VARIABILITY OF HARBOUR SEAL (*PHOCA VITULINA*) FORAGING BEHAVIOUR DURING OUT-MIGRATIONS OF SALMON SMOLTS

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Abstract

There is increasing evidence that predation by harbour seals (*Phoca vitulina*) on young salmon (smolts) out-migrating from rivers may be a significant source of mortality for coho (*Oncorhynchus kisutch*) and Chinook (*O. tshawytscha*) salmon populations in British Columbia. Studies supporting this have focused on documenting what and how much harbour seal populations eat—and the potential impact this has on salmon populations. However, little attention has been given to understanding where, when and how this predation occurs, and the extent to which it might be opportunistic or specialist feeding behaviour by a few or many individual seals. I documented the spatiotemporal foraging behaviour of harbour seals in the Salish Sea by equipping 17 seals with GPS loggers and Daily Diary tags—and tracking them before and after the release of thousands of coho and Chinook smolts from the Big Qualicum Hatchery. Reconstructing the high-resolution movements of the seals—and quantifying feeding using counts of prey chasing events (PCEs) detected by accelerometry—revealed that the Big Qualicum estuary was a feeding hotspot for 47.0% of the 17 tracked seals, but was relatively small geographically (accounting for 3% of PCEs) compared to the largest feeding area outside the estuary (26% of PCEs). Comparing the foraging behaviours of smolt specialists with non-specialist seals revealed 4 different foraging strategies. One consisted of seals (17.6%) that only fed on coho smolts and ignored Chinook in the river mouth, while a second group of seals (17.6%) appeared to target larger fish that preyed on Chinook smolts near the river mouth. The two other seal groups did not feed at the river mouth in association with the concentrated numbers of smolts, but either remained resident (52.9%) and fed near their main haul-out sites, or were transient (11.8%) and left the study area all together. My results suggest a high degree of individual foraging and diet specializations—and show that a small number of seals were specialized in consuming coho smolts, but did not appear to respond to the large pulse of the smaller bodied Chinook smolts. Such information concerning the fine-scale foraging behaviour of harbour seals in relation to pulses of out-migrating smolts can be used to design mitigation strategies to enhance coho and Chinook populations.

Lay Summary

I sought to estimate the impact of harbour seal predation on juvenile coho and Chinook salmon in the Salish Sea when the fish leave rivers and enter the ocean by documenting when, where, and how harbour seals feed. Tracking their high-resolution movements and behaviours before and after the release of coho and Chinook smolts from the Big Qualicum Hatchery revealed four groups of seals that used different foraging strategies. Only one of the four groups targeted the coho smolts, and all appeared to not respond to the pulse of the smaller bodied Chinook in the river mouth. Such information concerning the foraging behaviour of harbour seals in relation to pulses of out-migrating smolts can be used to design mitigation strategies to enhance coho and Chinook populations.

Preface

I was the primary designer of all my research project presented in this thesis and received suggestions and support from my supervisor Andrew Trites and colleagues Austen Thomas and Tiphaine Jeanniard du Dot. I performed all data collection with the help of the Marine Mammal Research Unit, Washington Department of Fish and Wildlife, Fisheries and Oceans Canada, Big Qualicum First Nation, Vancouver Aquarium, British Columbia Conservation Foundation, and Wildlife Computers. I also, performed all data analysis and prepared all manuscripts. Chapter 2 and 3 were formatted as manuscripts for submission in scientific journals for which co-authors Andrew Trites, Austen Thomas and Yang Liu provided edits and comments. All procedures and data collection from harbour seals were approved by the UBC Animal Care Committee (permit # A14-0322) and the Department of Fisheries and Oceans (permit # XMM 2 2015).

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Chapter 1: Introduction

The spatial and temporal variability of resources is a cornerstone of ecology and is ubiquitous in all ecosystems. Amounts and qualities of available resources directly affect individual foraging behaviours, and have consequences for the structure of population dynamics and the organization of biological communities (Odum 1969; Stephens & Krebs 1986; Sanders & Gordon 2010). This is particularly true of resource pulses (Ostfeld & Keesing 2000; Holt 2008; Yang *et al.* 2008, 2010)—temporary events of increased resource availability in space and time relative to the scale of their consumers (Ostfeld & Keesing 2000; Yang *et al.* 2008).

Resource pulses are characterized by three main components: low frequency, large magnitude, and short duration (Yang *et al.* 2008). Most common examples of resource pulses include mast fruiting by trees and herbs (Kelly 1994; Herrera *et al.* 1998), periodic irruptions of palatable insects (Itô 1998), and storm-induced transport of terrestrial resources (e.g., organic nitrogen or phosphorus) to aquatic systems (Burkholder *et al.* 1997). While the majority of the studies on resource pulses have focused on terrestrial ecosystems, it has been shown that resource pulses also commonly occur in aquatic ecosystems (Willson & Womble 2006; Nowlin *et al.* 2008; Yang *et al.* 2010). Examples of aquatic resource pulses include seasonal storm nutrient runoff (Lancelot *et al.* 1987; Van Boekel *et al.* 1992; Hoover *et al.* 2006), nutrient release from migrating bird fecal matter deposits (Kitchell *et al.* 1999), and large seasonal aggregations of spawning fish such as herring or salmonids (Naiman *et al.* 2002; Yanai & Kochi 2005).

Pacific salmonids are anadromous fish that provide seasonal food throughout their life cycle phases, in the form of resource pulses, to numerous predators in different ecosystems (Fresh 1997). They have a complex life history involving a fresh-water phase and an oceanic phase (Willson & Halupka 1995; Naiman *et al.* 2002)—and begin their life cycle in the autumn in fresh water habitats when eggs are fertilized by males as females deposit them in gravel beds. The young emerge from the gravel beds the following spring and either start migrating to salt water or spend one or more years in fresh water before initiating their out-migration. After completing a feeding and growing phase in the ocean for one or more years, adults return to their native river where they spawn and subsequently die (Groot & Margolis 1991). Their carcases subsequently provide significant amounts of nutrients to freshwater biotas at various trophic levels (Willson *et al.* 1998).

There are 5 species of Pacific salmon returning to hundreds of different streams and rivers, which means multiple sources of significant resource pulses for predators.

