural and social contexts of Hector's dolphin vocalizations. *Ethology.* 88**:** 265–276.

Dawson, S.M. and Thorpe, C.W. 1990. A quantitative analysis of the acoustic repertoire of Hector's dolphin. *Ethology.* 86: 131-145.

DOC. 2008. Marine Mammal (and other wildlife) Code Of Management: Doubtful Sound/Patea. Available from Doc Te Anau. 12pp.

dos Santos, M. E., Caporin, G., Moreira, H. O., Ferreira, A. J. and Bento-Coelho, J. L. 1990. Acoustic behaviour in a local population of bottlenose dolphins. In J. A. Thomas and R. A. Kastelein (Eds.). *Sensory abilities of cetaceans: Laboratory and field evidence*. New York: Plenum Press. 585-598,710 .

dos Santos, M.E. and Almada, V.C. 2004. A case for passive sonar: analysis of click train production patterns by bottlenose dolphins. In J. Thomas (eds). *Echolocation in bats and dolphins.* Chicago, Illinois: University of Chicago Press. 400– 403.

Elliott, R.G. 2008. The T-POD: an innovative way to assess habitat use for the conservation of bottlenose dolphins in Doubtful Sound, Fiordland, New Zealand. BSc Honours dissertation. Department of Marine Science. Dunedin, New Zealand, University of Otago.

Evans P.G.H. 1997. *Ecological studies of the harbour porpoise in Shetland, North Scotland*. Report to WWF-UK. Sea Watch Foundation, Oxford.106pp.

Evans, W. E. and Powell, B. A. 1967. Discrimination of different metallic plates by an echolocating delphinids. In R.G. Busnel. Jouy-en-Josas (eds). *Systems sonar animaux: Biologie and biunique.* Vol 2, ed. France: Laboratoire de Physiologie Acoustique. 363-382.

Finneran, J.J., London, H.R. and Houser, D.S. 2005. Modulation rate transfer functions in bottlenose dolphins (*Tursiops truncatus*) with normal hearing and high-frequency hearing loss. *Journal of Comparative Physiology of America*. 193:835–843.

Foote, A.D., Osborne, R.W. and Hoelzel, A.R. 2004. Whale-call response to masking boat noise. *Nature.* 428 : 910.

Fre´on, P., Gerlotto, F. and Soria, M. 1996. Diel variability of school structure with special reference to transition periods. *ICES Journal of Marine Science*. 53: 459–464.

Freeman, S., Mackinson, S. and Flatt, R. 2004. Diel patterns in the habitat utilisation of sandeels revealed using integrated acoustic surveys. *Journal of Experimental Marine Biology and Ecology*. 305: 141–154.

Gannon, D.P., Barros, N.B., Nowacek, D.P., Read, A.J., Waples, D.M. and Wells, R.S. 2005. Prey detection by bottlenose dolphins, *Tursiops truncatus*: an experimental test of the passive listening hypothesis. *Animal Behaviour*. 69: 709–720.

Gibbs, M. T. 2001. Aspects of the structure and variability of the low-salinity-layer in Doubtful Sound, a New Zealand fiord. *New Zealand Journal of Marine and Freshwater Research.* 35: 59-72.

Gibbs, M. T., Bowman, M. J. and Dietrich, D. 2000: Maintenance of near-surface stratification in Doubtful Sound, a New Zealand fiord. *Estuarine, Coastal and Shelf Science.* 51: 683-704.

Gish, S.L. 1979. A quantitative description of two-way acoustic communication between captive Atlantic bottlenosed dolphins (*Tursiops truncates* Montague). PhD Thesis. University of California, Santa Cruz.

Goodson, A.D., Klinowska, M. and Bloom, P.R.S. 1994. Enhancing the acoustic detectability of gillnets. In W. F. Perrin, G. P. Donovan and J. Barlow (eds). *Gillnets and Cetaceans.* Cambridge: Black Bear Press. 585-595.

Goodson, A.D., Klinowska, M. and Morris, R. 1988. Interpreting the acoustic pulse emissions of a wild bottlenose dolphin (Tursiops truncatus). *Aquat. Mamm*. 14: 7-12.

Grange, K.R., 1990. Unique Marine Habitats in the New Zealand Fiords: A Case for Preservation. N.Z. Department of Conservation, 1990/7, p. 70.

