KINEMATICS AND ACOUSTICS OF FORAGING BEHAVIOUR BY A SPECIALIST PREDATOR, THE NORTHERN RESIDENT KILLER WHALE (*ORCINUS ORCA*)

by

Brianna Margaret Wright

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Abstract

Foragers with narrow dietary niches often exhibit specialized hunting behaviours that improve their efficiency for capturing preferred prey, but can leave them vulnerable if the abundance of this prey declines. I examined the specificity of foraging behaviour by a highly selective predator, the northern resident killer whale (*Orcinus orca*), which specializes on Chinook salmon (*Oncorhynchus tshawytscha*). Northern residents are undoubtedly well adapted to capture Chinook, however, their hunting tactics have never been described due to the challenges of quantifying underwater behaviour. To address this research gap, I deployed archival tags (DTAGs) on 32 killer whales to measure their acoustic and kinematic behaviour during foraging dives. Reconstructed 3-dimensional tag tracks indicated that foraging and non-foraging dives were kinematically distinct. While engaged in hunting behaviour, whales dove deeper, remained submerged longer, swam faster, increased their dive path tortuosity, and rolled their bodies more than during other activities. Maximum foraging dive depths reflected both the deeper vertical distribution of Chinook (compared to other salmonids), as well as the tendency of these fish to evade predation by diving steeply. Inferences from whale movements further revealed that salmon engaged in other anti-predation strategies, including increasing swim speeds and evasive manoeuvring. DTAG records also provided the first definitive link between echolocation and prey captures by resident killer whales, who displayed significantly higher clicking rates and spent proportionally more time echolocating prior to capturing a fish than they did afterward. Rapid 'buzz' click sequences were often produced before fish captures, which is consistent with their hypothesized function of close-range prey targeting. Furthermore, prey handling 'crunches' were usually detected following kills and, with buzzes, provide possible acoustic proxies for capture attempts and successes that could be used to estimate foraging efficiency. My thesis determined that northern resident killer whales possess specialized foraging behaviours for targeting Chinook salmon. The specificity of these behaviours may make the whales less effective at capturing other types of fish. If northern residents have limited flexibility to modify their foraging behaviour to successfully exploit other prey types when Chinook availability is reduced, prey capture efficiency (and thus per capita energy intake) could decline.

Preface

The Cetacean Research Program at the Pacific Biological Station, Fisheries and Oceans Canada provided the DTAG data analysed in this thesis. DTAG fieldwork was conducted by myself, V. Deecke, M. deRoos, G. Ellis, A. Shapiro, and J. Towers and was funded by Fisheries and Oceans Canada. Field research and tagging protocols were approved by both the Committee on Animal Care at the University of British Columbia and the Animal Care Committee of the Pacific Biological Station, Fisheries and Oceans Canada. This research was conducted under UBC Animal Care Permit no. A11-0140 and Fisheries and Oceans Canada Marine Mammal Research License no. MML-001. The DTAGs and Matlab calibration toolboxes were rented from Woods Hole Oceanographic Institution (DTAG2, 2009-2011) and the Sea Mammal Research Unit, University of St. Andrews (DTAG3, 2012). Fish scales and tissue samples were analysed by the Fish Ageing Laboratory and the Molecular Genetics Laboratory at the Pacific Biological Station, Fisheries and Oceans Canada, Nanaimo, BC.

I performed the 2010-2012 DTAG calibrations and all of the tag data analysis and writing, with assistance where noted. A. Shapiro conducted the tag calibrations for the DTAGs deployed in 2009. I received advice and assistance with the calibrations from S. DeRuiter, T. Hurst, A. Shapiro and W. Zimmer. I received guidance on the use of TrackPlot visualization software from C. Ware. B. Battaile provided R code and assistance for georeferencing tag tracks and calculating dive path tortuosity. W. Zimmer and S. DeRuiter provided Matlab code and advice about determining arrival time delays for killer whale echolocation clicks between the DTAG hydrophones. V. Deecke provided verification and confidence ratings for recordings of prey handling sounds and buzzes. I received advice on the multivariate statistical methodology used in Chapter 2 from R. Joy, and assistance with linear mixed effects models in R from C. Gerlinsky.

Table of Contents

List of Tables

List of Figures

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Dedication

For my parents, who first introduced me to the beauty and wonder of nature.

“It will be universally admitted that instincts are as important as corporeal structure for the welfare of each species [...] it is at least possible that slight modifications of instinct might be profitable to a species, and if it can be shown that instincts do vary ever so little, then I can see no difficulty in natural selection preserving and continually accumulating variations of instinct to any extent that may be profitable. It is thus, as I believe, that all the most complex and wonderful instincts have originated.”

Charles Darwin, “On the Origin of Species”, © 1859

Chapter 1: Introduction

Foraging behaviour is of particular interest to population ecologists, because successful resource acquisition (in terms of both quantity and quality of prey) has direct consequences for an individual's fitness. Individuals that maximize the efficiency of their foraging behaviours are more likely to survive and reproduce (Pyke 1984), which has implications for long-term population trends. Furthermore, if foraging behaviour is heritable, then hunting tactics that enhance prey capture efficiency should increase in a population over time because the individuals that exhibit them are more likely to survive and pass these behaviours on to the next generation (Pyke 1984). In social animals, the perpetuation of effective foraging behaviours often occurs by social learning, rather than genetic inheritance (Galef and Giraldeau 2001). In this way, it is possible for predator populations to develop extremely specialized foraging behaviours for targeting a single or very narrow range of prey species (Futuyma and Moreno 1988, Beissinger et al. 1994).

Resource specialization is often selectively favoured because it reduces the negative effects of foraging competition between sympatrically occurring species or populations (Miller 1967, Futuyma 2001). Optimal foraging theory predicts that foragers should specialize on prey resources that are the most energetically profitable, so long as they are encountered regularly (Krebs et al. 1977). Lower quality prey may thus be selectively ignored, even when found in greater abundance (e.g., Krebs et al. 1977, Ford and Ellis 2006, Spitz et al. 2010). Predators that exhibit specialized foraging tactics for capturing higher-energy preferred prey will therefore maximize their foraging efficiency; however, behavioural specificity can also become detrimental if the availability of preferred prey declines. Specialized behaviours that are adapted for capturing preferred prey may be poorly suited for capturing other species, so reversion to a generalist mode of foraging or a different specialization is unlikely (Futuyma and Moreno 1988). Instead, prey capture efficiency (and thus energy intake) of specialist predators will probably decline under a scenario of reduced preferred prey availability, leading to increased mortality (e.g., Trowbridge 1991, Ford et al. 2010). For many specialist foragers, vulnerability to decreased prey abundance (or other ecological changes) often results in a correlation between dietary specialization and increased extinction risk (Biesmeijer et al. 2006, Boyles and Storm 2007, Colles et al. 2009). The specialization of foraging behaviour therefore represents an evolutionary trade-off between the benefits of increased feeding efficiency and the costs of being unable to tolerate environmental variability (Futuyma 2001).

Although foraging behaviours represent an observable mechanism by which evolved resource specializations are expressed (Futuyma and Moreno 1988, Beissinger et al. 1994), the adaptive significance of particular behaviours exhibited by specialist foragers is often not well understood. Describing specialized foraging behaviours, their mode of transmission to naïve individuals, and their correlation to the distribution and behaviour of preferred prey species provides insight into how foraging specializations are expressed and maintained within a population. In addition, understanding the relative degree of behavioural plasticity exhibited by specialist foragers should provide information about their sensitivity to changes in prey resources, which can be directly related to extinction risk (Colles et al. 2009). Given the coevolutionary nature of predator hunting behaviour and evasive behaviour of prey (Dawkins and Krebs 1979), analysis of specialized foraging tactics can also reveal information about the predator avoidance strategies used by preferred prey species.

1.1 Northern resident killer whales: Chinook salmon specialists

Northern resident killer whales (*Orcinus orca*) are one of two regional subpopulations of 'residents', a piscivorous ecotype of killer whale that preferentially feeds on Pacific salmon (*Oncorhynchus* spp.) for at least half of the year (96% of 529 recorded feeding events, primarily from May to October) (Ford and Ellis 2006). They range throughout the coastal waters of the eastern North Pacific, from central Vancouver Island to southeastern Alaska (Ford et al. 2000). Critical habitat for northern residents has been identified in the Johnstone Strait area of northeastern Vancouver Island (Ford 2006). This region experiences high use by the whales, particularly in the summer months, when they congregate to exploit runs of salmon returning to the Fraser River (Ford 2006).

Northern resident killer whales are listed as 'Threatened' under Canada's Species at Risk Act (SARA) (Fisheries and Oceans Canada 2008) and currently number 261 individuals (2010 census, Ellis et al. 2011). Since the first photo-identification census in 1974, the northern resident population has increased at annual rates of approximately 3.0% from ~120 to 220 individuals by 1997 (Fisheries and Oceans Canada 2011). It then declined by 7% to 205 whales in 2003 (Fisheries and Oceans Canada 2011), but has since increased to 261 whales in 2010 (Ellis et al. 2011). Although their numbers have grown over the last forty years, northern resident killer whales are designated as a threatened species due to their small population size, low reproductive rates, and threats to their continued population growth from various human activities (Fisheries and Oceans Canada 2011). The most important identified threats to northern residents include reductions in the availability and quality of their prey, and physical or acoustic disruption of their behaviour (including foraging) (Fisheries and Oceans Canada 2011). Northern residents are not expected to achieve very great numbers, because the population is closed to immigration and emigration, and its growth rate is restricted by delayed reproductive maturity, long calving intervals, and small numbers of reproductive adults (Fisheries and Oceans Canada 2011). Management goals thus focus on ensuring that the number of reproductive individuals is adequate to preserve a level or increasing population growth rate (Fisheries and Oceans Canada 2011).

Piscivorous resident killer whales exhibit an extreme degree of foraging specialization, which minimizes resource competition with two other sympatric killer whale ecotypes: Bigg's (transient) killer whales that specialize on marine mammals (Ford et al. 1998), and offshore killer whales that likely specialize on elasmobranchs (Ford et al. 2011). Not only do resident killer whales primarily consume Pacific salmon, they preferentially target a single species of salmon (Chinook, *O. tshawytscha*) for at least 4 months of the year (May to August) (Ford et al. 1998, Ford and Ellis 2006). Identification of prey remains collected following the foraging dives of resident killer whales (May to December) indicated that Chinook made up 71.5% of all salmon kills identified to species (Ford and Ellis 2006). Chum salmon (*O. keta*) are the second-largest and were the next most commonly consumed species (22.7%) of Pacific salmon (Ford and Ellis 2006). Chum made up the majority of sampled kills in autumn (September to October), although Chinook were still preferentially targeted during this season when they were available (Ford and Ellis 2006, Ford et al. 2010). While the winter and spring dietary composition of resident killer whales remains uncertain (Ford et al. 1998, Ford and Ellis 2006, Ford et al. 2009, Fisheries and Oceans Canada 2011, Hilborn et al. 2012), the available data suggest that Chinook are probably still important (Ford et al. 2009).

Despite being one of the least abundant Pacific salmon species in British Columbia (Riddell 2004), Chinook are likely preferred by residents due to their large size, high lipid content, and year-round availability in coastal waters (Ford and Ellis 2006). The high exploitation rate of chum salmon (90%) in the fall is probably due to the increased coastal availability of this species during their seasonal spawning migration (Ford and Ellis 2006). However, despite similar seasonal increases in the abundance of smaller migrating salmonids, such as pinks (*O. gorbuscha*) and sockeye (*O. nerka*), these species do not make up a significant part of resident killer whale diet

(Ford et al. 1998, Ford and Ellis 2006). Groundfish such as lingcod (*Ophiodon elongatus*), Pacific halibut (*Hippoglossus stenolepis*), sablefish (*Anoplopoma fimbria*), greenling (*Hexagrammos* sp.) and rockfish (*Sebastes* spp.) have also appeared infrequently in resident killer whale prey samples and stomach contents (Ford et al. 1998, Ford and Ellis 2006, Ford et al. 2010). However, there is no indication that groundfish contribute significantly to the diet from May to October, when salmon are the predominantly consumed prey species (Ford and Ellis 2006, Fisheries and Oceans Canada 2011).

Reduced prey availability, specifically depressed Chinook salmon stocks, has been identified as a important factor that may be limiting the population growth and recovery of resident killer whales (Fisheries and Oceans Canada 2011). Correlations between relative annual Chinook salmon abundance and resident killer whale survival and birth rates have been observed (Ward et al. 2009, Ford et al. 2010). In addition, Foster et al. (2012) determined that the social networks of southern resident killer whales have a reduced degree of connectivity in years with low Chinook salmon abundance. This correlation implies that when prey are less available, southern residents must invest more time in locating fish, and thus have fewer opportunities to engage in social interactions (Foster et al. 2012). Similarly, Parsons et al. (2009) found that southern resident social cohesion during the summer months (as measured by the level of intrapod associations) decreased in concurrence with a decline in their population size during the mid to late 1990s. Coinciding reductions in population size and the social association rates of southern resident killer whales may be driven by changes in the abundance or distribution of their prey (Parsons et al. 2009), as annual abundance indices for Chinook were also lower than average for multiple consecutive years during the same time period (1993-2001) (Ford et al. 2010).

It is probable that the high degree of resource specialization displayed by residents is accompanied by equally specialized foraging behaviours. The specificity of these hunting tactics likely restricts the ability of resident killer whales to exploit alternative prey species when Chinook availability is reduced (Ford et al. 2010). Behavioural constraints on resident killer whale foraging efficiency for non-preferred prey could lead to nutritional stress, which may be responsible for the observed correlation between decreased Chinook abundance and increased whale mortality (Ford et al. 2010). Mitigating human activities that disturb foraging behaviour or significantly reduce the availability of Chinook salmon (particularly in critical habitat during the summer months) will therefore help to ensure the continued population recovery of northern resident killer whales.

1.2 Studying underwater behaviour using acoustic biologging tags

Animal behaviour is complex, difficult to quantify, and its study is frequently subject to observer biases that arise from sampling methodology (Altmann 1974). Studying the behaviour of cetaceans presents additional challenges, since these species often have large home ranges, are highly mobile or migratory, and spend long periods of time underwater (Mann 1999). To overcome some of these problems, acoustic biologging tags (e.g., Johnson and Tyack 2003, Akamatsu et al. 2005) have been developed that can record information on the fine-scale movement and coinciding vocal behaviour of individual cetaceans. By deploying these tags on individual whales, previously undescribed behaviours can be indirectly observed and quantified in detail. Acoustic tags are particularly useful for studying the foraging behaviour of toothed whales that emit sonar clicks, as acoustic behaviour (echolocation) is thought to be critical to the detection and pursuit of prey by these species (Johnson et al. 2009).

For my study, I used a suction-cup-attached archival tag known as the DTAG to visualize the short-term (< 1 day) diving behaviour of northern resident killer whales. DTAGs are equipped with sensors for measuring depth, water temperature, and orientation, as well as on-board hydrophones to record underwater sound (Johnson and Tyack 2003). Depth is determined by a pressure sensor with a range of 0-2000 m and resolution of 0.5 $m \cdot H_2O$ (Johnson and Tyack 2003). Three-dimensional body orientation is determined by measuring the Euler angle parameters of pitch, roll and heading, which requires two sets of sensors. Pitch and roll are measured by capacitive and triaxial accelerometers that sense the animal's dynamic acceleration, as well as its orientation relative to gravitational pull. Heading is measured by a triaxial magnetometer that detects the direction of the earth's magnetic field relative to that of the tag (Johnson and Tyack 2003). Body orientation can be measured at sampling rates of up to 50 Hz (Johnson and Tyack 2003). The DTAG uses a low-power digital signal processor to combine the hydrophone audio recording with coinciding sensor measurements, which it archives on solid-state flash memory (Johnson and Tyack 2003). The tag components are powered by a lithium-ion battery and housed in an external polyethylene casing or embedded in moulded polyurethane to reduce drag (Johnson and Tyack 2003).

1.3 Study goals and thesis structure

The primary goal of my study was to quantitatively describe the foraging behaviour of northern resident killer whales, which was expected to show adaptations for selectively targeting and capturing Chinook salmon. To accomplish this, I deployed acoustic biologging tags (DTAGs) to obtain high resolution, three-dimensional movement data during northern resident feeding dives, and determined which kinematic traits best distinguished foraging from other behaviours. I then compared the structure of foraging dives to the distribution and behaviour of Chinook and other species of Pacific salmon to identify the specificity of this behaviour for capturing preferred prey species. I also sought to investigate the role of social learning in the transmission of foraging behaviours to juvenile resident killer whales, as this could help to explain the maintenance of resource selectivity in this population despite past fluctuations in Chinook abundance.

The acoustic recordings collected by the DTAGs provided the first opportunity to definitively link echolocation behaviour with foraging dive behaviour and prey captures by wild resident killer whales. Since echolocation is assumed to function in the detection and capture of prey, I expected that northern resident killer whales would invest greater effort in echolocation before capturing a fish than they would afterward. I therefore compared the relative click repetition rates and the total proportion of time spent echolocating between the pre- and post-capture phases of northern resident foraging dives. I also analysed the acoustic recordings for sounds that could signify prey capture attempts (e.g., rapid click sequences, or 'buzzes') or successes (e.g., prey handling sounds), to determine whether acoustic tag data could be used to estimate resident killer whale foraging efficiency.

My thesis contains four chapters: a general introduction, two data chapters, and a general conclusion. The two data chapters are written in manuscript style for publication as peer-reviewed journal articles. This led to a certain degree of repetition, particularly in the Methods sections, as the data for both chapters were collected using the same DTAG instrumentation over the same field seasons (2009-2012). Chapter 2 examines the movement characteristics that distinguish foraging and non-foraging dives by northern resident killer whales, and identifies ways in which foraging dives are behaviourally adapted to target their preferred prey, Chinook salmon. I also used the DTAG data to investigate the role of social learning in the transmission of these specialized foraging behaviours. Chapter 3 analyses the functional significance of echolocation during successful salmon captures by relating the occurrence of sonar clicks to the diving kinematics of foraging northern residents. This chapter also identifies acoustic indicators of capture attempts and successes that could be useful for calculating foraging efficiency. As a whole, my thesis endeavours to provide the first quantitative description of underwater foraging behaviour (acoustic and kinematic) by individual resident killer whales using high-resolution, multi-sensor biologging tags.

Chapter 2: Movement characteristics of foraging dives by northern resident killer whales indicate effective targeting of preferred prey

2.1 Summary

Northern resident killer whales (*Orcinus orca*) of the northeastern Pacific Ocean are specialist predators that rely on Pacific salmon, and preferentially feed on Chinook salmon (*Oncorhynchus tshawytscha*). However, little is known about how resident killer whales search for, pursue, and capture their preferred prey. I used high-resolution 3D movement data collected by digital archival tags (DTAGs) to obtain the first quantitative description of underwater hunting behaviour by northern resident killer whales. I determined the movement characteristics that differentiate foraging dives from other behaviours and tested how well they corresponded to the swimming behaviour of six species of Pacific salmon. Tags were deployed on 34 occasions involving 32 different killer whales in coastal British Columbia over four field seasons (2009-2012). I calculated a set of 16 kinematic variables to quantitatively describe the movements of tagged whales during 11,319 dives (>1 m). Multivariate analyses of these kinematic dive characteristics revealed three main dive types: foraging dives (n=701), respiration maintenance dives (n=7,050), and dives encompassing all other behaviours (n=3,568). Relative to respiration dives and other behaviours, foraging dives were typically longer (mean ± SD: 3.1 ± 1.7 min), deeper (64.5 ± 61.0 m), and had greater path tortuosity (straightness index <0.90). Whales also swam at greater speeds (2.1 ± 0.8 m s^{-1}), descended (0.8 ± 0.5 m s^{-1}) and ascended (0.8 ± 0.6 m s^{-1}) faster, and rolled their bodies to a greater extent (mean: 32.6 ± 27.1°, mean maximum: 115.5 ± 64.1°) while foraging. Of the six Pacific salmon species, hunting tactics used by northern resident killer whales corresponded best to the behaviour of Chinook salmon. Maximum foraging dive depths overlapped considerably with average Chinook swimming depths (43.4 ± 15.4 m) measured by previous telemetry and ultrasonic tagging studies, as well as to catch depths for Chinook reported by scientific test fisheries. I demonstrate that hunting behaviour by northern residents is fine-tuned for capturing this species of salmon. Quantitative analysis of killer whale foraging dives also provided indirect evidence of escape behaviours used by Pacific salmon. Understanding the selective foraging tactics of northern residents contributes new information to conservation planning that can help to minimize human disturbance of their feeding behaviour.

2.2 Introduction

As a species, killer whales (*Orcinus orca*) are globally distributed and exploit an extremely diverse array of prey types (Ford 2002). At the population scale, however, killer whales often exhibit multiple sympatric forms (ecotypes) that have distinct dietary specializations. These ecologically divergent forms have arisen in the absence of geographic isolation, likely because dietary specialization reduced the potential for harmful resource competition between groups (Foote 2012, Riesch et al. 2012). Extreme resource specialization often leads to development of ecotype-specific foraging behaviours that are adapted to target a single or very narrow range of prey types. For example, pack-ice killer whales (one of several Antarctic ecotypes) employ coordinated echelon swimming to generate waves that wash seals off of ice floes (Pitman and Durban 2012). Intentional self-stranding has been documented as a specialized hunting tactic used by killer whales in Patagonia (Lopez and Lopez 1985) and the Crozet Archipelago (Guinet and Bouvier 1995) to capture pinnipeds. Furthermore, a Norwegian ecotype engages in cooperative 'carousel' herding with stereotyped tail-slapping movements to corral, stun and consume herring (Simila and Ugarte 1993, Domenici et al. 2000).

The 'resident' killer whales of the eastern North Pacific are another ecotype that displays a high degree of dietary specialization. They feed almost exclusively on salmon, and prefer Chinook salmon (*Oncorhynchus tshawytscha*) over any other species (Ford and Ellis 2006). The resident ecotype is composed of two regional populations: the northern and southern resident killer whale communities (Ford et al. 2000). The northern resident community ranges from central Vancouver Island, British Columbia to southeastern Alaska (Ford et al. 2000) and as of the 2010 population census, numbered 261 individuals (Ellis et al. 2011). It is listed as 'Threatened' under Canada's Species at Risk Act (Fisheries and Oceans Canada 2008). The 'Endangered' southern resident community (Fisheries and Oceans Canada 2008) numbered 87 individuals as of 2011 (Hilborn et al. 2012), and ranges from coastal California to Haida Gwaii, off the northern coast of British Columbia (Ford et al. 2009).

Diet composition of resident killer whales has been studied intensively using techniques such as stomach contents analysis and prey fragment identification (via genetics or sclerochronology) to determine the relative importance of different prey species (e.g., Ford et al. 1998, Ford and Ellis 2006, Ford et al. 2009). Although Chinook salmon is one of the least abundant Pacific salmon species in British Columbia (Groot and Margolis 1991, Riddell 2004), it is the principal prey species targeted by resident killer whales and accounted for 71.5% of all identified salmon kills (May to December) in a long-term foraging study (Ford and Ellis 2006). Selectivity for Chinook was most prevalent during the summer (May to August), when this species made up the majority of sampled prey remains by month (Ford and Ellis 2006).

Chinook are thought to be preferred by resident killer whales (Ford and Ellis 2006) due to their large size and high lipid content (Stansby 1976), which make them energetically profitable, as well as their consistent year-round availability in the coastal waters of North America (Groot and Margolis 1991). Unlike the smaller species of Pacific salmon and stream-type Chinook (yearling smolts), which are distributed offshore until reaching reproductive maturity, ocean-type Chinook (sub-yearling smolts) remain in coastal habitats throughout their lives (Healey 1983). Killer whales exploit ocean-type Chinook more frequently (75% of aged prey samples, n=325) than stream-type Chinook (25%, n=106), which is probably due to the consistent availability of ocean-type fish within the whales' habitat (Ford et al. 2009). Chum salmon (*O. keta*) is the second largest and next most commonly consumed species (22.7%), and becomes a particularly important food source in September and October when its coastal availability increases during the spawning migration (Ford and Ellis 2006). The composition of resident killer whale diet during the winter and spring (November to April) remains largely undescribed (Ford et al. 1998, Ford and Ellis 2006, Ford et al. 2009, Hilborn et al. 2012), due to the difficulty of collecting prey fragments during this season. Although the dataset for winter is small, Chinook is still by far the predominant prey species, even more so than in the fall (Ford et al. 2009).

Smaller salmonids, such as sockeye (*O. nerka*) and pink (*O. gorbuscha*), are occasionally consumed by residents, but do not make up a significant part of the diet (Ford et al. 2010). Although these species are seasonally abundant within the whales' range (Ford et al. 2010), they spend the majority of their lives maturing in the open ocean, and only return to nearshore habitat prior to spawning in freshwater (Groot and Margolis 1991). Despite the predictability of these seasonal returns, the absence of sockeye and pink salmon from the coast during much of the year (as well as their relatively small body sizes) probably makes them less desirable as prey. It is more likely that they are taken opportunistically by foraging whales, rather than being targeted specifically. A recent experimental study suggests that killer whales can acoustically distinguish between Chinook and other species of salmon based on swim bladder shape and orientation, which is indicated by the structure of returning echolocation clicks (Au et al. 2010).

Correlations between the vital rates of resident killer whales (survival and births) and the relative abundance of Chinook (Ford et al. 2010) suggest that resident population recovery may be affected by the availability of this prey species (Fisheries and Oceans Canada 2011). The switch to chum salmon predation in the fall, as well as the occasional consumption of non-salmonids, indicates that resident killer whales are capable of capturing alternative prey when Chinook are not available (Ford et al. 1998, Ford and Ellis 2006). However, given the high degree of resource specialization exhibited by residents, their hunting techniques are likely to be most efficient for capturing Chinook and the range of potential alternative prey may therefore be limited (Ford et al. 2010). Adaptations that facilitate specialized diets (such as species-specific foraging behaviours) may impede individuals from either adjusting to a generalist mode of resource use, or switching to a different resource specialization (Futuyma and Moreno 1988) following a change in availability of the preferred resource. Killer whales that are less efficient at catching alternative prey when Chinook become unavailable could experience nutritional stress, which may help to explain the negative correlation between relative Chinook abundance and resident mortality (Ford et al. 2010). A lack of behavioural flexibility in foraging strategies could thereby result in reduced population growth when preferred prey are not available in sufficient quantities. However, current data are inadequate to link evidence of poor resident body condition to nutritional stress caused by reduced abundance of Chinook salmon (Hilborn et al. 2012).

In addition to establishing dietary composition, past studies have also described general patterns of foraging behaviour for resident killer whales based on observations of activity visible at the water's surface. While hunting, pods tend to separate into smaller subgroups that spread out over several square kilometres, but travel in the same general direction (Ford 1989). Dives by individuals in these subgroups are typically asynchronous, and often coincide with sudden changes of direction, lunges or milling behaviour (Ford 1989). Foraging whales usually have dive sequences of several short dives followed by a longer 1-2 min dive (Ford 1989). Capture success following these longer dives is often apparent based on the presence of fish scales and flesh in the upper water column after the whale has surfaced (Ford and Ellis 2006). Such physical remains from kills are especially evident when fish are broken up and shared, a behaviour that occurs frequently between related individuals (Ford and Ellis 2006). Although dietary specialization for Chinook salmon has been predicted to significantly affect the expression of resident killer whale foraging behaviour (Ford and Ellis 2006), much of this behaviour occurs underwater and cannot be observed directly. The specific hunting tactics that make these whales such effective salmon predators have therefore remained largely unknown. Recent advances in cetacean tagging technology (e.g., Johnson and Tyack 2003), however, have now provided the necessary tools for describing underwater hunting behaviour in detail. This new information can provide insight into the adaptive significance of various behaviours, as well as helping to explore the influence of prey selectivity on the structure of foraging dives.

The primary goal of my study was to quantitatively describe the kinematic behaviours used by resident killer whales during foraging dives, and to compare these to the distribution and behaviour of Pacific salmon. To accomplish this, I recorded fine-scale underwater movements of whales during foraging and other behaviours using digital archival tags (DTAGs; Johnson and Tyack 2003). Dive behaviour during hunting was expected to show adaptations for the targeting of preferred prey (Chinook salmon). To test this hypothesis, I compared the kinematics of resident killer whale foraging behaviour to published data on Pacific salmon swimming behaviour. Information about how these predators selectively target Chinook underwater can be used to inform resident killer whale conservation planning and ensure that preferred prey availability is sufficient to support continued population recovery.

2.3 Methods

2.3.1 Study area and DTAG instrumentation

The diving behaviour of northern resident killer whales was studied over four field seasons in August and September, 2009-2012 in the coastal waters of northeastern Vancouver Island and the central coast of British Columbia, Canada (Figure 2.1). The main study area off northeastern Vancouver Island was chosen because northern residents are predictably found there during summer and fall, as this region is a primary migration corridor for salmon returning to the Fraser River (Nichol and Shackleton 1996, Ford 2006, Ford and Ellis 2006). Consequently, whales are known to spend substantial time engaged in foraging behaviour within this nearshore habitat (Ford 1989, 2006, Ford and Ellis 2006).

Kinematic dive data were collected using suction-cup attached DTAGs (Johnson and Tyack 2003) equipped with sensors that simultaneously recorded pressure (depth), sound (using two on-board hydrophones), and three-dimensional body orientation (using tri-axial accelerometers and magnetometers to determine changes in pitch, roll and heading over time).

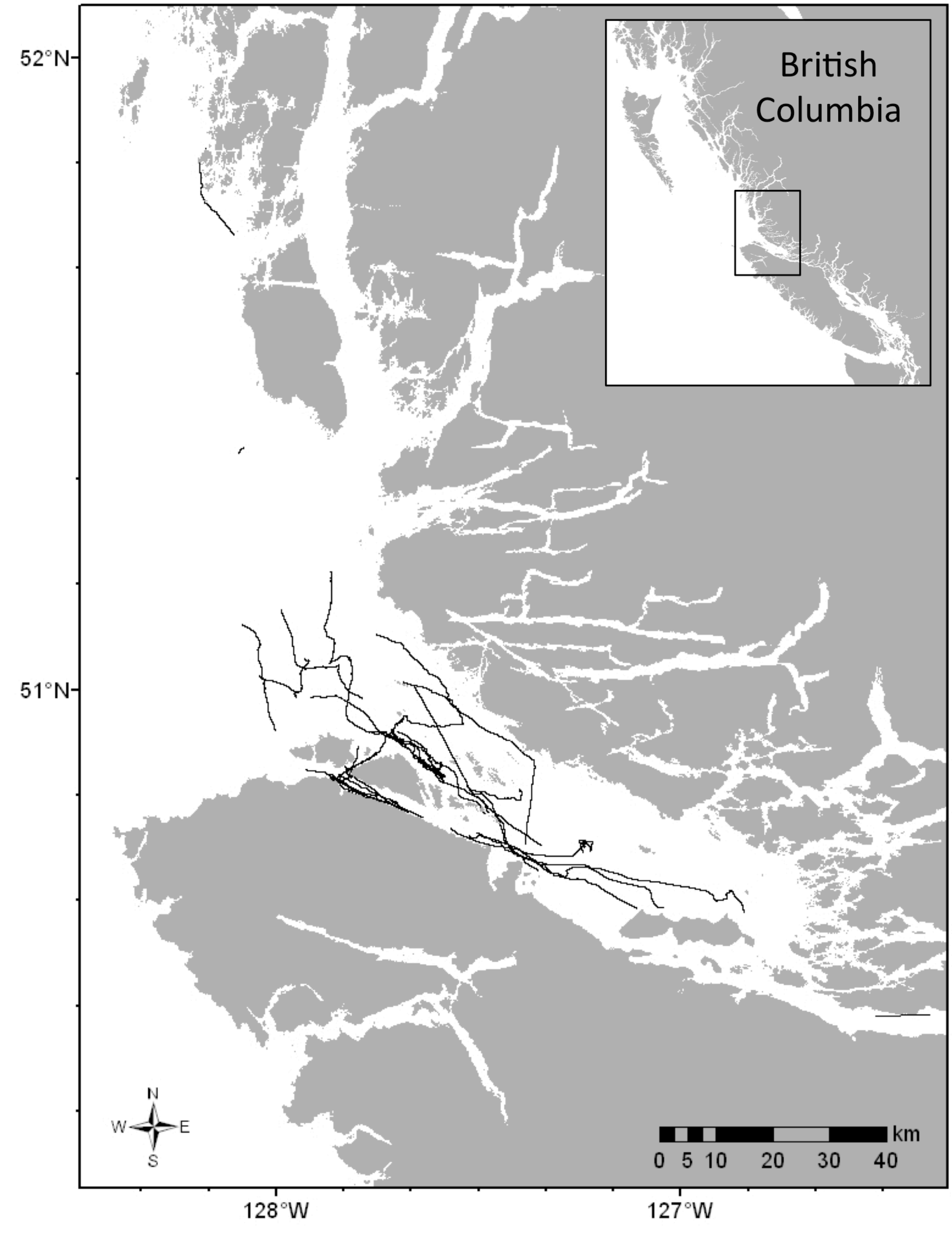

Figure 2.1 Georeferenced tracks (black lines) obtained by dead reckoning for 31 deployments of digital archival tags (DTAGs) on northern resident killer whales in British Columbia during August and September, 2009-2012.

On-board flash memory stored the data until tags were retrieved and the data were transferred to a computer (Johnson and Tyack 2003). The sampling rate for the pressure and orientation sensors was 50 Hz for 2009-2011 tags and 250 Hz for 2012 tags, and all sensor data were eventually reduced to 5 Hz during tag calibration.

After visually establishing the identities of encountered whales using an existing photo-identification catalogue of individual dorsal fin and saddle patch morphology (Ellis et al. 2011), a single whale was selected for tagging. The research platform was a 10-m command-bridge powerboat that provided an elevated vantage point, allowing the boat operator to see the whale underwater just prior to surfacing and position the vessel accordingly for DTAG deployment. To minimize the potential impacts of tagging, only adults and larger-sized juveniles were tagged and repeat deployments on previously tagged whales were avoided where possible. Calves and younger juveniles were not tagged because they were small and the least likely to be engaged in foraging behaviour, relying instead on milk or shared fish caught by related individuals. Repeated deployments on the same whale were also avoided to minimize the relative influence of idiosyncratic behaviours on the statistical analysis and ensure a maximally diverse sampling of behaviour.

2.3.2 DTAG deployments and focal follows

Whales selected for tagging were paralleled by the research vessel to match their speed of travel and swimming direction. The DTAG was then deployed from the bow of the vessel using a 7-m long, hand-held carbon-fibre pole. The preferred placement of the tag was on the back just below the insertion of the dorsal fin, so that it would clear the water when the whale surfaced to allow for tracking of the tag's VHF radio beacon. The tagged whale was followed slowly at distances of 10-200 metres for up to 12 hours until the suction cups detached via a timed, burn-wire release mechanism. In some cases, tags were dislodged prior to the programmed release time by sudden animal movements (e.g., breaching) or by suction cup failure. Once released, the floating DTAG was located using a directional VHF receiver and recovered to upload the kinematic dive data.

DTAG deployments were combined with focal follows of tagged individuals to correlate surface observations of foraging activity with archived tag data. The need for concurrent surface observations limited the tag deployments to daylight hours. The tagging vessel operated on a surface-drive propulsion system, which greatly reduced underwater noise by eliminating propeller cavitation. This minimized the chance that noise disturbance from the tagging vessel would affect the behaviour of the tagged whales during the focal follows. Whale surfacing locations (determined periodically by GPS fixes from the tagging vessel) and behavioural observations were noted using a digital voice recorder that was time-synchronized with the DTAG sensor instrumentation. This allowed tag sensor data to be referenced against simultaneous behavioural cues observed at the surface. Following the methodology of Ford and Ellis (2006), scales and tissue fragments were collected from the water (at depths of up to 2-3 m) using a long-handled dip net. These samples were used to confirm successful foraging dives and to identify the species and age of fish captured. Fish species were identified using either schlerochronology methods (MacLellan 2004) or genetic analysis (Withler et al. 2004); schlerochronology was also used to establish the age of each fish.

2.3.3 DTAG calibration and identification of dives

Sensor data uploaded from the DTAGs were calibrated to correct for the orientation of the tag relative to the body axes of each tracked whale using established methods (Johnson and Tyack 2003) in MATLAB (MATLAB 2009). Changes in the position of the DTAG on the animal due to tag slippage required performing new calibrations for every new orientation of the tag. Calibration converted raw sensor measurements of pressure into depth, and raw acceleration data into the three rotational measures of pitch, roll, and heading.

I visualized the time series of whale body orientations for each tag deployment using the software package TrackPlot 2.3 (Ware et al. 2006), which combines the calibrated pitch, roll, heading and depth values to create a three-dimensional representation (termed “pseudotrack”) of tagged whale movements (Figure 2.2). Since DTAGs do not directly measure swim speed, the pseudotracks were constructed by assuming a constant velocity of 1.6 m s^{-1}, which is a measured average swimming speed of foraging resident killer whales (Ford 1989). The exception to this assumption occurred when the whale was diving steeply, in which case TrackPlot estimated swim speed using the rate of change in depth, corrected by the sine of the whale’s pitch angle (Ware et al. 2006, Ware et al. 2013).