Previous studies have highlighted two different strategies of resource pulse consumers: 1) mobile and specialist consumers and 2) opportunistic and resident consumers. Mobile and specialist consumers often travel long distances to exploit sporadic and asynchronously resource pulses (Yang *et al.* 2008). Long-tailed parakeets (*Psittacula longicauda*), for example, feed on the seed production of mast-fruiting dipterocarp forests in Indonesia (Curran & Leighton 2000). In contrast, opportunistic and resident consumers are generalist feeders that exploit infrequently available resources (Ostfeld & Keesing 2000; Yang *et al.* 2008).

Many studies have shown that generalist consumers tend to opportunistically switch their diets in favour of resource pulses. Examples of this include sea otters that switch from eating benthic invertebrates to feeding on spawning lumpsucker fish (Watt *et al.* 2000), or passerine birds that feed on insect pulses (Hogstad 2005), or American black bears (*Ursus americanus*) that feed more heavily on acorns in mast years (when more nuts are produced than usual) compared to non-mast years (McDonald & Fuller 2005). Generalist consumers often have to travel to take advantage of resource pulses, and will significantly increase their rates of consumption when preying on resource pulses (Rose & Polis 1998; Schlacher *et al.* 2013). Those that take advantage of periodical superabundance of resources are able to feed on alternative prey when the pulse is absent (Ostfeld & Keesing 2000). Moreover, these generalist consumers tend to exhibit fast functional and numerical responses that are synchronous with the resource pulses (Rose & Polis 1998; Schlacher *et al.* 2013).

Generally, resource pulses integrate a first phase of bottom-up control of ecosystems followed by a second phase of top-down control (Ostfeld & Keesing 2000; McShea 2000). The bottom-up effect is characterized by a numerical increase in predator abundance, which is driven by behavioural aggregative and reproductive responses to prey pulses. The behavioural aggregation is usually a fast response to short periods of high resource abundance, whereas, the reproductive response tends to be delayed and persistent over time, which has an important impact on local communities (Yang *et al.* 2008). However, in some cases, the reproductive response may occur before resource pulses if consumers can predict and anticipate the availability of these resources—such as tree squirrels (*Tamiasciurus hudsonicus* and *Sciurus vulgaris*) that will increase their reproductive activity in anticipation of seed masts (Boutin *et al.* 2006).

In addition to direct bottom-up effects, resource pulses initiate indirect bottom-up effects spreading across multiple trophic levels (Yang *et al.* 2008). For instance, in the Gulf of California, Mexico, the El Niño rainfalls initiated multiple trophic interactions going from primary production to insect herbivores, mammalian granivores, sea birds, and spiders (Polis *et al.* 1997, 1998; Anderson & Polis 1999; Stapp & Polis 2003). Finally, following the bottom-up effect, the top-down effect is characterized by a crash in prey populations resulting in an expansion of the consumer's diet to include alternative prey due to increased competition (Schmidt & Ostfeld 2008).

1.1 Harbour seals foraging behaviour

Harbour seals (*Phoca vitulina*) are one of the smallest, abundant, and widespread pinniped species throughout the northern hemisphere (Scheffer 1958). They are considered a non-migratory species that is faithful to their main haul-out sites (Yochem *et al.* 1987; Van Parijs *et al.* 2000; Härkönen & Harding 2001; Cordes & Thompson 2015). This is particularly the case during breeding and moulting seasons when they limit their foraging range to less than 50 km from these haul-out sites (Thompson & Miller 1990; Tollit *et al.* 1998; Suryan & Harvey 1998). Mitochondrial differences indicate that harbour seal populations in the Pacific and Atlantic Ocean are genetically distinct and spatially predictable at a scale of few hundred kilometres (Stanley *et al.* 1996; Burg *et al.* 1999). However, individual harbour seals have been documented using multiple areas and haul-out sites (Brown & Mate 1983; Thompson *et al.* 1996; Simpkins *et al.* 2003) and travelling long distances (> 220 km in Oregon, Brown & Mate 1983; 280 km in western Canada, Peterson *et al.* 2012; 520 km in eastern Canada, Lesage *et al.* 2004; 525 km in Alaska, Lowry *et al.* 2001; and 144 km in Scotland, Cunningham *et al.* 2009).

Harbour seals are generalist and opportunistic predators that feed on locally abundant prey and commonly change their diets as prey abundances change seasonally and annually (Tollit *et al.* 1998; Middlemas *et al.* 2006; Lance & Jeffries 2007; Thomas *et al.* 2011). Harbour seal diets incorporate a variety of fish and invertebrate species such as clupeids, salmonids, gadids, rockfish and cephalopods. Nevertheless, their diets are typically dominated by a few targeted species (Scheffer & Sperry 1931; Tollit *et al.* 1997; Lance & Jeffries 2007). In the Salish Sea (eastern

Pacific), a large proportion of the harbour seal diet consistes of Pacific herring (*Clupea pallasii*), Pacific hake (*Merluccius productus*), walleye pollock (*Gadus chalcogrammus*), and salmonid species (Olesiuk 1993; Lance *et al.* 2012; Thomas 2015). World-wide, harbour seal diets and foraging behaviours vary in space and time due to different intrinsic and extrinsic factors including sex (Thompson *et al.* 1998), age (Hastings *et al.* 2004), time of day (Frost *et al.* 2001), tides (Zamon 2001), season (Lowry *et al.* 2001), weather conditions (Grellier *et al.* 1996), and dominant and available prey species (Tollit *et al.* 1997).

Harbour seals opportunistically take advantage of seasonal resource pulses such as spawning herring (Thomas *et al.* 2011) and migrating salmon (Zamon 2001). In Washington State, the largest numbers of pink salmon (*Oncorhynchus gorbuscha*) return to spawning rivers in odd-numbered years, while a smaller proportion returns in even years. Diet analyses conducted on local Washington State harbour seal populations in 2005 (a pink salmon year) noted seals switching from eating mainly herring to eating pink salmon at the end of July (Lance *et al.* 2012). Moreover, during even years (e.g., 2006 and 2008), rockfish occurrence in the diets of these seals increased by ~22-fold compared to years when pink salmon were present (Ward *et al.* 2012). However, prey abundance alone is not necessarily always the main factor affecting harbour seal diet composition.