Gregory, P.R. and Rowden, A.A. 2001. Behaviour patterns of bottlenose dolphins (*Tursiops truncatus*) relative to tidal state, time-of-day, and boat traffic in Cardigan Bay, West Wales. *Aquatic Mammals*. 27(2): 105–113.

Haase, P.A. and Schneider K., 2001. Birth demographics of bottlenose dolphins, *Tursiops truncatus,* in Doubtful Sound, Fiordland, New Zealand – preliminary findings. *N. Z. J. Mar. Freshw. Res.* 35: 675- 80.

Hammond, P.S. and Thompson, P.M. 1991. Minimum estimates of the number of dolphins *Tursiops truncates* in the Moray Firth, NE Scotland. *Biological Conservation*. 65: 79-87.

Hanson, L.J. 1983. Population biology of the coastal bottlenose dolphin off southern California. MSc. Thesis. California State University, Sacramento, CA.

Hanson, L.J. 1990. California Coastal Bottlenose Dolphins. In S. Leatherwood and R.R. Reeves (eds). *The Bottlenose Dolphin*. Academic Press, San Diego. 403-420.

Hays, G.C., Webb, P. I. and Frears, S.L. 1998. Diel changes in the carbon and nitrogen content of the copepod *Metridia lucens. Journal of Plankton Research*. 20(4):727-737.

Herzing, D.L. 1996. Vocalizations and associated underwater behaviour of free-ranging Atlantic spotted dolphins, *Stenella frontalis* and bottlenose dolphin, *Tursiops truncates*. *Aqua. Mamm*. 22: 61–79.

Herzing, D.L. 2004. Social and nonsocial uses of echolocation in free-ranging *Stenella frontalis* and *Tursiops truncatus*. In J. A. Thomas, C. F. Moss and M. Vater (eds). *Echolocation in Bats and Dolphins.* Chicago, IL: The University of Chicago Press. 404-410.

Holler, P. 1995. Orientation by the bat *Phyllostomus discolor* (Phyllostomidae) on the return flight to its resting place. *Ethology*. 100:72-83.

IWC, International Whaling Commission. 2008. Report of the Scientific Committee. Annex M. Report of the Sub-Committee on Whale watching. *J. Cetacean Res. Manage. (Supple.)* 9:326-40.

Janik, V. M. 2000. Whistle matching in wild bottlenose dolphins (*Tursiops truncatus*). *Science*. 289: 1355-1357.

Janik, V.M. 2000a. Whistle matching in wild bottlenose dolphins *(Tursiops truncutm). Science.* 289: 1355-1357.

Janik, V.M. 2000c. Source levels and the estimated active space of bottlenose dolphin (*Tursiops truncatus*) whistles in the Moray Firth, Scotland. *J. Comp. Physiol. A.* 186: 673 680.

Jefferson, T.A., Hung, S.K., Law, L., Torey, M. and Tregenza, N. 2002. Distribution and abundance of finless porpoises in Hong Kong and adjacent waters of China. *The Raffles Bulletin of Zoology*. 10: 43–55.

Johnson, C.S. 1967. Sound detection thresholds in marine mammals. In *Marine bioacoustics*. Oxfrod, UK: Pergamon Press. 2: 247-255.

Johnson, M., Hickmott, L. S., Soto, N. A. and Madsen, P. T. 2008. Echolocation behaviour adapted to prey in foraging Blainville's beaked whale (Mesoplodon densirostris). *Proc. Biol. Sci*. 275: 133-139.

Johnson, M., Madsen, P.T., Zimmer, W.M.X., Aguilar de Soto, N. and Tyack, P.L. 2004. Beaked whales echolocate on prey. *Proc. Biol. Sci.* 271(6): 383- 386.

Johnson, M., Madsen, P.T., Zimmer, W.M.X., Aguilar de Soto, N. and Tyack, P.L. 2006. Foraging Blainville's beaked whales (Mesoplodon densirostris) produce distinct click types matched to different phases of echolocation. *J. Exp. Biol.* 209: 5038-5050.

Jones, B.A., Stanton, T.K., Lavery, A.C., Johnson, M.P., Tyack, P. and Madsen, P.T. 2008. Classification of broadband echoes from prey of a foraging Blainville's beaked whale. *J. Acoust. Soc. Am.* 123: 1753-1762.

Jones, G.J. and Sayigh L.S. 2002. Geographic variation in rates of vocal production of free-ranging bottlenose dolphins. *Marine Mammal Science*. 18: 374–393.