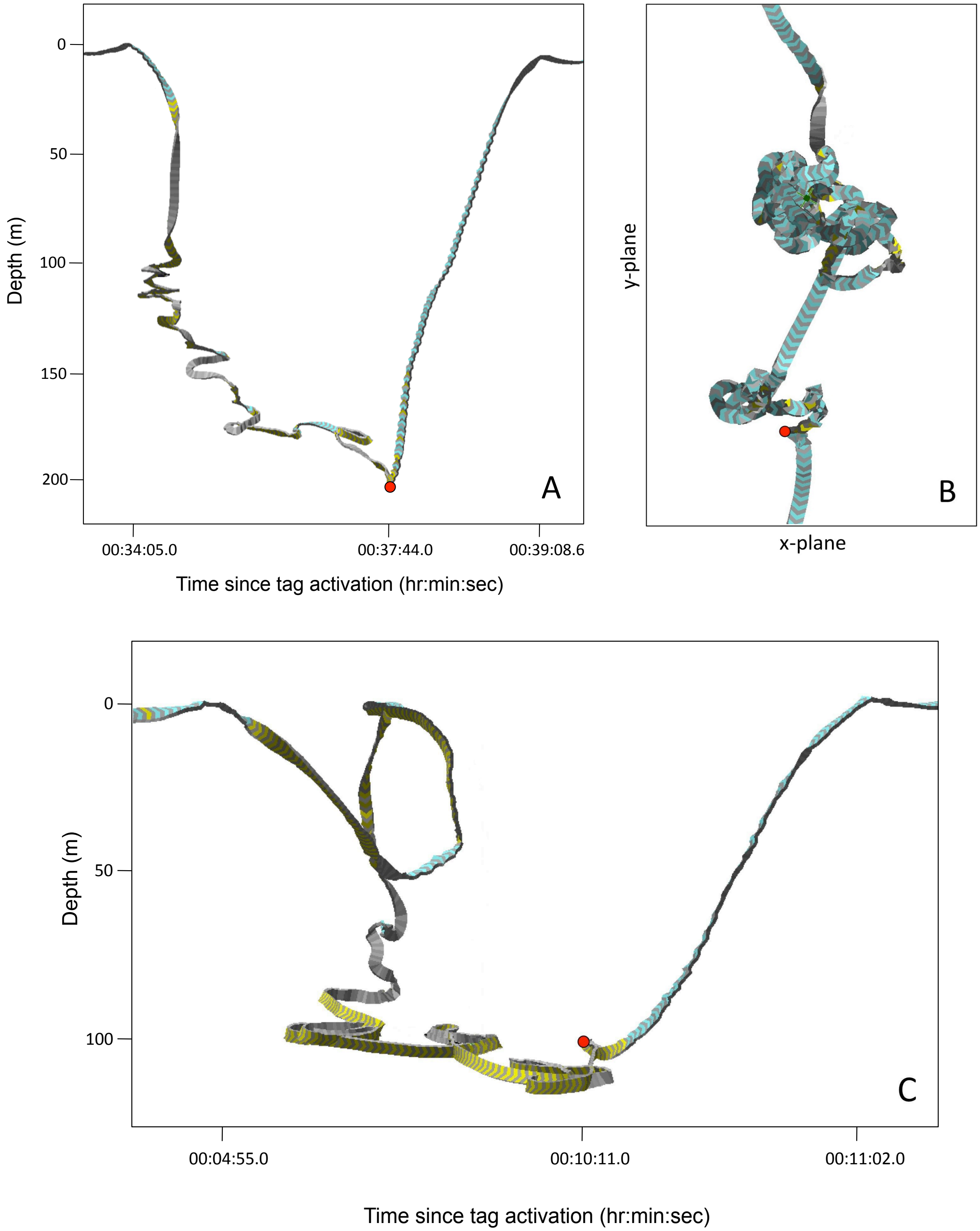

Figure 2.2 Three-dimensional reconstructions of 3 foraging dives by northern resident killer whales. A and C are side views of Chinook captures at depth, while B is an aerial view of a surface chase resulting in a chum capture. Red dots represent the probable positions of fish captures. Yellow portions of the track indicate when the whale rolled >40 degrees in either direction, while blue portions indicate roll values of <40 degrees.

Once calibrated, dives were identified using an automated filter in MATLAB (2009) that defined a dive as any event with a depth of 1 m or greater, bounded by surfacing events of <1 m depth. I chose a shallow depth threshold to ensure that all submersions and surfacings would be detected. Generally, each surfacing represented a single breath and immediate submersion by the tagged animal, although very rarely logging behaviour with multiple breaths per surfacing was also noted. Logging behaviour was not included in the dive behaviour analysis. The dive detection filter calculated start and end times (in seconds since tag activation) and maximum depth (m) for each of the identified dives.

The first 10 minutes of dive data for each tag deployment were excluded from further analysis to discount potentially atypical behaviours caused by reactions of the whales to being tagged. Ten minutes was selected as a conservative threshold for excluding any reactions to tag deployment, as most whales displayed mild behavioural responses (rolling or a slight flinch as the tag was applied) and resumed their pre-tagging swimming patterns within a few surfacings (typically <1-2 min). The whale that responded the most dramatically to tag attachment (A37, oo09_240a) dove to a depth of 426 m, and returned to its pre-tagging behaviour within 9.4 min of the tag deployment. In addition, another tagged whale (A66, oo12_235b) successfully caught a Chinook salmon only 14.8 min after it was tagged. I concluded that whales would be unlikely to engage in successful feeding behaviour if they were still reacting to the presence of the tag, so a 10 min threshold was chosen to prevent the loss of this important true-positive Chinook feeding dive from the data set, while maintaining reasonable confidence that all tagging reaction behaviours had been excluded. Thirty-two dives from tag oo09_235a (A72) that occurred during an acoustic playback experiment were also discounted to exclude potentially anomalous behaviours.

The accuracy of the automated dive detection filter was checked using 50 randomly selected dives that were visually inspected against the three-dimensional pseudotrack representation generated by TrackPlot. The start time, end time and maximum depth of each dive, as calculated by MATLAB, were manually checked against the corresponding values generated by TrackPlot. Overall, the MATLAB dive detection filter was 96% accurate: only two of the 50 dives displayed by TrackPlot showed minor deviations from the start and end times identified by the filter. These two dives were both from the same tag (oo09_238a), were extremely shallow (maximum depths of 1.12 and 1.67 m), and were bounded by indistinct surfacing events, which likely made them difficult for the filter to resolve.

2.3.4 Georeferencing of tag tracks by dead reckoning

A time-series of geographical locations for each whale was derived via dead reckoning, and was georeferenced using the periodic GPS fixes obtained during focal follows, since DTAGs do not have a GPS sensor or provide a direct measure of swimming speed. Generic x-y location data (no units) were generated in MATLAB with an existing program (ptrack) developed by Woods Hole Oceanographic Institute that uses a Kalman filter to estimate swim speed from the pressure (depth) and pitch sensor measurements. These estimates of speed, along with the tag sensor measurements of swimming direction (heading), were used to determine the x-y position of each whale relative to its starting location over the length of the deployment. The resulting tag tracks were then georeferenced by forcing them to pass through a series of GPS points (Wilson et al. 2007, Battaile 2014) collected from the research vessel at occasional surfacing locations by each tagged whale.

Accurate surfacing location fixes were obtained using the boat's GPS with minimal disturbance to the tagged whales by placing the boat over the 'fluke print' of a previous dive. Fluke prints are circular areas of smooth water created from displacement by the whale's body and turbulence from its tail stroke as it dives, and remain temporarily visible on the surface after the whale has moved on. I then matched the fluke print coordinates to the corresponding surfacing time on the tag record using the time-synchronized audio field notes. Because dead reckoning uses an estimated prior position to calculate later locations along the track, position estimates were subject to compounding error. Tracks with relatively fewer GPS surfacing location fixes therefore contain a greater degree of error than those with more frequently collected reference locations. Georeferenced tracks were plotted using ArcGIS software (ESRI 2011).

2.3.5 Calculation of kinematic dive variables

To summarize whale movements, a set of kinematic variables was calculated for each dive using both raw sensor data and the dead reckoned whale locations. These variables included descriptors of entire dives, such as dive duration (s), maximum dive depth (m), two-dimensional dive path tortuosity, mean vectorized Dynamic Body Acceleration (VeDBA), maximum absolute roll (degrees), mean absolute roll (degrees), overall dive speed (m s^{-1}), and the ratio of descent to ascent duration. Additional variables were calculated for the descent and ascent phases separately, including three-dimensional dive path tortuosity, vertical velocity (m s^{-1}), mean rate of change in roll (degree s^{-1}), and mean rate of change in pointing angle (degree s^{-1}). All kinematic variables were chosen based on their hypothesized ability to distinguish foraging dives from other behaviours.

Tortuosity is the degree of convolution in an animal's path of movement, and was estimated using a simple straightness index (Batschelet 1981, Weimerskirch et al. 2002, Benhamou 2004, Miller et al. 2011). This index, hereafter referred to simply as straightness, was calculated as the ratio of the shortest (straight line) distance between two surfacing locations (*D*) and length of the actual path travelled by the tagged whale between those two locations (*L*):

$$straightness = \frac{D}{L} \qquad \text{Eq. 1}$$

Straightness yields values between 0-1, with 1 representing a completely straight path and smaller values signifying a more convoluted, tortuous path. Using the dead-reckoned whale positions, I calculated straightness in both two-dimensions (x-y only) over whole dives and in three-dimensions over each descent and ascent phase. Estimates of *D* and *L* calculated from the dead-reckoned pseudotracks were rounded to the nearest 0.1 m prior to calculating straightness.

For two-dimensional straightness, the distance (*D*) portion of the equation was calculated using the Spherical Law of Cosines to determine the Great Circle distance between consecutive surfacing locations (where ϕ=latitude, λ=longitude, and R=radius of the Earth, or 6,371,000 m).

$$D = \arccos(\sin(\phi_{initial}) \times \sin(\phi_{final}) + \cos(\phi_{initial}) \times \cos(\phi_{final}) \times \cos(\Delta\lambda)) \times R \qquad \text{Eq. 2}$$

For three-dimensional straightness, the distances of descents and ascents were calculated as the Euclidean distance between each surfacing location and the coordinates at maximum dive depth using a three-dimensional extension of the Pythagorean Theorem (where ϕ=latitude, λ=longitude, d=depth).

$$D = \sqrt{(\Delta\phi)^2 + (\Delta\lambda)^2 + (\Delta d)^2} \qquad \text{Eq. 3}$$

Path lengths (*L*) for the straightness index were determined by first calculating the Euclidean distance travelled over each sampling interval (0.2 s) using the Pythagorean Theorem in either two- or three-dimensions. These distances were then summed over the entire time period of interest (i.e., whole dive, descent, or ascent) to obtain its path length. Dive speed (m s^{-1}) was also calculated using the same dead-reckoned, three-dimensional dive path lengths; these path lengths were divided by total dive duration to determine overall dive speed. Vertical velocities, conversely, are based solely on sensor data rather than dead-reckoned positions, and were determined by calculating the change in depth over time (m s^{-1}) for each dive phase.

Dynamic Body Acceleration (DBA) is a measure that summarizes tri-axial body acceleration and is believed to be a proxy for an individual's movement-based metabolic rate (i.e., its energy expenditure as indicated by the rate of oxygen consumption, or VO_2) (Wilson et al. 2006, Qasem et al. 2012). I chose to calculate VeDBA (the vectorial sum of DBA), rather than the more commonly used Overall Dynamic Body Acceleration (ODBA), as VeDBA is a better proxy for VO_2 in cases when tag orientation may vary over time (Qasem et al. 2012). To obtain VeDBA, I followed the methodology of Qasem et al. (2012) and derived the static acceleration for each axis by smoothing the raw accelerometer data using a running mean of 3 s (every 15 samples, given the calibrated sampling rate of 5 Hz). DBA is sensitive to the length of the running mean used to smooth the data (Shepard et al. 2008), and therefore this value must be chosen carefully. Changing the length of the running mean produces variability in DBA that correlates with the animal's stroke period and thus its body size (Shepard et al. 2008).

To derive static acceleration, Shepard et al. (2008) recommend a minimum 3 s running mean for species whose dominant stroke period does not exceed this value. This includes killer whales, which I calculated to have a mean stroke period of 2.33 s based on a published mean stroke cycle frequency of 0.43 Hz (obtained from 9 Norwegian and Alaskan killer whales using DTAG data) (Sato et al. 2007). Once static acceleration was determined by smoothing the raw accelerometer data, I subtracted the static values from the raw values to produce estimates of dynamic acceleration (Qasem et al. 2012). I then calculated VeDBA by taking the vectorized sum of these derived dynamic accelerations (A) for all three axes (x, y, and z), using the following equation:

$$VeDBA = \sqrt{(A_x^2 + A_y^2 + A_z^2)} \qquad \text{Eq. 4}$$

The mean value of VeDBA over the duration of each dive was then calculated.

Mean change in roll and pointing angle both estimate the rate of change in whale body orientation and were calculated following the methodology of Miller et al. (2004), with minor modifications. I calculated the absolute value of the change in each whale's roll orientation over each sampling interval (0.2 s) of the calibrated roll data. I then smoothed these values by taking the running sum of the change in roll over every 1 s interval (i.e., summing every 5 samples). The smoothed data (5 Hz) were down-sampled to 1 Hz before determining the mean change in roll (degree s^{-1}) for both the descent and ascent phases of every dive. To eliminate ambiguity in the rotational direction when taking the absolute value of change in roll, I assumed that roll orientation changes by killer whales could not exceed 180 degrees within each 0.2 s sampling interval.

'Pointing angle' is a variable that combines the pitch and heading orientations to describe the three-dimensional angle of the whale's longitudinal axis (Miller et al. 2004). Calculating the change in pointing angle ($\Delta\hat{\sigma}$) is analogous to finding the central angle between two locations on the surface of a sphere. Therefore, change in pointing angle can be calculated using the Spherical Law of Cosines with the substitution of pitch (p) and heading (h) for latitude and longitude, respectively.

$$\Delta\hat{\sigma} = \arccos(\sin(p_{initial}) \times \sin(p_{final}) + \cos(p_{initial}) \times \cos(p_{final}) \times \cos(\Delta h)) \qquad \text{Eq. 5}$$

I calculated the change in pointing angle over each sampling interval (5 Hz) of the calibrated pitch and roll data. Following the same methodology used to determine the rate of change in roll orientation, I then calculated a running sum over every 1 s interval and down-sampled to 1 Hz before determining the mean rate of change in pointing angle (degree s^{-1}) over each descent and ascent.

2.3.6 Multivariate statistical analysis of kinematic dive variables

All statistics were performed using R software (R Development Core Team 2010). Kinematic dive variables for the confirmed feeding dives (>1 m, with associated fish scale and/or tissue samples, n=15) were used as the training set in an iterative linear discriminant analysis (LDA) to identify other dives that were also likely to represent foraging behaviour. LDA is a statistical method for building a predictive model to determine group membership. It constructs a function that discriminates between groups (e.g., dive types) using linear combinations of predictor variables (e.g., kinematic dive variables). The standardized coefficients (weights) of this discriminant function indicate which of the predictor variables provides the greatest separation between the groups. LDA assumes multivariate normality and homogeneity of within-group variance-covariance matrices, and while it is fairly robust to violations of these assumptions, it is also quite sensitive to outliers.

Prior to running the LDA, the 16 kinematic dive variables were transformed to achieve the closest possible approximation to multivariate normality. I transformed all dive variables (except the three measures of tortuosity) by first adding 0.01 to eliminate zeros and then taking the natural logarithm of the resulting values. Since the straightness index used to calculate relative tortuosity is a proportion with values between 0 and 1, the logit transformation (Warton and Hui 2011) was applied to the three dive tortuosity variables, as follows:

$$\ln\left(\frac{p}{1-p}\right) \qquad \text{Eq. 6}$$

where p is the sample value of the proportional variable being transformed. I added a small value (ε) to the numerator and the denominator of this function to prevent the logit transformation from returning undefined values of $-\infty$ and ∞ for sample proportions of 0 and 1, respectively (Warton and Hui 2011). In this case, ε was equivalent to the minimum non-zero value of $1 - p$ for each tortuosity variable. Histograms and Q-Q plots were visually examined and Anderson-Darling normality tests were performed to assess the distribution of each kinematic variable before and after transformation.

Two of the confirmed fish captures (n=17) had to be discounted from the LDA training set, as both these pursuits occurred at the surface of the water, rather than during a dive. I standardized the transformed dive variables by group membership (i.e., the 15 feeding dives making up the training set versus all other unclassified dives) prior to running each iteration of the LDA. Multiple iterations were run in succession, with reassignment of misclassified dives prior to each iteration, until no more dives were misclassified in either category ('foraging' or 'non-foraging'). The 15 confirmed feeding dives with prey samples were permanently allocated to the 'foraging' training set regardless of whether the algorithm detected them as misclassified.

Due to the small size of the first training set (n=15) and the relatively small number of whales represented by these dives (n=7), there was a potential for idiosyncratic behaviour to unduly influence how the LDA identified foraging dives. As with most behavioural data sets, this study involved repeated measures on the same individuals, and so applying the LDA to these data also violated the assumption of sample independence (Mundry and Sommer 2007). To determine the relative influence of repeated measures (i.e., the factor of "individual") on the LDA results, I cross-validated the model's ability to correctly identify foraging dives regardless of within-individual behaviour patterns by re-running the analysis with the removal of each whale's dives in turn from the first training set (the 'leave-one-out' method, see description by Mundry and Sommer 2007). This provided a direct test of the LDA's capacity to correctly classify dives that were not used to calculate the original discriminant function (Mundry and Sommer 2007).

All foraging dives identified by the LDA were interpreted as the independent pursuit of single, isolated prey, as ocean-going Pacific salmon occur individually or in small groups (Nero and Huster 1996), rather than in large schools. In addition, long-term resident killer whale diet studies (Ford et al. 1998, Ford and Ellis 2006) have shown that prey remains collected following a feeding dive do not originate from multiple fish, and that whales hunt either individually or in very small subgroups (e.g., a female with one or two associated offspring). Furthermore, residents have not been observed to engage in cooperative herding of fish (Heimlich-Boran 1988, Ford 1989, Ford et al. 1998), so their foraging dive behaviour is unlikely to reflect a strategy for consuming numerous, aggregated prey.

Following the iterative LDA, I analysed the dives assigned to the 'non-foraging' set using *X*-means clustering to identify further dive types unrelated to feeding behaviour. *X*-means clustering is a variation of the widely used non-hierarchical *k*-means clustering technique, but does not require prior designation of the number of clusters. Instead, this analysis uses iterations of *k*-means in combination with a Bayesian Information Criterion (BIC) stopping rule that automatically determines the appropriate number of clusters (Ishioka 2000, 2005). Unlike discriminant analysis, *X*-means clustering does not rely on *a priori* knowledge of group membership (Ishioka 2000), which made it suitable for identifying dive types with no 'true positive' examples that could be used to construct a training set. Wilk's lambda tests were performed to determine if the two pairs of dive type groupings, as determined by the LDA (foraging and non-foraging dives) and X-means clustering (two non-foraging dive types) algorithms, were statistically different from one another.

2.3.7 Meta-analysis of Pacific salmon vertical distribution studies

To determine the relative vertical distributions of Pacific salmon species, I conducted a meta-analysis of available scientific test fishery, ultrasonic telemetry and archival tagging studies. The test fishery studies I included (n=8 studies) were either specifically designed to measure the vertical distribution of Pacific salmon, or contained information about salmon bycatch depths during fisheries that targeted other commercial species. A variety of gear types were used to conduct these studies, including gillnets, trolling, and mid-water and bottom trawls. Test fishery studies had to contain catch depth data for at least 10 individual fish per species to be included. Data from all seasons and all times of day were considered to ensure that the full variation in depth distribution for each salmon species (including seasonal and diurnal variation) would be apparent. Using this test fishery research, I compiled a list by species of the depth ranges over which the majority of fish were caught during each of the studies. These species-specific depth ranges were then compared to the maximum foraging dive depths of tagged killer whales to determine whether feeding dives corresponded to the depth range of preferred prey.

Using published mean swimming depths from ultrasonic telemetry and tagging studies (n=12 studies) of Pacific salmon, I also calculated an overall average swimming depth for each species, which was similarly compared to whale foraging dive depths. All of the studies used for the salmon tagging meta-analysis were conducted in either summer or autumn. Where possible, I included the means for night and day depth distributions of tagged salmon as separate values in the calculation of overall mean swimming depth. This allowed the meta-analysis to account for diurnal variation in preferred swimming depth. If separate day and night values were not available, I used the mean swimming depth for all times of day combined. Test fishery and tagging studies were generally conducted on maturing or adult fish (i.e., their scales had 1 or more marine scale annuli, indicating an age of ≥ 2 years), but in some cases ages were not specified or studies combined data from juvenile and adult individuals. I did not include studies involving only juvenile fish (first year at sea) because this age group is not consumed by resident killer whales (Ford and Ellis 2006). To obtain a sufficiently large data set, studies in both coastal and high seas habitat types were considered.

2.4 Results

2.4.1 Tag deployments and dive identification

DTAGs were deployed on 34 occasions on 32 different northern resident killer whales in the late summer and early autumn of 2009-2012 (Table 2.1, Figure 2.1). Two individuals, A66 and A83, were tagged twice, although the second deployment on A83 was too brief to include in the dive analysis. The tagged whales represented a range of demographic categories, including 8 adult females (≥12 y), 14 adult males (≥12 y), and 10 juveniles (3-11 y). Of the 10 juveniles tagged, 3 were female, 1 was male, and 6 were of undetermined sex. Adult males were slightly over-represented in this data set because of their tendency to travel alone at the periphery of a group (Heimlich-Boran 1988, Ford and Ellis 2006), as well as their larger dorsal fins and overall body size, which made them somewhat easier to tag. Data from three tagged individuals were not analysed because the tag deployments (oo09_237a, oo09_237b and oo12_235a) had extremely short durations and lacked completed dives deeper than 10 m, which are necessary for calibration.

The 31 analysed tag deployments ranged from 0.3-11.8 h in duration, for a total of 126.1 h (Table 2.1). Prey fragments (fish scales and/or flesh) were collected in the field for 17 confirmed kills that were made by 7 of the tagged individuals (Table 2.2). Scale morphological analysis revealed that 9 of these kills were Chinook salmon (*Oncorhynchus tshawytscha*), 6 were chum (*O. keta*), and 2 were coho (*O. kisutch*). Salmon caught by the tagged whales ranged in age from 2-5 y, with the majority (n=11, 65%) being 4-5 y (Table 2.2). Once the tags were calibrated and the first 10 minutes of diving had been omitted from each deployment, a total of 11,319 dives (≥1 m) were available for multivariate statistical analysis.

2.4.2 Multivariate statistical analysis of kinematic dive variables

Linear discriminant analysis (LDA) of the 11,319 identified dives detected a total of 701 potential foraging dives over 25 iterations, including the 15 confirmed feeding dives used in the original training set. This left 10,618 dives that were categorized by the LDA as non-foraging dives. The final iteration used a weighted mean cut-off score of -3.11 to classify dives, and the probabilities for the two dive type assignments were 6.2% (foraging) and 93.8% (non-foraging). The coefficients of the linear discriminant function indicated the weights applied to each kinematic dive variable (Table 2.3). Variables with larger discriminant coefficients (absolute values) therefore provided the most separation (Tabachnick and Fidell 2013) between foraging and non-foraging dive types. In the final iteration (n=25) of the discriminant function, the variables that best distinguished foraging from non-foraging dives were dive duration (min), vertical descent velocity (m s^{-1}), vertical ascent velocity (m s^{-1}), and the ratio of descent to ascent duration (Table 2.3).

Following the linear discriminant analysis, *X*-means clustering of the non-foraging dives grouped them into two additional types, designated 'respiration' (n=7,050) and 'other' (n=3,568), for a total of three overall dive types by tagged whales. The Wilks' lambda test statistic confirmed

Table 2.1 Summary of DTAG deployments on 34 northern resident killer whales in British Columbia (2009-2012) showing date, location and total duration of each deployment, the name, sex and age of each individual tracked, and the number of dives that were analysed (first 10 minutes of each deployment were omitted prior to dive analysis).

Tag ID	Deployment date (dd/mm/yyyy)	Deployment location	Individual	Sex	Age (years)	Deployment time (hours)	# dives analysed
oo09_231a	19/08/2009	50° 46.500 N 127° 24.066 W	G52	F	16	7.41	542
oo09_234a	22/08/2009	50° 56.870 N 127° 47.920 W	A46	M	27	3.92	342
oo09_235a	23/08/2009	50° 49.758 N 127° 43.463 W	A72	F	10	5.22	486
oo09_236a	24/08/2009	50° 51.032 N 127° 31.560 W	I45	M	24	2.37	151
oo09_237a	25/08/2009	50° 47.670 N 127° 31.891 W	I57?	F	20	0.07	0
oo09_237b	25/08/2009	50° 48.336 N 127° 36.855 W	I71	F	16	0.28	0
oo09_237c	25/08/2009	50° 49.336 N 127° 41.669 W	I83	F	12	1.15	93
oo09_237d	25/08/2009	50° 56.672 N 128° 02.190 W	I53	M	23	3.28	314
oo09_238a	26/08/2009	50° 51.117 N 127° 49.327 W	I111	?	3	11.64	1123
oo09_239a	27/08/2009	50° 49.516 N 127° 42.441 W	A66	M	13	2.15	145
oo09_240a	28/08/2009	50° 56.073 N 127° 41.825 W	A37	M	32	3.63	353
oo09_243a	31/08/2009	50° 53.767 N 127° 39.881 W	I39	M	29	3.11	233
oo09_244a	01/09/2009	51° 00.065 N 127° 49.085 W	R25	M	22	4.24	299
oo09_245a	02/09/2009	50° 47.268 N 127° 32.671 W	I46	M	24	5.89	483
oo09_245b	02/09/2009	50° 46.975 N 127° 15.357 W	I62	M	21	1.52	109
oo09_247a	04/09/2009	50° 30.813 N 126° 23.110 W	A62	F	15	1.27	157
oo10_256a	13/09/2010	50° 57.047 N 127° 44.552 W	G64	F	10	7.59	828
oo10_260a	17/09/2010	50° 53.982 N 127° 38.038 W	A75	F	8	6.97	604
oo10_261a	18/09/2010	50° 54.141 N 127° 38.604 W	A38	M	39	3.22	291
oo10_264a	21/09/2010	51° 03.696 N 127° 58.168 W	G39	M	24	1.60	116
oo10_265a	22/09/2010	50° 51.936 N 127° 33.151 W	G49	F	20	2.92	299
oo11_224a	12/08/2011	51° 51.844 N 128° 15.430 W	R40	?	10	2.12	215
oo11_224b	12/08/2011	51° 23.548 N 128° 08.301 W	G32	M	29	0.34	12

Tag ID	Deployment date (dd/mm/yyyy)	Deployment location	Individual	Sex	Age (years)	Deployment time (hours)	# dives analysed
oo11_240a	28/08/2011	50° 57.018 N 127° 43.853 W	I104	?	9	3.95	361
oo11_244a	01/09/2011	50° 55.329 N 127° 42.107 W	C14	M	26	2.84	175
oo11_244b	01/09/2011	51° 00.448 N 127° 58.949 W	C24	?	11	1.15	82
oo11_245a	02/09/2011	50° 47.917 N 127° 35.362 W	I43	M	28	11.80	856
oo11_246a	03/09/2011	50° 48.852 N 127° 39.618 W	G31	F	30	3.81	466
oo11_248a	05/09/2011	50° 49.609 N 127° 42.700 W	A83	?	6	0.48	21
oo11_248b	05/09/2011	50° 50.738 N 127° 46.718 W	A80	M	7	2.97	298
oo11_267a	24/09/2011	50° 40.754 N 127° 03.117 W	A34	F	36	7.19	620
oo12_232a	19/08/2012	51° 01.358 N 127° 41.391 W	I106	?	8	5.78	751
oo12_235a	22/08/2012	50° 55.672 N 127° 42.149 W	A83	?	7	0.07	0
oo12_235b	22/08/2012	50° 49.325 N 127° 28.907 W	A66	M	16	4.51	494

Table 2.2 Summary of confirmed feeding dives (n=17) resulting in fish kills by 7 tagged northern resident killer whales over three seasons (2009-2012) of digital archival tag (DTAG) deployments, showing the date and estimated time of capture, estimated capture depth, and the species and age of fish caught. Capture times and depths were determined from the behavioural transition between ascent and descent phases evident on Trackplot pseudotracks of confirmed foraging dives, as well as pressure sensor depth measurements. Surface captures (<1 m depth, denoted by †) could not be included in the linear discriminant training set for identifying foraging dives, as they did not occur during a dive.

Tag ID	Whale ID	Sex	Age (y)	Date of kill (dd/mm/yyyy)	Capture time (hh:mm:ss)	Capture depth[a] (m)	Fish species	Fish age[b] (European)	Fish age (y)
oo09_234a	A46	M	27	22/08/2009	18:46:35	101.6	Chinook	1.1	3
oo09_240a	A37	M	32	28/08/2009	13:02:28	165.7	coho	x.1	≥ 2
oo09_240a	A37	M	32	28/08/2009	13:29:29	119.4	coho	1.1	3
oo10_256a	G64	F	10	13/09/2010	16:26:52	134.5	chum	0.4	5
oo10_256a	G64	F	10	13/09/2010	16:44:18	123.7 *	chum	0.4	5
oo10_265a	G49	F	20	22/09/2010	17:46:02	130.5	chum	0.4	5
oo10_265a	G49	F	20	22/09/2010	17:53:26	133.7	chum	0.3	4
oo11_246a	G31	F	30	03/09/2011	13:24:46	201.9	Chinook	0.3	4
oo11_246a	G31	F	30	03/09/2011	13:39:04	264.8	Chinook	0.3	4
oo11_246a	G31	F	30	03/09/2011	14:43:15	131.1	Chinook	0.3	4
oo11_246a	G31	F	30	03/09/2011	14:50:32	204.5	Chinook	0.3	4
oo11_246a	G31	F	30	03/09/2011	15:05:47	180.7	Chinook	0.3	4
oo12_232a	I106	?	8	19/08/2012	15:43:54	0.7 †	chum	0.3	4
oo12_232a	I106	?	8	19/08/2012	16:51:35	87.6	chum	0.2	3
oo12_235b	A66	M	16	22/08/2012	14:36:49	102.7 *	Chinook	0.1	2
oo12_235b	A66	M	16	22/08/2012	15:43:56	6.6 *	Chinook	0.2	3
oo12_235b	A66	M	16	22/08/2012	15:57:38	0 †	Chinook	0.3	4

a. Excluding the two surface captures (†), all but three foraging dives (*, maximum depths=141.4, 103.9 and 32.0 m, respectively) had estimated capture depths that corresponded to the maximum dive depth, as measured by the DTAG pressure sensor.

b. Fish ages are displayed according to the European system, which indicates the number of freshwater and marine annuli (rings) found in the scales, separated by a decimal point. For example, a fish aged 0.4 has no freshwater annulus and 4 ocean annuli and therefore migrated to the sea shortly after hatching and is currently in its 5th year of life. Scales for which the number of annuli could not be determined are denoted by an “x” in place of a number.

Table 2.3 Summary of mean values of untransformed kinematic dive variables (standard deviations shown in parentheses) by dive type for 31 northern resident killer whales carrying digital archival tags (DTAGs). Dives were classified into three types using iterative linear discriminant and *X*-means clustering analyses. Loading values (coefficients of linear discriminant) of the transformed, group standardised kinematic dive variables for the final iteration (25th) of the discriminant function are also displayed.

Dive variable	Foraging dives n=701	Respiration dives n=7050	Other dive behaviours n=3568	Coefficients of linear discriminant
dive duration (min)	3.14 (1.73)	0.41 (0.37)	0.47 (0.45)	-1.7075
maximum dive depth (m)	64.54 (61.03)	3.03 (1.78)	3.88 (2.70)	0.2537
2D dive straightness index	0.88 (0.16)	1.00 (0.004)	0.93 (0.11)	-0.1045
3D descent straightness index	0.89 (0.12)	0.98 (0.02)	0.89 (0.10)	-0.1066
3D ascent straightness index	0.89 (0.11)	0.98 (0.02)	0.91 (0.08)	0.0362
mean VeDBA	0.11 (0.07)	0.09 (0.05)	0.13 (0.09)	0.1421
maximum absolute roll (deg)	115.47 (64.15)	20.76 (17.67)	39.02 (35.75)	-0.1204
mean absolute roll (deg)	32.56 (27.15)	8.19 (8.08)	14.03 (16.04)	-0.0770
overall dive speed (m s^{-1})	2.14 (0.81)	1.96 (0.69)	1.27 (0.60)	0.0801
descent : ascent duration	1.18 (1.01)	1.17 (0.68)	1.21 (0.83)	-5.1212
vertical descent velocity (m s^{-1})	0.78 (0.53)	0.32 (0.22)	0.35 (0.20)	-5.9038
vertical ascent velocity (m s^{-1})	0.75 (0.57)	0.36 (0.38)	0.39 (0.39)	4.9175
descent Δroll/time (deg s^{-1})	14.02 (14.87)	6.76 (5.75)	10.48 (14.80)	0.1164
ascent Δroll/time (deg s^{-1})	14.57 (15.68)	5.23 (4.15)	10.08 (16.86)	0.1094
descent Δpointing angle/time (deg s^{-1})	31.69 (26.37)	26.43 (24.07)	38.55 (42.50)	0.0352
ascent Δpointing angle/time (deg s^{-1})	27.74 (19.50)	14.43 (19.4)	23.82 (36.46)	-0.2077

that the foraging and non-foraging dives detected by the LDA were significantly different from one another ($\lambda = 0.3213$, df = 16, $p < 0.001$), as were the two non-foraging dive types detected by the *X*-means clustering algorithm ($\lambda = 0.3227$, df = 16, $p < 0.001$). Due to the non-independence of the samples (i.e., dives) making up this data set, the level of significance implied by the Wilks' lambda p-values is likely to be inflated. However, both p-values are much lower than the α=0.05 required to show significance, and the LDA separated dive types consistently even when reduced training sets were used during the leave-one-out validations. This suggests that within-group variance is much lower than between-group variance, and I can therefore be reasonably confident that the dive types are differentiable from one another. Wilks' lambda represents the proportion of variance in the combined predictor variables that is not explained by the grouping factor in the model. In this case, the majority of variance in the kinematic dive variables (~68%) can be attributed to the grouping factor (dive type), meaning that both the LDA and *X*-means models were able to distinguish dive types that differed significantly in their overall kinematic structures.

Compared to other dive types, foraging dives were typically deeper (mean ± SD: 64.5 ± 61.0 m), lasted longer (3.1 ± 1.7 min) (Figure 2.3), and foraging whales travelled at greater overall speeds (2.1 ± 0.8 m s^{-1}) (Figure 2.4, Table 2.3). Rates of descent (0.8 ± 0.5 m s^{-1}) and ascent (0.8 ± 0.6 m s^{-1}), measured as vertical velocities, were also faster during foraging dives than non-foraging dives (Figure 2.4, Table 2.3). Straightness index values in both two- (whole dive) and three-dimensions (descent and ascent phases) were generally lower for foraging dives (means = 0.88-0.89) than respiration dives (mean $\geq$ 0.98), indicating that whale movement paths were more convoluted and less directional during foraging (Figure 2.5, Table 2.3). However, mean straightness values (0.89-0.93) for other dive behaviours were similar to those displayed during foraging dives. Whales engaged in foraging dives also rolled their bodies to a greater extent than they did during non-foraging dives (Figure 2.6). Both overall mean (32.5 ± 27.2º) and mean maximum (115.5 ± 64.2º) body roll values were considerably higher during foraging dives (Table 2.3).

Visual inspection of TrackPlot pseudotracks for the confirmed feeding dives (n=17) revealed a general pattern of convoluted, spiralling and kinematically complex paths during descents, with relatively abrupt transitions (usually at the point of maximum depth) to directional, linear ascents (see Figure 2.2). These sudden behavioural transitions likely occurred immediately following prey capture, which allowed the time and depth of captures to be determined for these successful kills (Table 2.2). While not as frequent as deeper foraging dives, a few surface chases were also observed. One chum salmon capture involved only a surface chase (Figure 2.2B), while four other captures (2 chum, 2 coho) showed surface pursuits followed by a deeper dive that eventually resulted in the fish kill. One surface-caught Chinook was taken by a tagged whale (oo12_235b, Table 2.2) that made a sudden leap at the surface, without any evidence of a pursuit prior to the capture event.

In all but three of the non-surface captures (n=15), the probable capture depth corresponded to the maximum depth attained by the whale during the dive (Table 2.2). The majority of capture depths, regardless of salmon species, were deeper than 100 m (Figure 2.3). Most of the deeper confirmed feeding dives were V-shaped (n=11, Figure 2.2A), however, a few were U-shaped (n=4) with relatively flat bottom phases accompanied by a maintained body roll of approximately 90° (i.e., swimming on their sides) (Figure 2.2C). Body roll was most often to the right (3 of the 4 U-shaped dives); however, during one dive a tagged whale switched between right and left rolls. The sample-size for these U-shaped dives was too limited to determine if this rolling behaviour is lateralized with a right-sided bias, as has been observed for other cetacean species during feeding along the sea floor (Woodward and Winn 2006, Ware et al. 2013). The bottom phases of U-shaped dives also typically contained many tight loops and swim paths were very convoluted.

The kinematic structures of the two non-foraging dive types identified by the *X*-means clustering analysis were very different from those of the foraging dives. The first type of non-foraging dive was extremely shallow (mean ± SD: 3.0 ± 1.8 m), very brief in duration (0.4 ± 0.4 min), and while only slightly slower in terms of overall speed (2.0 ± 0.7 m s^{-1}), it had considerably slower mean vertical descent (0.3 ± 0.2 m s-1) and ascent (0.4 ± 0.4 m s^{-1}) velocities (Figure 2.4, Table 2.3). Movement within these dives was extremely directional, with almost no tortuosity (mean straightness index ≥0.98, all 3 measures, Figure 2.5) and limited mean (8.2 ± 8.1°) and mean maximum (20.8 ± 17.7°) body roll (Figure 2.6, Table 2.3). The kinematics of this dive type corresponded well with surface observations of breathing behaviour by killer whales, and were therefore designated as ‘respiration maintenance dives’. In other words, the majority of diving behaviour by tagged killer whales, regardless of surface-observed activity states, consisted of extremely short submersions occurring between single breaths. Typically these respiration type

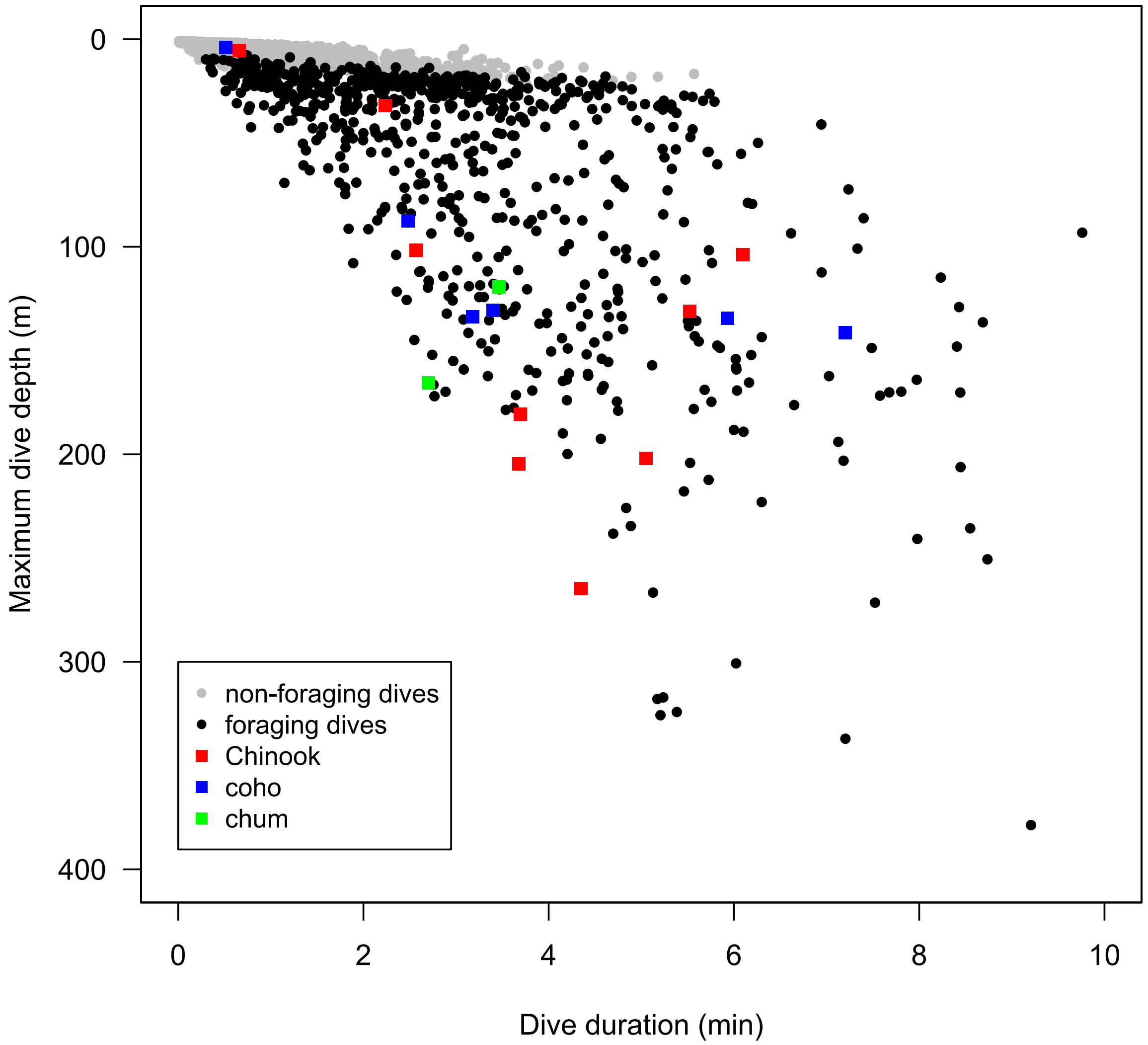

Figure 2.3 Maximum dive depths (m) and dive durations (min) of foraging (n=701) and non-foraging (n=10,618) dives by 31 tagged northern resident killer whales. Confirmed foraging dives (n=17) are marked by coloured data points indicating the species of salmon killed (Chinook, coho or chum). Non-foraging dives (gray data points) did not exceed 21 m in depth.