Factors other than prey abundance that influence predator foraging behaviour include prey energy density, prey handling time, availability of alternative prey, inter and intra-competition, and predation risk (Stephens & Krebs 1986; Abrams 2000; Sih & Christensen 2001; Creel & Christianson 2008). Overall, predators should minimize energy expenditure while maximizing energy intake in the goal to maximize the net energy gain when foraging (Stephens & Krebs 1986). This appears to be the case in the Puget Sound, northern Pacific coast, where harbour seals mostly fed on more energetically but less abundant juvenile Pacific herring instead of the spawning aggregation of adult Pacific herring that were numerically higher but energetically lower (Thomas *et al.* 2011).

1.2 Coho and Chinook salmon in the Salish Sea

In the Salish Sea (i.e., Puget Sound, Strait of Juan de Fuca, and Strait of Georgia), coho (*Oncorhynchus kisutch*) and Chinook (*O. tshawytscha*) salmon are economically valuable species. These two salmon species peaked in the 1970s (coho) and 1980s (Chinook), and subsequently experienced a drastic decline in abundance and productivity (Nehlsen *et al.* 1991; Beamish *et al.*

1995, 1999, 2010, 2012; Preikshot *et al.* 2013). Numerous biotic and abiotic explanations have been hypothesized to explain the declines of coho and Chinook salmon. These include loss of vital habitat (Nehlsen *et al.* 1991; Magnusson & Hilborn 2003), overfishing (Rutter 1997), interspecific competition (Ruggerone & Goetz 2004; Ruggerone & Nielsen 2004; Springer & van Vliet 2014), changes in ocean conditions (Beamish *et al.* 1995; Coronado & Hilborn 1998; Mueter *et al.* 2005) and changes in prey abundance (Beamish *et al.* 1994; Ruzicka *et al.* 2011; Mackas *et al.* 2013).

Although, factors driving coho and Chinook salmon productivity in the eastern Pacific Ocean still remain unclear, the core evidence suggests that the highest mortality occurs within the first months of marine life stages (Zimmerman *et al.* 2015). During the 1990s, commercial and recreational harvests of adult Pacific salmon, particularly coho salmon, were reduced in the Salish Sea (PSC 2013, 2014). In addition, attempts to increase coho and Chinook salmon populations were taken by releasing large numbers of hatchery-raised fish into the Salish Sea (Labelle 2009). However, reducing fishing caused mortality from the 1990s to present, and augmenting salmon production with Canadian and American hatcheries, have failed to increase numbers of returning coho and Chinook salmon. Marine survival rates of coho and Chinook salmon remain low and their recruitment is still depressed. This represents significant economic and conservation challenges (Lindley *et al.* 2009).

The failure of coho and Chinook populations to respond to reduced fishing pressure and hatchery enhancement has led to speculation that changes in early natural mortality from predators may be impeding recovery of these salmon populations (Miller *et al.* 2013). During their migration to the open ocean, coho and Chinook juveniles (i.e., smolts) face predation from a variety of fish, bird, and mammal species either in the fresh water or ocean environment (Fresh 1997). These predators of salmon smolts include Pacific herring (*Clupea pallasii*; Ito & Parker 1971), rainbow trout (*Oncorhynchus mykiss*; Fresh & Schroder 1987), adult coho and Chinook salmon (Sholes & Hallock 1979; Hargreaves 1988), walleye pollock (*Theragra chalcogramma*; Armstrong & Winslow 1968), spiny dogfish (*Squalus acanthias*; Beamish *et al.* 1992), river lamprey (*Lampetra ayresi*; Beamish & Neville 1995), common mergansers (*Mergus merganser*; Wood 1987), double crested cormorants (*Phalacrocorax auritus*; Robertson 1974), bald eagles (*Haliaeetus leucocephalus*; Angell & Balcomb III 1982), river otters (*Lutra canadensis;* Dolloff 1993), harbour seal (Olesiuk 1993), Steller sea lion (*Eumetopias jubatus*; Fiscus 1980) and harbour porpoise (*Phocoena phocoena*; Fiscus 1980).

Although, predation on out-migrating smolts by multiple predator species has been considered important sources of mortality (e.g., Evans *et al.* 2012; Sebring *et al.* 2013), harbour seals alone may be the biggest contributor to smolt predation (Riddell *et al.* 2009). In the Salish Sea, harbour seals are present year-round and are the most abundant pinniped species (Olesiuk 2010) and their relatively large body sizes imply high energy needs (Stenson *et al.* 1997; Trites *et al.* 1997). In addition, harbour seals can inflict significant damage to prey populations, and may limit recovery of declining populations (Fu *et al.* 2001; Bundy 2001; Butler *et al.* 2006; Trzcinski *et al.* 2006). Such may be the case in the Moray Firth, Scotland, where models predict that removing harbour seals from a small river during the spring when salmon are relatively small would increase overall number of Atlantic salmon (Butler *et al.* 2006).

1.3 Seal-Salmon interactions

Historically, harbour seal populations in the Salish Sea were culled from 1943 to 1960, which decreased their abundance and kept them at low numbers (Scheffer & Sperry 1931; Newby 1973). Legislation enacted in the early 1970s protected marine mammals in Canada and US, and led to an exponential recovery and stabilization of harbour seal numbers at carrying capacity in the 2000s (Jeffries *et al.* 2003; Olesiuk 2010). This recovery of the harbour seal numbers occurred concomitantly with declines of coho, Chinook, and rockfish (Palsson *et al.* 2009).

It is not clear whether harbour seals are responsible for the decline of coho and Chinook salmon, or whether their predation impedes recovery of the depressed stocks (NMFS 1997). However, the recovery of harbour seals following culling and hunting in the Salish Sea has led to speculation that predation by seals might be the main factor impeding the recovery of coho and Chinook salmon (Miller *et al.* 2013). Salmon species are one of the most important seasonal prey in harbour seal diet particularly during the fall when adults return to their natal rivers to spawn (Lance *et al.* 2012). Harbour seals are well known to consume adult and juvenile salmon (Thomas *et al.* 2016), but have not been thought to consume large amounts of juveniles. While overall predation on returning adult salmon is generally considered minimal relatively to numbers of fish, there is new evidence that high mortality of coho and Chinook smolts might be occurring during their out-migration when they leave rivers to reach the ocean (Beamish *et al.* 2010; Welch *et al.* 2011; Neville *et al.* 2015; Zimmerman *et al.* 2015).