Kalko, E.K.V. and Schnitzler, H.U. 1998. How echolocating bats search and find food. In T. H. Kunz and P. A. Racey (eds). *Bat Biology and Conservation*. Washington, DC: Smithsonian Institution Press. 183- 196.

Kastelein, R., Schooneman, N.M., Au, W.W.L., Verboom, W.C. and Vaughan, N. 1997. The ability of a harbour porpoise (*Phocoena phocoena*) to discriminate between objects buried in sand. In A. J. Read, P. R. Wiepkema and P. E. Nachtigall (eds). *The Biology of the Harbour Porpoise*. Woerden, The Netherlands: De Spil. 329-342.

Kenney, R.D. 1990. Bottlenose dolphins off the northeastern United States. In S. Leatherwood and R.R. Reeves (eds). *The Bottlenose Dolphin*. Academic Press, San Diego. 369-386.

Koschinski, S., Ansgar, D. and Amundin, M. 2008. Click train patterns of free-ranging harbour porpoises acquired using T-PODs may be useful as indicators of their behaviour. *J. Cetacean Resource Management.* 10(2): 147-155.

Koschinski, S., Culik, B.M., Damsgaard Henriksen, O., Tregenza, N., Ellis, G., Jansen, C. and Kathe, G. 2003. Behavioural reactions of free-ranging porpoises and seals to the noise of a simulated 2 MW windpower generator. *Marine Ecology Progress Series*. 265: 263–273.

Koschinski, S., Culik, B.M., Trippel, E.A. and Ginzkey, L. 2006. Behavioral reactions of free-ranging harbor porpoises *Phocoena phocoena* encountering standard nylon and BaSO4 mesh gillnets and warning sound. *Mar Ecol Prog Ser.* 313: 285-294

Lamb J. 2004. Relationships between presence of bottlenose dolphins, environmental variables and boast traffic; visual and acoustic surveys in New Quay, Wales. MSc. Thesis. University of Wales, Bangor.

Lammers, M.O., Au, W.W.L. and Herzing, D.L. 2003. The broadband social acoustic signalling behaviour of spinner and spotted dolphins.*J. Acoustic. Soc. Amer.* 114(3): 1629-1639.

Lampert, W. 1989. The Adaptive Significance of Diel Vertical Migration of Zooplankton. *Functional Ecology*. 3:21-27.

Leaper R., Chappell O. and Gordon , J. 1992. The development of practical techniques for surveying sperm whale populations acoustically. *Report of the International Whaling Commission.* 42: 549–560.

Leatherwood, S.1979. Aerial surveys of the bottlenose dolphins and the West Indian manatee in the Indian and Banana rivers, Florida. *Fishery Bulletin.* 74: 47-59.

Leatherwood, S. and Reeves, R.R. 1983. *The Sierra Club Handbook of Whales and Dolphin*s. Sierra Club Books, San Francisco, California. 302.

Leeney, R.H., Berrow, S., McGrath,D., O'Brien, J., Cosgrove R. and Godley, B.J. 2007. Effects of pingers on the behaviour of bottlenose dolphins. *J. Mar. Biol. Ass. U.K.* 87: 129–133.

Lilly, J.C., and A.M. Miller. 1961. Sounds emitted by the bottlenose dolphin. *Science*. 133: 1689-1693.

Lorenz, K.Z. 1950. The comparative method in studying innate behaviour patterns. In *Physiological Mechanisms in Animal Behaviour, Symposium of the Society of Experimental Biology*. Academic Press, London. 4: 221-268.

Lusseau, D. 2003a. The state of the scenic cruise industry in Doubtful Sound in relation to a key natural resource: bottlenose dolphins. In M. Hall & S. Boyd (eds). *Nature-based Tourism* *in Peripheral Areas: Development or Disaster?* Channel view Publications, Cleventon, England.

Lusseau, D. 2003b. Effect of tour boats on the behaviour of Bottlenose dolphins: Using Markov chains to model anthropogenic impacts. *Conservation Biology.* 17: 1785-1793.

Lusseau, D. and Slooten, E. 2002. Cetacean sightings off the Fiordland coastline: Analysis of commercial marine mammal viewing data 1996–99, Science for Conservation 187. Department of Conservation, Wellington: 42.

Lusseau, S.M. and Wing, S.R. 2006. Importance of local production versus pelagic subsidies in the diet of an isolated population of bottlenose dolphins *Tursiops* sp. *Marine Ecology Progress Series.* 321: 283-293.