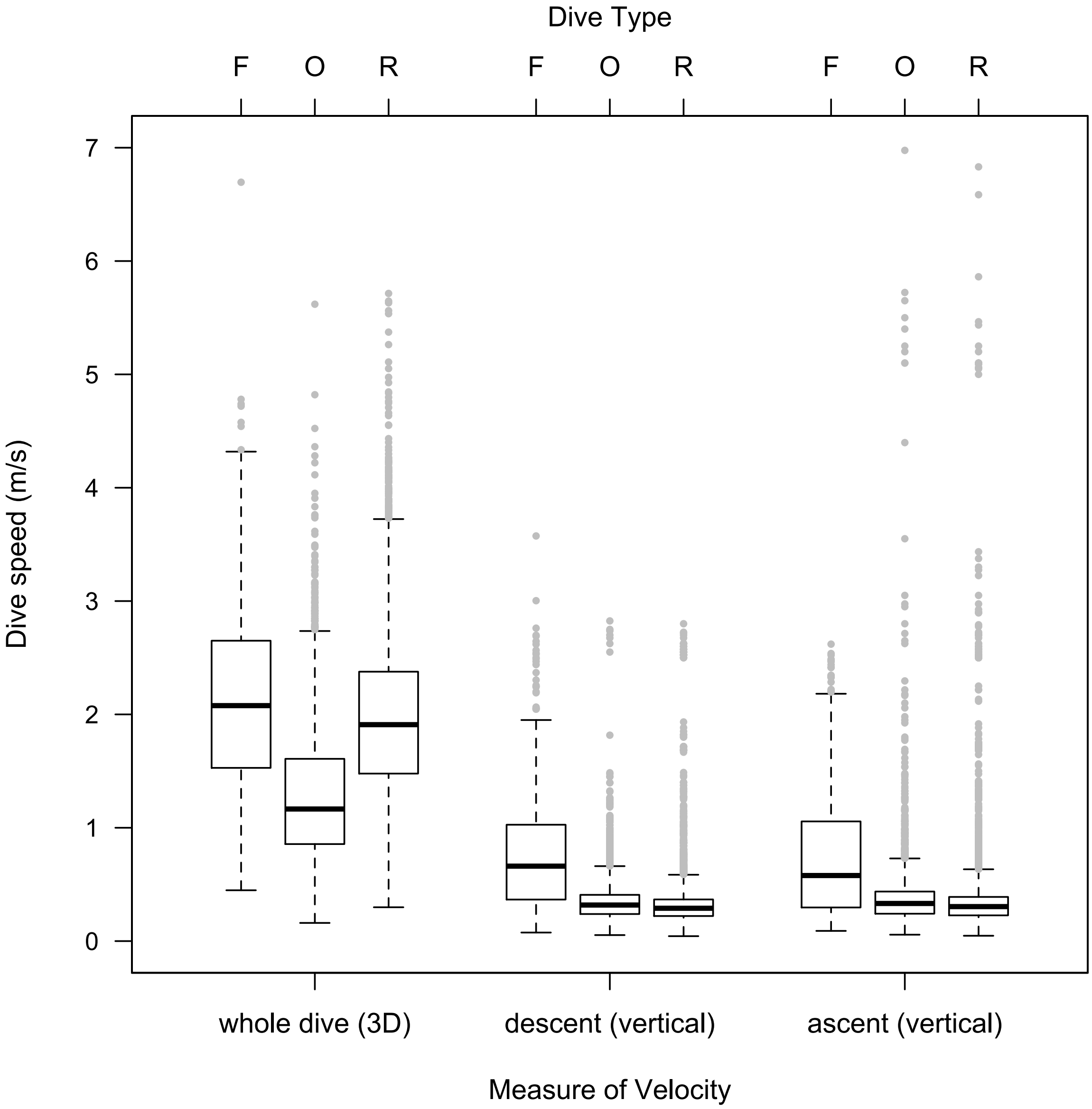

Figure 2.4 Comparison of dive velocities between the three identified dive types made by 31 tagged northern resident killer whales (F=foraging, R=respiration, O=other behaviours; total dives=11,319). Whole dive velocity was calculated by dividing the three-dimensional dive path length (determined using dead-reckoning techniques) by the total dive time, and included both descent and ascent phases. Vertical velocities for descent and ascent phases were based solely on depth sensor data.

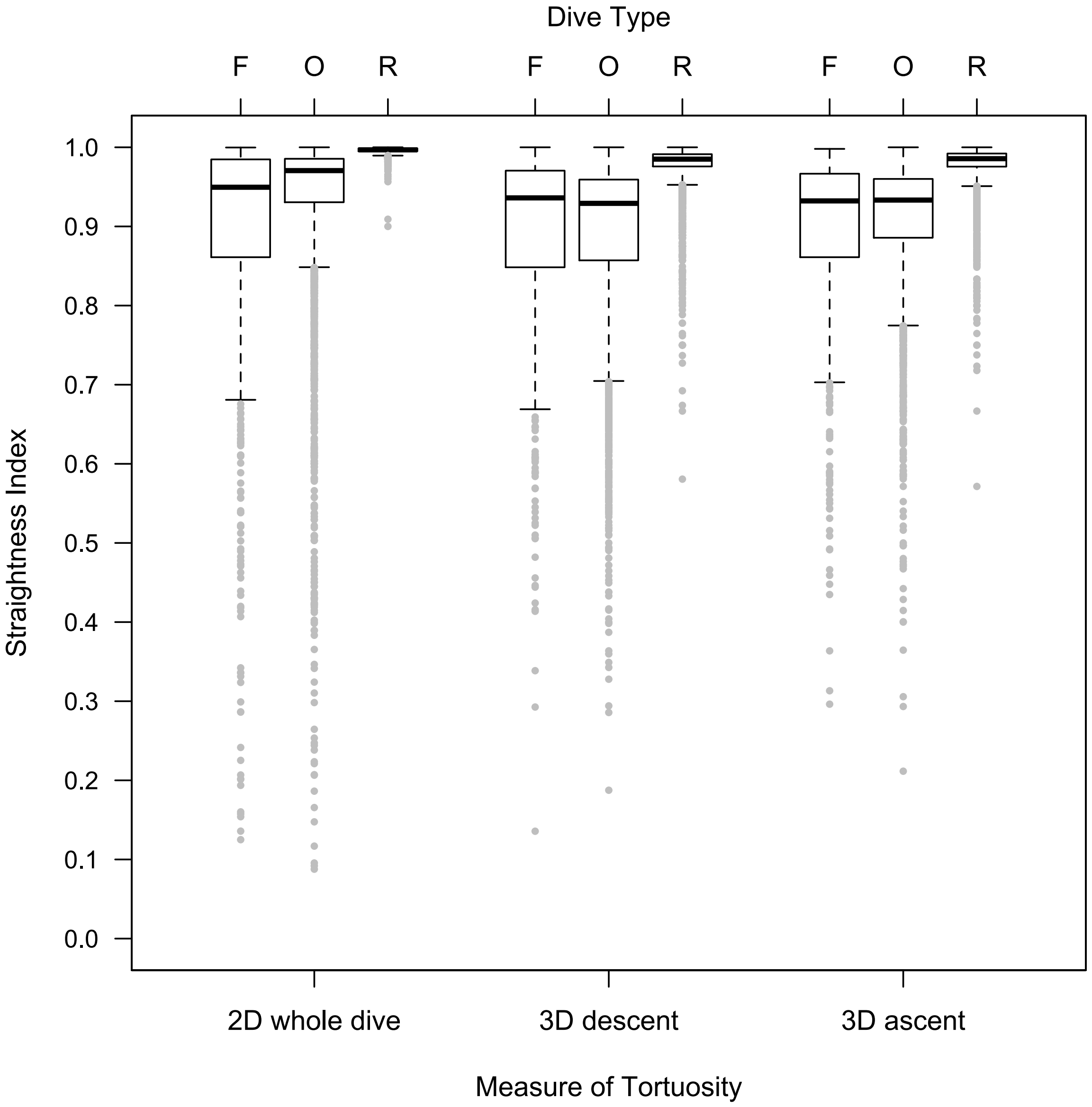

Figure 2.5 A comparison of kinematic tortuosity variables between the three identified dive types made by 31 tagged northern resident killer whales (F=foraging, R=respiration, O=other behaviours; total dives=11,319). A straightness index indicating relative tortuosity was calculated in two dimensions (x-y plane only) over entire dives and in three dimensions for the descent and ascent phases. Lower values of the straightness index indicate more convoluted paths of whale movement, while values approaching 1 indicate directional, straight-line paths.

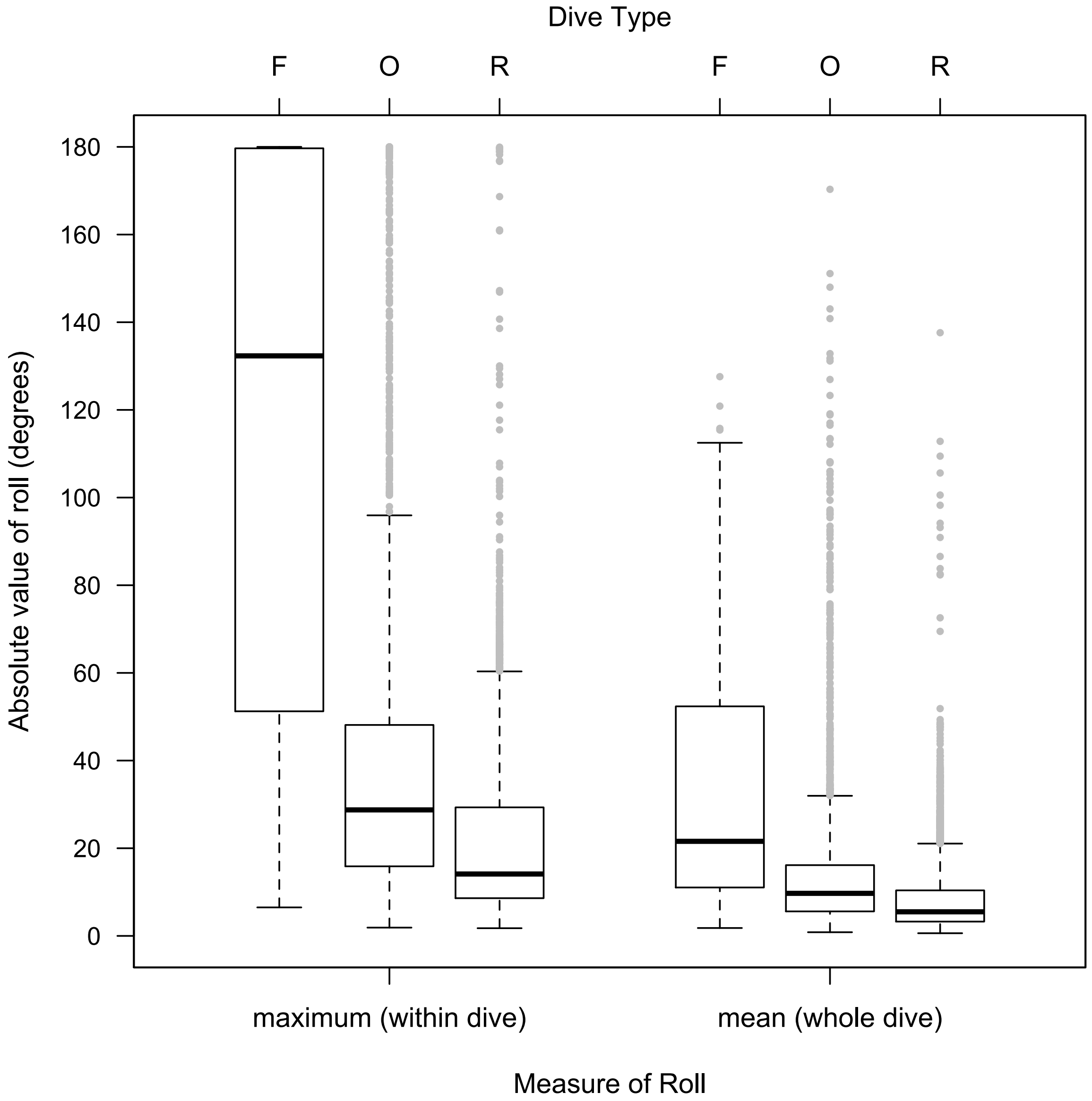

Figure 2.6 Comparison of maximum and mean absolute values of body roll (degrees) by 31 tagged northern resident killer whales engaged in three identified dive types (F=foraging, R=respiration, O=other behaviours; total dives=11,319).

dives were repetitive and interspersed between deeper dives. Since they were observed to occur during all activity states (e.g., resting, foraging, travelling), they likely have no behavioural significance beyond simple respiratory maintenance.

The second type of non-foraging dive was designated as 'other' dive behaviour because the overall kinematic structure was intermediate between foraging and respiration dives, with a higher degree of variability. Like respiration dives, these dives were also comparatively shallow (mean ± SD: 3.9 ± 2.7 m) and short in duration (0.5 ± 0.5 min). Overall dive speed (1.3 ± 0.6 m s^{-1}), as well as descent (0.3 ± 0.2 m s^{-1}) and ascent (0.4 ± 0.4 m s^{-1}) vertical velocities, were also comparable to those of respiration dives and were slower than during foraging dives (Figure 2.4, Table 2.3). However, 'other' dive behaviours had tortuosity values that were more similar to those of foraging dives (mean straightness index = 0.89-0.93, Figure 2.5) (Table 2.3). Whales also exhibited a higher level of mean (14.0 ± 16.0°) and mean maximum (39.0 ± 35.8°) body roll than during respiration dives, although not to the same extent as during foraging dives (Figure 2.6, Table 2.3). Given the large number of dives in this category (n=3,568) and the higher variability of the kinematic dive characteristics (Table 2.3), it likely includes a variety of other previously described behaviours by resident killer whales, such as socializing, travelling, resting and beach rubbing (Ford 1989). It is likely that the *X*-means clustering analysis was unable to further separate the different behaviours within the 'other' dive type category because the kinematic predictor variables were chosen specifically for their hypothesized ability to distinguish foraging dives from all other behaviours.

A few of the kinematic variables were somewhat ambiguous in their ability to separate foraging from non-foraging dive types. Vectorized Dynamic Body Acceleration (VeDBA) was similar between foraging dives (mean ± SD: 0.11 ± 0.07), respiration dives (0.09 ± 0.05), and other dive behaviours (0.13 ± 0.09) (Table 2.3). Rates of change (degree s^{-1}) for both roll and pointing angle (descents and ascents) tended to be similar between foraging dives and other behaviours, but were lower for respiration dives (Table 2.3). The ratio of descent to ascent durations was expected to be higher for foraging dives, on the basis that descents involving tortuous chase behaviour should take longer than directional ascents covering the same depth range. This variable was also assigned a higher linear discriminant coefficient (-5.12) value (Table 2.3), which implies that it was relatively important in predicting group membership (i.e, dive type). However, the mean ratio of descent to ascent durations for the untransformed dive data was similar between foraging dives (1.18 ± 1.01), other behaviours (1.21 ± 0.83), and respiration dives (1.17 ± 0.68) (Table 2.3). A simple comparison of group (dive type) means and standard deviations of untransformed, non-normal (often skewed) kinematic variables may therefore not fully reflect the contribution of the transformed variable to the discriminant function.

All three dive types were detected in each of the 31 analysed tag deployments, except for deployment oo11_224b (n=12 dives), which did not contain any foraging dives. On average, foraging dives made up 6.7% (SD: ±3.5%) of an individual's dive behaviour, while respiration dives comprised 64.7% (±21.0%) and other dive behaviours 28.6% (±20.0%). A cross-validation of the LDA, in which each individual's (n=7 whales) dives were removed from the original training set (n=15 dives) in turn, revealed that the discriminant function was not unduly influenced by individual variations in foraging dive structure. In all cases, the confirmed foraging dives of the omitted individual were still reclassified as 'foraging' by the final iteration of the LDA, even though dives by that individual were no longer used to derive the initial discriminant function. Additionally, the same LDA cutting point (-3.11) for classifying dives was identified regardless of which animal was removed from the training set, and the same 701 dives were placed in the foraging group by the final LDA iteration.

Visual inspection of a multivariate Q-Q plot for the combined kinematic dive variables, as well as examination of histograms and individual Q-Q plots for each variable, indicated that data transformation achieved a considerable improvement towards approximating multivariate normality. However, Anderson-Darling normality tests indicated that only one of the transformed kinematic variables (maximum dive depth) actually achieved an approximately normal distribution. As more than one dive per whale was included in the LDA, the analysis also contained unavoidable pseudoreplication due to the inclusion of a second factor (individual) in addition to the grouping factor of interest (dive type), which violates the assumption of statistically independent replicates (Mundry and Sommer 2007). Despite the non-independence of dives, the extremely successful 'leave-one-out' cross-validation provided evidence that the factor of 'individual' did not greatly influence the algorithm's ability to classify dives by behaviour type. Furthermore, discriminant analysis has advantages that are not provided by other multivariate tests, such as robustness to multicollinearity and the ability to estimate a variable's contribution to the separation of classes (Mundry and Sommer 2007). Since no equivalent techniques exist that could also account for non-independence of samples (Mundry and Sommer 2007), an iterative

LDA was deemed the best possible approach even given the non-independent samples making up the DTAG data. Dives were therefore treated as though they were independent replicates.

2.4.3 Meta-analysis of Pacific salmon vertical distribution studies

The meta-analysis of ultrasonic telemetry and archival tagging studies showed that Chinook salmon swim at an average depth of 43.4 ± 15.4 m (mean ± SD; Figure 2.7) in coastal and offshore Pacific waters (Ogura 1994, Candy and Quinn 1999, Hinke et al. 2005, Walker et al. 2007). In contrast, chum salmon swim at a shallower average depth of 22.0 ± 19.0 m (Soeda et al. 1987, Yano and Nakamura 1992, Ogura 1994, Ishida et al. 2001, Tanaka et al. 2001, Azumaya and Ishida 2005, Tanaka et al. 2005, Walker et al. 2007), while coho (9.4 ± 2.2 m), sockeye (9.4 ± 6.1 m), pink (9.0 ± 3.7 m), and steelhead (4.6 ± 3.2 m) are all found at average depths of less than 10 m (Figure 2.7) (Quinn et al. 1989, Ruggerone et al. 1990, Ogura 1994, Walker et al. 2007). The meta-analysis of test fishery and bycatch studies indicated a similar vertical distribution of these species, with the majority of Chinook being caught at depths below 30 m (range = 15-100 m) (Milne 1955, Parker et al. 1959, Taylor 1969, Argue 1970, Godfrey et al. 1975, Walker et al. 2007), while all other species tended to be caught in surface waters shallower than 30 m (range = 0-45.5 m) (Figure 2.8) (Milne 1955, Parker et al. 1959, Manzer 1964, Machidori 1966, Taylor 1969, Argue 1970, Godfrey et al. 1975). More detailed summaries of the studies used for the telemetry and test fishery meta-analysis of salmon vertical distributions are provided in Appendix A.

2.5 Discussion

Multivariate analysis of movement patterns by northern resident killer whales revealed that dive depth, tortuosity, body rotation and estimates of velocity are reliable metrics for distinguishing foraging from non-foraging behaviour. Most notably, the DTAG-recorded kinematics of foraging dives showed that resident killer whale hunting techniques match the behaviour of Chinook salmon, their preferred prey. Foraging dives attained the expected depth distribution of Chinook and revealed movement patterns consistent with whales responding to escape strategies used by Pacific salmon (i.e., rapid descent, evasive manoeuvring, and increased swimming speeds). Foraging dive kinematics may be further optimized for improving acoustic detection and convergence on highly mobile prey using echolocation. These documented foraging

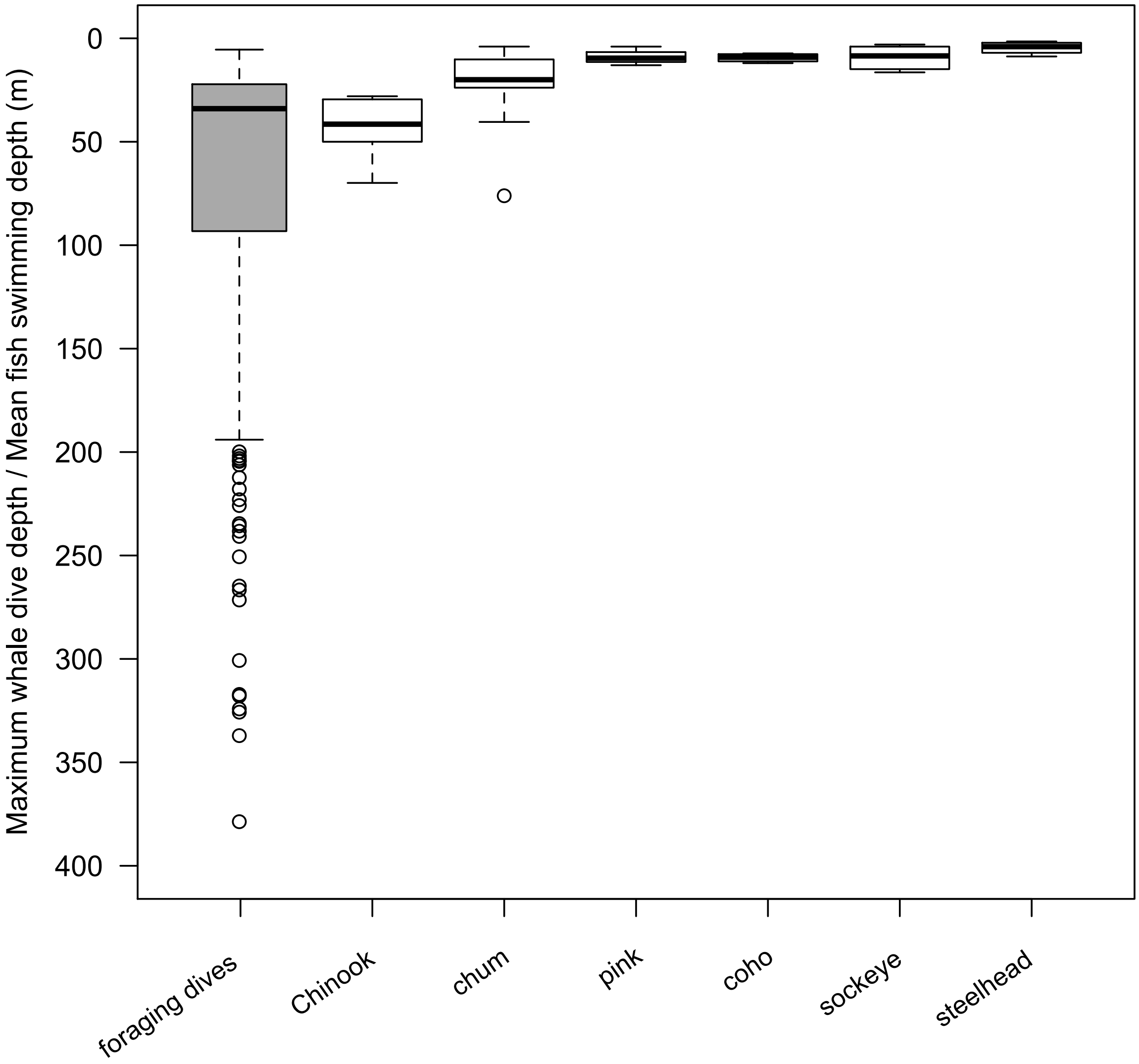

Figure 2.7 Maximum depths (m) of foraging dives (n=701) by 31 tagged northern resident killer whales (grey box plot) and overall mean ocean swimming depths (white box plots) of six species of Pacific salmon reported in tagging and ultrasonic telemetry studies (n=12) of maturing or adult fish (2 years or older) in summer or autumn.

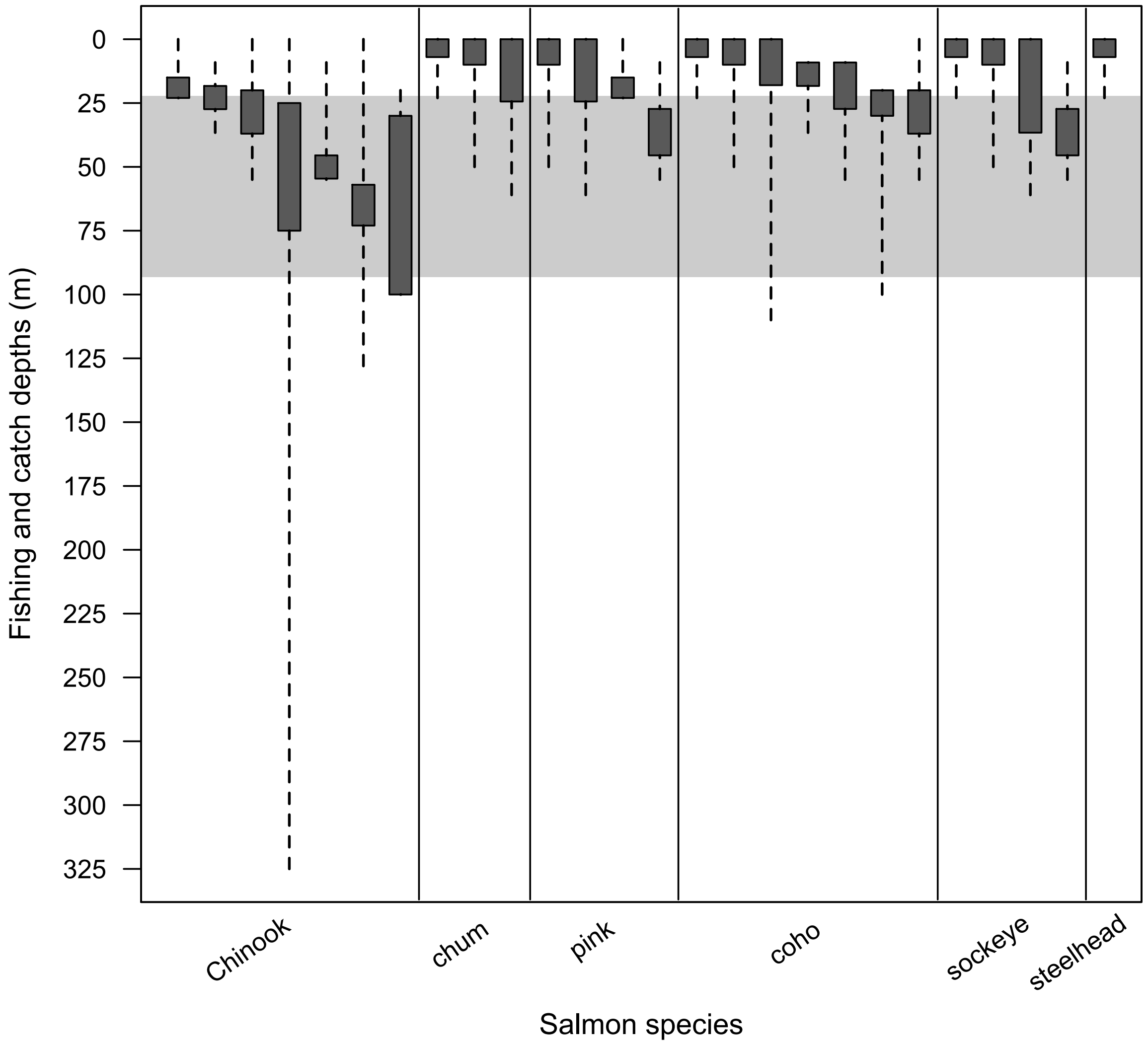

Figure 2.8 Catch depths (m) of six species of Pacific salmon taken by troll, gillnet or trawl fishing (boxes), and maximum foraging dive depths of 31 tagged northern resident killer whales (shaded band). The range of maximum foraging depths spans the interval between the 25th and 75th percentiles (22.2-93.2 m) of all detected foraging dives (n=701), and the fishery catch depths are from salmon vertical distribution and bycatch studies. Within each species of salmon, each box plot represents a separate study (some studies appear more than once if conducted on multiple species). Dashed lines indicate the total depth intervals fished, and dark shaded boxes represent the depth intervals in which the largest percentage of fish were caught during each study. Catch data are from all seasons and times of day, taken in both coastal and high seas habitats (n=8 studies, minimum of 10 fish/species/study).

behaviours appear to be specialized for capturing Chinook salmon, and are likely maintained in this population through social learning.

2.5.1 Killer whale dive depth selectivity and salmon evasive response

The maximum depths of foraging dives (predicted fish capture depths) by northern resident killer whales (64.5 ± 61.0 m SD) overlapped considerably with the average swimming depth of Chinook salmon (43.4 ± 15.4 m SD) tracked during tagging studies (Figure 2.7), as well as with test fishery catch depths (15-100 m) for Chinook (Figure 2.8). Conversely, there was almost no correspondence between maximum dive depths of foraging whales (64.5 ± 61.0 m SD) and the average swimming depths of other tagged salmon species (Figure 2.7), except to a small extent for chum (22.0 ± 19.0 m), which is the second most preferred prey species of northern residents (Ford and Ellis 2006). This overlap between maximum foraging dive depths (generally equivalent to fish capture depths) and the vertical distributions of Chinook and chum salmon provides evidence that resident killer whales may be selectively diving to depths where preferred prey are more likely to occur. This means that in years of reduced Chinook availability, whales could be expending considerable effort diving in search of their preferred prey but would experience relatively poor encounter rates (and thus low energetic return). Vertical distributions of salmon change both seasonally and diurnally, and are affected by many physiological and ecological factors, including temperature, salinity, olfactory homing cues, prey distributions, predator avoidance behaviour, and bathymetric limitations (Candy and Quinn 1999, Quinn 2005, Walker et al. 2007). Despite these many sources of variation, however, tagging and fisheries studies that analysed vertical distribution patterns invariably concluded that Chinook were located deeper in the water column than other salmonids (see Appendix A).

While maximum foraging dive depths overlapped with the area of the water column usually occupied by Chinook salmon, tagged whales also extended their foraging dives to much greater depths of up to 379 m (Figure 2.3 and Figure 2.7). Chinook have been documented to occur at comparably great depths by bottom-trawling studies, which have taken them as by-catch at up to 325 m (Walker et al. 2007) and 482 m (Erickson and Pikitch 1994). Ultrasonic tracking of tagged fish has similarly indicated that Chinook can swim to depths of 300-400 m, and furthermore, that fish performing deep dives (>200 m) are significantly larger than those remaining in shallower water (Candy and Quinn 1999). This implies that resident killer whales must dive beyond the average swimming depth of most Chinook to find the largest individuals that would supply the greatest energetic return. The mean size of deep-diving Chinook salmon tracked by Candy and Quinn (1999) was 87.2 cm (compared to 77.3 cm for shallow-diving Chinook), which corresponds to the intermediate average fork lengths of 4-5 year old seine-caught Chinook (80.8 and 93.9 cm, respectively) measured by the Fisheries and Oceans Canada's Mark Recovery Program (Kuhn 1988, Ford and Ellis 2006). Four and 5 year-old Chinook are the age classes most commonly consumed by resident killer whales (Ford and Ellis 2006), so it is likely that whales routinely dive beyond average Chinook swimming depths to locate these larger fish.

Killer whales may also swim to depths greater than those typical for Chinook if salmon are using diving as an escape response to avoid predation. Highly tortuous dive paths that resembled chasing behaviour occurred primarily during the descent phase for 12 of the 15 confirmed feeding dives that were not surface captures (Table 2.2). For these dives, the probable capture point corresponded precisely to the maximum depth of the dive (e.g., Figure 2.2A), regardless of the salmon species caught. It is therefore likely that rapid descents are a typical reaction of Pacific salmon to predator pursuit. The remaining three deeper feeding dives had capture points that did not correspond to maximum dive depths (Table 2.2). Of these, however, 2 were U-shaped dives with flat bottom phases that contained the same high track tortuosity evident in the descent phases of the other 12 dives (Figure 2.2C). The level bottom phases of these 2 dives imply that the tagged whales were pursuing fish along the sea floor, and therefore these fish did not have the ability to flee to deeper water. This could explain why the capture points for these dives, as estimated by the behavioural transition from tortuous to directional swimming, did not correspond to the maximum dive depths.

Other than one surface chase, the confirmed kills of chum and coho (n=7), which are normally shallow-swimming species (Figure 2.7), had estimated capture depths exceeding 80 m (Table 2.2, Figure 2.3). This provides further evidence that diving steeply is an escape response common to all species of Pacific salmon. It is likely that foraging whales opportunistically encountered chum and coho closer to the surface, where they are usually found, and subsequently pursued them to greater depths before making a successful capture. The DTAG pseudotracks indicated that surface or shallow water chases preceded captures of coho and chum for 5 of the 8 (63%) confirmed foraging dives that resulted in kills of these two species. An underwater video collected by Ellis et al. (2008) of two juvenile northern residents hunting a chum salmon further supports the hypothesis that surface-oriented salmon species will dive when threatened with predation by killer whales. The footage shows two young whales echolocating on a chum salmon that appears to be stunned and is relatively stationary at the surface; however, the salmon becomes active again after one of the juvenile whales bites its caudal fin, and immediately swims towards the bottom (Ellis et al. 2008).

Tagging studies of Pacific salmon also provide further evidence that diving steeply could represent an escape response, as fish often performed very deep dives directly following post-tagging release (Soeda et al. 1987, Quinn et al. 1989, Ruggerone et al. 1990, Ogura and Ishida 1992, Yano and Nakamura 1992, Ogura and Ishida 1995, Candy and Quinn 1999, Wada and Ueno 1999). In addition, tagged chum salmon were observed to dive to the sea floor in 12 of 16 encounters with Dall's porpoises (*Phocoenoides dalli*), a potential predator (Yano et al. 1984). Schools of herring (*Clupea harengus*) have similarly been observed to swim downward upon encountering killer whales, and whales often attempted to prevent this escape behaviour by corralling the fish against the surface (Simila and Ugarte 1993).

Although fleeing is energetically costly (Godin 1997), rapid descents may be an effective strategy for fish (particularly non-schooling species) to escape an air-breathing predator, such as a killer whale. The likelihood that a pursuing whale would have to return to the surface to breathe before intercepting its prey would increase with greater dive depths. Salmon may also swim downward to avoid presenting the visual target of a dark body silhouette against light coming from the surface (Denton 1970, A. Farrell 2013, pers. comm.). Furthermore, a previous study of resident killer whale habitat found that whales engaged in foraging behaviour more frequently in areas with high relief bathymetry (Heimlich-Boran 1988). Salmon may prefer areas with complex bottom topography because it provides good habitat for hiding from large predators. By rapidly swimming toward the sea floor when pursued, fish are able to make use of these refuges. Although another study (Hoelzel 1993) failed to find a correlation between bottom topography and the incidence of southern resident feeding behaviour, this may have been because recorded feeding behaviour was limited to those chases that could be observed at or near the surface.

Since salmon appear to dive in response to predator pursuit, pinpointing the depth at which chases are initiated (rather than the depth at capture) may provide a more accurate estimate of the depth ranges the whales are targeting. This would involve determining the depth of the transition between the searching and pursuit phase of each foraging dive, which might be accomplished by a combination of kinematic and acoustic analyses. The beginning of a chase is probably indicated by increases in swimming velocity, path tortuosity, and the production rate of echolocation clicks. Since echolocating killer whales can detect Chinook salmon approximately 100 m away in quiet conditions (Au et al. 2004), it is also probable that killer whales perceive fish at depth during surface transits, and then initiate a foraging dive in response. Kinematic analysis of foraging dive behaviour would therefore benefit from knowledge about how close a killer whale must be to a fish before it is energetically worth pursuing (Au et al. 2004), as well as the threshold distance at which Pacific salmon are capable of detecting large predators. Such information is currently lacking and extremely challenging to obtain.

2.5.2 Behavioural significance of killer whale dive tortuosity and body rotation

The tortuous and non-linear swim paths exhibited by foraging whales (Figure 2.2) support field observations (Hoelzel 1993) that, in addition to performing steep dives, salmon also attempt to avoid capture by unpredictably altering their swimming trajectories. The smaller body size of salmon relative to that of killer whales allows them to execute tighter turning angles at faster rates, making them more manoeuvrable than their larger predators (Godin 1997, Domenici 2001). Evasive movements increase the probability of escape by taking the fish out of the direct pursuit path of the predator (Godin 1997). In order to intercept erratically-swimming prey, killer whales must attempt to match these convoluted flight paths. In my study, the behavioural response of tagged whales to evasive manoeuvres of salmon resulted in noticeably lower straightness indices for foraging dives (means = 0.88-0.89) as compared to respiration dives (means ≥ 0.98, Figure 2.5). However, mean straightness indices for the foraging dives were only marginally lower than those of other dive behaviours (means = 0.89-0.93), indicating that measures of tortuosity alone may be insufficient to distinguish foraging from non-foraging dives.

The rate of change in pointing angle was also expected to be noticeably higher during foraging dives (particularly for descents, where the majority of chasing occurred) than non-foraging dives, since the orientation of the whale's longitudinal axis should change more rapidly when it is responding to prey manoeuvres. While the change in pointing angle was higher during foraging dives than during respiration dives, other dive behaviours displayed comparable or even higher values (Table 2.3). This implies that other behaviours, for instance socializing or beach-rubbing, may also involve rapid orientation changes. Change in pointing angle over time was higher for descents (chasing) than ascents (transiting), as expected (Table 2.3), however, this was true for all dive types, not just foraging.