Some studies that have quantified seal diets from scats (faeces) collected in the Salish Sea have suggested that harbour seals are capable of consuming significant percentages of salmon runs under certain conditions (Lance *et al.* 2012; Ward *et al.* 2012; Howard *et al.* 2013). One study reported that the proportion of juvenile salmonids in the diet of harbour seals in Drayton Harbor (central Salish Sea) was 17.1% in the spring, and 35% in the summer and fall (Luxa & Acevedo-Gutiérrez 2013). Other studies have observed harbour seal moving into river mouths and estuaries to take advantage of temporal pulses of adult and smolt salmon (Yurk & Trites 2000; London *et al.* 2002). Another study in the Strait of Georgia identified the remains of all 5 species of Pacific salmon in seal scats—and noted that harbour seals targeted adult salmon of lesser conservation concern during the fall (i.e., chum and pink salmon), but preferred smolt salmon of greater conservation concern during spring (i.e., coho and Chinook salmon) (Thomas *et al.* 2016). Although, coho and Chinook smolts represent only a small proportion (5.8 %) of the overall seal diet in the spring, they may represent a significant source of mortality when converted into numbers of individuals consumed (Irvine *et al.* 2009; Welch *et al.* 2011; Thomas *et al.* 2016).

1.4 Research goals

Diet composition has provided important quantitative knowledge about the role harbour seals play in the lack of recovery of coho and Chinook salmon (Lance *et al.* 2012; Ward *et al.* 2012; Thomas *et al.* 2016). However, these diet studies provide only a partial understanding of the predator-prey interactions between seals and salmon smolts. Most notably, they tell little about where, when and how harbour seal predation occurs (Yurk & Trites 2000; Berejikian *et al.* 2016), and the extent to which harbour seal predation on salmon smolts may be an opportunistic or specialist feeding behaviour that is adopted by a few or many individuals from the overall harbour seal population. Knowledge about predator-prey dynamics between harbour seals and salmons is essential for implementing effective mitigation management strategies and ultimately, promoting salmon recovery.

The overall goal of my thesis was to determine harbour seal fine-scale foraging behaviours during the out-migrations of coho and Chinook smolts in the Strait of Georgia, Canada. In particularly, I sought to track the fine-scale movements and behaviours (mainly feeding behaviour) of individual harbour seals near the Big Qualicum River where a hatchery annually releases millions of coho and Chinook salmon smolts. My thesis includes two chapters that were written as independent manuscripts in the goal to be submitted for publications in peer-reviewed journals. The overall aim of the first manuscript (Chapter 2) was to describe how feeding areas of harbour seals, at the population scale, vary in space and time according to smolt release timings. Specially, I sought to identify areas of high feeding intensity (i.e., feeding "hotspots") in order to evaluate whether or not these harbour seal feeding hotspots overlap in space and time with salmon smolt out-migrations. In contrast, the primary objective of the second manuscript (Chapter 3) was to evaluate harbour seal foraging behaviours at the individual level during the coho and Chinook smolt out-migrations, and how they vary spatially and temporally. I sought to quantify differences between individual seals in their impact on outmigrating salmon smolts. I therefore examined the differences between the foraging strategies of individuals—including differences in geographical areas, depths and times of feeding.

Overall, I sought to extend the understanding of fine-scale foraging behaviour of harbour seals in relation to pulses of prey abundance. Combining detailed knowledge of feeding behaviour with existing diet information contributes to understanding the extent to which seals are impacting salmon, as well as science-based evidence needed to design effective mitigation strategies that might enhance coho and Chinook populations in the Salish Sea.

Chapter 2: Harbour seal foraging hotspots during out-migrations of coho and Chinook salmon smolts

2.1 Summary

There is increasing evidence that predation by harbour seal (*Phoca vitulina*) on young salmon (smolts) out-migrating from rivers may be a significant source of mortality for coho (*Oncorhynchus kisutch*) and Chinook (*O. tshawytscha*) salmon populations in British Columbia. Studies supporting this have focused on documenting what and how much harbour seals eat—and the potential impact this has on salmon populations. However, little attention has been given to understanding where, when and how this predation occurs, and the extent to which it might be opportunistic or specialist feeding behaviour by a few or many individuals. We documented and assessed the temporal and spatial foraging behaviour of seals during the out-migration of smolts in the Salish Sea by capturing and equipping 17 harbour seals with GPS loggers and Daily Diary tags—and tracking them before and after the release of thousands of coho and Chinook smolts from the Big Qualicum Hatchery. Reconstructing the high-resolution movements of the seals using GPS locations combined with dead reckoning tracks—and quantifying feeding using counts of prey chasing events (PCE) detected by accelerometry—revealed that the Big Qualicum estuary was a feeding hotspot for 47.0% of the 17 tracked seals. This estuary hotspot was relatively small (accounting for 3% of PCEs) compared to the largest feeding area outside the estuary (26% of PCE), suggesting that only a small portion of the seal population capitalizes on the arrival of the small salmonids into the Salish Sea. We detected a notable change in foraging behaviour of harbour seals that corresponded to the pulse of coho smolts flowing into the estuary, but found no change in feeding intensity of seals in response to the pulse of out-migrating Chinook. Our data indicate that a small number of seals were specialized in consuming smolts, but that these individuals did not appear to target the smaller Chinook smolts. Such information concerning the fine-scale foraging behaviour of harbour seals in relation to pulses of out-migrating smolts can be used to design mitigation strategies to enhance coho populations.