Lusseau, D., Schneider, K., Boisseau, O.J., Haase, P.A., Slooten, E. and Dawson, S.M. 2003. The bottlenose dolphin community of Doubtful Sound features a large proportion of long-lasting associations – can geographic isolation explain this unique trait? *Behav. Ecol. Sociobiol.* 54: 396-405.

Lusseau, D. Slooten, L. and Currey, R.J. 2006. Unsustainable dolphin watching tourism in Fiordland, New Zealand. *Tourism in Marine Environments.* 3: 1-6.

Lusseau, D., Slooten, E., Higham, J.E.S. and Dawson, S.M. 2002. The effects of tourism activities on bottlenose dolphins in Fiordland: towards a sustainable solution. Department of Conservation, Wellington, NZ. (unpublished). 75.

Madsen, P.T., Johnson, M., Aguilar de Soto, N., Zimmer, W.M.X. and Tyack, P.L. 2005. Biosonar performance of foraging beaked whales (Mesoplodon densirostris). *J. Exp. Biol.* 208: 181-194.

Madsen, P.T., Payne, R., Kristiansen, N.U., Wahlberg, M., Kerr, I. and Møhl, B. 2002. Sperm whale sound production studied with ultrasound time/depth-recording tags. *J. Exp. Biol.* 205: 1899-1906.

Malme, C.I. 1995. Sound Propagation. Pp. 59-86. In W.J. Richardson., C.R. Greene., C.I. Malme., D.A. Mann., Z. Lu., M.C. Hastings. and A.N. Popper. 1998. Detection of ultrasonic tones and simulated dolphin echolocation clicks by a teleost fish, the American shad (Alosa sapidissima*). J. Acoust. Soc. Am.* 104: 562-568.

McDonald M.A. and Fox C.G. 1999. Passive acoustic methods applied to fin whale population density estimation. *Journal of the Acoustical Society of America*. 105:2643–2651.

Miller, B. and Dawson, S.M. 2009. A Large aperture, low-cost hydrophone array for tracking whales from small boats. *Journal of the acoustical Society of America.* 126 (5): 2248-2256.

Miller, L. A., Pristed, J., Møhl, B. and Surlykke, A. 1995. The click-sounds of narwhals (*Monodon monoceros*) in Inglefield Bay, Northwest Greenland. *Mar. Mamm. Sci*. 11: 491 502.

Miller, P. J. O., Johnson, M. P. and Tyack, P. L. 2004. Sperm whale behaviour indicates the use of echolocation click buzzes “creaks” in prey capture. *Proc. Biol. Sci*. 271: 2239-2247.

Morozov, B. P., Akapiam, A. E., Burdin, V. I., Zaitseva, K. A. and Solovykh, Y. A. 1972. Tracking frequency of the location signals of dolphins as a function of distance to the target. *Biofizika*. 17: 139–145.

Nowacek, D.P. 2005. Acoustic ecology of foraging bottlenose dolphins (*Tursiops truncates)*, habitat-specific use of three sound types. *Marine Mammal Science.* 21(4):587-602.

Ohizumi, H., Kuramochi, T., Amano, M. and Miyazaki, N. 2000. Prey switching of Dall’s porpoise Phocoenoides dalli with population decline of Japanese pilchard Sardinops melanostictus around Hokkaido, Japan. *Marine Ecology Progress Series*. 200: 265–275.

Overstrom, N. A. 1983. Association between burst-pulse sounds and aggressive behaviour in captive Atlantic bottlenose dolphins (*Tursiops truncates*). *Zoo Biol*. 2: 93–103.

Philpott, E., Englund, A., Ingram, S. and Rogan, E 2007. Using T-PODs to investigate the echolocation of coastal bottlenose dolphins. *J. Mar. Biol. Ass.* 87: 11–17.

Pickrill, R.A. 1987. Circulation and sedimentation of suspended particulate matter in New Zealand fjords. *Marine geology*. 74: 21-39.

Rayment, W. Dawson, S.M. and Slooten, E. 2009. Trialing an automated passive acoustic detector (T-POD) with Hector's dolphins (*Cephalorhynchus hectori*). *Journal of the Marine Biological Assiociation.*. 89(5):1015-1022.

Reyes-Zamudio, M. 2005. Acoustic behaviour of bottlenose dolphins (*Tursiops truncatus*): a comparison between T-POD and visual surveys. MSc. Thesis. University of Wales, Bangor.