Given that smaller fish have smaller minimum turning radii and faster maximum turning rates than larger fish (Domenici 2001), it follows that coho and other smaller salmonids are more manoeuvrable and therefore could be more difficult for killer whales to catch compared to the larger-bodied Chinook. Individually, smaller fish would provide a poorer net energy benefit if killer whales require more energy to catch what constitutes a smaller meal. This may provide an additional explanation for why Chinook are preferentially pursued by northern residents, as prey size choices of predators can be influenced by size-dependent differences in the locomotor performance of prey (Domenici 2001). Other killer whale populations that do preferentially feed on small, highly manoeuvrable fish tend to do so by cooperatively aggregating them, rather than pursuing them individually. However, this strategy is only effective if the targeted fish species engages in schooling behaviour as a response to the threat of predation. For example, the Norwegian population of killer whales that cooperatively herds herring are always observed to stun fish with high acceleration tail-slaps prior to consuming them (Simila and Ugarte 1993, Domenici et al. 2000). Tail-slaps are hypothesized to be more efficient than direct pursuit because acceleration and swimming manoeuvrability of herring is far superior to that of killer whales (Domenici et al. 2000). Unlike herring, Pacific salmon do not form densely populated schools (Nero and Huster 1996), so cooperatively herding and stunning them prior to capture is not likely to be effective. Furthermore, cooperative prey aggregation or pursuit has not been observed as a foraging tactic undertaken by resident killer whales, which capture their prey individually (Heimlich-Boran 1988, Ford and Ellis 2006). Individual pursuit is probably inefficient for capturing smaller salmon species because these fish can more readily out-manoeuvre the whales during chases than can the larger Chinook. Without a behavioural strategy to effectively aggregate and capture smaller-bodied prey in larger quantities (to ensure a greater net energy return), it is not surprising that northern residents tend to selectively ignore sockeye and pink salmon even when they are more plentiful.

The spiralling and highly tortuous descent paths of foraging killer whales are also possibly the result of acoustic searching behaviour, rather than simply a response to the evasive manoeuvres of fleeing prey. Odontocetes have narrow, conically-shaped sonar beams, a trait that allows them to effectively discriminate the size and distance of targets once they have been detected (Akamatsu et al. 2010). However, during the initial search phase of a foraging dive, an area much larger than the animal's beam width must be scanned in order to locate prey. Akamatsu et al. (2010) found that finless porpoises (*Neophocaena phocaenoides*) rolled their bodies extensively during dives that also had higher rates of echolocation and shortened inter-click intervals. Since these acoustic cues signify an increase in search effort, porpoise rolling behaviour probably functions to broaden the scanned area by continuously altering their sonar beam-axis (Akamatsu et al. 2010). Additionally, an experimental study of echolocation by two captive harbour porpoises (*Phocoena phocoena*) found that both clicking rate and variance in roll angle increased around the time of fish capture (DeRuiter et al. 2009). This implies that acoustic targeting and body manoeuvrability may serve complementary functions to improve the likelihood of intercepting highly mobile prey. Similar increases in rolling behaviour were strikingly prevalent in foraging dives conducted by tagged northern resident killer whales (Figure 2.6), and could serve a related purpose. Measures of mean and maximum roll per dive, as well as the rate of change in roll for both descents and ascents, were noticeably higher during foraging than other behaviours (Table 2.3). Roll measurements could therefore be useful as reliable metrics for identifying foraging behaviour in future studies.

Sustained off-axis body roll positions performed by hunting northern residents may also function to improve manoeuvrability and swimming performance during fish pursuits along the sea floor. Since cetaceans generate hydrodynamic thrust for swimming by moving the posterior third of their bodies and tail flukes dorso-ventrally (Fish et al. 2006), tail stroke amplitude (and thus forward propulsion) would be impeded when moving along the bottom in an upright position. Tagged northern residents often rotated their bodies approximately 90º to the right or left during confirmed foraging dives with U-shaped profiles (Figure 2.2C). The level bottom phases of these dives imply that the whales were probably chasing salmon along the sea floor, and turning sideways would ensure that fluke strokes were not inhibited by contact with the bottom and high swimming speeds could still be achieved.

Body rotation during swimming is also hypothesized to play a role in the echolocation behaviour of odontocetes foraging for benthic prey. Narwhals (*Monodon monoceros*) often swim in an upside-down position when moving along the sea floor, which is thought to improve prey detection by directing the sonar beam downward, where fish are more likely to be located (Dietz et al. 2007). Indus river dolphins, or susu (*Platanista gangetica minor*), also display an unusual swimming pattern in which they roll their bodies 90º to one side and orient their heads downward while trailing one flipper along the bottom (Herald et al. 1969). Susu echolocate continuously and make constant sweeping motions with their heads while conducting this swimming behaviour (Herald et al. 1969), implying that it may be related to searching for benthic fish. The prominent dorsal fins of killer whales prevent upside-down swimming along the sea floor; however, side-swimming displayed by tagged northern residents during U-shaped foraging dives might also serve to improve acoustic prey targeting. Au et al. (2004) determined that the target strength for Chinook salmon is highest when killer whale echolocation signals are oriented perpendicularly to the long axis of the fish, so rolling sideways might improve prey detection by reorienting the angle of outgoing echolocation clicks to maximize backscatter.

2.5.3 Comparative swimming velocities of killer whales and salmon

In addition to dive depth and tortuosity, estimates of swimming velocity were also an effective way to identify foraging dives. Adult resident killer whales have been previously shown to have maximum swimming rates of up to 2.7 m s^{-1} (females) and 3.0 m s^{-1} (males) (Williams and Noren 2009). The average foraging dive speed of northern residents in my study was only slightly lower than these maximum speeds, at 2.1 ± 0.8 m s^{-1} (mean ± SD, n=701, Table 2.3). However, average foraging speeds greater than 4.0 m s^{-1} were also observed for several dives conducted by tagged whales (Figure 2.4). Dives resulting in successful kills (n=17) ranged in speed from 1.1-4.2 m s^{-1} (mean ± SD = 2.6 ± 0.7 m s^{-1}), which is slightly faster than the average speed of 2.1 m s^{-1} for all statistically identified foraging dives (n=710), a category that also included unsuccessful chases. I calculated overall dive velocities from the DTAG data by using dive path lengths that relied on dead-reckoned positions, and therefore the resulting velocity values contained an undetermined amount of error. To eliminate this source of error, future accelerometry tag designs would benefit from the inclusion of a sensor that can accurately and directly measure swimming speed. Since descent and ascent vertical velocities were calculated using only direct depth sensor measurements, they provide a more accurate measure than overall dive velocity; however, these values are considerably lower than the true speed of the animal because movement in the x-y plane was not taken into account. Despite this, as with overall dive velocity, vertical velocities for both descents (0.78 ± 0.53 m s^{-1}) and ascents (0.75 ± 0.57 m s^{-1}) show the same trend of being much higher for foraging dives than for any other dive type (means $\leq$ 0.39, Table 2.3).

Most studies of salmon swimming performance focus on testing swimming stamina against current (to simulate upstream migration) by calculating critical swimming speeds (U_{crit}) achieved during incremental velocity tests, which can last for several hours. Mean foraging dive duration of tagged whales (including post-capture ascent) was 3.14 ± 1.73 min (Table 2.3), which implies that the chase (descent) portion of a feeding dive is probably between 1-2 minutes long at most. U_{crit} endurance swim speeds are therefore not useful for estimating salmon escape capabilities during a killer whale pursuit. Unfortunately, there are very few studies that document maximum or burst swimming speeds of adult salmon in saltwater, a measure that is more relevant to predator evasion (Reidy et al. 2000). This makes comparison with resident killer whale swimming velocities difficult. Data logger measurements from a wild adult chum salmon (ocean age 0.4) in the Bering Sea measured a maximum swimming speed of 2.8 m s^{-1} (Tanaka et al. 2005), which is comparable to the average foraging dive speed (2.6 ± 0.7 m s^{-1}, n=17) for tagged northern residents that were confirmed to have caught a fish. Average foraging dive speeds are expected to approximate or marginally surpass the maximum speeds of Pacific salmon, since whales should not expend additional energy by swimming faster than is required for prey capture.

2.5.4 Multivariate clustering to identify foraging dives

Dive depth, tortuosity, body roll, and estimates of swimming velocity were all useful measures to distinguish foraging dives from other behaviour types in resident killer whales. Overall, the LDA did a good job of identifying foraging dives using these and other metrics, despite a comparatively small initial training set (n=15) of feeding dives. The usefulness of this technique was indicated by the successful cross-validation results that saw all omitted feeding dives correctly re-assigned to the foraging category. While the LDA appeared to readily separate foraging dives from the rest of the data set, the *X*-means cluster analysis was only able to identify two additional behaviour types within the 10,618 non-foraging dives. The inability of the cluster analysis to resolve finer-scale behavioural differences is likely the result of the dive variables being chosen with the specific goal of discerning foraging from non-foraging dives. An additional study using different kinematic variables that might better distinguish non-foraging dive types from one another (e.g., resting from travelling) would result in an improved quantitative description of these additional behaviours.

Because the discriminant analysis used individual dives as the behavioural sampling unit, two confirmed feeding dives that occurred on the surface could not be included in the statistical training set for classifying dives. Surface chases were made up of multiple brief, shallow “dives” terminating in a fish capture, so unlike deeper, single-dive pursuits, these events were very difficult to detect statistically. This is because the dive-by-dive LDA could only consider very small portions of the entire surface chase at a time, rather than analysing all the dives comprising the chase as a single event. Consequently, the multivariate analysis probably did a relatively poor job of identifying surface pursuit behaviour as ‘foraging’ and therefore could not resolve potential captures occurring at the surface (< 1 m depth).

Of the confirmed feeding dives, surface captures (n=2) were observed less frequently than deeper foraging dives (n=15), probably because whales were primarily focused on capturing the more deeply distributed Chinook. This contrasts directly with Alaska’s Prince William Sound resident killer whale population, which feeds primarily on coho during the summer months, a season when Chinook are largely unavailable in this area (Saulitis et al. 2000). Surface chases are the prevailing salmon foraging tactic displayed by Prince William Sound residents during the summer (Saulitis et al. 2000), which is unsurprising given that coho typically occupy the upper 25 m of the water column (Figure 2.7 and Figure 2.8). For the tagged northern residents in my study, surface chases probably arose from opportunistic detections of fish in shallow water, rather than representing a targeted foraging effort by the whales. This is evident in the case of a surface-caught Chinook captured by A66 (tag deployment oo12_235b, Table 2.2), as this capture consisted of a single leap at the surface and was not preceded by any behaviours that resembled chasing. Because surface pursuits were not the main foraging tactic used by northern residents during the season and years in which this study took place, the LDA’s inability to detect them probably resulted in only a minor number of false-negatives when detecting foraging dives.

2.5.5 Juvenile whale foraging behaviour and social learning

Killer whales are already known to be capable of learning complex behaviours, such as vocal dialects (Ford 1991, Deecke et al. 2000), and the transmission of specialized feeding behaviours has been similarly hypothesized to occur through learning of group traditions (Ford et al. 1998). The behaviour of juvenile tagged whales in this study provides some evidence that species-specific foraging tactics are learned, either through imitation or active teaching by mothers and other experienced relatives. For instance, the tagged juvenile I106 made three dives that were classified as foraging behaviour by the LDA; however, in all three cases a confirmed fish kill was attributed to its mother, I51, who was observed diving simultaneously in the same locations. There were also other cases of tagged juveniles that dove with their mothers but had dive pseudotracks that failed to show active participation in the chase, despite the mother successfully taking a fish. These dives may represent learning by juveniles through the observation of fish pursuit and capture by a more experienced whale. Similar following behaviour was verified from DTAG data collected from a tagged humpback whale (*Megaptera novaeangliae*) mother-calf pair, which had the highest degree of correlated dive behaviour when both individuals were feeding (Tyson et al. 2012). The calf probably engaged in synchronized diving in order to share prey or learn foraging techniques from its mother (Tyson et al. 2012).

There is widespread evidence that specialized foraging behaviours are transmitted by social learning in other killer whale populations, as well as in other cetacean species. Observations of self-stranding behaviour by killer whales hunting pinnipeds have shown that this risky hunting tactic requires a high degree of skill to execute (Lopez and Lopez 1985, Guinet and Bouvier 1995). Juveniles only become proficient after several years of practice, learning, and assistance from more experienced individuals (Lopez and Lopez 1985, Guinet and Bouvier 1995). There is also evidence that intentional beaching behaviour by foraging bottlenose dolphins (*Tursiops* sp.) is learned, as animals displaying this behaviour were always born to mothers that engaged in beach hunting (Sargeant et al. 2005). Specialized sponge-carrying behaviour by bottlenose dolphins in Shark Bay, Australia, is likewise maternally transmitted to calves via vertical learning and takes several years to develop (Sargeant and Mann 2009). This behaviour is never displayed by calves whose mothers did not carry sponges and, additionally, 71% of calves with sponge-carrying mothers were also observed to use this tactic (Sargeant and Mann 2009). The occurrence of various specialized feeding behaviours in baleen whales has also been attributed to social learning, including lobtail (Weinrich et al. 1992) and reverse-loop (Ware et al. 2010) lunge feeding in humpbacks, and bird-association and lunge feeding in minke whales (*Balaenoptera acutorostrata*) (Hoelzel et al. 1989).

Sociality provides a mechanism by which specialist foraging behaviours can easily proliferate from individuals to the population or species level. Resident killer whales have extremely stable group membership with no dispersal of either sex from the matriline into which they were born, as well as a prolonged period of maternal investment (Ford et al. 2000). This high degree of social stability allows learned behaviours, such as hunting tactics, to be effectively passed from one generation to the next with great conservatism. Cultural transmission may therefore contribute greatly to maintaining an ecotype's prey selectivity over multiple generations. Bonsall and Wright (2012) provide support for the hypothesis that resource specialization is more likely to evolve in populations with threshold levels of cooperation and altruistic behaviour. In northern resident killer whales, cooperative prey sharing between related individuals serves to minimize intra-group competition (Ford and Ellis 2006, Ford et al., unpublished data). In this way, specialization on a spatially predictable but comparatively rare prey species, like Chinook salmon, is possible without leading to increased resource competition as the population grows.

Should environmental change outpace the rate of learning, however, transmission of behaviours via social learning will become a detrimental strategy (Boyd and Richerson 1988). If it takes several years or more to develop the foraging skills needed to effectively hunt Chinook salmon, species-specific foraging behaviours may become too culturally engrained to allow for dietary shifts to more plentiful prey species when Chinook are less abundant. This lack of behavioural plasticity could be the root cause of the observed negative correlation between resident mortality rates and Chinook salmon availability (Ford et al. 2010), and may prevent continued resident population growth if Chinook stocks remain low or experience future declines.

2.5.6 Conclusions

DTAG-recorded kinematics of feeding dives by northern resident killer whales indicated that foraging techniques are specialized to match the behaviour of their preferred prey, the Chinook salmon. Foraging dives targeted the expected depth distribution of Chinook and showed that whales effectively responded to escape strategies displayed by Pacific salmon. Dive depth, tortuosity, body roll, and estimates of swimming velocity were determined to be the most useful measures for distinguishing foraging from other dive behaviours in resident killer whales. Based on the kinematic behaviour of tagged juveniles that conducted synchronous foraging dives with their mothers, specialized foraging tactics appear to be learned. Social learning has probably led to a culturally stable, population-wide foraging tradition that precludes efficient prey-switching or generalist strategies, even in the event of a decline in Chinook availability.

Chapter 3: Echolocation and prey handling sounds are linked to foraging dive kinematics in northern resident killer whales capturing Pacific salmon

3.1 Summary

Piscivorous resident killer whales (*Orcinus orca*) are assumed to use echolocation to find and capture their prey. The functional significance of echolocation clicks produced by residents foraging in the wild, however, has not yet been investigated. Furthermore, patterns of echolocation by individual whales during different stages of prey capture, as well as the relationship between echolocation and kinematic diving behaviour, remain unknown. I used multi-sensor biologging DTAGs to study the association between echolocation and foraging dive kinematics for 7 northern resident killer whales during 17 successful captures of Pacific salmon (*Oncorhynchus* spp.) off the northeast coast of Vancouver Island (2009-2012). The tagged killer whales produced 260 regular echolocation click trains with mean repetition rates of 6.7 ± 7.2 (SD) clicks s^{-1}, and 82 buzzes with extremely rapid click rates in excess of 50 clicks s^{-1}. The whales produced an average of 15.3 ± 6.6 regular click trains per fish capture, which likely assisted in locating and identifying their prey. In addition, echolocation during the pre-capture phase often coincided with sideways roll orientations that could improve the reception of returning echoes or facilitate benthic pursuit of fish. Buzzes were produced at a rate of 5.9 ± 2.9 per capture and most occurred in deep water (117.0 ± 62.5 m) prior to or concurrent with fish captures (89%), which supports their hypothesized function of providing fine-scale targeting information just prior to prey capture. After salmon were successfully captured, both the percentage of time that whales spent echolocating and the mean repetition rate within regular click trains decreased significantly. Distinctive 'crunching' sounds (11.3 ± 7.4 per capture) were also evident on the DTAG recordings, and likely signified the fish being torn apart prior to consumption or prey sharing. The majority of crunches were produced at relatively shallow depths (21.1 ± 28.9 m) after the estimated time of prey capture (70%), indicating that most prey was brought to the surface before being eaten. The occurrence of some crunches (21.1%) prior to estimated prey capture times might reflect multiple prey captures per dive, but most likely represent misidentified flow noise (which can have similar acoustic properties). My analysis indicates that buzzes (capture attempts) and crunches (capture successes) are potentially useful metrics of foraging efficiency, which could be used to determine whether killer whales are meeting their daily energetic requirements.

3.2 Introduction

The ability of toothed whales to produce pulses of clicks similar to those described for echolocating bats (Griffin et al. 1960) first came to light in the 1950s (e.g., Kellog et al. 1953). However, determining the functional significance of these clicks has proved extremely difficult, given that most behaviours by diving marine mammals occur underwater and cannot be directly observed. Since the initial discovery of dolphin sonar, studies of captive cetaceans (whose behaviours can be readily observed and manipulated) have sought to fill this knowledge gap, and have provided valuable information about the echolocation capabilities of these animals. Captive studies have shown that dolphins can find and distinguish a large variety of targets with great accuracy using sonar clicks, even when their vision is restricted (e.g., Norris et al. 1961, Nachtigall 1980, Verfuss et al. 2009). Experimental studies with trained animals have also provided an understanding of how cetacean echolocation functions during target detection tasks. For instance, many studies (e.g., Evans and Powell 1967, Johnson 1967, Morozov et al. 1972, Au et al. 1982) have shown that delphinid click intervals are equivalent to the two-way transit time of the click to a target, plus a lag time for signal processing, which means that click repetition rates are correlated with target range (Au 1993). Based on captive studies of dolphin sonar, and its similarity to the clicking behaviour of insectivorous bats during prey captures (Madsen and Surlykke 2013), it has been assumed that toothed whale echolocation clicks also facilitate the detection and tracking of prey. However, field-based evidence with greater ecological relevance is still needed to explain the functional significance of echolocation by wild odontocetes.

Although captive studies have provided detailed information about the sonar capabilities of small cetaceans, translating these findings into an understanding of how echolocation is used by wild odontocetes presents a significant challenge. Recent studies using acoustic biologging tags (e.g., DTAGs, Johnson and Tyack 2003) have supplied the first data that link echolocation behaviour to foraging and prey captures by wild individuals. Click echoes rebounding from prey were first recorded in the wild using DTAGs deployed on beaked whales (family Ziphiidae) (Johnson et al. 2004). These deep-diving whales produce echolocation clicks almost continuously at the bottom of their dives but are largely silent during the descent and ascent phases (Johnson et al. 2004). Given the large energetic cost associated with these extremely deep dives, they are presumably conducted to capture prey. The restriction of echolocation to the bottom phase therefore indicates that its function is specifically related to feeding. Similarly, the proportion of time that finless porpoises (*Neophocaena phocaenoides*) spent echolocating almost doubled when they were performing manoeuvres associated with chasing prey, such as body rotations and sudden turns (Akamatsu et al. 2010). Porpoises also shortened their inter-click intervals when conducting these types of movement, indicating that their intended targets were increasingly close in proximity and were probably prey (Akamatsu et al. 2010). These are just two examples from the growing body of evidence provided by acoustic tags to support the theory that wild odontocetes use echolocation for prey detection and tracking.

Acoustic biologging tags have also supplied the first verification that rapid bursts of clicking (known as 'buzzes') are used by odontocetes for fine-scale tracking during the final moments of prey pursuit. Echo structures from buzzes by Blainville's beaked whales (*Mesoplodon densirostris*) showed that buzz clicking rates were correlated to prey range and allowed the whales to focus on a single target during a capture attempt (Johnson et al. 2008). This has been corroborated in other species by relating the occurrence of buzzes to body movements that are consistent with close-range prey pursuit or captures. Buzzes by beaked whales, for example, often coincide with movements that are consistent with chase behaviour, such as increased dynamic body acceleration (Johnson et al. 2004) or tight, circling swim paths (Johnson et al. 2008). In addition, short-finned pilot whales (*Globicephala macrorhynchus*) perform directional high-speed (9 m s^{-1}) sprints at the bottom of deep dives that are immediately followed by buzzes (Aguilar Soto et al. 2008). Short range sonar sounds (inter-click intervals of < 10 ms) produced by finless porpoises were similarly observed to occur at increased frequencies during rolling dives and were often associated with abrupt declines in swimming speed (indicative of small radius turns made during prey pursuit) (Akamatsu et al. 2010). Furthermore, DTAGs deployed on sperm whales (*Physeter macrocephalus*) recorded rapid click bursts called 'creaks' that coincided with increased changes in body orientation during the bottom phases of dives, when prey captures were probably occurring (Miller et al. 2004). Evidence from acoustic biologging tags has thus far supported the hypothesis that buzzes are produced during the terminal phase of prey capture (Madsen and Surlykke 2013).

Schevill and Watkins (1966) first described the echolocation behaviour of fish-feeding 'resident' killer whales (*Orcinus orca*) of the eastern North Pacific from recordings of vocalizations by a subadult male that was captured off Vancouver Island. They noted that this individual produced series of clicks that appeared to function in echolocation, as he was only able to consistently avoid a hydrophone placed in his path at night when he was clicking (Schevill and Watkins 1966). Following this initial work, echolocation by wild resident killer whales has also been described using passive acoustic methods (Ford 1989, Barrett-Lennard et al. 1996, Holt et al. 2013). However, concurrent behavioural information collected during these studies was limited to surface observations of group behaviour. Barrett-Lennard et al. (1996) determined that resident killer whales produced comparatively louder and more variable echolocation clicks, and used echolocation significantly more often while feeding than during all other activity states combined. Similarly, Holt et al. (2013) found that the occurrence of clicking by southern resident killer whales increased during group activities that were consistent with foraging, as compared to those indicative of travel or other behaviours. These two studies suggest that resident echolocation probably serves important functions specific to their feeding behaviour. Killer whales of various ecotypes, including residents, have also been recorded producing buzzes (Awbrey et al. 1982, Ford 1989, Holt et al. 2013), but the occurrence of these sounds has not yet been specifically linked to prey captures by killer whales, as it has for other species of toothed whales.

In addition to general descriptions of echolocation behaviour by resident killer whales, the acoustic properties of their clicks have also been well-documented using hydrophone arrays (Au and Benoit-Bird 2003, Au et al. 2004). These studies confirmed that the structure of clicks made by resident killer whales is consistent with the traits required to produce an effective sonar signal: they have broad bandwidths, brief durations and high amplitudes (Au et al. 2004). Quantitative analysis of click properties showed that echolocating killer whales can detect prey at distances of 100 m or greater, and are capable of fine target discrimination (Au et al. 2004). Click source levels are also highly coupled to target distance, indicating that killer whales possess a type of time-varying gain control that can be used to discern relative target size (Au and Benoit-Bird 2003). Furthermore, an experimental study of backscatter created by exposing live fish to simulated killer whale clicks determined that echo structures differed between Pacific salmon species, probably as a result of variation in their swimbladder morphologies (Au et al. 2010). It is therefore likely that resident killer whales use echolocation to identify the sizes and types of fish they encounter (Au et al. 2010), a function that is especially significant given their preference for consuming mature (4-5 y) Chinook salmon (*Oncorhynchus tshawytscha*) over other species and age classes (Ford et al. 1998, Ford and Ellis 2006).

Understanding how resident killer whales use echolocation to forage is important because anthropogenic noise, such as boat traffic, has the potential to disrupt prey captures by masking click echoes. Although most shipping noise is low frequency, broadband cavitation noise produced by fast-moving ships extends into higher frequencies (Arveson and Vendittis 2000), and has been shown to reduce the maximum detection ranges of echolocation clicks by another odontocete species, Cuvier's beaked whales (*Ziphius cavirostris*) (Aguilar Soto et al. 2006). An experimental study of resident killer whale echolocation clicks determined that detection ranges for Chinook salmon would be reduced from 100 m to less than 40 m in the presence of significant ambient noise, such as moderately heavy rainfall (Au et al. 2004). Resident killer whales in British Columbia, particularly southern residents, are frequently exposed to anthropogenic noise from a considerable fleet of small commercial and private whale-watching boats (Foote et al. 2004), as well as larger vessels like ferries and cruise ships. Southern residents are already known to increase their call durations (Foote et al. 2004) and call amplitudes (Holt et al. 2008) in the presence of increased boat noise, but no field studies have been undertaken to determine how engine noise impacts their echolocation behaviour. Model estimates of click detection thresholds, however, indicated that a single whale-watching boat could cause masking approximately 20-30 dB above that of ambient noise, which would result in a 3-fold decrease in resident killer whale click detection ranges (Bain et al. 2014).

Resident killer whales also reduce the time they spend feeding when boats are present (Williams et al. 2006, Lusseau et al. 2009), possibly because the noise renders their echolocation clicks ineffective. This would lead to decreased energy intake (Williams et al. 2006), and eventually, population level effects (Bain et al. 2014). Exposure to anthropogenic noise that interferes with echolocation could therefore limit the population growth of resident killer whales by reducing prey capture rates. To mitigate the potential impacts of boat noise on foraging efficiency, the normal use of echolocation during feeding dives by resident killer whales must first be understood. In particular, the impact of reduced echolocation detection ranges on foraging success is highly dependent on the type of prey searching tactics that resident killer whales employ (Bain et al. 2014).

Although general characteristics of echolocation have been described for resident killer whales, a definitive link between echolocation and prey captures by wild individuals has yet to be established. In this study, I deployed acoustic biologging DTAGs on northern resident killer whales to investigate how they used echolocation during successful salmon captures, and analysed the relationship between echolocation and concurrent diving behaviour. I also examined the occurrence of buzzes in relation to the timing of prey captures to determine whether these sounds were used in fine-scale targeting at the end of chases, as has been demonstrated for other species of toothed whales. Other sounds that could reflect prey handling behaviour were also identified, and the potential applicability of DTAG data as a means of estimating resident foraging efficiency was explored.

3.3 Methods

3.3.1 Study area and DTAG instrumentation

I documented the acoustic behaviour of foraging northern resident killer whales over four field seasons (August and September, 2009-2012) in the coastal waters of northeastern Vancouver Island and the central coast of British Columbia. Northeastern Vancouver Island was chosen as the primary study site because northern residents are predictably found there during summer and fall, when they intercept migrating salmon returning to the Fraser River (Nichol and Shackleton 1996, Ford 2006, Ford and Ellis 2006). Consequently, whales are known to spend substantial periods of time engaged in foraging behaviour within this important nearshore habitat (Ford 1989, 2006, Ford and Ellis 2006).

I recorded vocalizations and simultaneous body movements of foraging whales using suction-cup attached digital archival tags (DTAGs). These tags log high-resolution data describing the three-dimensional orientation of the tag (and by proxy, the animal's body position) using a pressure sensor, triaxial accelerometers and magnetometer, as well as continuously record underwater sound on two hydrophones (Johnson and Tyack 2003). All data were archived on a flash memory array within the DTAG (Johnson and Tyack 2003). The sampling rate for the pressure sensor, accelerometers, and magnetometer was 50 Hz for DTAG-2 deployments (2009-2011) and 250 Hz for DTAG-3 deployments (2012); all sensor data were eventually reduced to 5 Hz sampling frequencies during tag calibration. Audio was recorded with 16-bit resolution at frequencies of 96, 192 or 240 kHz, depending on the tag model used (DTAG-2 or DTAG-3) and the year of deployment (Table 3.1). Prior to analysis, hydrophone recordings with sampling frequencies of 240 kHz were down-sampled to 192 kHz to allow for real-time audio playback.

Table 3.1 Overview of DTAG deployments used to analyse echolocation behaviour by northern resident killer whales (n=7) during successful fish capture events (n=17), 2009-2012.

Tag ID	Whale ID	Sex	Age (y)	Audio sampling rate (kHz)	Tag model	Recording time (h)	Number of fish capture events
oo09_234a	A46	male	27	96	DTAG-2	3.9	1
oo09_240a	A37	male	32	96	DTAG-2	3.6	2
oo10_256a	G64	female	10	192	DTAG-2	7.6	2
oo10_265a	G49	female	20	192	DTAG-2	2.9	2
oo11_246a	G31	female	30	192	DTAG-2	3.8	5
oo12_232a	I106	unknown	8	240	DTAG-3	5.8	2
oo12_235b	A66	male	16	240	DTAG-3	4.5	3

A single whale was selected for tagging after the identities of encountered whales were visually established using an existing photo-identification catalogue of individual dorsal fin and saddle patch morphology (Ellis et al. 2011). The research platform was a 10 m command-bridge powerboat that provided an elevated vantage point from which the whale could be seen underwater just prior to surfacing. This allowed the tagging vessel to be positioned accordingly for DTAG deployment. Only adults and larger juvenile killer whales were approached for tagging, and repeat deployments on previously tagged individuals were avoided where possible.

3.3.2 DTAG deployments and prey sampling

The whale selected for tagging was approached in the research vessel by paralleling its swimming path and matching its speed of travel. The DTAG was then deployed from the bow using a 7 m long, hand-held carbon fibre pole. Ideally, tags were attached to the back just below the insertion of the dorsal fin and would clear the water when the whale surfaced to allow for tracking of the tag's VHF radio beacon. We photographed tagged whales to confirm their identities and followed them at a distance throughout each deployment in order to correlate surface observations of foraging activity with the archived tag data. The need for concurrent surface observations limited the tag deployments to daylight hours only. Tagged whale behaviours were noted using a digital voice recorder that was time-synchronized with the DTAG sensor instrumentation. This allowed the tag sensor data to be referenced against simultaneous behavioural cues observed at the surface. Following the methodology of Ford and Ellis (2006), scales and tissue fragments observed floating in the vicinity of tagged whales were collected from using a fine-meshed dip net. These samples were used to confirm which dives resulted in successful prey captures and provided information about the species and age of fish caught. Species and ages of fish were determined using schlerochronology methods (MacLellan 2004), or by genetic analysis (Withler et al. 2004).

3.3.3 DTAG calibration, pseudotrack construction, and dive identification

Sensor data downloaded from the DTAGs were calibrated to correct for the orientation of the tag relative to the body axes of each tagged whale using established methods (Johnson and Tyack 2003) in MATLAB (MATLAB 2009). For some deployments, changes in the position of the DTAG on the animal due to tag slippage required performing new calibrations for every new orientation of the tag. Calibration converted the raw sensor measurements of pressure into depth, and raw acceleration data into the three rotational measures of pitch, roll, and heading.

I visualized the time series of whale body orientations for each tag deployment using the software package TrackPlot 2.3 (Ware et al. 2006), which combines the calibrated pitch, roll, heading and depth values to create a three-dimensional representation (termed "pseudotrack") of tagged whale movements (see Chapter 2, Figure 2.2). Since DTAGs do not directly measure swim speed, the pseudotracks were constructed by assuming a constant velocity of 1.6 m s^{-1}, which is a measured average swimming speed of foraging resident killer whales (Ford 1989). The exception to this assumption occurred when the whale dove steeply, in which case TrackPlot estimated swim speed using the rate of change in depth, corrected by the sine of the whale's pitch angle (Ware et al. 2006, Ware et al. 2013). Dives were identified from the calibrated tag data using an automated filter in MATLAB (2009) that defined a dive as any submersion with a depth of 1 m or greater, bounded by surfacing events of <1 m depth. I chose a shallow depth threshold to ensure that all submersions and surfacings would be detected. The dive detection filter calculated the start and end times (in seconds since tag activation) and the maximum depth (m) for each of the identified dives.

3.3.4 Defining successful fish capture events

The beginning and end times of every successful fish capture event were determined by matching the times at which prey samples were collected (n=17) to the corresponding kinematic behaviour displayed in the TrackPlot pseudotracks. Each fish capture event included all dives immediately preceding the prey sample collection that contained behaviour indicative of prey searching or pursuit (i.e., convoluted, spiralling and kinematically complex dive paths). The time of the capture itself was predicted to occur when this pursuit behaviour ceased abruptly, and generally corresponded to the maximum depth of the dive just before the prey sample was collected at the surface (see Chapter 2, Table 2.2). At the predicted time of fish capture, tagged whales usually transitioned from a complex, spiralling descent to a directional, linear ascent. Dives that took place after the fish was caught were also included in the event if the pseudotracks contained circling or milling behaviour that could be associated with prey handling or sharing. The capture event was considered to end when the tagged whale resumed shallow, directional swimming at the surface. After identifying the beginning and end times for each fish capture event, I then isolated and analysed the concurrent acoustic segment from the DTAG hydrophone recordings.

3.3.5 Distinguishing focal (tagged whale) from non-focal sounds

All DTAG hydrophone recordings were amplified by 10 dB on both channels to improve visualization of the acoustic spectrograms prior to analysis. The resulting audio files were then examined both visually (using spectrograms) and aurally for the occurrence of sounds potentially made by the tagged whale. Whale vocalizations were broadly categorized as either echolocation clicks, buzzes, pulsed calls, or whistles, based on definitions of sound types from a detailed acoustic study of the same population (Ford 1989). Sounds that were likely associated with prey handling and consumption were also identified on the DTAG recordings. I noted the beginning and end times (relative to the start of each fish capture event), and the total duration for every sound of interest. Only those sounds that were likely to have been made by the tagged whale (i.e., 'focal' sounds) were analysed; non-focal sounds produced by conspecifics were omitted. This distinction was achieved using a combination of qualitative and quantitative approaches, depending on the sound category.

Focal echolocation clicks (tagged whale) were distinguished from non-focal clicks using two different methods, as described by Ward et al. (2008) and Jensen et al. (2011). First, I examined the spectrograms of each click for the presence of a low frequency energy component. Increased low frequency content (generally <20 kHz) results from the passage of sounds through the tissue of the whale's body prior to reaching the DTAG, and is therefore evident in focal clicks but largely missing from non-focal clicks (Zimmer et al. 2005, Figure 3.1). The second method calculated the delay between the arrival times of each click at the two DTAG hydrophones, and was used to confirm that clicks with low frequency components originated from the focal whale. Given the fixed position of the DTAG on the whale's body, sounds made by the focal individual should originate from a consistent angle relative to the tag. Consequently, the difference in the arrival times of a sound at the two tag hydrophones should also be consistent over time and close to zero (Zimmer et al. 2005, Johnson et al. 2006). Conversely, clicks recorded on the tag from non-focal whales would originate from continuously changing angles as the relative locations of these individuals shift with respect to the focal whale (and the DTAG) (Johnson et al. 2006). Arrival time differences for non-focal echolocation clicks were therefore expected to be inconsistent over time (and have values ≠ 0), so long as both whales were not stationary.

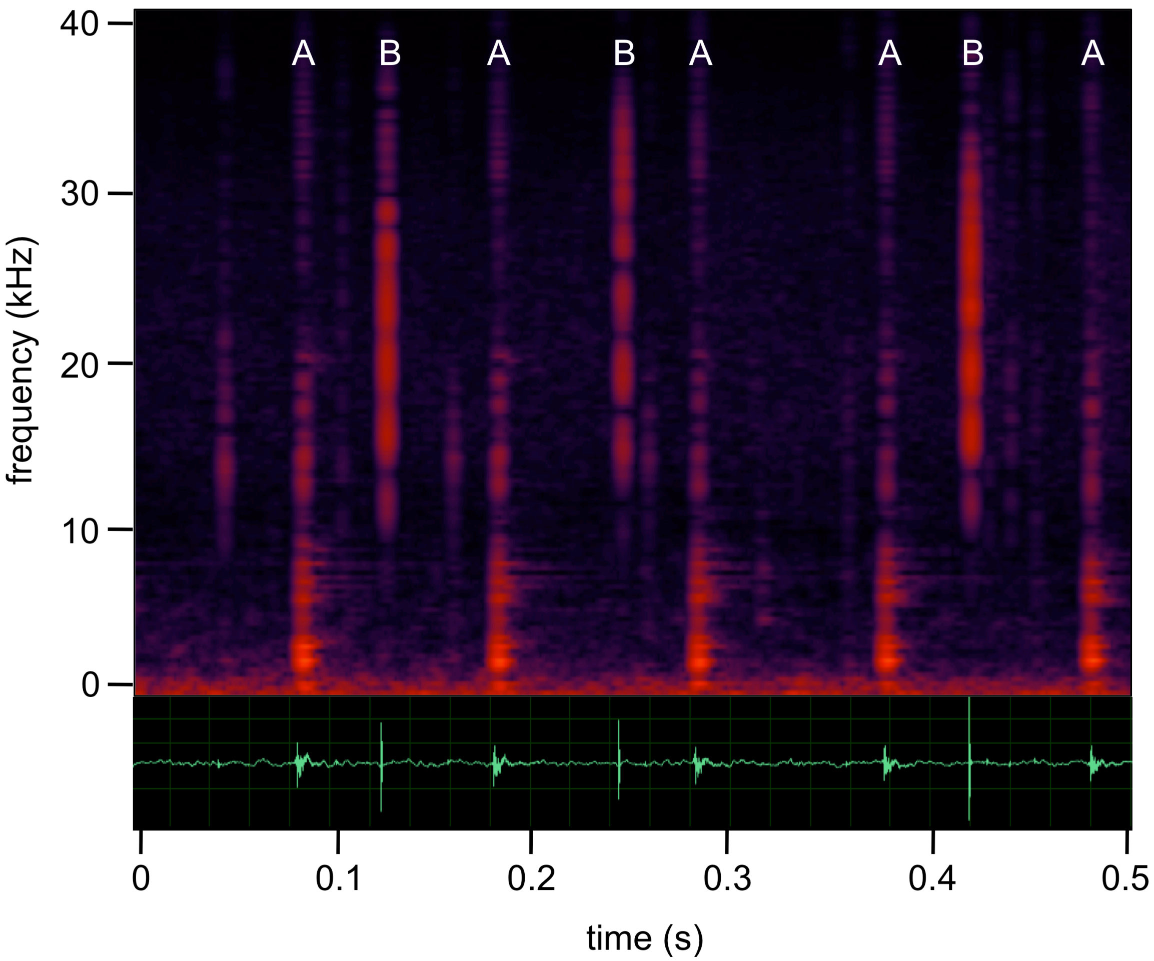

Figure 3.1 Spectrogram (top) and waveform (bottom) of focal echolocation clicks (A) made by tagged northern resident killer whale I106 (tag deployment oo12_232a) during a foraging dive, along with simultaneous non-focal clicks (B) originating from a conspecific. The focal clicks display coupling of low frequency sound energy (≤ 10 kHz) that is absent in the non-focal clicks. Originally recorded with 12 dB gain and amplified by an additional ~20 dB to improve visualization of the spectrogram.