2.2 Introduction

Two economically valuable species of salmon—coho (*Oncorhynchus kisutch*) and Chinook (*O. tshawytscha)*—have declined to critically low numbers in the Salish Sea, i.e., Puget

Sound, Strait of Juan de Fuca, and Strait of Georgia (Nehlsen *et al.* 1991; Beamish *et al.* 1995, 1999, 2010, 2012; Preikshot *et al.* 2013). Different biotic and abiotic explanations have been proposed to explain their declines, such as overfishing (Rutter 1997), loss of vital habitat (Nehlsen *et al.* 1991; Magnusson & Hilborn 2003), interspecific competition (Ruggerone & Goetz 2004; Ruggerone & Nielsen 2004; Springer & van Vliet 2014), changes in ocean conditions (Beamish *et al.* 1995; Coronado & Hilborn 1998; Mueter *et al.* 2005) and changes in prey composition and availability (Beamish *et al.* 1994; Ruzicka *et al.* 2011; Mackas *et al.* 2013). However, none of these possible explanations are supported by data. Attempts to increase coho and Chinook by releasing large numbers of hatchery-raised fish—and reducing commercial and recreational exploitation rates—have been unsuccessful. Both species of salmon have remained at low levels and continue to present significant economic and conservation challenges (Lindley *et al.* 2009).

The recovery of harbour seals (*Phoca vitulina*) following culling and hunting in British Columbia has led to speculation that it might be predation by seals that is impeding the recovery of coho and Chinook salmon (Miller *et al.* 2013). Harbour seals are known to consume both adult and juvenile (smolt) salmon, but have generally not been thought to consume large amounts of them. While predation on returning adult salmon is generally considered low relative to numbers of returning fish, there is evidence that high mortality of coho and Chinook salmon is occurring in the early marine stage (i.e., smolt stage) as the fish move downstream and enter the ocean (Beamish *et al.* 2010; Welch *et al.* 2011; Neville *et al.* 2015; Zimmerman *et al.* 2015).

The exponential increase in harbour seal populations in the Strait of Georgia correlates with the decline in numbers and poor marine survival rates of coho and Chinook salmon (Olesiuk 2010). Harbour seals are the most abundant and the only year-round resident pinniped in the Strait of Georgia (Olesiuk 2010). They are considered generalist predators that feed on a variety of fish and cephalopod species, but show preferences for Pacific herring (*Clupea pallasii*), walleye pollock (*Gadus chalcogrammus*), Pacific hake (*Merluccius productus*) and salmonid spp. (Scheffer & Sperry 1931; Tollit *et al.* 1997; Lance *et al.* 2012). Harbour seals are also considered opportunistic predators that vary their diet seasonally and annually according to locally abundant prey (Middlemas *et al.* 2006; Lance & Jeffries 2007; Thomas *et al.* 2011).

In the Strait of Georgia, the scats (faeces) of harbour seals contain the remains of many prey species—including juvenile coho, Chinook, and sockeye (*O. nerka*) salmon during spring when smolts are out-migrating (Thomas *et al.* 2016). The seals appear to preferentially target these three species of salmon over the smaller-bodied chum (*O. keta*) and pink (*O. gorbuscha*) salmon smolts (Thomas *et al.* 2016). Although the consumed juvenile salmon species appear as small percentages in the overall harbour seal diet, they may in fact represent a significant source of mortality on salmon populations when converted into numbers of individual salmon consumed—particularly for coho and Chinook salmon that are of conservation concern (Irvine *et al.* 2009; Welch *et al.* 2011; Thomas *et al.* 2016)

The majority of studies to date on predation by seals on salmon smolts have focused on documenting what harbour seals eat and the potential impact this has on salmon populations (Lance *et al.* 2012; Ward *et al.* 2012; Thomas *et al.* 2016). However, relatively little attention has been given to understanding where, when and how this predation occurs (Yurk & Trites 2000; Berejikian *et al.* 2016), and the extent to which it might be opportunistic or specialist feeding behaviour by a few or many individuals. Documenting and assessing the temporal and spatial foraging behaviour of seals during the smolt migration is needed to fully understand the predator-prey dynamics, and guide the development of adequate conservation actions that may be necessary to enhance salmon numbers (Lima 2002; Caro 2007).

The objectives of our study were to 1) track and document the fine-scale movement of harbour seals in the Strait of Georgia, 2) map their feeding distribution in space and time during the out-migration of coho and Chinook smolts, and 3) identify areas of high feeding intensity (i.e., feeding "hotspots"). We expected harbour seals to concentrate their feeding effort in the river mouth and estuary where smolts are in denser schools and spatially restrained, and more vulnerable to predation compared to open waters (Yurk & Trites 2000). We therefore captured and equipped 17 harbour seals from the surrounding area with GPS and biologging tags, and tracked them before and after the release of thousands of coho and Chinook smolts from the Big Qualicum Hatchery. We were thereby able to identify feeding events from changes in body acceleration relative to the presence of salmon smolts and identify high feeding intensity areas. Such information is needed to assess ways which predation by seals on salmon smolts might be mitigated.

2.3 Material and Methods

2.3.1 Study location

The study was conducted in the Big Qualicum area (49° 26' 58" N, 124° 31' 43" W) located on the western side of the Strait of Georgia, on Vancouver Island, British Columbia, Canada (Figure 2.1). This area is surrounded by Denman, Hornby, Texada and Lasqueti Islands—and is home to pinniped (e.g., Steller and California sea lions and harbour seals) and seabird colonies. It is an ecologically important marine habitat (e.g., Pacific herring spawning areas, and nursery for juvenile fish).

The Big Qualicum River flows into our study area and is an important spawning river for chinook, coho, pink, chum, and steelhead (*O. mykiss*) salmon. In addition to wild Pacific salmon populations, the Big Qualicum Hatchery artificially enhances the coho and Chinook salmon stocks in the river to increase recreational and commercial fishing opportunities (Cross *et al.* 1991). The different species and breeding sites result in different marine habitats in the vicinity of the Big Qualicum River being important salmon migration routes in the spring when smolts leave the river to reach the ocean — or in the fall when adults return to their natal river to spawn and die. In the spring of 2015 when we conducted our study, the Big Qualicum Hatchery released approximately ~350,000 coho smolts on May 4th and ~3 million Chinook smolts on May 14th.

A number of harbour seal haul-out sites surround the Big Qualicum area. These include Norris Rocks, Flora Islet, Seal bay, Sisters Islets, Fegen Islets and Jenkins Island, which are less than 30 km distance from where smolts leave the Big Qualicum River and enter the estuary (49° 23' 55.7" N, 124° 36' 33.1" W). All of these sites are within foraging distance of the River mouth (Hardee 2008; Peterson *et al.* 2012). These haul-out sites are estimated to be used by over 1000 harbour seals (Olesiuk 2010).