Rice, W.R. 1989. Analysing tables of statistical tests. *Evolution.* 43(1): 223-225.

Rutger, S. and Wing, S.R. 2006 Effects of freshwater input on shallow-water infaunal communities in Doubtful Sound, New Zealand. *Marine Ecology Progress Series.* 314: 35-47.

Saayman, G. S., Tayler, C. K. and Bower, C. 1973. Diurnal activity cycles in captive and free-ranging Indian Ocean bottlenose dolphins (*Tursiops aduncus* Ehrenberg). *Behaviour.* 44:212–233.

Scarpaci, C., Dayanthi, N. and Corkeron, P.J. 2003. Compliance with regulations by 'swim-with-dolphins' operations in Port Phillip Bay, Victoria, Australia. *Environ. Manage.* 31(3): 342-47.

Schneider, K., 1999. Behaviour and ecology of bottlenose dolphins in Doubtful Sound, Fiordland, New Zealand. PhD. Thesis. University of Otago, Dunedin, NZ.

Schultz, K.W., Cato, D.H., Corkeron, P.J. and Bryden, M.M. 1995. Low frequency narrow-band sounds produced by bottlenose dolphins. *Mar. Mamm. Sci.* 11(4): 503-509.

Scott, M.D. and Chivers, S.J. 1990. Distribution and herd structure of bottlenose dolphins in the eastern tropical Pacific Ocean. In S. Leatherwood and R.R. Reeves (eds.). *The Bottlenose Dolphin*. Academic Press, San Diego. 387-402.

Shane, S.H. 1980. Occurance, movements and distribution of bottlenose dolphins, *Tursiops truncates*, in southern Texas. *Fishery Bulletin.* 78: 593-601.

Simon, M., Nuuttila, H., Reyes-zamudio, M.M., Ugarte, F., Verfub, U. and Evans, P.G.H. 2010. Passive acoustic monitoring of bottlenose dolphin and harbour porpoise, in Cardigan Bay, Wales, with implications for habitat use and partitioning. *Journal of the Marine Biological Association of the United Kingdom*. 10: 1-7.

Smith, W.J. 1986. Signalling behaviour: contributions of different repitoires. In (R.J. Schusterman et al (eds). *Dolphin cognition and behaviour: a comparative approach.* LEA. 315-330.

Smolker, R.A., Mann, J. and Smuts, B.B.1993. Use of signature whistles during separations and reunions by wild bottlenose dolphin mothers and infants. *Behaviour Ecol.and Sociolbiol.* 33(6): 393-402.

Smolker, R.A., Richards, A.F., Connor, R.C. and Pepper, J.W. 1992. Sex differences in patterns of association among Indian Ocean bottlenose dolphins. *Behaviour.* 123:38–69

Stanton, B.R. and Pickard, G.L. 1981. Physical oceanography of the New Zealand fiords. *New Zealand Oceanographic Institute Memoir.* 88: 3–37.

Teilmann, J., Henriksen, O.D., Carstensen, J. and Skoy, H. 2002. Monitoring effects of offshore windfarms on harbour porpoises using PODs (porpoise detectors). *Technical Report to the Ministry of the Environment Denmark*, 95pp.

Thomas, J. A., Moss, C. F. and Vater, M. 2004. *Echolocation in Bats and Dolphins*. Chicago: University of Chicago Press.

Thomsen, F., van Elk, N., Brock, V. and Piper, W. 2005. On the performance of automated porpoise-click-detectors in experiments with captive harbor porpoises (*Phocoena phocoena*) (L). *Journal of the Acoustical Society of America.*118: 37–40.

Todd, V.L.G., Pearse, W.D., Tregenza, N.C., Lepper, P.A. and Todd, I.B. 2009. Diel echolocation activity of harbour porpoises (*Phocoena phocoena*) around North Sea offshore gas installations. *ICES Journal of Marine Science*. 66: 734–745.

Tougaard, J., Rosager Poulsen, L., Amundin, M., Larsen, F., Rye, J. and Teilmann, J. 2006. Detection function of T-PODs and estimation of porpoise densities. In R. Leeney and N.J.C. Tregenza (eds). *Proceedings of the workshop; Static acoustic monitoring of cetaceans. Held at the 20th Annual Meeting of the European Cetacean Society, Gdynia, Poland 2 April 2006* ECS Newsletter No 46. Special Issue July 2006.