To calculate the arrival time difference for each echolocation click, I cross-correlated the waveform signals from the two DTAG hydrophones and calculated the time lag at which the cross-correlation became maximal, according to the following integral (Zimmer 2011):

$$C(\tau) = \int_{-\infty}^{\infty} s_0(t)s_1(t+\tau)dt \qquad \text{Eq. 7}$$

where s_0 and s_1 represent the respective time series of the two hydrophones and τ is the variable time lag between them; the cross-correlation $C(\tau)$ is maximized when the signal delay between s_0 and s_1 corresponds to τ (Zimmer 2011). Since one of the two hydrophones was set to record with a gain of 12 dB, the amplitude of the waveform recorded on the second hydrophone (gain = 0 dB) was multiplied by a factor of 4 prior to performing the cross-correlation. The value of this multiplier was determined using the formula for calculating relative amplitude, or sound pressure level:

$$R_{dB} = 20 * \log_{10}\left(\frac{A_1}{A_0}\right) \quad \text{Eq. 8}$$

where the multiplier equals the ratio of the two waveform amplitudes ($A_1/A_0 = 4$), given a gain difference between them of R_{dB} = 12 dB. Effective cross-correlation requires signals with definitive temporal or spectral features (e.g., substantial amplitude modulation) (Zimmer 2011); therefore, arrival time delays could only be estimated for echolocation clicks and not for other types of vocalizations. The estimated differences in arrival time for echolocation clicks were then compared to the results from the qualitative visual and audio method (i.e., presence of low frequency sound energy) to determine the relative agreement between these two methods for identifying focal echolocation clicks. The results of this comparison led me to retain all clicks identified using the initial qualitative method in the subsequent analyses.

Further analysis of pulsed calls and whistles was not attempted because it was impossible to distinguish whether these types of vocalizations were from focal or non-focal whales, either qualitatively or by waveform cross-correlation. It was also not possible to reliably distinguish focal and non-focal buzzes from one another using these methods. However, I included most audible buzzes in my analysis under the assumption that they were more likely to have originated from the focal whale than from conspecifics. This assumption was based on the fact that buzzes do not travel as far as regular echolocation clicks, since click source levels decline as killer whales approach a target (Au and Benoit-Bird 2003), and clicks within buzzes thus have lower relative amplitudes and apparent output levels (Miller et al. 1995, Madsen et al. 2005, DeRuiter et al. 2009). Recorded levels of returning echoes from buzz clicks are also lower than those for regular clicks (Johnson et al. 2006). The only situations in which buzzes could be ruled out as non-focal occurred when the buzz either began or ended as a regular click train that lacked the low frequency sound energy present in focal clicks, or the buzz overlapped with a focal click train that had clear low frequency content (assuming that killer whales cannot emit more than one click train at a time the buzz would therefore be non-focal).

Prey handling sounds, termed 'crunches', were interpreted to arise from a whale catching a fish in its jaws, or tearing the carcass into pieces following a capture. Such sounds were unlikely to be audible unless they occurred very close to the tag hydrophones, and therefore all identified crunches were also assumed to come from the focal animal. This approach likely over-estimates the total number of buzzes and crunches, due to the possible inclusion of similar sounds made by non-focal whales when in close proximity to the tag. Once identified, crunches were rated by a more experienced listener on their relative likelihood (confirmed, probable, or possible) of actually representing prey handling behaviour. 'Confirmed' crunches shared acoustic similarities with prey handling sounds previously described for transient killer whales (termed KRaCS, or 'killing, ramming and crushing sounds'). 'Probable' and 'possible' crunches had decreasing levels of certainty because air bubbles and water flowing through the tag housing could not be ruled out as the sound source (V. Deecke, pers. comm.).

3.3.6 Analysis of echolocation and concurrent kinematic behaviour

Consecutive echolocation clicks were considered to be part of the same click train if they had similar frequency structures and were separated by intervals of 2 s or less (based on Barrett-Lennard et al. 1996). Mean click duration (s) and mean inter-click interval (ICI, s) were calculated for all focal echolocation clicks produced during the 17 fish capture events. The mean duration of all click trains (s) produced during the fish capture events was also determined. Click repetition rate (clicks s^{-1}) was calculated for every second within each fish capture event, and each second was then binned by clicking rate using intervals of 10 click s^{-1} (i.e., 5 bins, ranging from 1-10 clicks s^{-1} to 41-50 clicks s^{-1}). Mean click repetition rate was determined by averaging the number of clicks produced during every second for all fish captures pooled together (periods where whales were not echolocating were excluded). Buzzes occurred when echolocation clicks became so close together as to be visually indistinguishable when viewing the acoustic spectrogram in 1 s windows (generally this occurred at click rates exceeding 50 clicks s^{-1}).

Acoustic recordings were synchronized with kinematic data from the DTAG accelerometers to explore the relationship between whale body position, the production of echolocation clicks, and the relative foraging phase (either pre- or post-capture). All measurements of body position on the roll axis were converted to absolute values to eliminate directionality (+/-), which could have led to artificially lowered rates of orientation change if whales abruptly switched their direction of body rotation. Roll orientation changes by killer whales were assumed not to exceed 180° within each 0.2 s sampling interval. Thus, roll orientations of 0° indicated upright swimming (dorsal fin oriented upward), orientations of 90° signified that a whale was swimming on its side, and 180° indicated a whale swimming upside-down. I examined the measures of instantaneous body roll (degrees, down-sampled to 1 Hz) and rate of change in body roll (calculated as the sum of the change in body roll every 0.2 s, in degrees, over 1 s intervals) relative to whether or not clicks were being produced, and whether these clicks were made before or after a fish was captured. I also compared the relative clicking rates (clicks s^{-1}) before and after the fish capture for each event, as well as the amount of time spent clicking (%) during each of these two foraging phases.

To determine if body position varied simultaneously with clicking rate, instantaneous body roll (degrees) was also compared to the time-synchronized, binned clicking rates (clicks s^{-1}) that were calculated over each second of a fish capture event. Clicking rates were similarly compared to the rate of change in body roll (degrees s^{-1}) to determine if a relationship existed between clicking rate and movement rate. The timing of buzzes and crunches relative to fish captures was also examined to verify the usefulness of these sounds as proxies for prey capture attempts and successes, respectively.

All statistical comparisons of summarized echolocation behaviour were made using linear mixed-effects models (lme) from the nlme package in R (Pinheiro et al. 2014), with individual whale ID included as a random effect. The mixed effects models were run using the restricted maximum likelihood method, and significance was set at α=0.05. No statistical tests were performed to analyse the relationship between body position (roll) and echolocation, since both of these data sets were temporally autocorrelated, and thus violated the assumption of random, independent samples. All non-normal numeric variables were log transformed prior to running the linear mixed effects models.

3.4 Results

3.4.1 Tag deployments and prey sampling

Thirty-four DTAGs were deployed on 32 different northern resident killer whales in the late summer and early autumn of 2009-2012 (see Table 2.1, Chapter 2). Prey fragments (fish scales and/or flesh) were collected for 17 confirmed fish captures made by 7 of the 32 tagged individuals: 3 adult males (oo09_234a, oo09_240a, oo12_235b), 2 adult females (oo10_265a, oo11_246a), and 2 juveniles (oo10_256a, oo12_232a) (Table 3.1). Scale morphological analysis revealed that 9 of these kills were Chinook salmon, 6 were chum (*O. keta*), and 2 were coho (*O. kisutch*). Salmon caught by the tagged whales ranged in age from 2-5 y, with the majority (n = 11, 65%) being 4-5 y (Table 2.2).

3.4.2 Comparison of two methods for identifying focal clicks

Click trains that were qualitatively identified as focal did not have arrival time difference variances and modes equal to zero, as would have been expected if the two methods for identifying focal clicks were in agreement. Of the 260 qualitatively identified focal click trains (2 or more consecutive clicks separated by intervals of < 2 s) within the 17 fish capture events, only 61 trains (23.5%) had variances in arrival time differences equal to zero. The majority of variances (n = 199, 76.5%) were greater than zero, implying that arrival time delays for clicks within these trains were largely inconsistent. In addition, less than half (n = 107, 41.2%) of the qualitatively identified focal click trains had the expected arrival time difference mode of zero.

Differences in tag housing design between study years may explain some of the discrepancies between the qualitative identification method for focal clicks and the calculated arrival time differences. In 2009-2011, the DTAG-2 generation of tags that were used had external polyethylene housings that allowed water and air bubbles to pass around the electronics package containing the tag hydrophones. In 2012, DTAG-3 tags with components encased in moulded polyurethane were used, thereby eliminating trapped air bubbles and turbulence between the tag housing and the hydrophones. As a consequence, low frequency flow noise levels were significantly reduced on the DTAG-3 recordings compared to those made using the older DTAG-2. High levels of flow noise probably obscured the signal clarity of the echolocation click waveforms recorded on the DTAG-2 deployments, which may have caused cross-correlation errors since this technique requires clear amplitude modulation in order to be effective. Consequently, cross-correlation of poor quality waveform signals probably led to incorrectly calculated arrival time differences for the 2009-2011 echolocation clicks.

Examination of the variances and modes for the 2012 arrival time delays provided verification that the qualitative and quantitative methods were generally consistent with one another so long as the flow noise was minimal: 100% of arrival time difference modes (n = 69) for DTAG-3 click trains were equal to zero, and the majority of arrival time difference variances (n = 50, 72.5%) for click trains were also equal to zero. This suggests that for all 2012 focal click trains, the delay in arrival times was generally consistent between clicks and rarely deviated from zero, confirming that these clicks were correctly identified as focal using the initial qualitative method. In contrast, only 5.6% of DTAG-2 click trains had variances in arrival time difference equal to zero, and only 20.4% had modes equal to zero.

Based on the high level of agreement between the qualitatively identified focal clicks and the corresponding arrival time difference calculations for the 2012 DTAG-3 click trains, I concluded that the qualitative method alone was sufficient and that I could be fairly confident in its ability to distinguish focal from non-focal clicks. For this reason, I included all clicks that were identified as focal using the qualitative method in the analysis of tagged whale echolocation behaviour, regardless of whether the arrival time differences were in agreement or not.

3.4.3 Patterns of echolocation and movement during fish capture events

A total of 9985 focal echolocation clicks were identified for the 17 fish capture events, using the qualitative method described previously. The majority of focal clicks consisted of single broadband pulses; however, clicks with doublet structures resembling those described by Awbrey et al. (1982) for Antarctic killer whales were occasionally recorded. Excluding periods when tagged whales were not echolocating, the mean click repetition rate during fish capture events was 6.7 ± 7.2 clicks s^{-1}. Echolocation clicks had a mean duration of 13 ± 4 ms (± SD, range = 6-51 ms) and a mean inter-click interval (ICI) within click trains of 0.114 ± 0.163 s (range = 0.002-1.990 s). No ICIs were calculated for clicks > 2 s apart, as these were considered to belong to separate click trains. A total of 260 separate click trains, as well as 7 isolated clicks were detected on the DTAG hydrophone recordings during the 17 fish capture events. Each capture event contained a mean of

15.3 ± 6.6 click trains (range = 6-26), and trains had a mean total duration of 5.0 ± 6.2 s (range = 0.1-41.7 s).

Examining the time and depth at which whales emitted their first echolocation click train showed that they initiated searching behaviour at comparatively shallow depths (< 20 m) for most fish capture events (70.6%, n = 12, Table 3.2, e.g., Figure 3.2). Furthermore, whales that began a fish capture by engaging in pursuit behaviour at the surface emitted their first echolocation trains at much shallower depths (mean ± SD: 1.8 ± 1.2 m, n = 5) compared to those that dove deeper to initially locate prey (33.0 ± 36.4 m, n = 12) ($F_{1,9} = 69.3$, $p = 0.0018$, n = 17). Depths of first echolocation trains were log transformed prior to running the linear mixed effects model. First click trains also tended to commence at greater depths for capture events involving Chinook salmon (31.5 ± 37.9 m, n = 9), compared to surface-oriented species like chum or coho (15.2 ± 27.8 m, n = 8). However, this difference was not statistically significant when tested using a linear mixed effects model (using log transformed depth data). The deepest depth at which an individual (adult female G31, oo11_246a) first began echolocating during a fish capture event was 118.2 m, which was equivalent to almost 60% of the maximum depth of 204.5 m for that particular capture (Table 3.2).

Comparing pre- and post-capture echolocation patterns showed that tagged killer whales produced echolocation clicks at significantly greater rates ($F_{1,7} = 11.3$, $p = 0.012$, n = 13) prior to capturing a fish (mean ± SD: 7.1 ± 2.8 clicks s^{-1}) than they did during the post-capture phase (3.9 ± 2.3 clicks s^{-1}) (Table 3.2). They also spent a significantly greater percentage of their time engaged in clicking behaviour ($F_{1,10} = 32.0$, $p < 0.001$, n = 17) before the capture (mean ± SD: 34.6 ± 9.6%) than they did once the fish had been caught (13.0 ± 12.1%). In four of the capture events, the tagged whale did not emit any echolocation clicks after the fish was successfully caught (Table 3.2). The only whale that engaged in sharing behaviour (G31, oo11_246a) did so on five occasions and appeared to have significantly higher post-capture clicking rates (6.1 ± 2.7 clicks s^{-1}, n = 5) than other whales who did not share their prey (2.6 ± 0.8 clicks s^{-1}, n = 10), although no statistical comparison could be made. There appeared to be no difference, however, in the percentage of post-capture time that was spent clicking when fish were shared with other whales (11.2 ± 9.2%, n = 5), compared to fish that were not shared (14.3 ± 13.9, n = 10) (2 'possible' shares were excluded, Table 3.2).

Table 3.2 Summary of fish capture events (n=17) and corresponding echolocation behaviour by 7 tagged northern resident killer whales (DTAGs deployed over four field seasons, 2009-2012). Fish capture depths (m) were determined using 3-dimensional pseudotracks by estimating the time and depth at which pursuit behaviour (i.e., convoluted, spiralling and kinematically complex dive paths) ceased abruptly. This typically corresponded to maximum depth of the dive immediately prior to the prey sample collection at the surface. The presence of chasing on the surface at the beginning of the event, the fish species caught and the occurrence of post-capture sharing with other whales was also noted.

Tag ID	Depth of first click train (m)	Initial surface pursuit? (y/n)	Depth of fish capture (m)	Fish species	Shared? (y/n)	Mean click rate (clicks s^{-1})		Seconds spent clicking (%)	
						pre-capture	post-capture	pre-capture	post-capture
oo09_234a	63.5	no	101.6	Chinook	no	3.4	2.2	14.9	29.1
oo09_240a	3.7	yes	165.7	coho	no	3.6	2.6	42.0	16.7
oo09_240a	10.7	no	119.4	coho	no	2.5	2.1	33.9	20.9
oo10_256a	83.1	no	134.5	chum	no	5.3	1.8	19.6	5.2
oo10_256a	6.0	no	123.7	chum	no	6.3	3.4	27.4	3.4
oo10_265a	1.8	no	130.5	chum	possible	6.1	5.3	39.7	21.3
oo10_265a	12.7	no	133.7	chum	no	7.1	4.0	33.6	5.3
oo11_246a	10.3	no	201.9	Chinook	yes	6.7	—	44.7	0
oo11_246a	11.9	no	264.8	Chinook	yes	7.0	9.5	31.3	10.4
oo11_246a	32.0	no	131.1	Chinook	yes	11.2	7.0	35.1	25.5
oo11_246a	118.2	no	204.5	Chinook	yes	10.7	3.7	37.7	12.0
oo11_246a	16.0	no	180.7	Chinook	yes	9.5	4.1	48.1	8.0
oo12_232a	2.3	yes	0.7	chum	possible	7.1	—	41.4	0
oo12_232a	0.9	yes	87.6	chum	no	9.5	—	24.5	0
oo12_235b	29.3	no	102.7	Chinook	no	12.4	1.8	31.1	21.2
oo12_235b	1.7	yes	6.6	Chinook	no	7.3	—	27.3	0
oo12_235b	0.6	yes	0	Chinook	no	5.2	2.8	61.6	41.5

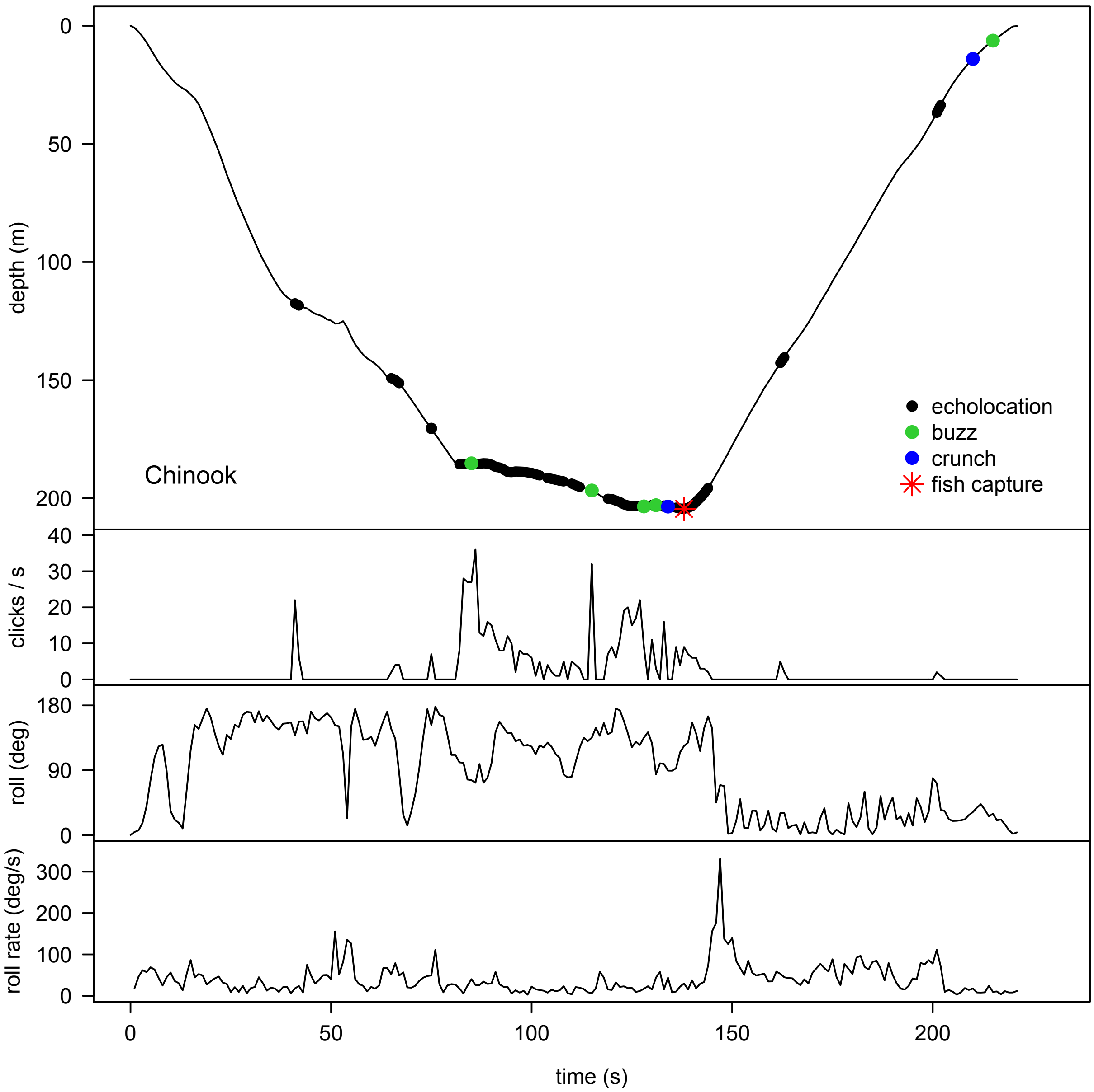

Figure 3.2 Time-depth profile (top) of a successful foraging dive resulting in a Chinook salmon capture, made by tagged northern resident killer whale G31 (deployment oo11_246a). The occurrence by time (s) and depth (m) of echolocation clicks, buzzes, prey handing sounds (crunches), and the fish capture (estimated based on changes in kinematic behaviour) are indicated with different symbols. Echolocation click rate (clicks s^{-1}, not including buzzes), instantaneous body roll (absolute values in degrees, sampled at 1 Hz), and rate of change in body roll (absolute values of change in degrees, sampled at 5 Hz and summed over 1 second intervals) throughout the fish capture event are also displayed (bottom 3 panels). G31 echolocated more often (> clicks s^{-1} and > time spent clicking) prior to the fish capture than she did afterward. Note that absolute body roll was also greater prior to the fish being caught, and a peak in roll rate occurred around the same time as the capture.

Kinematic data from the DTAG accelerometers were paired with the time-synchronized hydrophone recordings to investigate the role of body position during the production of echolocation clicks. An initial visual inspection of dive profiles and acoustics during individual fish capture events suggested that echolocation click rates (clicks s^{-1}) might be related to whale body orientation (deg) on the roll axis (e.g., Figure 3.2). When all capture events were considered collectively (n = 17), it appeared that whales were more likely to roll onto their sides when clicking at higher rates. When this relationship was examined on an individual basis, however, the trend was not consistent across all whales (Table 3.3). There was also no association between clicking rate (clicks s^{-1}) and the rate of change in body roll (deg s^{-1}), either for all capture events pooled together (n = 17), or at the level of the individual whale (Table 3.3). However, occasionally peaks in roll rate were observed to coincide with the time of fish capture for some individuals (e.g., Figure 3.2). Detailed dive profiles for each of the fish capture events, along with concurrent acoustic and roll orientation data, are provided in Appendix B.

Although no correlation existed between clicking rates and body rotation, there did appear to be an overall increase in roll angle when whales were echolocating (click rate > 0 click s^{-1}) compared to times when they were silent (Table 3.3). Whales generally spent more time rolled onto their sides when emitting echolocation clicks during prey searching and pursuit (i.e., pre-capture), but maintained more upright orientations when they were not clicking (both pre- and post-capture phases) or when they echolocated after catching a fish (post-capture, Figure 3.3, top). This pattern held true for all individuals except oo12_232a (I106), who did not emit any echolocation clicks following fish captures (n = 2). Roll orientations for oo12_232a were relatively upright and remained consistent between periods of pre-capture clicking and periods when no clicks were produced.

Unlike instantaneous body roll, the rate at which whales rolled (deg s^{-1}) did not change with the production of echolocation clicks, regardless of whether the fish was still being chased or had already been caught (Figure 3.3, bottom). This indicates that whales were more likely to roll sideways when echolocating during active pursuit of prey (versus when they were silent or echolocating after prey were captured), but that they probably maintained their roll positions rather than continuously changing them.

Table 3.3 Mean instantaneous body roll (absolute values in degrees, sampled at 1 Hz) and mean rate of change in body roll (absolute values of change in degrees, sampled at 5 Hz and summed over 1 second intervals) at different echolocation clicking rates (clicks s^{-1}, binned by intervals of 10) for 7 tagged northern resident killer whales during 17 successful fish capture events. Standard deviations for all individuals pooled are shown in parentheses.

Clicking rate (clicks s^{-1})		0	1-10	11-20	21-30	31-40	41-50
Tag ID	No. events	Mean instantaneous body roll (deg), (SD)					
oo09_234a	1	33.9	58.3	—	—	—	—
oo09_240a	2	34.5	46.5	17.7	—	—	—
oo10_256a	2	45.1	57.7	82.9	72.0	88.0	—
oo10_265a	2	35.2	88.0	92.1	46.4	—	—
oo11_246a	5	71.7	99.2	105.7	104.9	110.5	112.3
oo12_232a	2	39.7	37.4	57.5	50.8	59.6	13.5
oo12_235b	3	78.8	66.2	110.8	123.3	141.9	172.9
All whales	17	50.4 (51.3)	67.9 (57.2)	92.8 (50.0)	99.9 (35.3)	98.1 (36.8)	107.5 (45.3)
Clicking rate (clicks s^{-1})		0	1-10	11-20	21-30	31-40	41-50
Whale ID	No. events	Mean rate of change in body roll (deg s^{-1}), (SD)					
oo09_234a	1	16.2	25.8	—	—	—	—
oo09_240a	2	44.3	30.0	29.7	—	—	—
oo10_256a	2	31.6	28.7	41.2	25.6	27.6	—
oo10_265a	2	36.5	34.7	28.4	44.8	—	—
oo11_246a	5	30.0	22.5	24.1	28.4	22.0	28.4
oo12_232a	2	57.6	38.9	40.5	57.6	44.4	36.1
oo12_235b	3	31.5	25.8	34.7	32.8	73.5	8.5
All whales	17	35.4 (44.2)	29.1 (34.3)	30.9 (31.0)	33.4 (21.7)	33.9 (23.0)	26.8 (11.9)

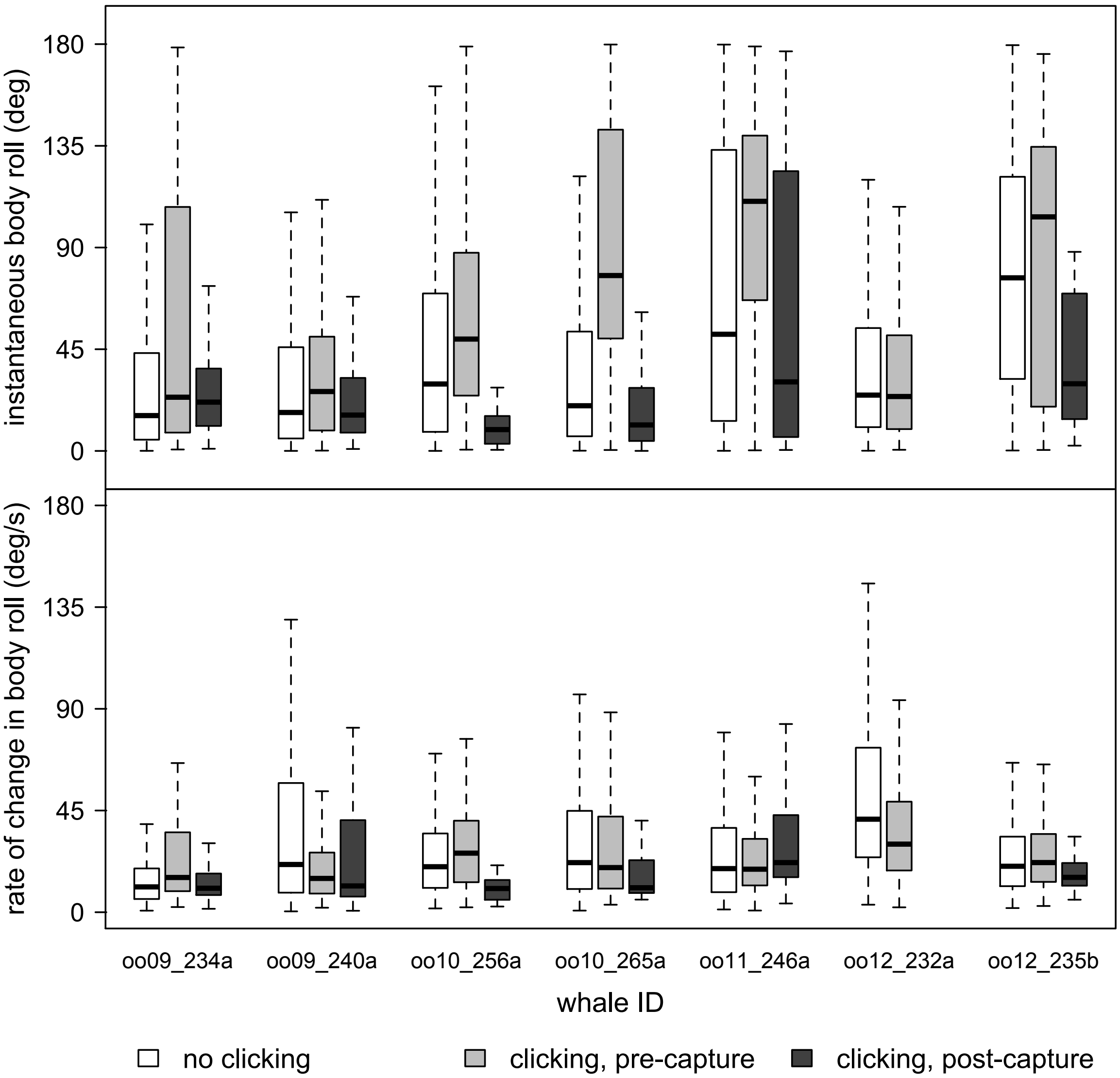

Figure 3.3 Instantaneous body roll (top, absolute values in degrees, sampled at 1 Hz) and rate of change in body roll (bottom, absolute values of change in degrees, sampled at 5 Hz and summed over 1 s intervals) per second, as a function of the presence of echolocation clicks and the relative foraging phase (white fill: no clicks, light grey: pre-capture clicks, dark grey: post-capture clicks). Recorded during 17 successful fish capture events by 7 tagged northern resident killer whales. Fish capture events were aggregated by individual (mean = 2.4 captures/whale, range = 1-5 captures/whale) and outliers were omitted. For instantaneous body roll, 0° indicates a whale swimming in an upright position (dorsal fin up) and 180° indicates a whale swimming upside-down. The boxplots indicate that most whales spent more time rolled onto their sides when producing echolocation clicks during the search and pursuit (pre-capture) phase of a dive (top). Whales maintained a more upright body position when they were not echolocating or when they were producing clicks after the fish had already been caught (post-capture phase). The rate of change in body roll (deg s^{-1}), however, did not change appreciably with the production of echolocation clicks during either foraging phase, as compared to portions of the capture events with no clicks (bottom).

3.4.4 Acoustic signals of prey capture attempts and successes

The assessment of whether the timing of buzzes could be used as a proxy for prey capture attempts produced mixed results. No buzzes (Figure 3.4) were audible for any of the fish capture events (n = 3) recorded on the tag deployments from 2009, however 82 buzzes were present on the 2010-2012 recordings of fish capture events (n = 14). These 14 capture events had an average of 5.9 ± 2.9 (SD) buzzes per capture, and a mean buzz duration of 1.9 ± 1.9 s (SD, range = 0.1-9.6 s). The majority of buzzes occurred prior to the estimated time of fish capture (78.0%, n = 64), some occurred around the same time (±5 seconds) as the capture itself (11.0%, n = 9), and a few occurred after the capture (11.0%, n = 9) (Figure 3.5). Buzzes that occurred either before or around the same time as the fish capture were produced at significantly ($F_{1,76} = 90.8$, $p < 0.0001$) greater depths (mean ± SD: 117.0 ± 62.5 m, n = 73) than those occurring after the capture (14.2 ± 27.4 m, n = 9) (Figure 3.5).

Prey handling sounds were found to be a reasonable proxy for estimating prey capture success provided they are interpreted carefully, as flow noise sometimes produced very similar sounds. Prey handling sounds, or ‘crunches’ (n = 180, Figure 3.6), were audible on the DTAG recordings for 16 of the 17 fish capture events, with an average of 11.3 ± 7.4 (SD) crunches per capture. There were no audible crunches for only one of the fish capture events, the second of the three Chinook captures made by the adult male A66 (deployment oo12_235b, Table 2.2). The majority of crunches occurred after the estimated time of fish capture (70.0%, n = 126) and a few occurred around the same time (±5 seconds) as the capture (8.9%, n = 16, Figure 3.7). Unexpectedly, an additional 38 crunches (21.1%) were audible well prior to the estimated times of fish captures. A large proportion of these pre-capture crunches (94.7%, n = 36), however, had the lowest level of identification certainty and most of them (84.2%, n = 32) were also recorded during a single deployment with higher relative flow noise (oo11_246a). The majority of the DTAG recordings (13 of 16 fish capture events with audible crunches) contained no pre-capture crunches, and notably, none were recorded for any of the 2012 DTAG-3 prey capture events (n = 5). Only 2 of the 38 pre-capture crunches were identified with certainty (Figure 3.7), and these occurred during a chum fish capture event by a subadult female (G64, oo10_256a). Crunches occurring after the fish capture happened at significantly ($F_{1,172} = 272.5$, $p < 0.0001$) shallower depths (mean ± SD: 21.1 ± 28.9 m, n = 126) compared to those occurring either prior to or around the same time as the capture (124.9 ± 36.6 m, n = 54) (Figure 3.7).

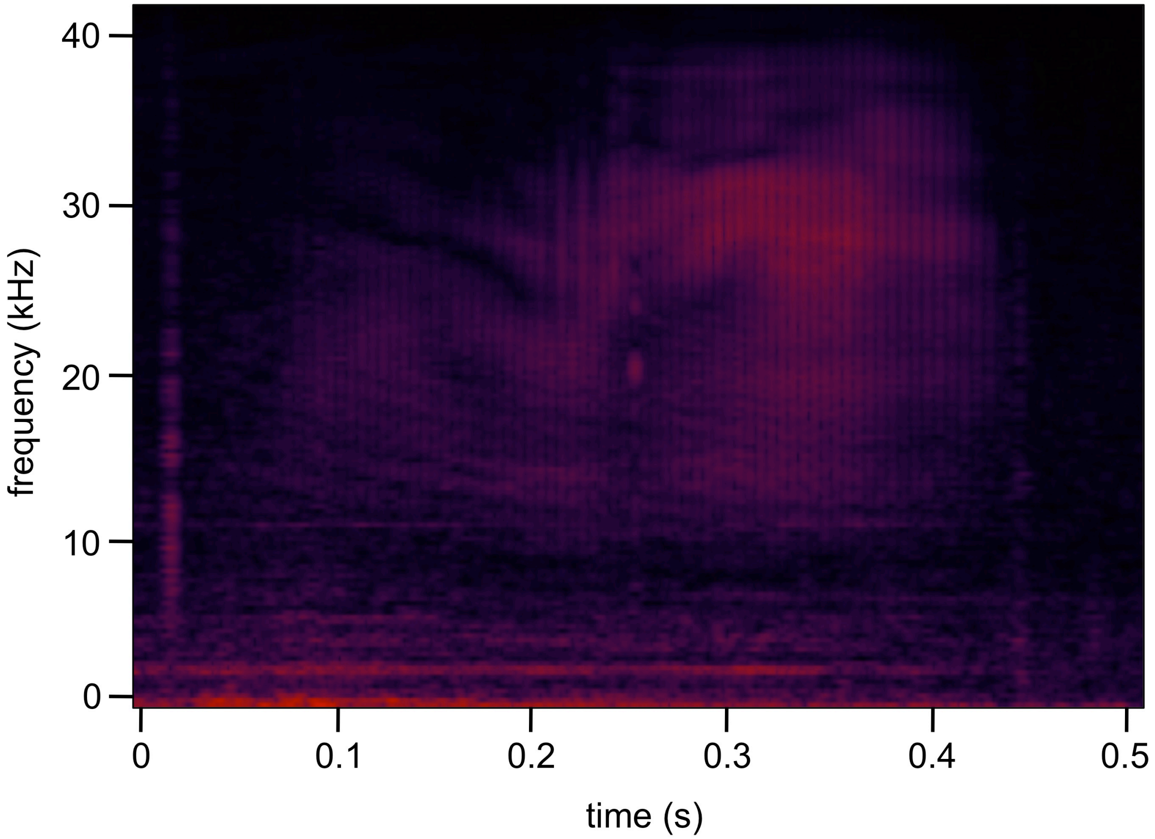

Figure 3.4 Spectrogram of a buzz, a series of extremely rapid echolocation clicks (>50 clicks s^{-1}), likely produced by tagged killer whale I106 (tag deployment oo12_232a) during a foraging dive. Originally recorded with 12 dB gain and then amplified by an additional ~20 dB to improve visualization of the spectrogram.

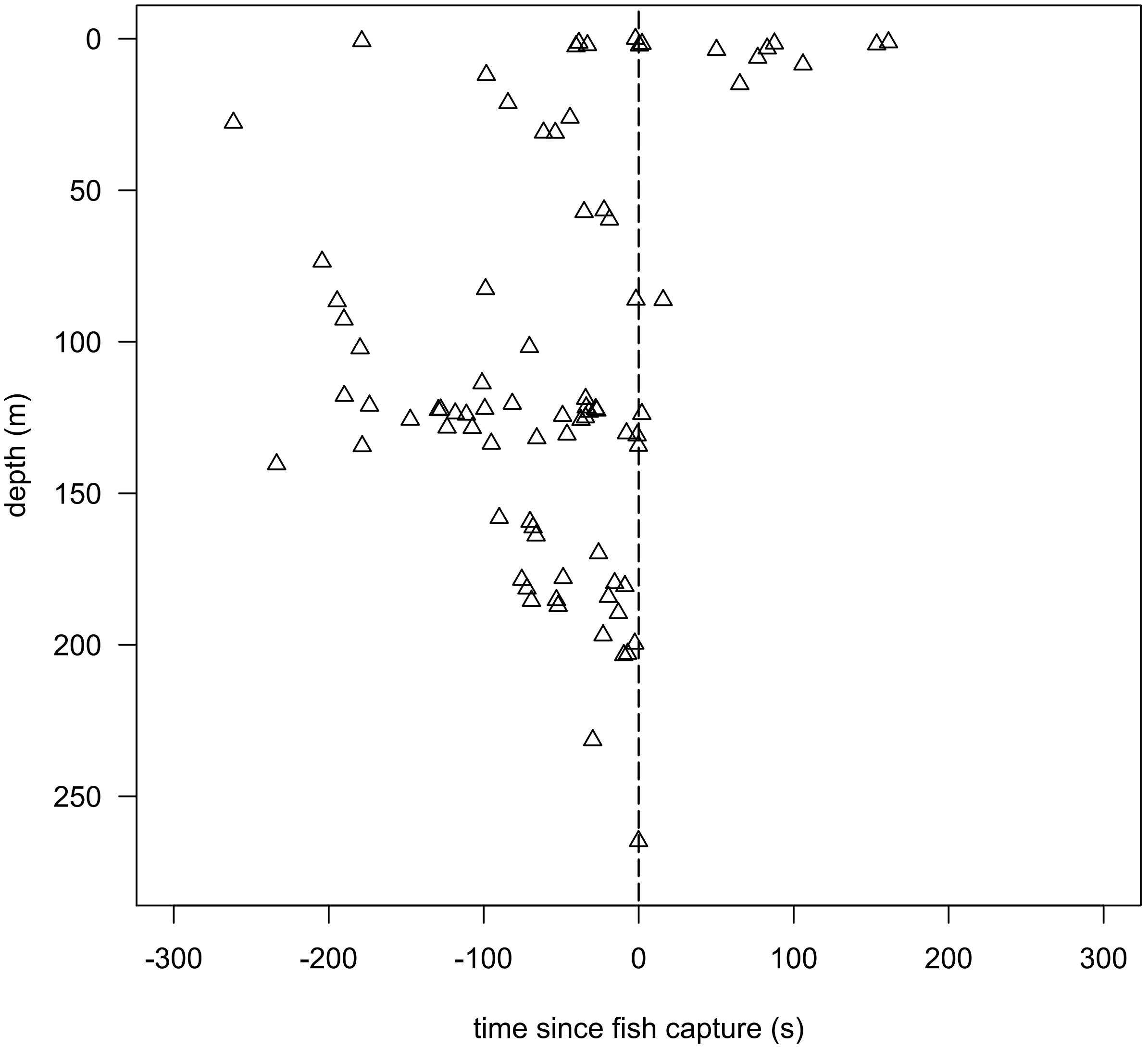

Figure 3.5 The occurrence of buzzes (n=82) made by tagged northern resident killer whales relative to dive depth (m) and the time elapsed (s) since the fish was captured. Plotted for 14 successful foraging dives for which prey fragment samples (fish scales and/or tissue) were collected at the surface. No prey handling sounds were detected on the DTAG hydrophone recordings for 3 of the successful foraging dives (all 2009 tag deployments). Mean number of buzzes per dive = 5.9 ± 2.9 SD. Post-capture buzzes were produced at significantly shallower depths (14.2 ± 27.4 m, $F_{1,76} = 90.8$, $p < 0.0001$) than those made prior to or simultaneously with the fish capture (117.0 ± 62.5 m).