2.3.2 Ethics statement

The UBC Animal Care Committee (permit # A14-0322) and Fisheries and Oceans Canada (permit # XMM 2 2015) approved all scientific procedures applied to the harbour seals. All animals used in this study were handled and cared for according to their guidelines and recommendations. Animal handling time for instrument deployment was less than 60 minutes.

2.3.3 *Device deployment and data collection*

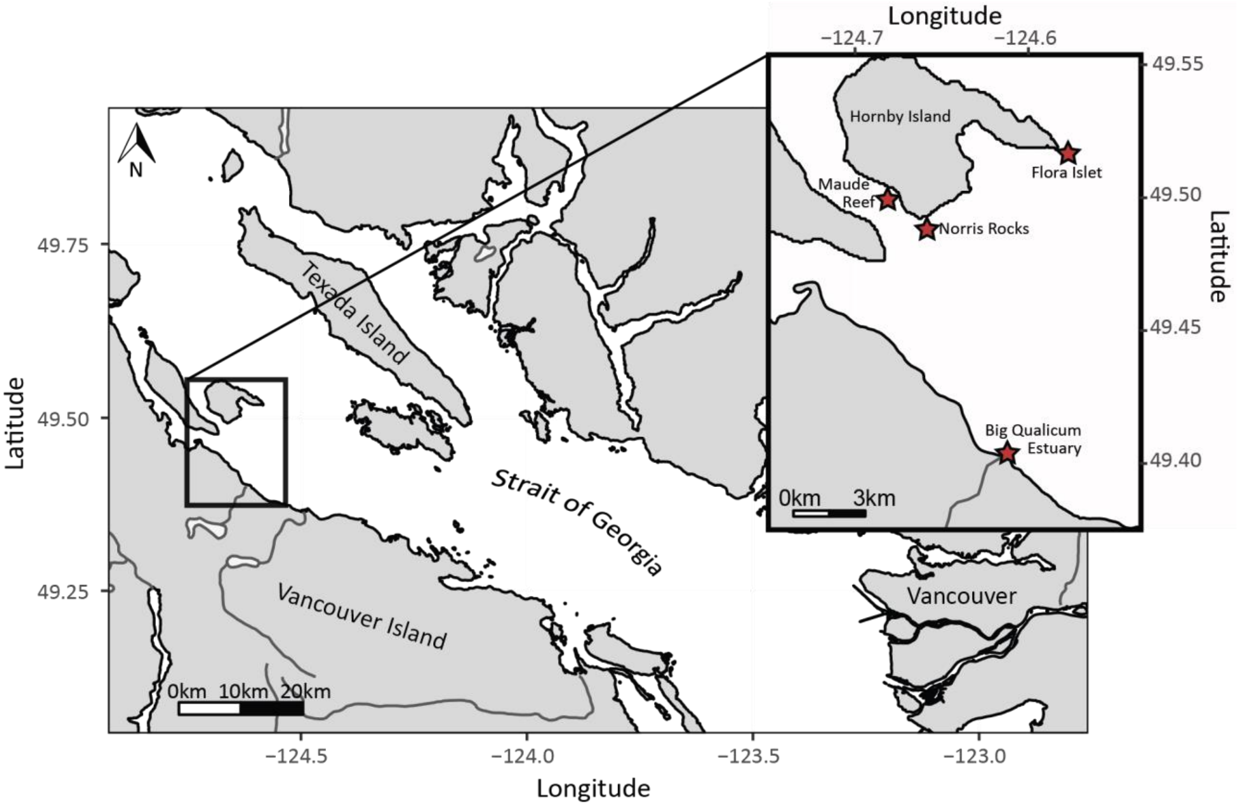

Figure 2.1: Map of the site locations where 20 harbour seals were captured in the Strait of Georgia, British Columbia, Canada. Big Qualicum Estuary (49°23'57''N, 124°36'31''W; n=9), Norris Rocks (49°23'57"N, 124°36'31"W; n=9), Maude Reef (49°29'57"N, 124°41'03"W; n=1), and Flora Islet (49°30'48"N, 124°34'12"W; n=1).

We captured 20 harbour seals in the Big Qualicum area from April 21st and May 1st 2015, using either a specialized beach seine (Jeffries *et al.* 1993) or a low-tech "boat rush" method at 4 locations (Figure 2.1): Big Qualicum Estuary (49°23'57"N, 124°36'31"W; n=9), Norris Rocks (49°23'57"N, 124°36'31"W; n=9), Maude Reef (49°29'57"N, 124°41'03"W; n=1), and Flora Islet (49°30'48"N, 124°34'12"W; n=1). All seals were individually transported in hoop nets and carried to a restraining board where they were sedated with an intramuscular injection of 0.1-0.2 mg/kg of butorphanol and then weighed (±0.2 kg) and measured (to the nearest 0.5 cm). Seals that weighed > 60 kg were equipped with a floating biologger package to their dorsal midline between shoulders using a quick-drying epoxy glue. The biologger packages included a Global Positioning System (GPS) satellite tag (Splash 10-F; Wildlife Computers, Redmond, WA, USA), a Daily Diary tag (Wildlife Computers, Redmond, WA, USA), a Very High Frequency (VHF) transmitter (MM190B; Advanced Telemetry Systems, Isanti, MN, USA), and a floating device (Figure A-1).

The Daily Diary tags were set to sample and archive depth and external temperature at 1 Hz, earth's magnetic field at 8 Hz and acceleration at 16 Hz. The GPS satellite tags were set to sample and archive Fastloc-GPS snapshots (Dujon *et al.* 2014) every 20 min when at the surface in May and June 2015, and then transmit them through satellite when seals are hauling out in July and August 2015. We recovered the biologger packages when they fell off the seals during the moulting season from August 17th to October 15th, 2015. During this time, we monitored harbour seal large-scale movements using Argos and GPS locations transmitted by satellite, and then used VHF radio signal to retrieve the biologger packages that were floating at the water surface, due to a floating device, or had washed ashore.