Townsend, C.H. 1914. The porpoise in captivity. *Zoologica* (N.Y.) 1: 289-299.

Turl, C.W. & Penner, R.H. 1989. Differences in echolocation click patterns of the beluga (*Delphinapteras leucas*) and the bottlenose dolphin (*Tursiops truncatus*). *J. Acoust. Soc. Am.* 86(2): 497-502.

Verfuss, U.K., Miller, L.A. and Schnitzier, H.U. 2005. Spatial orientation in echolocating harbour porpoises*, Phocoena phocoena. J. Exp. Biol.* 208:3385-94.

Verfuss, U.K., Miller, L.A., Pilz, P.K.D. and Schnitzler, H.U. 2009. Echolocation by two foraging harbour porpoises (Phocoena phocoena). *The Journal of Experimental Biology*. 212: 823-834.

Villadsgaard, A., Wahlberg, M. and Tougaard, J. 2006. Echolocation signals of wild harbour porpoises, Phocoena phocoena. *J Exp Biol*. 210: 56-64.

Wang , D.W., Würsig, B. and Evans, W.E. 1995. Whistles of bottlenose dolphins: comparisons among populations. *Aquat. Mamm.* 21: 65–77.

Wang K., Wang D., Akamatsu T., Li S. and Xiao J. 2005. A passive acoustic monitoring method applied to observation and group size estimation of finless porpoises. *Journal of the Acoustical Society of America.* 118: 1180–1185.

Weller, D.W. 1998. Global and regional variation in the biology and behavior of bottlenose dolphins. Ph.D. Thesis, Texas A&M University.

Wells, R.S. 1986. Structural aspects of dolphins societies. Ph.D. Thesis, University of California at Santa Cruz, California.

Wells, R. S. and Scott, M.D. 1994. Bottlenose dolphin. In S.H. Ridgeway and F.R.S. Harrison (eds). *Handbook of marine mammals. Small Cetace*ans. Academic Press, London. 1-55.

Wells, R.S., Hansen, L.J., Baldridge, A., Dohl, T.P., Kelly, D.L. and Defran, R.H. 1990. Northward extension of the range of Bottlenose dolphin along the Californian Coast. In S. Leatherwood R. R. Reeves (eds). *The Bottlenose Dolphi*n. Academic Press, San Diego. 421-431.

Whitt, A. and Read. A. 2006. Assessing compliance to guidelines by dolphin-watching operators in Clearwater, Florida, USA. *Tour. Mar. Environ.* 3(2): 117-30.

Wiley, D.N. Moller, J.C. Pace, R.M. and Carlson, C. 2008. Effectiveness of Voluntary Conservation Agreements: Case Study of Endangered Whales and Commercial Whale Watching. *Conservation Biology*. 22: 450–457

Williams, C. 2007. Doubtful Sound Bottlenose Dolphin, Threat Management Discussion Paper. Department of Conservation, Invercargill, NZ.: 42.

Williams, J.A., Dawson, S.M., and Slooten, E. 1993. The abundance and distribution of bottle-nosed dolphins (*Tursiops truncatus*) in Doubtful Sound, New Zealand. *Canadian Journal of Zoology*. 71(10): 2080-2088.

Wilson, B., Thompson, P.M. and Hammond, P.S. 1997. Habitat use by Bottlenose dolphins: seasonal distributions and stratified movement patterns in the Moray Firth, Scotland. J*ournal of Applied Ecology*. 34: 1365-1374.

Wing, S.R., Gibbs, M.T. and Lamare, M.D. 2003. Reproductive sources and sinks within a sea urchin, *Evechinus chloroticus*, population of a New Zealand fjord. *Mar Ecol Prog Ser*. 248: 109–123.

Wing, S.R., Lamare, M.D. and Vasques, J. 2001. Echinoderms. Population structure of sea urchins *(Evechinus chloroticus)* along gradients in benthic productivity in the New Zealand fjords. In Barker, M.F. (eds). *Echinoderms* 2000. Balkema, Rotterdam .

Xitco, M.J. & Roitblat, H.L. 1996. Object recognition through eavesdropping: passive echolocation in bottle-nose dolphins. *Anim. Learn. Behav*. 24: 355–365.

Zar, J.H. 1999. Biostatistical analysis, Fourth Edition. Prentice-Hall, Inc. Upper Saddle River, New Jersey, USA.