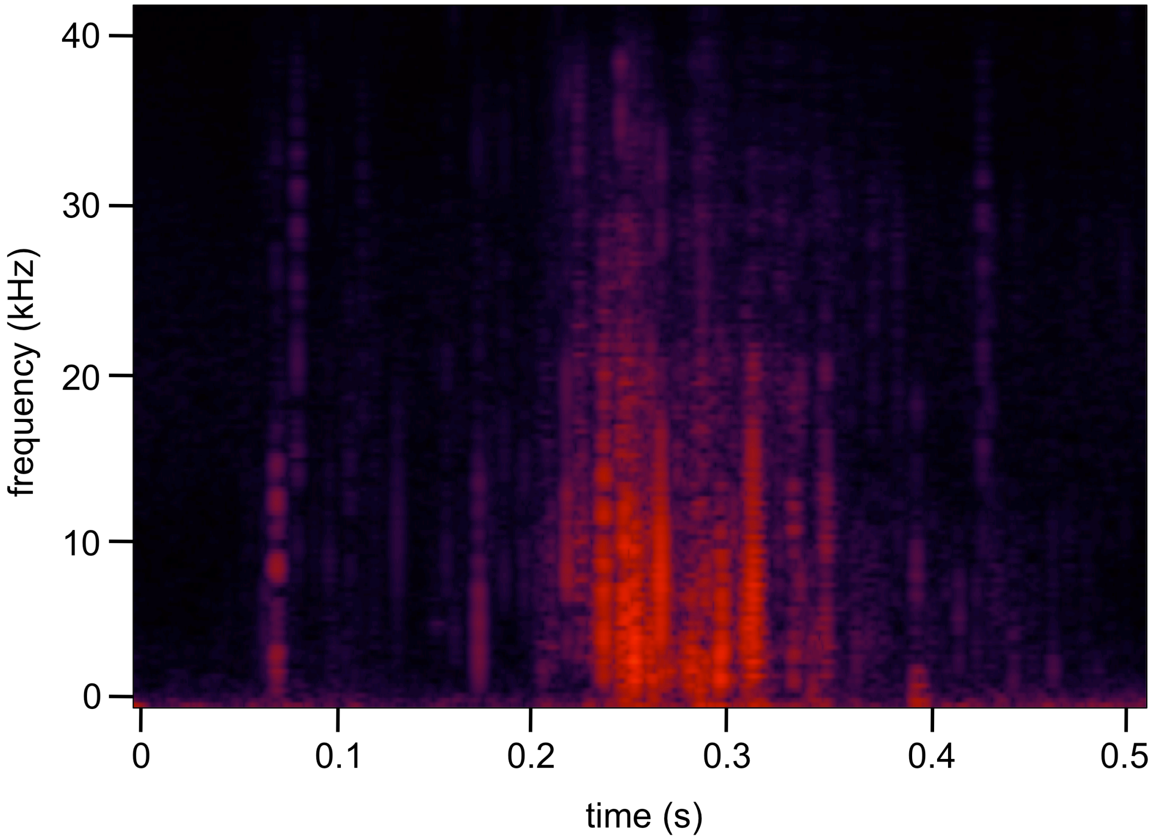

Figure 3.6 Spectrogram of a prey handing sound, or 'crunch', made by tagged resident killer whale I106 (tag deployment oo12_232a) following the capture of a chum salmon. This sound probably occurred as the whale tore the fish into pieces and consumed it. Originally recorded with 12 dB gain and then amplified by an additional ~20 dB to improve visualization of the spectrogram.

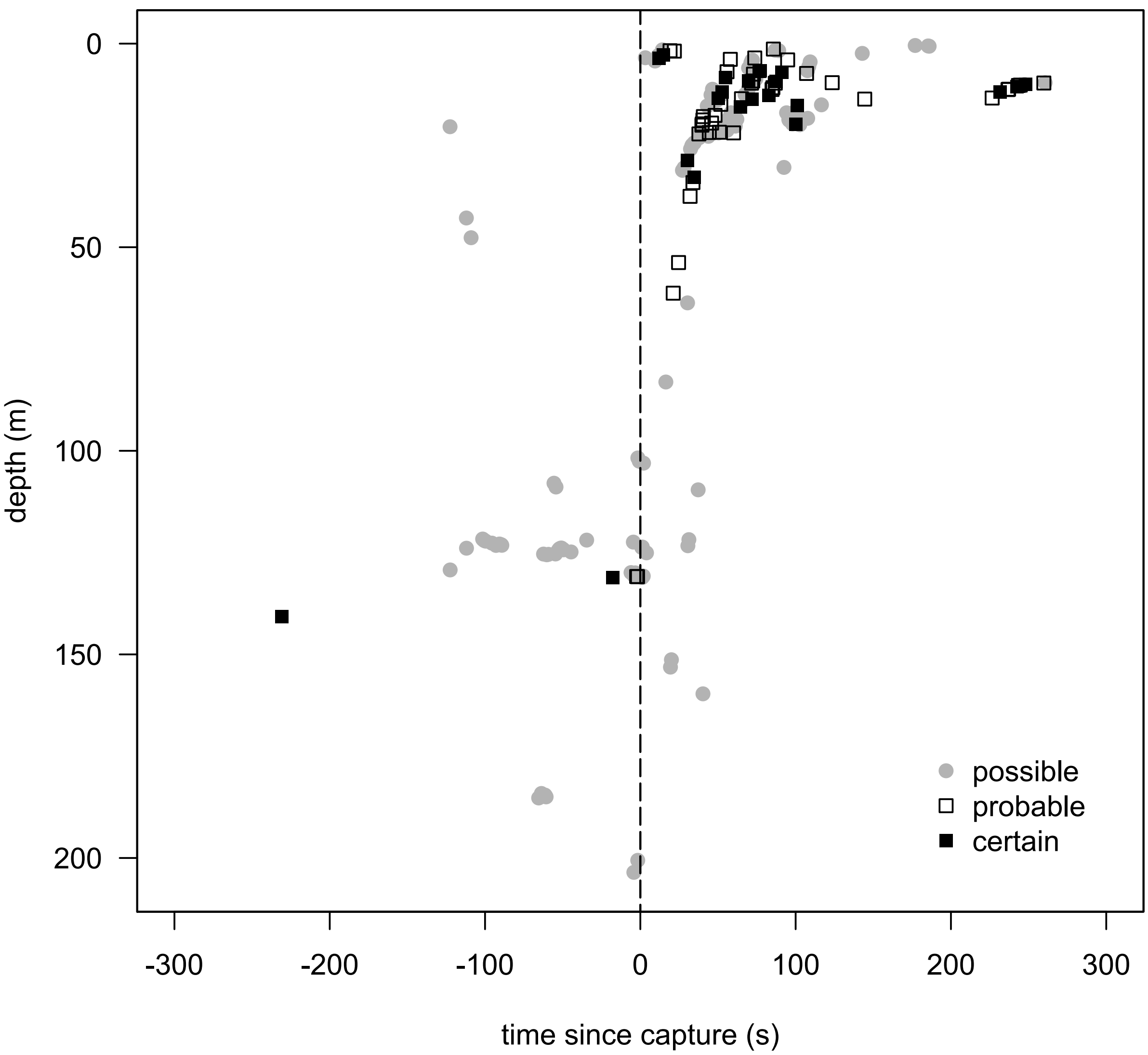

Figure 3.7 Time and depth of prey handling sounds (n=180), or 'crunches', made by 7 tagged northern resident killer whales relative to when each whale captured a fish (plotted for 16 successful foraging dives, mean number of crunches per dive = 11.3 ± 7.4 SD). Crunches were rated by increasing level of certainty (possible, probable, certain) of having been correctly identified and distinguished from similar sounds that arise from flow noise around the tag housing. Certainty ratings were performed by an experienced secondary observer. No prey handling sounds were detected on the DTAG hydrophone recording for 1 of the 17 successful foraging dives. Post-capture crunches were made at significantly shallower depths (21.1 ± 28.9 m, $F_{1,172}$ = 272.5, p < 0.0001) than those made prior to or simultaneously with the fish capture (124.9 ± 36.6 m).

3.5 Discussion

This study used biologging tags to provide the first description of individual echolocation behaviour by foraging resident killer whales. Patterns of echolocation appeared to be functionally similar to those of other odontocete species, with regular clicks produced for finding and identifying prey, and rapid click sequences (buzzes) for terminal targeting just prior to prey capture. The significantly higher incidence of echolocation prior to prey captures supports its hypothesized function in prey detection and tracking. Killer whales also frequently rolled sideways when they were echolocating (regular click trains) during prey searching and pursuit, which could improve the reception of returning echoes or facilitate the pursuit of fish along the sea floor. Buzzes and prey handling sounds can be used to identify prey capture attempts and successes, respectively, which in turn could be used to estimate northern resident foraging efficiency. This would provide valuable information about whether members of this threatened population are currently meeting their daily energetic requirements, and could be used to assess the impact of boat noise on foraging success.

3.5.1 Methods for identifying focal clicks

Acoustic recording tags (Johnson and Tyack 2003) provide a means of investigating the vocal behaviour of individual whales in conjunction with their diving kinematics during foraging and other activity states. However, these tags record vocalizations and echolocation clicks produced by all whales in the vicinity of the recording device, and it is not always clear which of them are made by the tagged animal (Johnson et al. 2009). Although resident killer whales pursue and capture salmon individually, they generally hunt in close proximity to matrilineal relatives that are also engaged in foraging (Ford and Ellis 2006). Overlapping click trains and simultaneous calls from multiple individuals are therefore quite common on acoustic recordings of foraging residents (Ford 1989). Discerning which of these sounds were actually made by tagged individuals presents a difficult and emerging challenge in acoustic biologging research (Johnson et al. 2009).

Many studies that successfully attributed sounds to focal whales have done so based on an increase in low-frequency energy content (e.g., Aguilar Soto et al. 2008), which occurs when focal sounds are conducted through the animal's tissue before being received by the tag (Zimmer et al. 2005). However, this technique relies on qualitative appraisal of sound spectrogram characteristics, and may be affected by the experience level of the person performing the analysis, as well as by the quality of the recording. Visual and aural processing also require significant analysis time, particularly if conducted by multiple independent observers as a means of minimizing observer bias.

A quantitative method has also been developed to identify focal sounds recorded by acoustic biologging tags. This technique involves calculating the difference in arrival time of the same sound between the two tag hydrophones (or the related measure of angle-of-arrival) (e.g., Akamatsu et al. 2005, Johnson et al. 2006, Johnson et al. 2009, Akamatsu et al. 2010). Although this method eliminates observer bias and can be automated to significantly reduce analysis time, it also has some limitations, as arrival time delays cannot be calculated accurately for sounds that overlap or have poor signal-to-noise ratios (Dunn et al. 2013). Variable tag placement between different study animals (or tag slips on a single study animal) may also impact the consistency of time delay values for focal sounds. Consistent tag placement allows accurate determination of the angles from which focal sounds should arise (Akamatsu et al. 2010), but this is unrealistic for most studies because animals cannot usually be captured for tag deployment. Currently, the most reliable way to identify focal sounds is probably to use the qualitative (low frequency sound energy) and quantitative (arrival time delay or angle-of-arrival) methods in combination as validations of one another (e.g., Johnson et al. 2006, Jensen et al. 2011, Dunn et al. 2013).

Most studies that combined the two techniques discounted qualitatively focal sounds that could not be verified using angle-of-arrival or time delay waveform cross-correlations (e.g., Jensen et al. 2011). In my study, however, I found that all of the DTAG-2 recordings (2009-2011) had fairly poor signal-to-noise ratios due to the tag housing configuration, which made it impossible to accurately calculate arrival time differences. Rather than lose a large portion of the data set by discounting the DTAG-2 recordings (12 of 17 fish capture events), I decided to validate my qualitative identification of focal sounds using only the DTAG-3 (2012) data. Since the arrival time differences were consistent with expected values for focal whales for the 2012 recordings, I was confident that my initial qualitative identifications were relatively accurate. I therefore retained the DTAG-2 (2009-2011) focal clicks that I identified using the qualitative method, despite the lack of accurate arrival time differences that normally would have confirmed my original classifications.

Although the arrival time difference technique has been used successfully by others, it merits further refinement as a quantitative tool for distinguishing focal from non-focal vocalizations. Finding ways to improve cross-correlation accuracy would eliminate the need for time-consuming qualitative validation of focal clicks by aural and visual processing. This would allow for more efficient analysis of larger acoustic data sets from biologging tags in the future. Maintaining a high level of recording quality is also very important for the success of this method, and recordings from acoustic tags with external plastic housings rather than embedded components will likely be inadequate. Although calculating arrival time differences for echolocation clicks is fairly straightforward (given sufficient recording quality), waveform cross-correlation of sounds that contain multiple amplitude modulations (e.g., killer whale pulsed calls and whistles) remains difficult (W. Zimmer, pers. comm.). Analysing these types of vocalizations will require further refinement of the cross-correlation technique for calculating arrival time difference, likely on a species-by-species basis.

3.5.2 Patterns of echolocation behaviour during successful fish captures

The mean click repetition rate (6.7 clicks s^{-1}) from the DTAG recordings of successful fish captures was comparable to the median repetition rate of 7.1 clicks s^{-1} reported for resident killer whales (all activity states) in an earlier study by Barrett-Lennard et al. (1996). Similarly, Ford (1989) reported that resident click repetition rates generally fell within 2-50 clicks s^{-1}, which matches my finding that click repetition rates rarely exceeded 50 clicks s^{-1}, and when they did, this almost invariably occurred during buzzes. The mean click train duration of 7.22 s recorded by Barrett-Lennard et al. (1996) is also fairly consistent with the mean click train duration of 5.0 ± 6.2 s (± SD) calculated from my DTAG data. Durations of individual clicks from tagged residents (6-51 ms) in my study also corresponded with those measured for wild Atlantic killer whales (4-13 ms) (Steiner et al. 1979) and for a captive Pacific resident killer whale (10-25 ms) (Schevill and Watkins 1966). Click durations for resident killer whales measured by Au et al. (2004) were significantly briefer (8-120 µs), but probably more accurate because an array of hydrophones was used to restrict the analysis to on-axis clicks with minimal off-axis distortion.

Echolocation began at relatively shallow depths (generally < 20 m) during fish captures, and was employed even when the whales chased fish along the surface (Table 3.2). This implies that vision and echolocation are not mutually exclusive methods for detecting and tracking prey, and that echolocation may be critical for successful prey captures even when visibility is good. This conclusion is supported by Barrett-Lennard et al. (1996), who found no correlation between water clarity and the frequency of echolocation use by resident killer whales. Echolocation was also not continuous throughout any of the 17 DTAG fish capture events: even during the search and pursuit (pre-capture) phase, whales typically echolocated less than 50% of the time (Table 3.2). Previous observations that resident killer whales emitted periodic echolocation trains during foraging behaviour, but were otherwise silent when pursuing and capturing salmon (Ford 1989) support these results. This implies that, in addition to echolocation and vision, whales likely use other sensory cues to track prey at depths where light is not available. These signals could include passive listening for fish swimming sounds (Barrett-Lennard et al. 1996), or sensing changes in water turbulence produced by prey movements.

Although most fish captures began with killer whales echolocating near the surface, occasionally individuals waited to attain greater depths before producing their first click train. Overall, whales that did not initially encounter and chase fish at the surface delayed emitting their first echolocation train until they had reached greater depths (33.0 ± 36.4 m) ($F_{1,9} = 69.3$, $p = 0.0018$, n = 17). This could be a tactic to specifically target Chinook salmon by achieving the depth range where this species is typically located before undertaking searching behaviour (mean swimming depth of Chinook from a meta-analysis of salmon tagging studies was 43.4 ± 15.4 m, see Chapter 2). By narrowing the potential distance between themselves and their prey at the time of detection, whales increase the profitability of pursuing a fish by reducing the energy required to intercept it (Au et al. 2004). The majority of fish capture events where echolocation was initiated at > 20 m (n = 5) were for Chinook (Table 3.2), whereas only one capture of chum or coho (typically surface-oriented species, see Figure 2.7, Chapter 2) involved a similar delay (first echolocation at 83.1 m, Figure 3.2). In addition, the overall mean depth of the first echolocation train was greater for Chinook captures (31.4 ± 37.9 m) than it was for the other two species pooled (15.2 ± 27.8 m). However, this difference was not statistically significant. The lack of a significant statistical trend may be due to the limited sample size of successful fish captures (n=17) that were recorded, and the relatively large group variances compared to the means.

Whales conducting bouts of consecutive foraging dives may also delay echolocating until reaching greater depths because they may not need to begin clicking near the surface for every dive if they already have previous knowledge of prey locations. This seemed to be the case for whale oo11_246a (G31), who successfully captured 5 fish within 2 h. For most of these fish captures, the initial echolocation train began in comparatively shallow water (Table 3.2); however, for her fourth capture, this whale did not echolocate until she had reached almost 120 m in depth.

In this case, the whale was probably able to forgo echolocation near the surface because she had already located fish during the preceding capture, which occurred only 4 minutes previously. Lastly, it is also possible that whales swam deeper before beginning to echolocate in order to avoid noise at the surface (e.g., from rain or boat propellers) that could mask returning echoes from prey (Au et al. 2004). Echolocating resident killer whales are theoretically capable of detecting salmon at ranges of 100 m, but this distance is reduced to less than 40 m in the presence of ambient environmental noise such as moderately heavy rainfall (Au et al. 2004), so consequently they may choose to swim deeper before initiating clicking behaviour.

The echolocation behaviour of foraging resident killer whales changed significantly once a fish had been caught, implying that echolocation may be modified within a fish capture event to satisfy different functions. For example, whales actively searching for or pursuing prey (i.e., pre-capture phase) spent a significantly greater proportion of their time echolocating (34.6%, $F_{1,10} = 32.0$, $p < 0.001$, n = 17) than they did after prey were caught (13.0%). Increased echolocation effort prior to captures was expected, since foraging whales are assumed to use echolocation to acoustically resolve potential prey while simultaneously navigating features of the underwater environment at relatively high speeds. Pursuing highly mobile prey like salmon requires resident killer whales to respond to fish evasive behaviours, which is likely accomplished by using echolocation to constantly update their awareness of prey movements. The significantly higher mean clicking rate (7.1 clicks s^{-1} compared to 3.9 clicks s^{-1} post-capture, $F_{1,7} = 11.3$, $p = 0.012$, n = 13) displayed by resident killer whales during the pre-capture phase was therefore also expected, since click repetition rate is directly related to target range. Continuous reductions in target distance during prey pursuit necessitates shorter intervals between clicks because the echoes are returning at increasingly faster rates (Madsen and Surlykke 2013). Similar increases in phonation effort (22.7% from 12.7%) and shortening of inter-click intervals (0.0295 s from 0.0425 s) were observed for finless porpoises when they were performing body movements consistent with prey searching and pursuit behaviour (Akamatsu et al. 2010). The significantly higher echolocation effort by northern residents prior to prey captures (both in time spent and relative click repetition rates) suggests that echolocation is central to their foraging success. Acoustic disturbances that mask echolocation behaviour are therefore of great concern, as they have the potential to reduce prey capture rates and lower the energetic intake of resident killer whales (Bain et al. 2014).

After capturing a fish, killer whales slowed their mean echolocation rates by almost 50% (3.9 clicks s^{-1} compared to 7.1 clicks s^{-1} prior to capture) and spent only 13% of their time engaged in clicking behaviour (Table 3.2). Post-capture clicking could aid in navigation back to the surface, or may be related to prey handling behaviour so that whales can track pieces of a carcass in the water as they tear their prey apart. Both of these tasks are unlikely to require continuous or rapid sensory updates using biosonar, hence the reduction in echolocation following a capture. In a few instances (n = 4), whales were completely silent after catching a fish, which indicates that echolocation is not critical to navigate back to the surface or to process prey, and that these tasks can be accomplished using other sensory inputs, such as visual cues.

Post-capture clicking may also be used by foraging whales to locate conspecifics (typically offspring, Ford et al., unpubl. data) with whom they may share their prey. Only 1 of the 7 tagged whales (G31, oo11_246a, Table 3.2) exhibited sharing behaviour, and although the amount of post-capture time she spent clicking did not appear to differ from that of whales who did not share their prey, the mean rate at which she clicked was noticeably higher (6.1 clicks s^{-1} compared to 2.6 clicks s^{-1} for non-sharing whales, Table 3.2). This whale probably increased her clicking rates during post-capture ascents in order to locate her juvenile offspring (G84 and G96) at the surface, or to facilitate prey handling during the provisioning of these offspring (see acoustic dive profile figures in Appendix B). Further investigation of echolocation behaviour during prey sharing would require a larger sample size of shared kills from multiple whales to account for the potential influence of idiosyncratic behaviours.

3.5.3 Body roll during echolocation

The DTAG data indicated that resident killer whales frequently rolled onto their sides when producing echolocation clicks during fish capture events, but only prior to when the capture took place (Figure 3.3). This suggests that body position may be functionally linked to the effectiveness of echolocation during either the detection or tracking of fish. Odontocete sonar beams are directional and quite narrow (Au 1993), which provides excellent range resolution once prey are detected, but also presents the challenge of locating small moving objects (prey) in three-dimensional space with only a narrow window of sensory information (Madsen et al. 2013). Like the tagged resident killer whales, Akamatsu et al. (2010) similarly determined that foraging finless porpoises displayed mean roll angles > 60° during periods of increased echolocation effort. In finless porpoise, body roll was interpreted as functioning to widen the area scanned for prey by changing the echolocation beam axis. In addition, captive echolocation trials found that harbour porpoises used beam scanning to inspect artificial targets, and that this was accomplished partially through whole-body movements (Wisniewska et al. 2012). Killer whales could likewise increase the volume of water they effectively scan by varying the direction of their outgoing clicks. However, unlike porpoises, which can also change their sonar axis direction using head movements (Akamatsu et al. 2010, Wisniewska et al. 2012), killer whales have fused cervical vertebrae (Buchholtz and Schur 2004) and thus limited flexion at the neck (Buchholtz 1998). This means that they would have to roll their entire bodies to achieve a similar scanning effect, as suggested by Evans (1973).

Rotating the body primarily to improve echolocation searching efficiency means that the rate of rotation (not just the absolute magnitude) should also increase during pre-capture clicking (so that more water volume could be scanned per unit of time). However, this was not observed for foraging residents, as the rate of body rotation was equivalent whether or not the whales were echolocating. Roll rates also did not decrease appreciably after a fish was caught as compared to before (Figure 3.3). This implies that body roll positions were maintained during prey searching and pursuit, rather than being continuously altered.

Rather than rolling to change the direction of outgoing clicks, whales could be maintaining a sideways orientation during echolocation to improve the reception of returning echoes. Delphinid hearing sensitivity is not equivalent in all directions, in either the vertical or the horizontal plane (Au and Moore 1983), and sounds from certain directions are therefore more effectively coupled to the ear than others (Ridgway and Au 2009). For example, Atlantic bottlenose dolphins (*Tursiops truncatus*) are sensitive to a greater range of sound source angles arising from below their heads than from above (Au and Moore 1983). Asymmetrical hearing sensitivity could relate to the role of the lower jaw in sound reception (Au and Moore 1983), and killer whales might rotate sideways to better orient their jaws for receiving returning echoes from prey.

It is also possible that the observed sideways roll positions are not related to echolocation function at all, but happen to coincide with periods of high clicking effort because killer whales adopt this orientation when pursuing salmon along the bottom. Sideways body rotation (instantaneous roll > 90°) often corresponded to portions of fish capture events with relatively level depth profiles (see acoustic dive profiles in Appendix), implying that whales may have been chasing salmon along the sea floor during these times. Rolling sideways could therefore be interpreted as a strategy to maintain high swimming speeds while moving along the bottom, because this orientation would prevent fluke strokes from being impeded by contact with the sea floor.

Since both instantaneous body roll and the rate of rolling were not correlated with click repetition rate (Table 3.3), it can be inferred that the rate of change in body orientation did not increase with target proximity during regular echolocation click trains. However, peaks in roll rate were often observed (usually synchronous with buzzes) at around the time a fish was caught for many of the capture events (e.g., Figure 3.2, see acoustic dive profiles in Appendix B). This is consistent with experimental findings for harbour porpoises, which increased the variability in their roll angle simultaneously with buzz production during prey captures (DeRuiter et al. 2009). Buzzes produced by beaked whales similarly coincided with peaks in dynamic body acceleration, which likely represented rapid movements made during prey captures (Johnson et al. 2004). Furthermore, sperm whale ‘creaks’, which are analogous to buzzes, are also accompanied by an increased rate of change in body orientation (Miller et al. 2004). Although the relationship between killer whale buzzes and changes in body orientation was not analysed in my study, it merits further investigation since peaks in roll rate coincident with buzzes could be useful indicators of successful prey captures.

3.5.4 Acoustic indicators of fish capture attempts and successes

Many odontocete species use buzzes to target their prey, during which they produce echolocation clicks at very high repetition rates to determine the distance between themselves and their selected target (Johnson et al. 2004, Aguilar Soto et al. 2008, Johnson et al. 2008, DeRuiter et al. 2009). Echolocating animals produce a new click only after they have received an echo from the previous one (Cahlander et al. 1964), so the clicking interval is roughly equivalent to the two-way travel time of the click between the whale and its target (Madsen and Surlykke 2013). Subsequently, the closer the whale gets to a fish, the faster it clicks until eventually a buzz is produced. While regular echolocation clicks function in the detection and classification of more distant prey targets, buzzes are produced during extremely close approaches (i.e., the capture phase), when rapid updates on prey movements become necessary (Johnson et al. 2006). The vast majority of buzzes (74.4%, n = 61) by resident killer whales were produced at depths > 50 m (Figure 3.5), with a mean depth for all buzzes of 105.8 m (± 67.8 m). This reflects the greater depths at which prey are likely to be caught, given the tendency of Pacific salmon to dive in response to predator pursuit (see Chapter 2). Buzzes were always preceded by trains of regular echolocation clicks that were probably used to search for and detect prey during the initial part of the foraging dive.

If whales only produce buzzes when making close approaches to a prey target, then no buzzes should be emitted after a fish has been caught. However, this was not always the case for tagged northern residents, as 11.0% (n = 9) of recorded buzzes occurred post-capture (Figure 3.5). A captive study by DeRuiter et al. (2009) similarly found that harbour porpoises continued buzzing even after catching a fish, and concluded that buzzes may also be used to re-detect escaped prey or to locate additional prey following a kill. Buzzes produced by these porpoises > 5 s after a fish capture were interpreted as aiding navigation back to the trainer (DeRuiter et al. 2009). Northern resident killer whales may use post-capture buzzes in a similar way, either to navigate back to the surface to breathe, or to locate nearby whales with whom to share their prey. In addition, the significantly shallower average depth of post-capture buzzes (14.2 ± 27.4 m, $F_{1,76} = 90.8$, $p < 0.0001$; Figure 3.5) suggests these sounds might also assist in handling prey near the surface. Possible inclusion of non-focal buzzes could also account for some of the post-capture buzzes recorded by the DTAGs, particularly if other individuals were emitting buzzes close to the tag as they investigated fish being shared by the tagged whale.

Buzzes were not a completely reliable estimator of prey capture attempts, however, as they were absent during the successful fish captures from 2009 (n = 3). Given the lower relative amplitudes of these sounds (Miller et al. 1995, Madsen et al. 2005, Johnson et al. 2006, DeRuiter et al. 2009), buzzes may have been present but were obscured on tag recordings due to poor signal-to-noise ratios. This may explain why no buzzes were audible on the 2009 DTAG prey capture recordings, which had high levels of flow noise. It is also possible that no buzzes were actually produced during these three captures, although this seems unlikely, since buzzes appear to be fundamental components of prey capture behaviour for echolocating odontocetes (DeRuiter et al. 2009, Madsen et al. 2013, Madsen and Surlykke 2013). Fish captures without buzzes occurred in only 1 of 67 cases for experimental trials with captive harbour porpoises (DeRuiter et al. 2009). It is also important that buzzes not be interpreted as a 1:1 indicator of capture attempts because killer whales often produced multiple buzzes while pursuing and capturing what was likely a single fish. The average number of buzzes made by foraging northern residents was 5.9 ± 2.9 (SD) per successful prey capture (n = 14). Other odontocetes, such as beaked whales, are also known to produce multiple buzzes in series during tracking of the same prey target (Johnson et al. 2008, Madsen et al. 2013).

Prey handling sounds, or ‘crunches’, could likewise be useful indicators of prey capture success that would provide information for estimating the foraging efficiency of northern resident killer whales. Like buzzes, multiple crunches were often produced during the capture and handling of a single fish (mean ± SD: 11.3 ± 7.4), so care should be taken when interpreting these acoustic cues. Most ‘crunches’ resulting from prey processing happened after the estimated time of capture (70.0%, n = 126), which is expected since these sounds are likely the result of whales tearing a fish into pieces for consumption or sharing it with other individuals. Post-capture crunches (n = 126) were also produced at relatively shallow depths (21.1 ± 28.9 m; Figure 3.7), which supports previous observations that resident killer whales routinely bring prey to the surface prior to consumption (Ford and Ellis 2006). Crunches that occurred around the time of prey capture (± 5 s) occurred at significantly greater depths (Figure 3.7) and were presumed to result from whales initially grabbing onto fish with their jaws.

Unexpectedly, prey handling sounds were also noted prior to the estimated time of fish capture (> 5 s) in 21.1% (n = 38) of cases over the 17 fish capture events by tagged northern residents (Figure 3.7). This could suggest that multiple prey were potentially being caught during some foraging dives, with only the last fish being brought to the surface by the whale. If killer whales sometimes consume fish underwater, as pre-capture crunches appear to indicate, then these prey are not available for sampling at the surface and current estimates of dietary composition may therefore be inaccurate. Diet estimates could be especially skewed if certain prey species, such as epibenthic fish like Pacific halibut (*Hippoglossus stenolepis*), are consistently consumed underwater (Ford et al. 1998). However, the continuity of pursuit behaviour visualized by the 17 capture event pseudotracks seems to negate this possibility for salmon captures. Killer whales could conceivably consume one fish while simultaneously pursuing additional prey, but a break in the kinematic pursuit pattern is more likely.

Given that most (94.7%, n = 36) pre-capture crunches were also identified with relatively low certainty (Figure 3.7), it is likely that these crunches could instead be attributed to similar noises produced by air bubbles or water turbulence within the DTAG housings. This conclusion is reinforced by results from the 2012 DTAG-3 recordings, which had minimal flow noise due to improvements in tag housing design and also had no recorded pre-capture crunches. In addition, the majority of pre-capture crunches (84.2%, n = 32) were recorded during a single tag deployment (oo11_246a) that had unusually high levels of flow noise. Furthermore, this deployment's prey captures also occurred along a steeply sloped shoreline with large kelp beds, and kelp stems impacting the tag might similarly have produced noises that resembled prey handling crunches. The 2 pre-capture crunches identified with high certainty occurred during a single fish capture event by subadult female G64 (oo10_256a), who captured a chum salmon. It is possible that she was able to capture and consume more than one of these smaller salmon during a single dive, despite the pseudotrack indicating relatively continuous pursuit behaviour.

To help verify that crunches are actually produced during prey handling, non-foraging dives should be acoustically analysed to ensure that no such sounds are evident when resident killer whales are not feeding. Foraging dives without prey samples should also be analysed to determine the occurrence, depth and timing of prey handling sounds when no prey remains were recovered. Crunches occurring in deeper water could explain why no prey samples were visible at the surface for these foraging dives, and would suggest that a re-examination of dietary composition is warranted. A lack of audible crunches on foraging dives that did not produce prey samples would indicate that most of these dives represented unsuccessful chases and that the current method of estimating diet is relatively accurate. Perhaps the only way to definitively verify how often resident killer whales consume prey below the surface (and also which species are taken) is to simultaneously deploy animal-borne video cameras with acoustic and accelerometry sensors (e.g., Calambokidis et al. 2008). Video recordings of foraging events could also validate whether or not crunches in fact represent prey handling sounds. Deployment of suction-cup-attached video cameras on a fast-swimming delphinids like killer whales, however, will remain extremely challenging until greater reductions in instrument size are achieved.

Careful interpretation of buzzes and prey handling sounds can provide valuable information about the foraging efficiency of individuals. Since prey availability may be limiting resident killer whale population growth and recovery (Fisheries and Oceans Canada 2008), it is important to establish whether or not individuals are meeting their daily energy requirements. Analysis of foraging dives for the presence of buzzes and prey handling sounds could be useful in this respect, as the frequency of these events indicate prey encounter rates (Johnson et al. 2009) and potential energetic gain (i.e., number of fish consumed). The amount of energy expended to successfully capture prey could also be determined from DTAG data using fluking stroke rate (Johnson et al. 2009) or possibly a measure of total body acceleration (Wilson et al. 2006). Combining acoustic indicators of energy acquired with kinematic estimates of energy expended would provide an indication of catch per unit effort (CPUE) for foraging resident killer whales. In addition, masking noise from boat traffic could further limit the prey available to be detected by resident killer whales by reducing their click detection ranges (Bain et al. 2014) and thus lowering CPUE. Comparing CPUE values to estimates of daily energetic requirements (e.g., Ford et al. 2009) under different acoustic disturbance scenarios would verify whether nutritional stress is impacting population growth rates, and whether vessel traffic significantly impacts foraging efficiency.

3.5.5 Conclusions

The DTAG has provided new insights into the individual echolocation behaviour of foraging resident killer whales relative to their diving behaviour and body positions. Analysis of the DTAG recordings confirms that patterns of echolocation produced by northern resident killer whales are consistent with its proposed function in prey detection and pursuit, as they are highly dependent on the relative stage (pre- or post-capture) of a fish capture event. It also revealed that killer whales frequently maintain sideways roll orientations while echolocating prior to fish captures. This positioning of the body may either be a strategy for pursuing prey along the bottom, or for improving the reception of click echoes through their lower jaws. Buzzes (capture attempts) and crunches (capture successes) were identified as potentially useful acoustic metrics that could be used to estimate killer whale foraging efficiency.

Chapter 4: Conclusions

4.1 Summary of research findings

My study provides the first quantitative description of underwater hunting behaviour by the northern resident killer whale, a specialist predator. Given that northern residents preferentially feed on Chinook salmon for much of the year, even when they are less abundant than other species of salmon (Ford and Ellis 2006), I expected their foraging behaviour to be adapted in some way for capturing Chinook. To obtain the first quantitative description of specialized foraging behaviour by northern resident killer whales, I deployed multi-sensor biologging tags (DTAGs) to obtain high-resolution 3D movement data from 32 whales and compared their foraging dive behaviour to the vertical distribution of six species of Pacific salmon. The northern resident population's preference for consuming Chinook salmon appeared to influence the specificity of their hunting behaviour, as maximum foraging dive depths corresponded to average Chinook swimming depths obtained from a meta-analysis of fish telemetry and tagging studies. Maximum dive depths of foraging whales also matched the distribution of test fishery catch depths reported for Chinook salmon, implying that northern resident killer whales target the depth range where Chinook are most likely to occur. Quantitative analysis of killer whale foraging dives also suggested possible escape behaviours that Pacific salmon use to avoid predation. These behaviours included descent to greater depths, increased swimming velocity, and continuous alteration of their escape trajectories.

To determine if the hunting behaviour of resident killer whales reflected their prey preference, I first developed a quantitative method for distinguishing foraging from non-foraging dives on the DTAG records. I accomplished this using an iterative linear discriminant analysis (LDA) of 16 kinematic dive traits, which revealed that some movement characteristics had greater utility than others when it came to differentiating foraging from other behaviours. More specifically, dive depth, duration, dive path tortuosity, swimming velocity, and body orientation along the roll axis were all observed to increase during foraging dives. Dives identified as foraging behaviour by the discriminant analysis were thus kinematically distinct from other behaviour types. Unfortunately, the LDA was not as useful for identifying surface foraging behaviours, since these chases consisted of multiple dives and the kinematic variables were only compared at the level of a single dive.

Several DTAGs were deployed on juvenile resident killer whales (<12 y), which provided an opportunity to collect data on the behaviour of individuals that were still developing their hunting skills. I found that young resident killer whales frequently dove in synchrony with their mothers, and often participated in chasing behaviour, but did not necessarily make the final prey capture. In other instances, tagged juveniles did not actively chase fish that were being pursued by their mothers, but they still dove concurrently and likely observed the hunt. Consequently, transmission of foraging tactics within this population appears to occur by social learning. This evidence supports the hypothesis that shared behavioural traditions affect the foraging tactics that resident killer whales use to capture prey (Ford and Ellis 2006).

The DTAG data also provided the first empirical evidence linking echolocation to salmon captures by wild northern resident killer whales. Echolocation has been assumed to function in prey detection and capture for this species, and previous field studies have detected correlations between the occurrence of echolocation and group activity states consistent with foraging (Barrett-Lennard et al. 1996, Holt et al. 2013). I was able to build on this work by analysing the echolocation behaviour of individual whales during successful feeding dives. Both the time that whales spent producing click trains, as well as the click repetition rates within these trains, were significantly greater prior to fish captures than they were afterward. These increases in clicking effort indicate that echolocation serves an important function during the search and pursuit phases of foraging dives. Furthermore, regular click trains during the pre-capture phase were often associated with sideways roll orientations by the whales. This body position could facilitate the pursuit of fish along the sea floor, or might improve the reception of click echoes through the lower jaw. Echolocation probably serves secondary functions in addition to locating and catching prey, as some clicks were emitted after fish captures. Post-capture echolocation could aid in prey handling, navigating back to the surface, or locating other whales.