2.3.4 Track reconstruction

We divided each seal's time series into either "haul-out" (i.e., resting on land) or "at-sea" state using the wet-dry sensor on the Daily Diary tag. The haul-out state started when the tag was dry for at least 10 min and ended up when the tag was wet for more than 40 sec (Russell *et al.* 2015). The seals were considered in the at-sea state the rest of the time. Some of the Daily Diary tags failed to record data for brief time intervals (<1 min), which we decided to ignore in our analysis as we believed such small gaps would not significantly affect the track reconstruction (Battaile *et al.* 2015).

The seals were equipped with a Fastloc-GPS which provides highly resolution locations even during short surface intervals (Costa *et al.* 2011). However, it has been shown that the accuracy of Fastloc-GPS locations could vary as a function of the number of available satellites (Dujon *et al.* 2014). We, therefore, applied the method outlined in Austin *et al.* (2003) using the function `austFilter` from the `diveMove` R package (Luque 2007) to filter GPS locations. We used a traveling speed threshold of 2.78 m/s (Williams & Kooyman 1985; Thompson & Miller 1990; Lesage *et al.* 1999), and a distance threshold of 160 km. We also conducted a final visual inspection and removed all GPS locations on land.

We used the "dead reckoning" method to reconstruct the seal pseudo-tracks between each two consecutive GPS locations (Wilson *et al.* 2007; Battaile *et al.* 2015). We ran the dead reckoning pseudo-tracks using the function `DeadReckoning` from the R package `TrackReconstruction` (Battaile 2014)—and extracted the inclination and declination of the earth's magnetic field for May 15th 2015 and the latitude and the longitude of approximately the center of the Strait of Georgia (49°24’00.0’’N 124°06’00.0’’W) using the World Magnetic Model 2010 Calculator from the British Geological Survey (http://www.geomag.bgs.ac.uk/data_service/models_compass/wmm_calc.html). We also used a 3 sec running mean window to extract the static acceleration (i.e., the earth’s gravitational field) from the three separate acceleration sensors. We then estimated the dynamic acceleration due to animal movement by subtracting the static acceleration from the total acceleration (Shepard *et al.* 2008). The running sum of this dynamic acceleration was used to estimate swimming speed of each animal. We used 2.78 m/s for the maximum speed of adult harbour seals (Lesage *et al.* 1999).

The raw dead reckoning tracks were generated giving the magnetometer resolution (i.e., 8 Hz), and then rescaled to each minute in order to maximize computational speed. We georeferenced the raw dead reckoning tracks by forcing them through GPS locations using the function `GeoRef` (Battaile 2014) which uses the conventional bias correction equation from Wilson *et al.* (2007):

$$\hat{\eta}_t = x_t + \frac{y_T - x_T}{T-1}(t-1) \qquad \text{Eq. 2.1}$$

where $\hat{\eta}_t$ is the corrected path in one dimension (i.e., Easting or Northing) at time $t = 1,2,\ldots,T$ between two GPS locations, x_t is the dead reckoning coordinate at time $t = 1,2,\ldots,T$ and y_T the GPS location at time T. In this equation, we assumed that $x_1 = y_1 = 0$. When georeferencing the dead reckoning tracks, we projected GPS locations from longitude and latitude to Easting and Northing in kilometers (km). While the seals were hauling-out (i.e., on land), we set their speed to zero and their position to the GPS location recorded during that haul-out time interval. Georeferencing allows to correct for error in the dead reckoning tracks which tends to grow with time, especially in aquatic environments, because each dead reckoning location depends on the previous one. Error in dead reckoning tracks could be due to many factors including accumulation of sensor errors, water currents, the animal buoyancy, the animal speed estimation (Bidder *et al.* 2012) and the violation of the assumption that the animal is only moving forwards in the caudo-rostral direction (Johnson *et al.* 2009). The Fastloc-GPS tags were programmed to record locations every 20 min (72 locations/day), but varied between seals and over time with an average of one location every 62.7±141.1 min.

Based on visual examination of the reconstructed pseudo-tracks, we noticed that there were not enough GPS locations to properly correct for the error induced by the dead reckoning, especially for pseudo-tracks that lasted more than an hour. We observed multiple pseudo-tracks crossing the land, so we applied an additional custom correction algorithm to the georeferenced tracks based on the spatial constraints of the seal movements. This correction algorithm was run in two steps. First, multiple pseudo-tracks were generated between each pair of GPS locations based on the original shape of georeferenced pseudo-track in Eq. 2.1. To do so, we added an extra parameter α into Eq. 2.1:

$$\hat{\eta}_t' = \alpha x_t + \frac{y_T - \alpha x_T}{T-1}(t-1) \qquad \text{Eq. 2.2}$$

where the parameter α proportionally modifies the original georeferenced track between two GPS locations while preserving its global movement shape. When $\alpha = 1$, $\hat{\eta}_t' = \hat{\eta}_t$, and hence the new pseudotrack is exactly the same than the original georeferenced pseudo-track. When $\alpha = 0$, $\hat{\eta}_t'$ is a straight line between the two GPS locations (i.e., y_1 and y_T). We generated 21 pseudotracks for each interval between two GPS locations with an α that ranged from -1 to 1 with a step of 0.1.

The second part of our correction algorithm selected the most likely pseudo-track between two GPS locations. To do so, we conducted a step-wise filtering process. First, we removed all pseudo-tracks where the seals exceeded the maximum speed of 2.78 m/s (Lesage *et al.* 1999). Second, we selected the tracks that minimized the error due to the pseudo-track passage on land while the seals were diving.