Tagged northern resident killer whales also produced series of extremely rapid echolocation clicks, known as buzzes, that usually occurred in deeper water and preceded prey captures. As determined by acoustic tagging studies of other echolocating odontocetes, buzzes made by northern residents likewise appeared to function in terminal prey targeting just before capture. In addition to buzzes, I also identified distinctive ‘crunching’ sounds on the DTAG recordings that primarily occurred after a successful capture had taken place. Given the similarity of crunches to transient killer whale prey processing noises, as well as their post-capture timing, I concluded that these sounds likely signified prey handling behaviour. Unexpectedly, however, a small proportion of the crunches occurred prior to the fish capture time. This could indicate that resident killer whales are capable of catching multiple prey during a single foraging dive, but the continuity of chasing behaviour within the dive pseudotracks suggested that pre-capture crunches were more likely the result of misidentified flow noise. Since buzzes were associated with close approaches to prey, and crunches with successful prey captures, both could be useful proxies for estimating foraging efficiency.

4.2 Study limitations and future research

Before the development of biologging tags, detailed behavioural studies of diving animals like cetaceans were extremely challenging. These tags have given biologists unprecedented access to behaviours that were previously unobservable and difficult to quantify, however, they also produce extremely large data sets that present a considerable analytical challenge. Furthermore, while vocal and kinematic information collected by these tags provide a relevant context for relating acoustic behaviour to an individual's movements, integrating these two sets of tag sensor data is a complex and often time-consuming task (Johnson et al. 2009). Future studies using acoustic biologging tags would benefit from improved standardization of analysis techniques, such as automated methods for the detection and categorization of behaviours and tagged whale vocalizations. In particular, further advancements in multivariate statistical techniques for analysing dive behaviour would be of considerable benefit. The DTAG data used in my study were spatially and temporally autocorrelated, which violated the assumption of independent sampling that is required for many statistical tests and introduced the potential bias of within-individual behavioural differences. Although I performed a 'leave-one-out' type validation to help minimize this bias, developing more rigorous multivariate statistical techniques (e.g., Mundry and Sommer 2007) to cope with the nonindependence of dive data (resulting from replicate measures taken on the same individuals) would improve the level of confidence in results from future studies.

Limitations in data storage capacity, in combination with high sampling rates and the density of audio data in particular, have restricted acoustic biologging tags to the collection of short-term behavioural information (Johnson et al. 2009). The current suction-cup attachment method also limits the amount of time that the tag will remain attached to a whale (Johnson et al. 2009). The DTAGs I deployed measured the behaviour of northern residents for 12 hours or less per tagged individual, and my study was also largely restricted to a single geographic area (northeastern Vancouver Island) and time of year (summer/fall). As such, it represents only a partial description of the feeding behaviour of this population. Tag deployments over a wider range of locations and during the winter would provide a greater understanding of resident killer whale foraging behaviour. Feeding tactics may differ in other locations due to differences in prey species availability and habitat characteristics (e.g., bathymetry, substrate type). The logistics of working in remoter areas, along with the unpredictability of resident killer whale distribution and weather conditions during the winter months, will unfortunately prevent this type of study from being carried out unless biologging tags that do not require retrieval are used. To accomplish this, the tags would have to incorporate on-board processing to reduce the volume of data and transmit this summarized information via satellite (e.g., Fedak et al. 2002). Consequently, the diving behaviour data obtained by satellite telemetry tags would be less detailed than those recorded by archival tags, such as the DTAGs in my study. Furthermore, telemetry of acoustic data is currently unfeasible because of the extremely high sampling frequencies (at least double the highest frequency of interest) required for audio recordings (Johnson et al. 2009). Satellite telemetry studies may become possible in the future with the advent of further innovations in tag data compression and processing.

My interpretations of salmon responses to pursuit by killer whales, as well as the spatial environments in which this interaction takes place, have relied solely on inferences from whale behaviours. The predator response behaviours of adult Pacific salmon, as well as relevant physiological measures (e.g., burst swimming speeds), remain virtually undescribed. My study objective of determining the specificity of whale foraging behaviour for Chinook salmon was thus limited to a comparison of their vertical distributions. Additional evidence for the specialization of resident killer whale hunting behaviour could be gained from experimental or tagging studies of Chinook that focused on understanding their predator avoidance responses. Furthermore, integrating spatial data with the DTAG pseudotracks would increase understanding of how both foraging whales and fleeing salmon make use of the surrounding habitat. For instance, by associating dive pseudotracks with bathymetric data, it may be possible to determine if whales roll sideways to facilitate the pursuit of prey along the sea floor (as I hypothesized in this study). Provided that the dead-reckoned pseudotracks were sufficiently accurate, it might also allow me to clarify whether fish were using the bottom topography as a refuge when threatened by predators. Quantifying the spatial characteristics (e.g., slope steepness, depth, bottom complexity) of preferred feeding areas for northern resident killer whales would provide better information for delineating additional areas of critical habitat. It could also help to reveal areas of spatial overlap between foraging resident killer whales and human activities that could potentially disrupt their feeding behaviour.

In other species of toothed whales, buzzes frequently coincide with significant changes in movement parameters and are thought to represent successful prey captures (e.g., Johnson et al. 2004, Miller et al. 2004, Aguilar Soto et al. 2008, Johnson et al. 2008, Akamatsu et al. 2010). I would like to investigate whether this is the case for resident killer whales, as it appears that body roll orientation might vary significantly during some buzzes. This was not done in the current study due to constraints on analysis time, because clicks had to be manually identified. Developing an automated click detection function would permit click rates within buzzes to be calculated and potential correlations with body orientation parameters could be tested. An automated click detection function for northern resident killer whales could also be used to examine their echolocation behaviour during foraging dives without prey samples (presumed unsuccessful) and during other activity states (e.g., travel, socializing, etc.). The importance of echolocation behaviour in facilitating prey captures, as well as its role in navigation and other functions, might thereby become more apparent.

The timing of 'crunch' sounds on the DTAG record imply that they are related to prey handling behaviour and could be a useful proxy for successful prey captures, however, this still requires validation. A blind analysis of prey handling sounds on the acoustic recordings of non-foraging dives and foraging dives without prey samples (as categorized by the cluster analysis) could be used to accomplish this validation. Crunches should not be present on recordings of non-foraging dives if these sounds reflect prey-handling behaviour. In addition, the presence of crunches during foraging dives without associated prey samples could help to determine whether fish are sometimes consumed at depth and are thus unavailable to be sampled. If this is the case, current estimates of diet composition based on surface collections of prey samples may need to be re-examined. An underwater video camera with audio recording capabilities (either animal-borne or pole-mounted on a research boat) could be used to record the consumption of prey by resident killer whales to help confirm that crunches are the result of prey handling behaviour.

Buzzes and crunches on the DTAG records could also be used to estimate the foraging efficiency (e.g., Catch Per Unit Effort) of individuals, which could be compared to existing model estimates of prey energy requirements for different demographic categories (Ford et al. 2009). This would provide an indication of whether northern residents are currently meeting their energetic requirements, or if individual fitness is being compromised by nutritional stress. Once the population-level consequences of foraging specificity have been examined, the impact of human activities can also be factored in. For instance, field studies investigating the effects of vessel noise on resident killer whale echolocation behaviour would reveal how human disturbance may impact their foraging efficiency. If boat noise causes reduced click detection ranges and prey capture rates, it could also have a negative effect on individual survival and reproductive success. To prevent this, management decisions such as changes to whale-watching guidelines or establishment of vessel exclusion zones in important feeding habitats could be implemented.

Although this thesis is primarily a study of individual behaviour, short-term responses of animals to their environments can have long-term, ecologically relevant consequences. In years of high Chinook availability, foraging behaviour that is highly specialized for capturing this preferred prey species would be beneficial, however, in years of poor availability it becomes detrimental and would probably prevent individuals from meeting their energetic requirements. Consequently, hunting behaviour has a direct effect on foraging efficiency and thus individual fitness, which ultimately determines population growth. A greater understanding of northern resident killer whale foraging behaviour could therefore help to inform management and conservation planning for this threatened population.

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Appendices

Appendix A: Summary of salmon vertical distribution meta-analysis data

Table A.1 Summary of tagging and telemetry studies (n=12) examining the vertical distribution of Pacific salmon (*Oncorhynchus* spp.) in the marine environment. All studies were conducted on maturing/adult fish (ocean age X.1 or older) in summer and autumn. Standard deviations of average swimming depth are provided where available.

Species	Study	Habitat type	Methodology	No. fish	Time of day	Average depth (SD) (m)
Chinook	Candy & Quinn 1999	coastal	ultrasonic telemetry	32	combined	69.9 (57.3)
O. tshawytscha	Hinke *et al.* 2005	coastal	archival data tags	15	combined	50
	Ogura 1994	high seas	ultrasonic telemetry	4	day	28.0 (9.0)
					night	29.5 (5.4)
	Walker *et al.* 2007	high seas	archival data tags	2	day	43
					night	40
Chum	Soeda *et al.* 1987	coastal	ultrasonic telemetry	7	day	23.9 (25.5)
O. keta				4	night	40.4 (20.4)
	Tanaka *et al.* 2001	coastal	archival data tags	7	combined	76.1 (33.6)
	Yano & Nakamura 1992	coastal	ultrasonic telemetry	21	combined	19.9
	Azumaya & Ishida 2005	high seas	archival data tags	5	day	20.3 (3.1)
					night	4.0 (2.0)
	Ishida *et al.* 2001	high seas	archival data tags	1	day	12.8
					night	4.8
	Ogura 1994	high seas	ultrasonic telemetry	5	day	20.1 (12.8)
					night	25.6 (21.8)
	Tanaka *et al.* 2005	high seas	archival data tags	1	combined	10.2 (12.5)
	Walker *et al.* 2007	high seas	archival data tags	11	day	20
					night	8
Coho	Ogura 1994	high seas	ultrasonic telemetry	4	day	10.3 (2.6)
O. kisutch					night	7.3 (3.4)
	Walker *et al.* 2007	high seas	archival data tags	10	day	12
					night	8
Pink	Ogura 1994	high seas	ultrasonic telemetry	3	day	9.9 (10.5)
O. gorbuscha					night	9.3 (9.5)

Species	Study	Habitat type	Methodology	No. fish	Time of day	Average depth (SD) (m)
	Walker *et al.* 2007	high seas	archival data tags	3	day	13
Pink (continued)					night	4
Sockeye	Quinn *et al.* 1989	coastal	ultrasonic telemetry	16	combined	14.9 (7.5)
O. nerka	Ogura 1994	high seas	archival data tags	4	day	8.5 (2.1)
					night	16.5 (18.2)
	Walker *et al.* 2007	high seas	archival data tags	12	day	4
					night	3
Steelhead	Ruggerone *et al.* 1990	coastal	ultrasonic telemetry	6	day	1.5
O. mykiss					night	2.8
	Ogura 1994	high seas	ultrasonic telemetry	3	day	8.8 (4.3)
					night	5.3 (1.3)

Table A.2 Summary of catch and fishing depth data for Pacific salmon (*Oncorhynchus* spp.) caught in vertical distribution test fishery and bycatch studies; all studies were conducted on maturing or adult fish (ocean age x.1 or older), data from all seasons and times of day were included.

Study	Region	Gear type	Fished depth (m)	Species	Catch depth[a] (m)	Proportion of catch[b]	No. fish
Argue 1970	Juan de Fuca Strait	troll	9-55	chinook	46-55	0.80	894
				coho	9-24	0.70	1176
				pink	27-46	0.64	452
				sockeye	27-46	0.72	91
Godfrey *et al.* 1975	Aleutian Islands & northeast Pacific	gillnet	0-23	chinook	15-23	0.64	11
				coho	0-7	0.62	87
				chum	0-7	0.47	431
				pink	15-23	0.57	28
				sockeye	0-7	0.72	821
				steelhead	0-7	0.82	10
Machidori 1966	Bering Sea & northwest Pacific	gillnet	0-50	sockeye	0-10	0.88	77
				chum	0-10	0.74	42
				pink	0-10	0.95	115
				coho	0-10	0.79	24
Manzer 1964	Gulf of Alaska	gillnet	0-61	chum	0-24	0.73	184
				pink	0-24	0.84	64
				sockeye	0-37	0.86	337
Milne 1955	Vancouver Island	troll	9-37	chinook	18-27	1.00	97
				coho	9-18	1.00	54
Parker *et al.* 1959	Gulf of Alaska	troll	20-100	chinook	30-100	not available	25
				coho	20-30	not available	115
Taylor 1969	Vancouver Island	trawl	0-128	chinook	57-73	0.46	194
			0-110	coho	0-18	0.71	56
			0-55	chinook	20-37	0.96	53
			0-55	coho	20-37	1.00	10
Walker *et al.* 2007	Bering Sea	trawl	0-325	chinook	25-75	0.72	4855

a. Refers to the depth interval at which the majority of the fish were caught

b. Refers to the proportion of the total catch per species that was caught at the catch depth interval indicated

Appendix B: Prey capture dive profiles with associated echolocation and roll behaviour

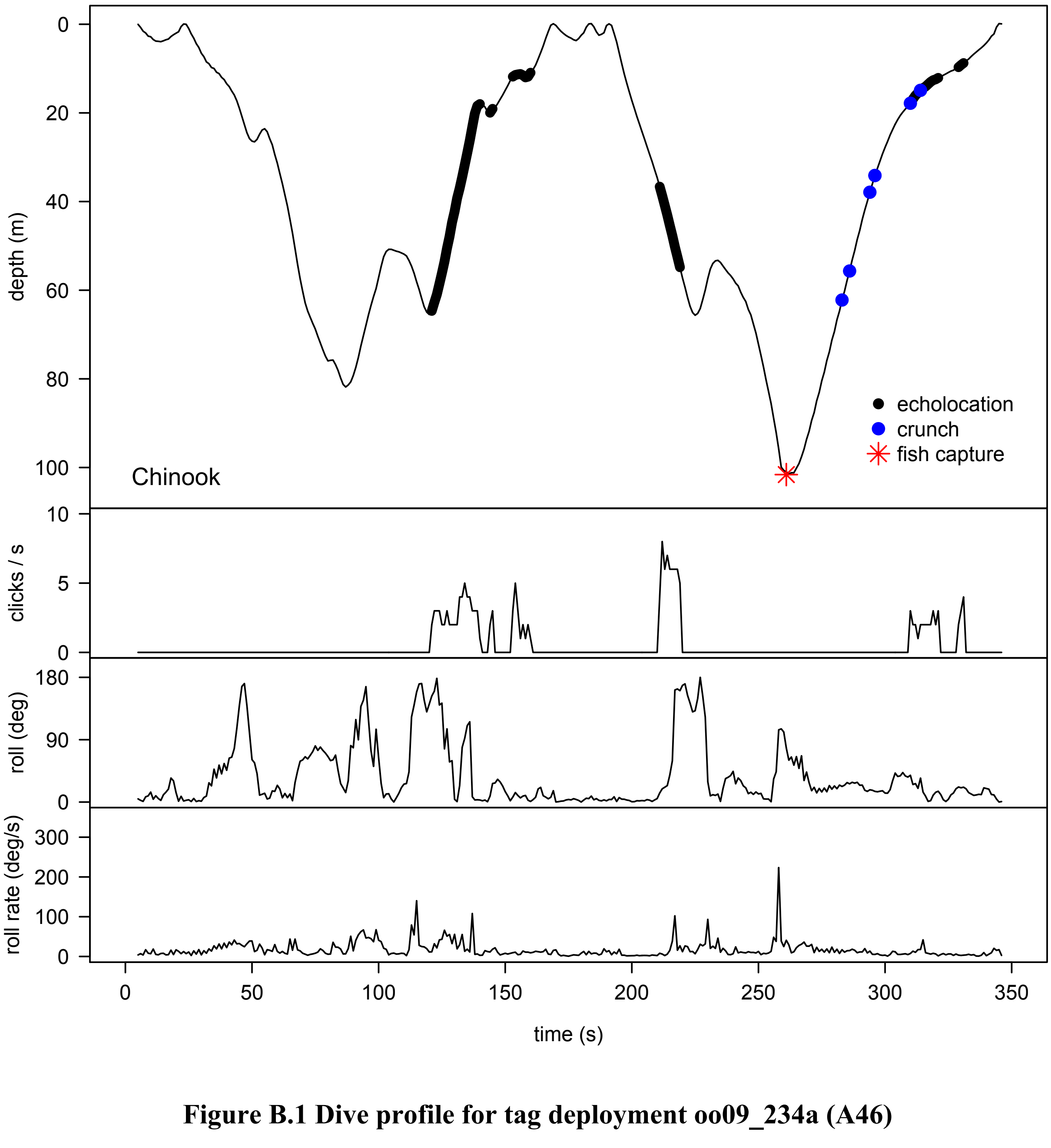

Figure B.1 Dive profile for tag deployment oo09_234a (A46)

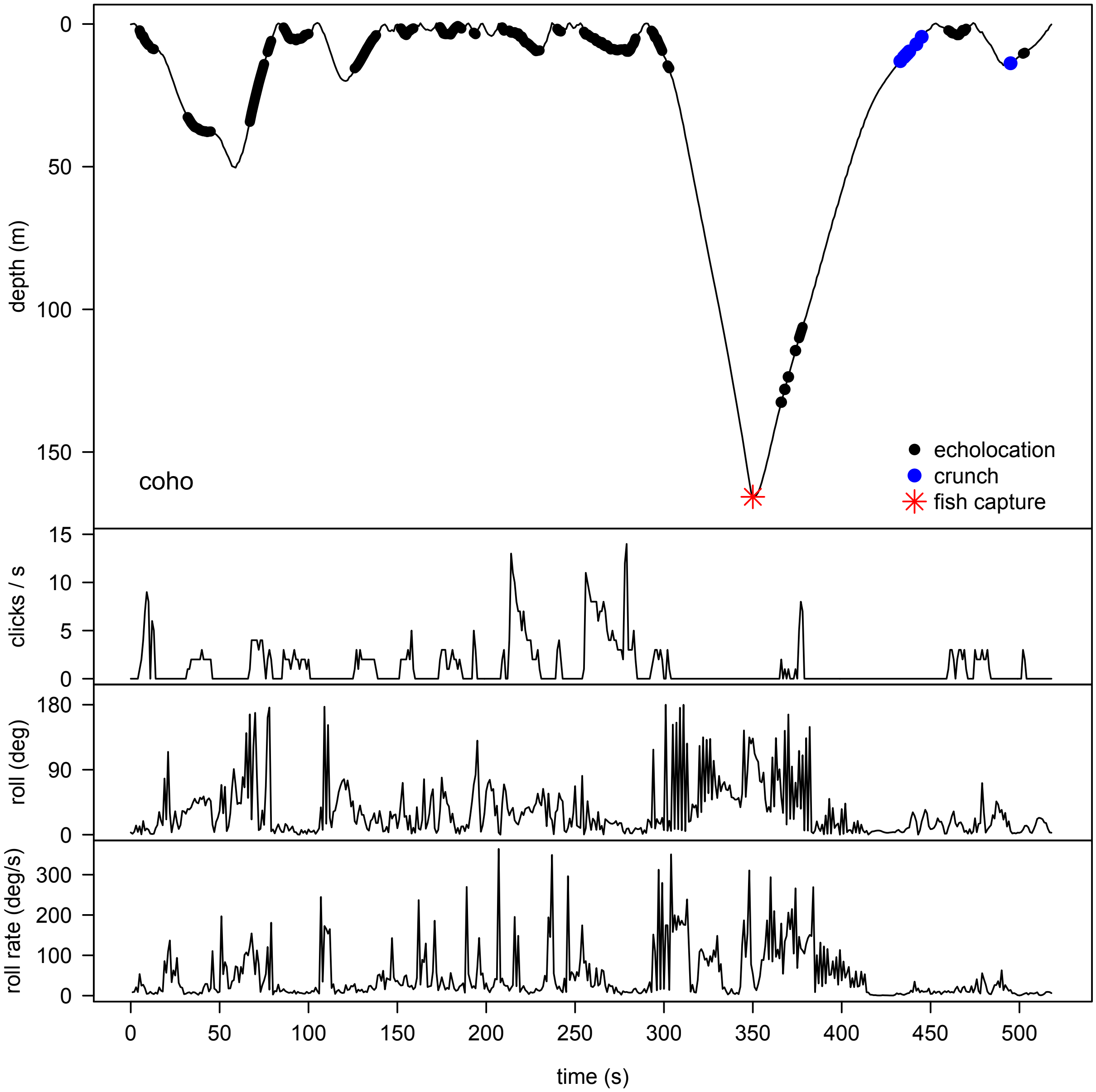

Figure B.2 Dive profile for tag deployment oo09_240a (A37)

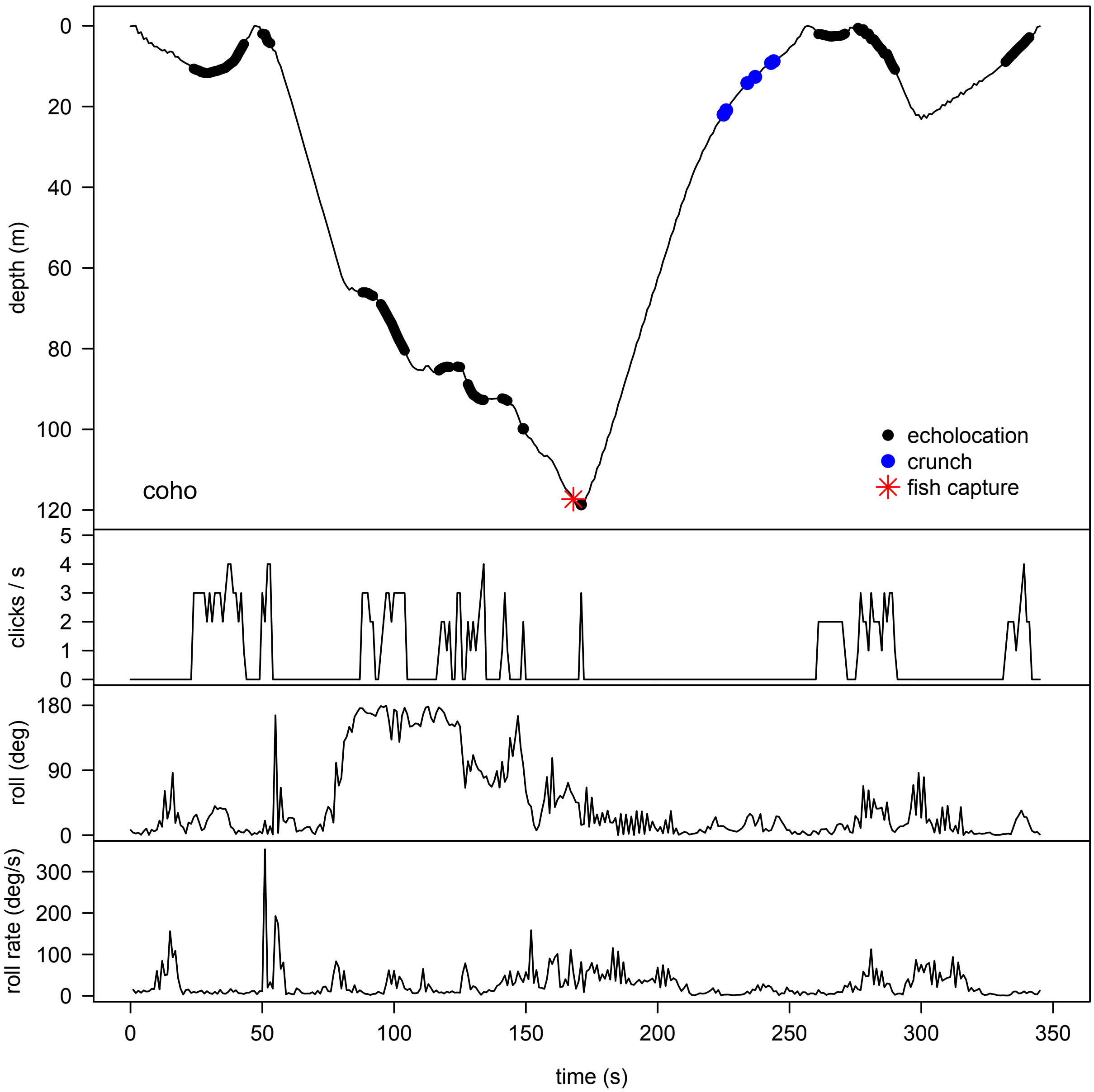

Figure B.3 Dive profile for tag deployment oo09_240a (A37)

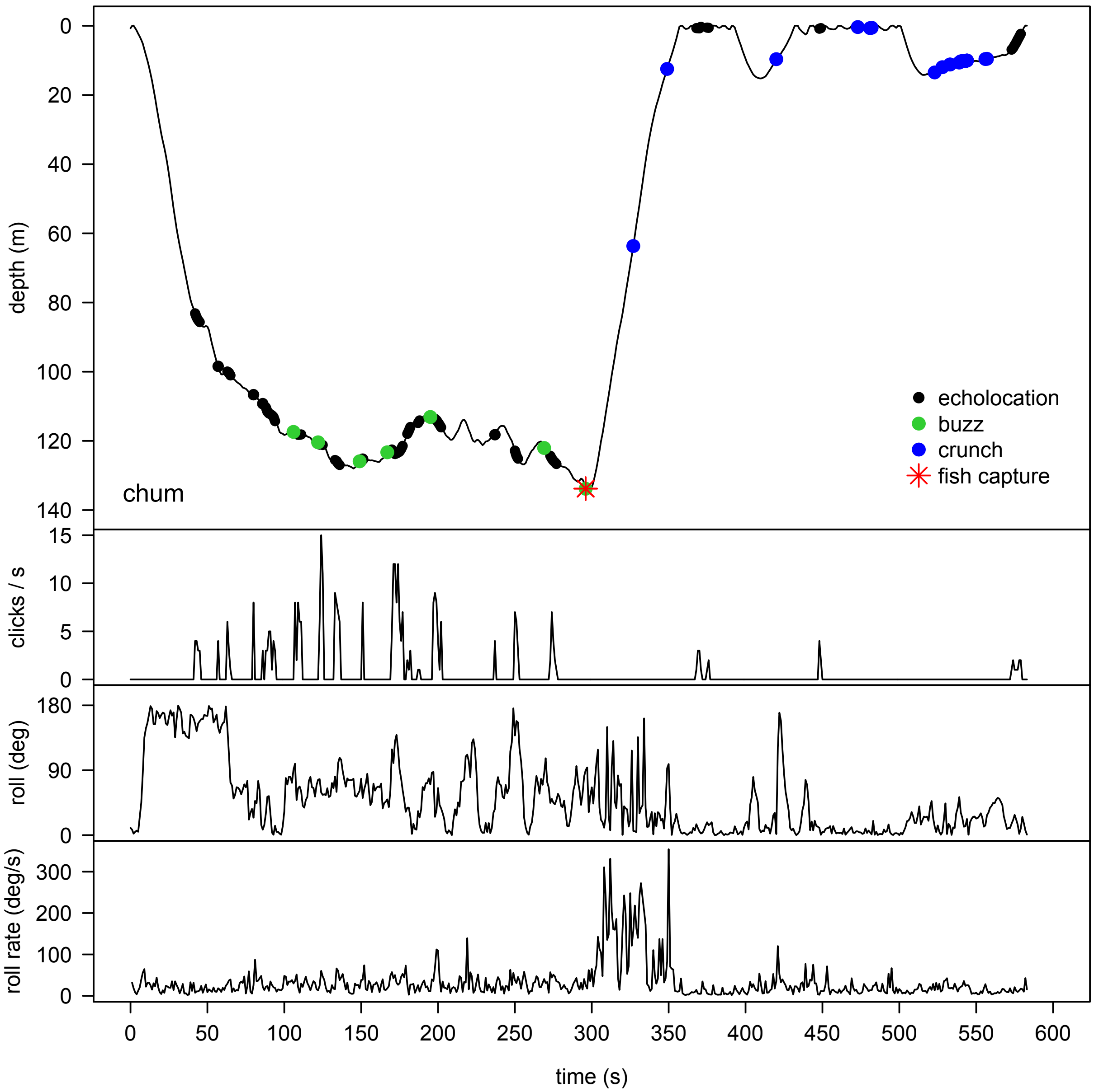

Figure B.4 Dive profile for tag deployment oo10_256a (G64)

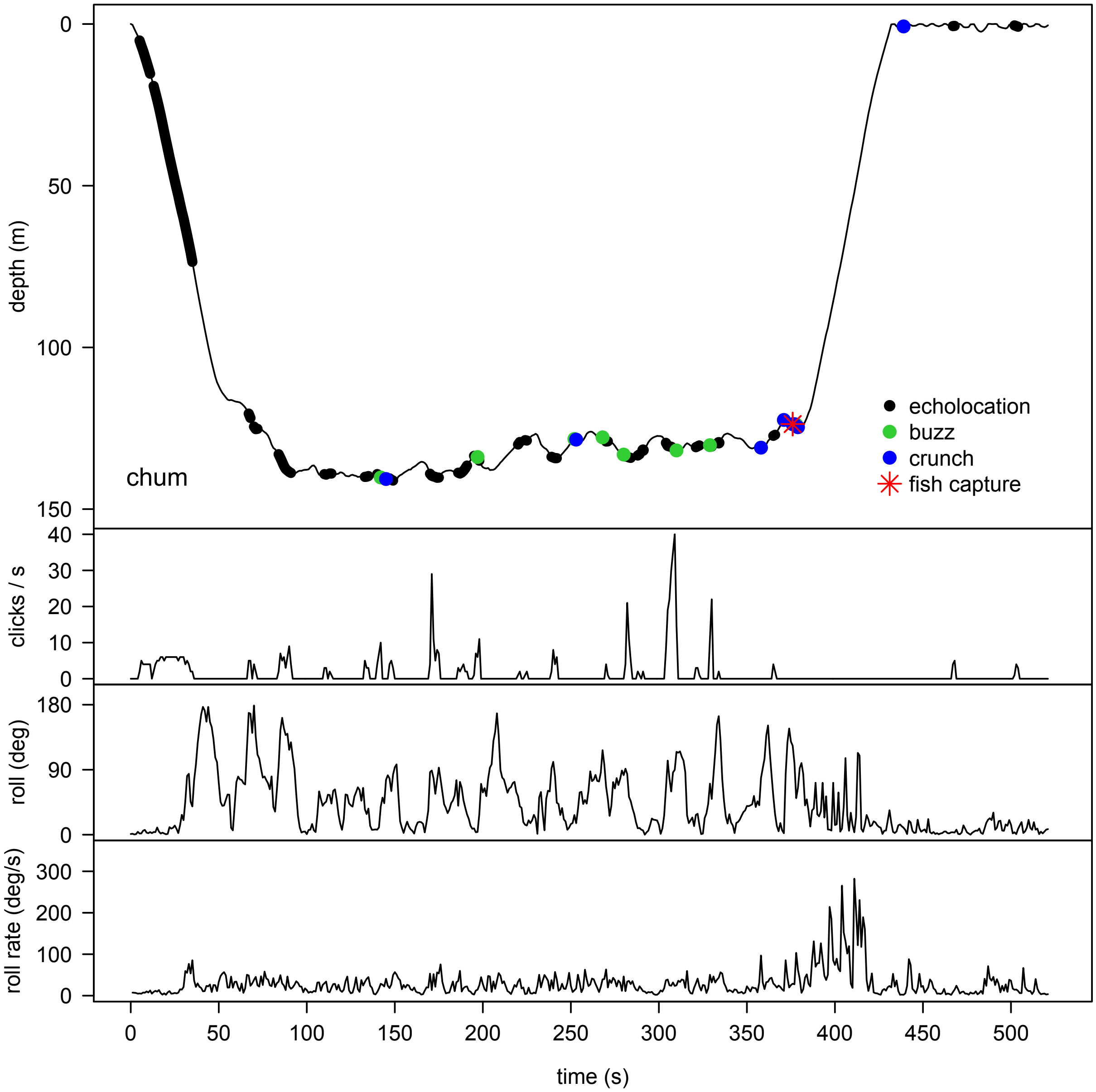

Figure B.5 Dive profile for tag deployment oo10_256a (G64)

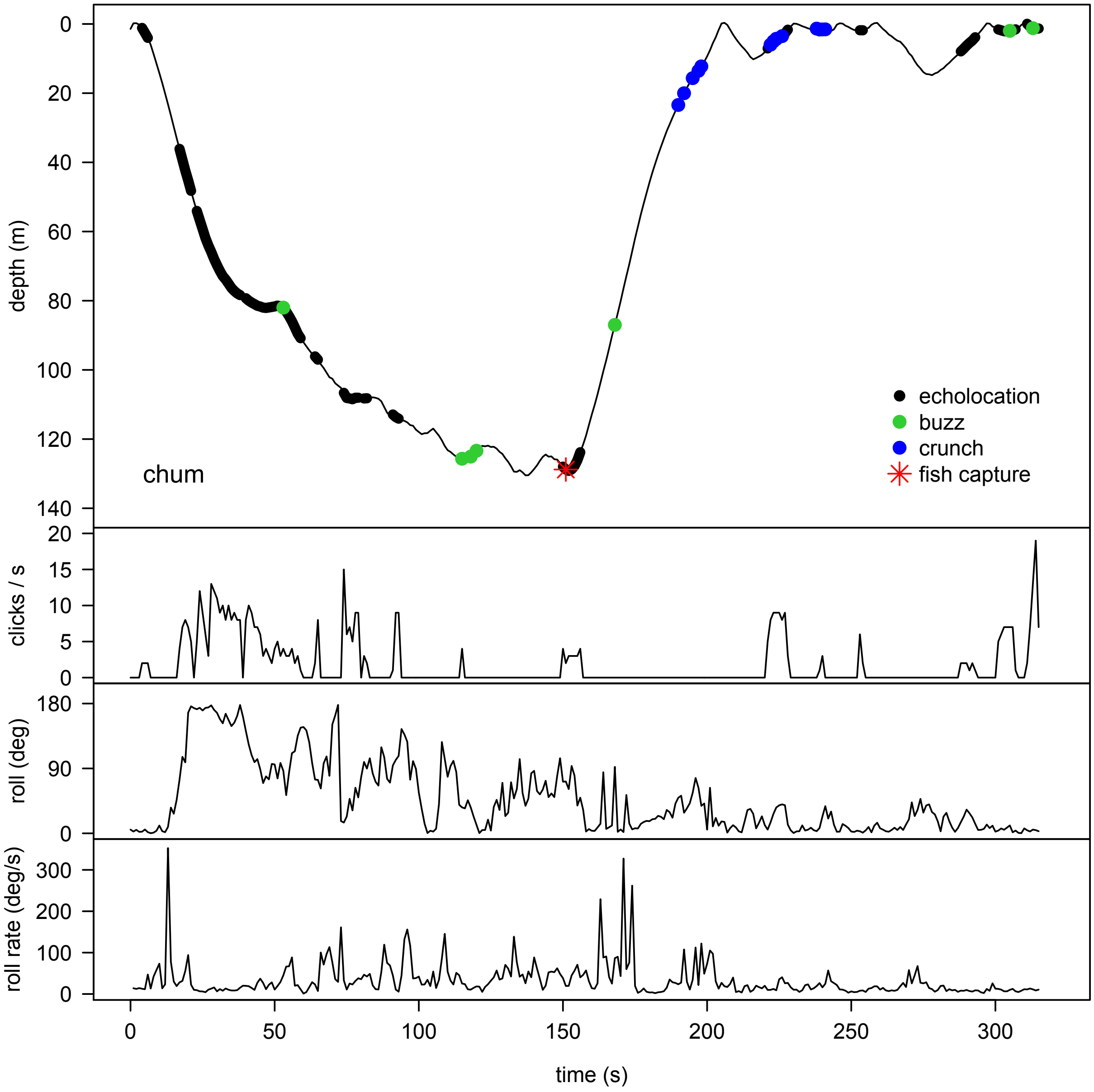

Figure B.6 Dive profile for tag deployment oo10_265a (G49)

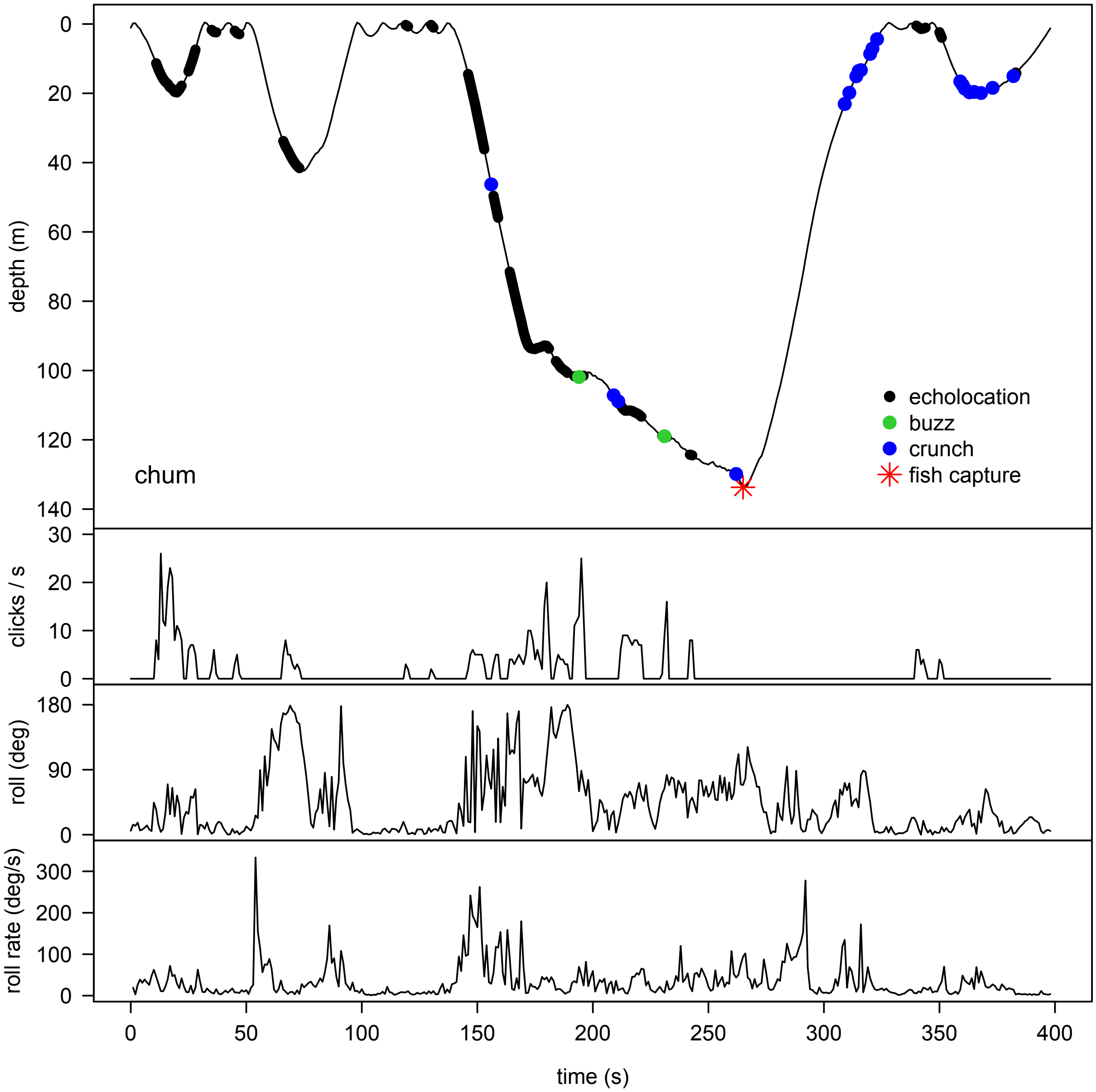

Figure B.7 Dive profile for tag deployment oo10_265a (G49)

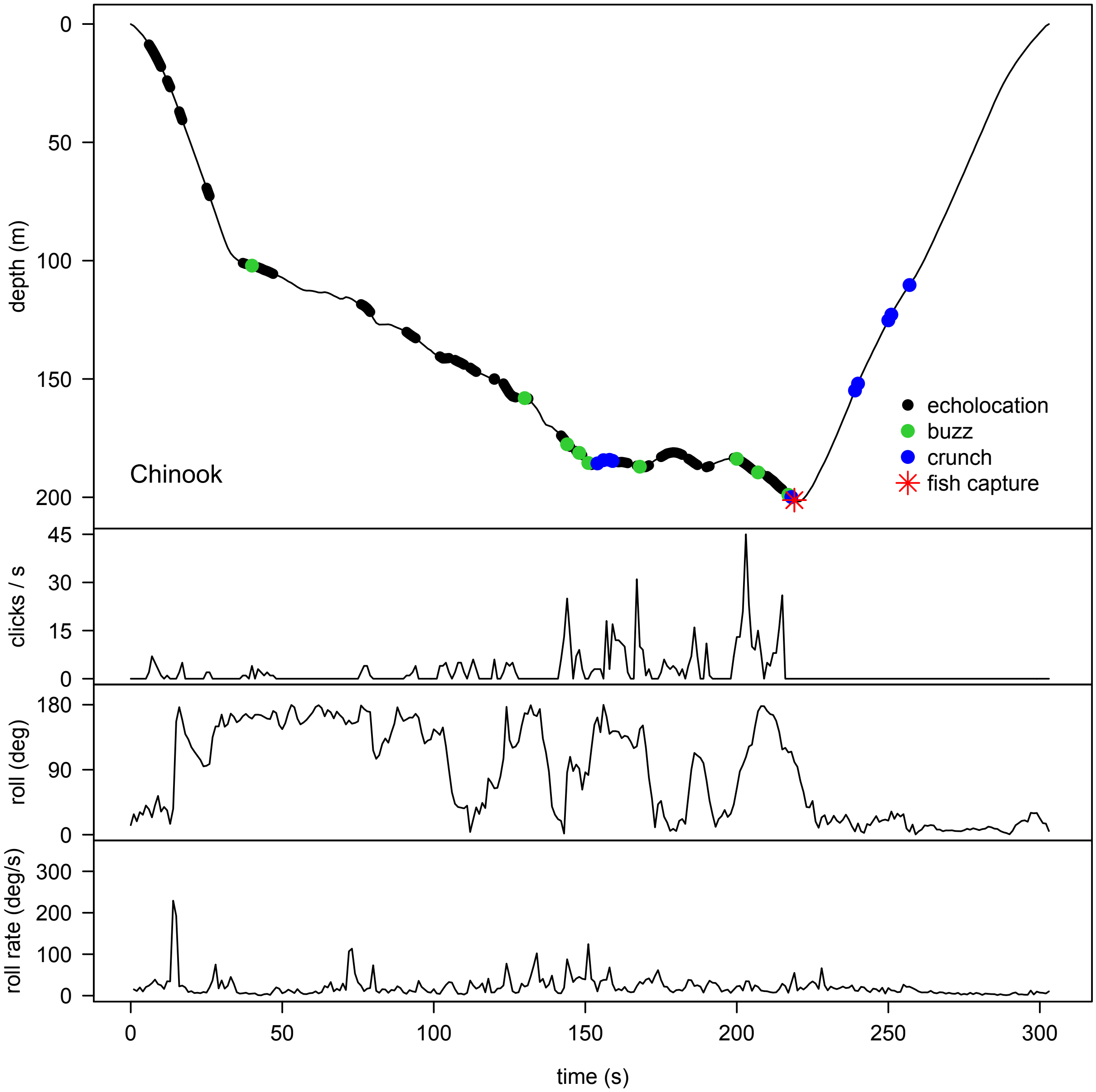

Figure B.8 Dive profile for tag deployment oo11_246a (G31)

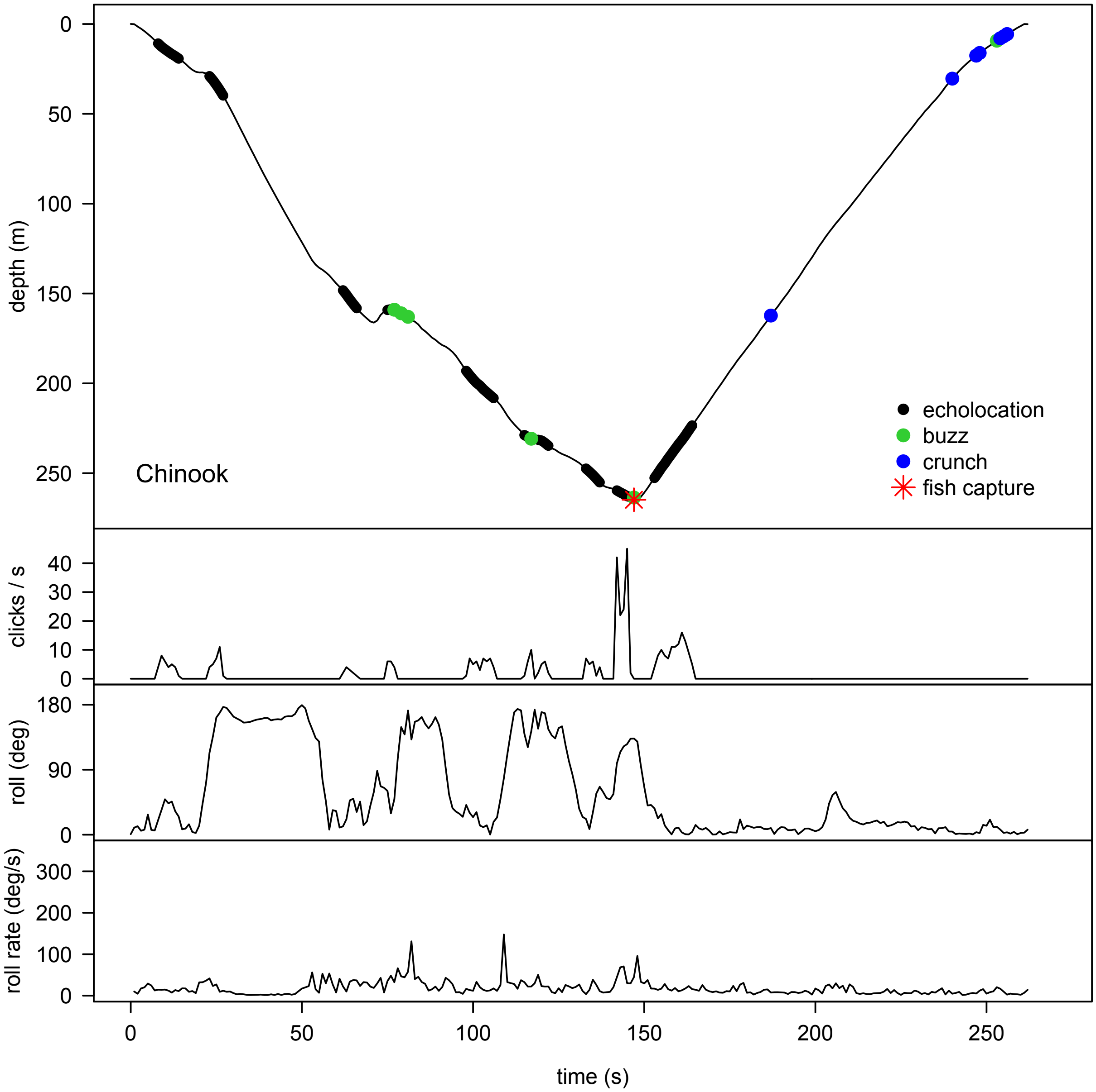

Figure B.9 Dive profile for tag deployment oo11_246a (G31)

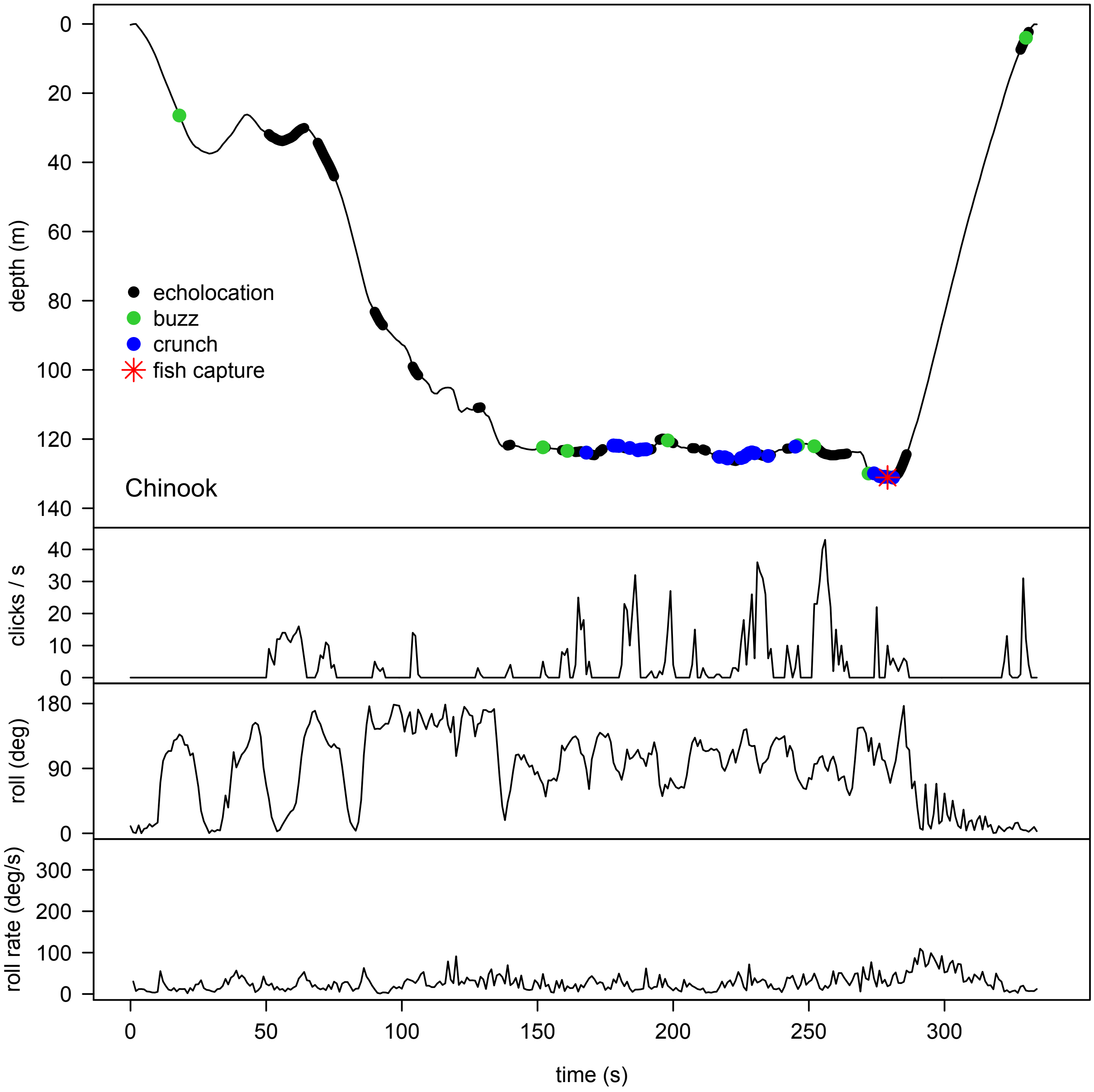

Figure B.10 Dive profile for tag deployment oo11_246a (G31)

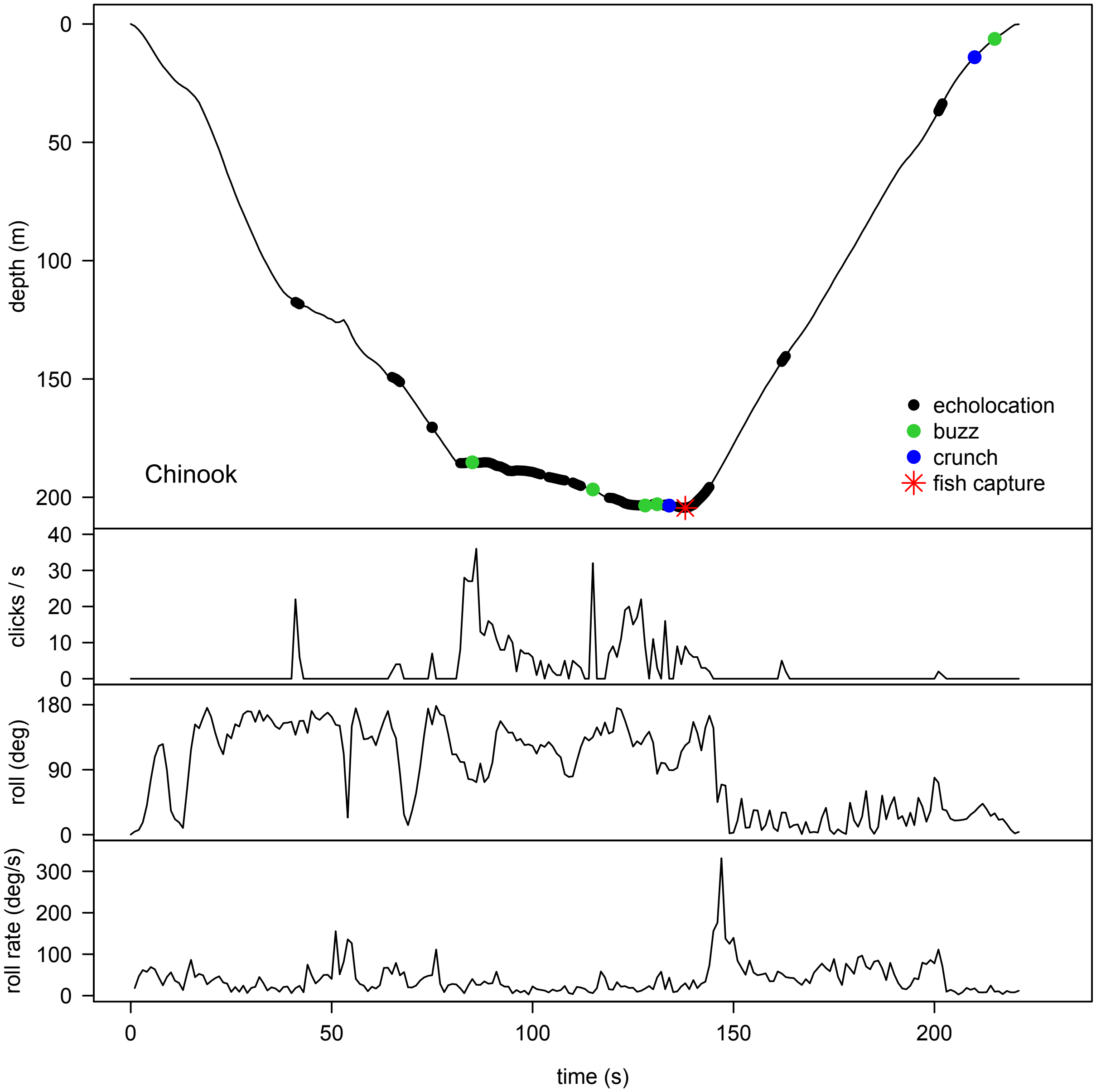

Figure B.11 Dive profile for tag deployment oo11_246a (G31)

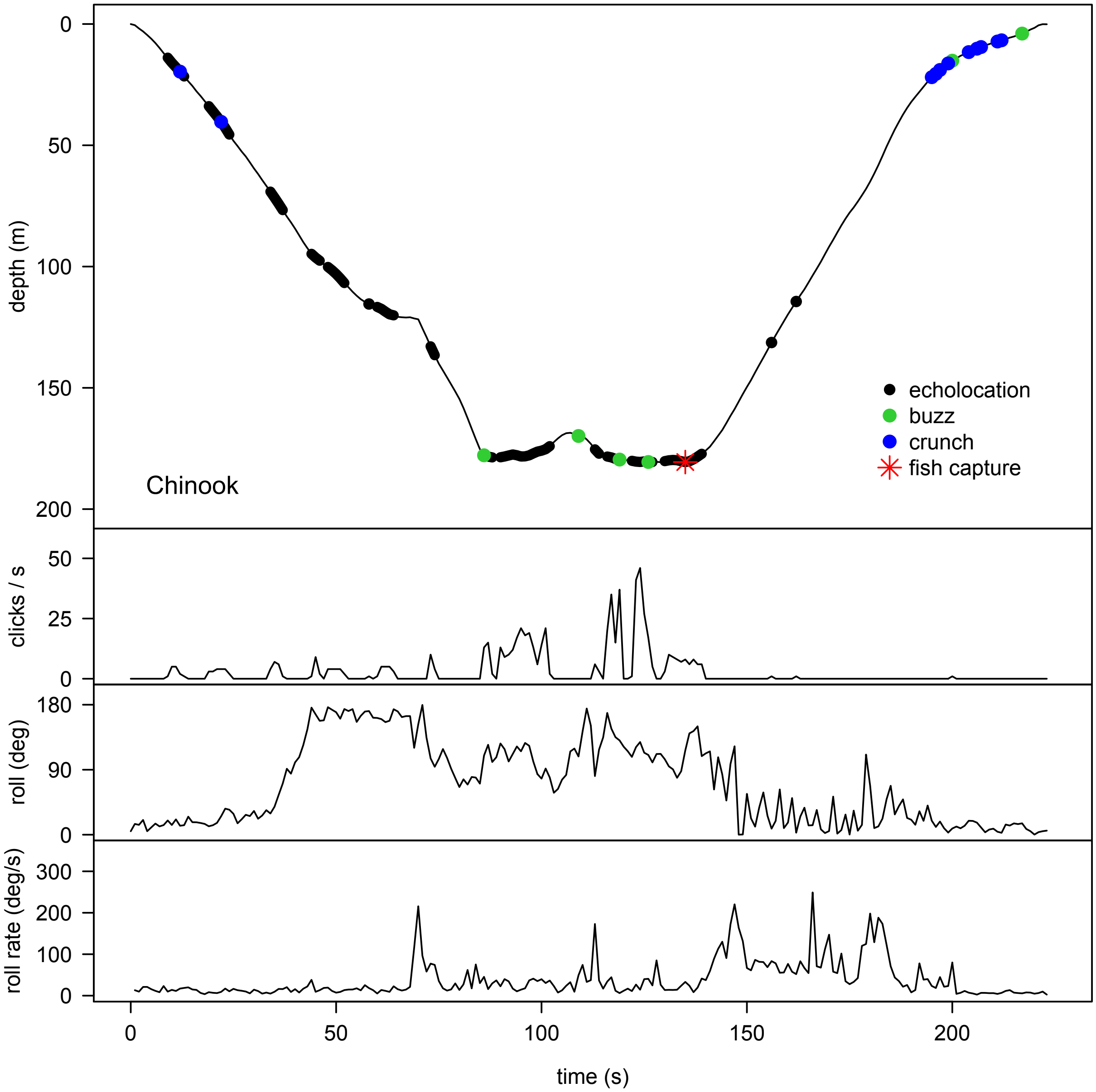

Figure B.12 Dive profile for tag deployment oo11_246a (G31)

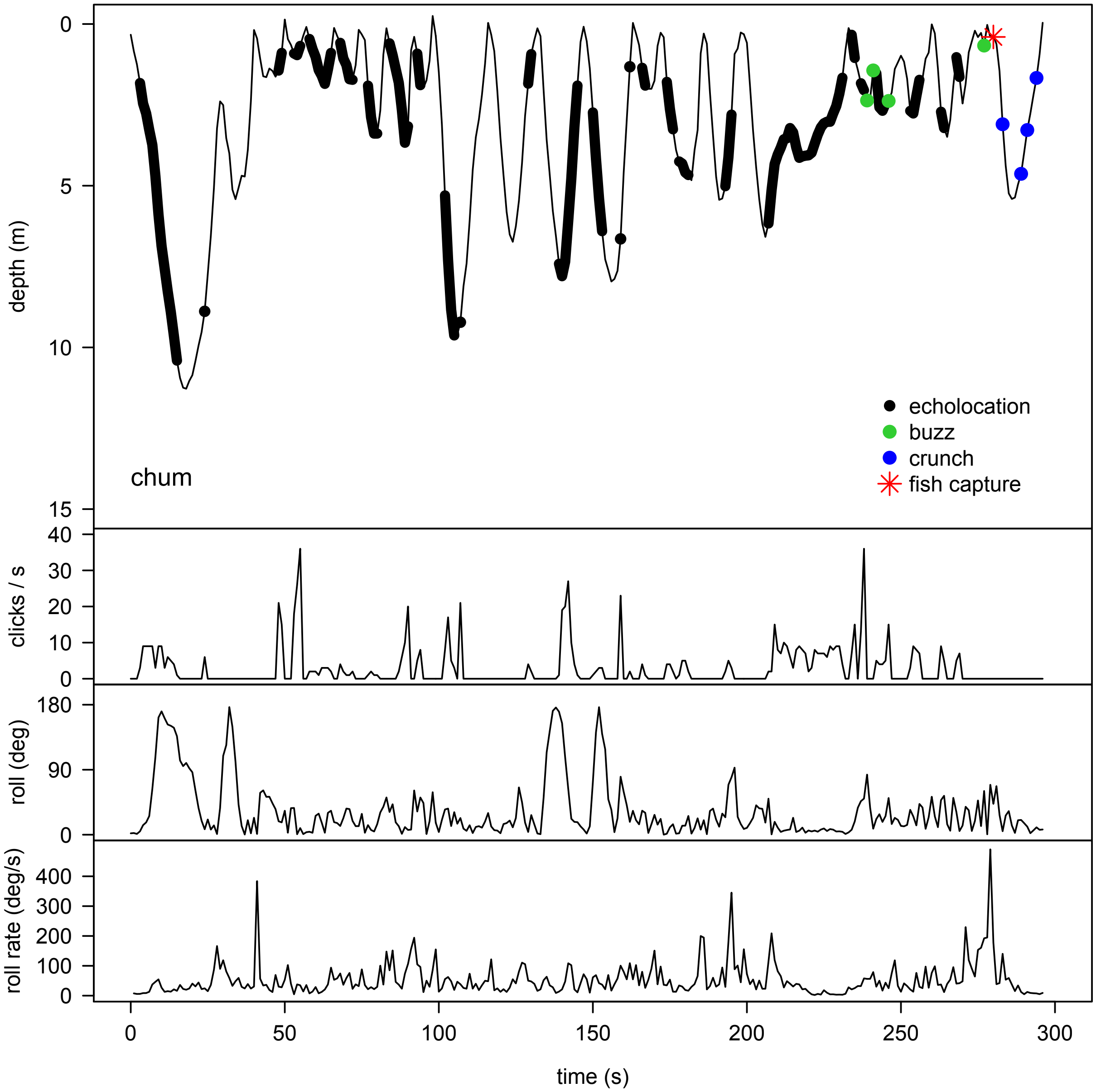

Figure B.13 Dive profile for tag deployment oo12_232a (I106)

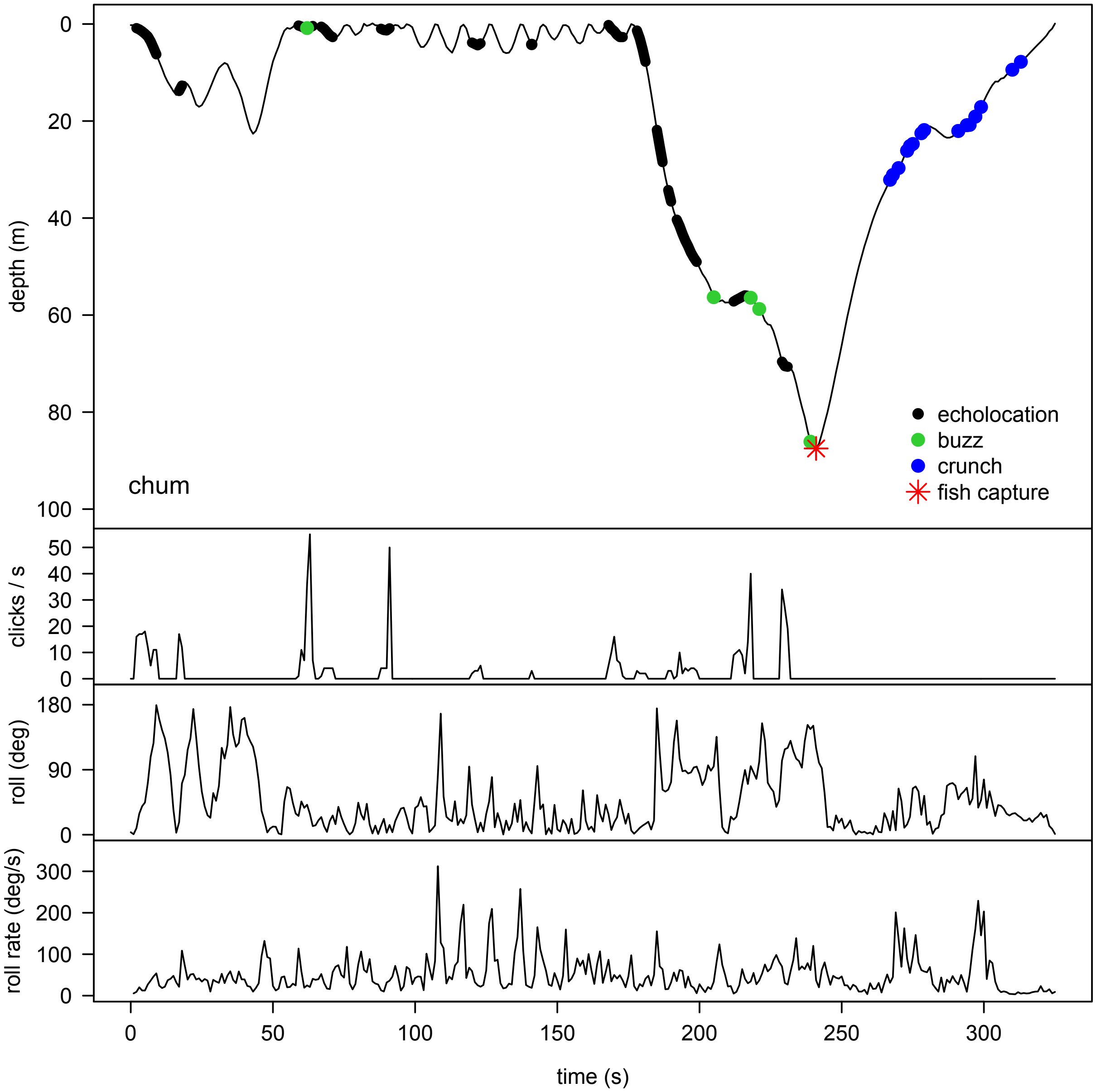

Figure B.14 Dive profile for tag deployment oo12_232a (I106)

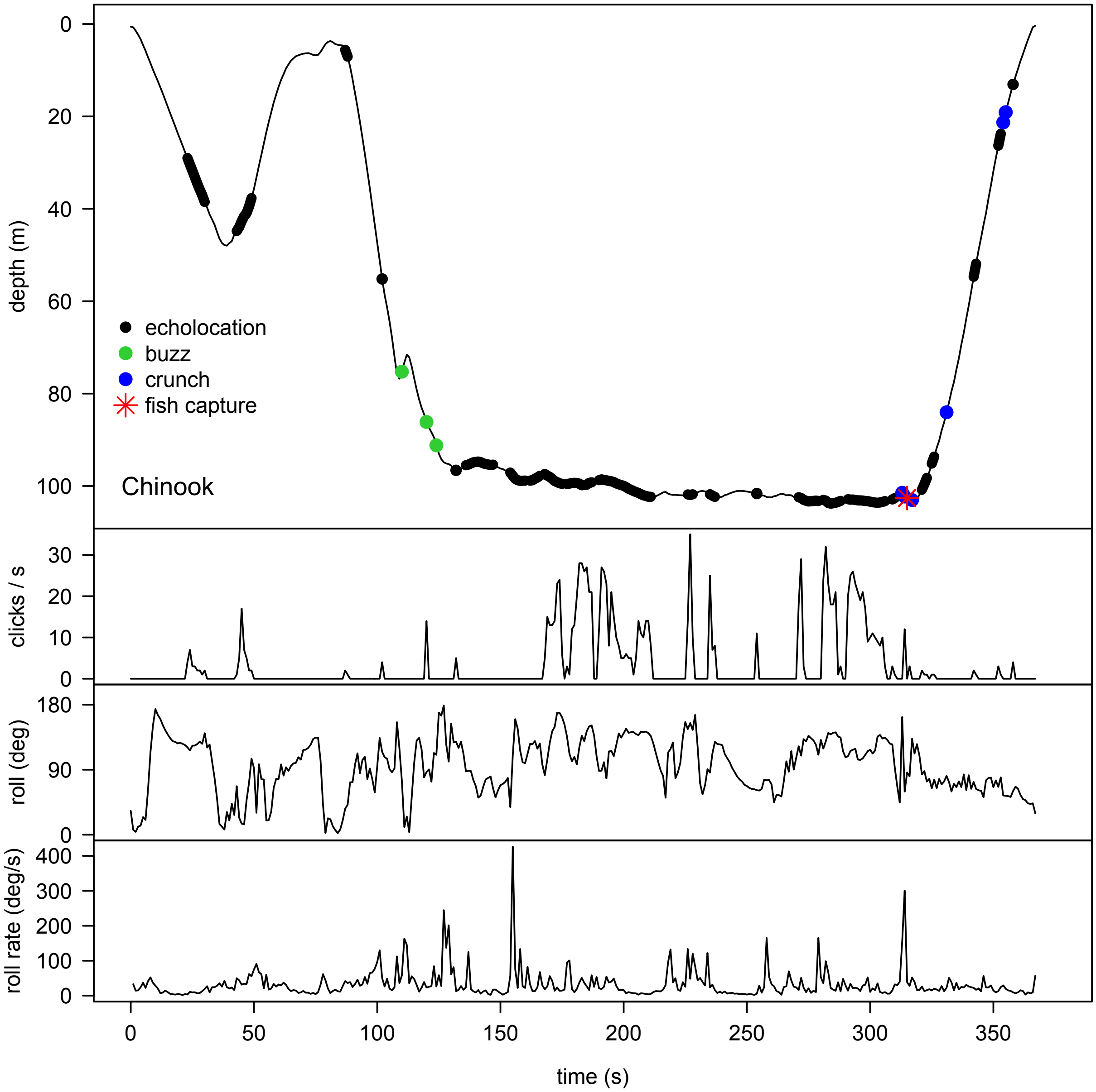

Figure B.15 Dive profile for tag deployment oo12_235b (A66)

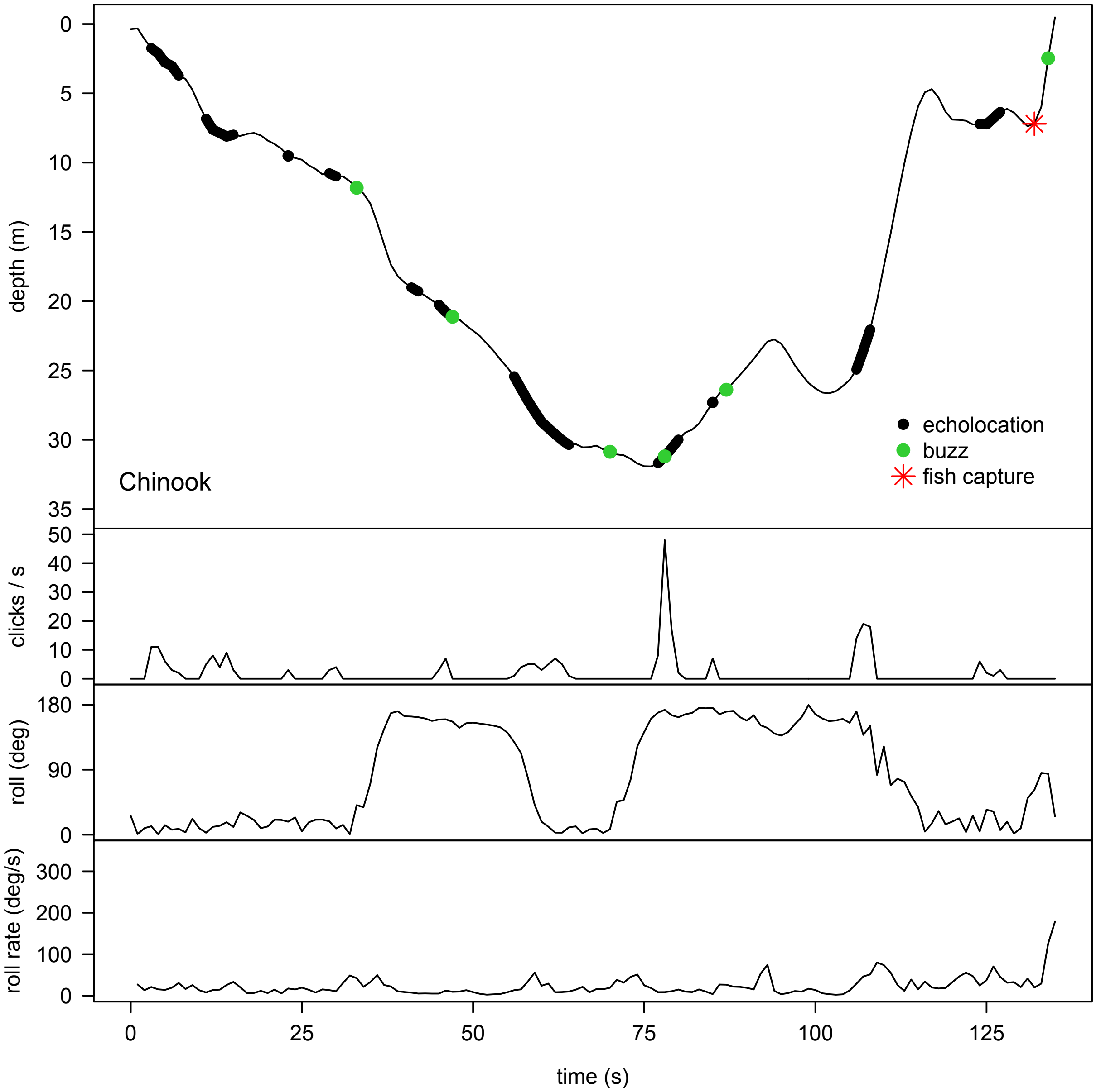

Figure B.16 Dive profile for tag deployment oo12_235b (A66)

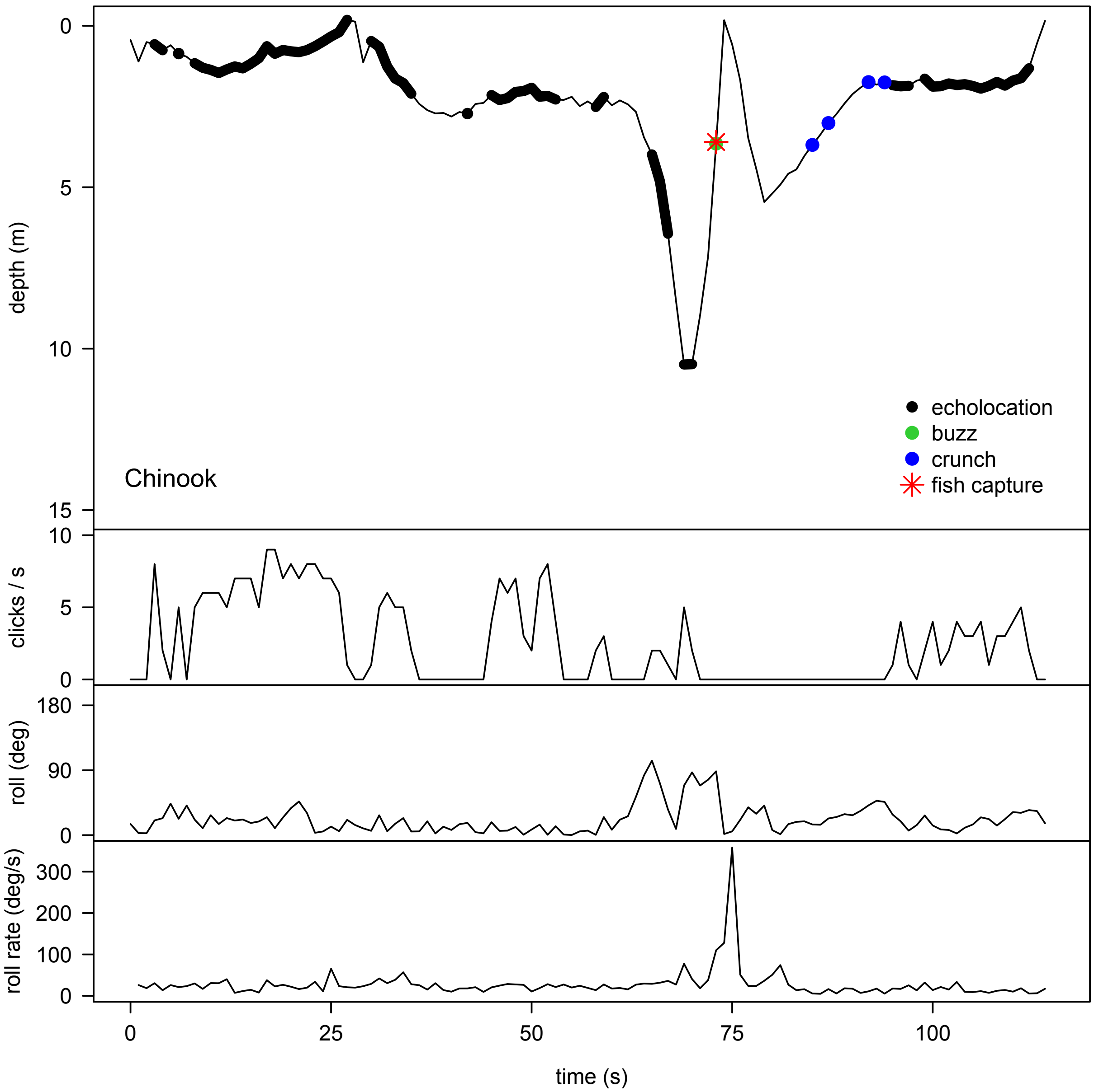

Figure B.17 Dive profile for tag deployment oo12_2435b (A66)