To quantify the pseudo-track error on land, we used the root-mean-squared error (RMSE):

$$RMSE_{on\ land} = \sqrt{\frac{\sum_{t=1}^{T} {\varepsilon_t}^2}{T}} \qquad \varepsilon_t = \begin{cases} at\ sea & , \quad 0 \\ on\ land & , \quad d_t \end{cases} \qquad \text{Eq. 2.3}$$

where ε_t is the error difference at time t between the seal diving depth and the surface (i.e., at 0 depth) when the estimated seal location is on land, d_t is the seal diving depth at time t, and T is the number of time steps between the two GPS locations. Finally, we selected the pseudotracks that minimized the error due to the seal diving below the bathymetry depth:

$$RMSE_{at\ sea} = \sqrt{\frac{\sum_{t=1}^{T} {\delta_t}^2}{T}} \qquad \delta_t = \begin{cases} b_t - d_t \geq 0, & 0 \\ else & , \quad d_t - b_t \end{cases} \qquad \text{Eq. 2.4}$$

where δ_t is the error difference at time t between the seal diving depth and the bathymetry depth, d_t is the seal diving depth at time t, b_t is the bathymetry value at time t and T is the number of time steps between the two GPS locations. If at this stage more than one pseudotrack remained, the pseudotrack with the closest α parameter to 1 (i.e., to the original georeferenced pseudotrack) was selected. The bathymetry data of the Strait of Georgia had a resolution of 3 arc-seconds, and was obtained from the National Oceanic and Atmospheric Administration (NOAA; https://data.noaa.gov/dataset/british-columbia-3-arc-second-bathymetric-digital-elevation-model).

2.3.5 Prey chasing events (PCE)

To quantify feeding events, which we used as a foraging proxy, we used Prey Chasing Events (PCE) by isolating bouts of high body accelerations while diving, similarly to the Prey Capture Attempts (PrCA) method which uses head or jaw acceleration data (Viviant *et al.* 2010; Iwata *et al.* 2012; Jouma'a *et al.* 2015; Volpov *et al.* 2015). Some unpublished results for Antarctic fur seals and southern elephant seals suggest that bouts of high body accelerations (i.e., the accelerometer is attached to the animal back) slightly overestimate total detection of PrCA compared to head accelerations (T. Jeanniard du Dot & C. Guinet, pers. comm.)

We first extracted the three axes (i.e., heave, surge and sway) of the dynamic acceleration (i.e., animal movement) by subtracting the static acceleration (i.e., gravity) from the total acceleration ($m.s^{-2}$, at 16 Hz). A rolling mean with a 2 sec window was applied on the total acceleration data to calculate the static acceleration. We then smoothed the three dynamic accelerations using a rolling variance with a 2 sec window and summed them to summarize the animal movement intensity in one value. Finally, we performed a two-mean clustering on the resulting data to separate the data into low and high intensity variance. We considered occurrence of PCE when the cluster analysis indicated the higher mean cluster. We combined PCEs that were separated by < 1 sec time interval—and recorded the date, time, depth and location at which each PCE occurred. To minimize PCE false positive detections (e.g., a PCE that is not related to feeding behaviour such as social behaviour), we excluded all PCEs when 1) the Daily Diary tag was in a "dry" state, 2) the depth was 0 (i.e., surface), 3) the seal was hauled-out, or 4) 10 min before and after the seal was in a "haul-out" state.

Depth sensors commonly drift over time (Hull 2000; Laidre *et al.* 2002; Spence-Bailey *et al.* 2007). We, therefore, applied a zero-offset correction using the software provided by the manufacturer (Wildlife Computers Inc., Redmond, WA). We specified an hour for the maximum dive duration and 0.5 m for allowable surface error. We also applied a 5 sec rolling median on the corrected depth data to remove quick spikes due to Argos transmission.

2.3.6 *Seal feeding intensity*

We considered the number of PCE as a proxy to quantify feeding intensity. We conducted a kernel density analysis on the locations of the PCE to highlight geographical regions of increasing feeding intensity. We used the R package `ks` (Duong 2007) to estimate the kernel density distribution for which we used an unconstrained bandwidth matrix (Wand & Jones 1993) and a smoothed cross-validation bandwidth selector (Hall *et al.* 1992) as recommended by Duong (2007). We also considered feeding hotspots as areas encompassing the top 30% of the kernel density estimate. Information for each hotspot was summarized including the location of the polygon centroid, the area, the number of seals that foraged in it, the number of PCE detected in it and the depth distribution of the PCEs.

We also calculated the daily number of PCE detected in the Big Qualicum estuary as well as the number of seals that conducted these PCE. The Big Qualicum estuary was delimited as the area within 500 m distance from the middle point of the estuary (9°23'55.7"N, 124°36'33.1"W). Our delimitation of the estuary included an intermediate zone that rapidly increased in depth as you move towards the open water (>100 m depth). Since we detected some PCE at deep depths (>100 m), we kept only the ones that occurred before 15 m depth given that smolts are more likely to swim close to the surface (Weitkamp & Neely 2002).

2.4 Results

2.4.1 *Telemetry performance and general spatial distribution*

Of the 20 harbour seals captured in the Big Qualicum area from April 21st and May 1st 2015, 15 were males and 5 were females (Figure 2.1). The seals weighed an average of 91.7 ± 13.9 kg and were 155.3 ± 9.5 cm long (Table 2.1). Although we were able to recover GPS locations for all 20 equipped seals either from satellite transmission or from the device itself, we recovered full data for only 17 of the 20 seals due to equipment failure or tag loss. Recording periods of the Daily Diary tags (48.2 ± 2.8 days) varied between devices due to variation in capture dates and battery lifespans (Table 2.1). To remove potential bias due to the Daily Diary tag recording variability in

Table 2.1: Morphometric measurements, and sites and dates of capture of 15 male (M) and 5 female (F) harbour seals in the Strait of Georgia, British Columbia. Capture sites include Big Qualicum Estuary (BQE; 49°23'57''N, 124°36'31''W) Norris Rocks (NR; 49°23'57"N, 124°36'31"W), Maude Reef (MR; 49°29'57"N, 124°41'03"W) and Flora Islet (FI; 49°30'48"N, 124°34'12"W). Daily Diary tags duration is the number of days the Daily Diary tags collected data following the date each seal was captured.

Seal ID	Mass (kg)	Length (cm)	Sex	Capture Site	Capture Date	Daily Diary tag duration (d)	# GPS/day	# PCE/day
1	91	165	M	BQE	21-Apr-2015	43.2	3.7	334.3
2	75.5	148	M	BQE	21-Apr-2015	51.8	27.7	82.7
3	78.5	142	F	BQE	22-Apr-2015	46	38.4	31.1
4	81.5	162	M	NR	22-Apr-2015	51.2	20.8	224
5	93	163	M	NR	22-Apr-2015	-	13	-
6	103	164	M	NR	22-Apr-2015	46.1	28.9	156.2
7	110	168	M	FI	01-May-2015	-	17.4	-
8	117.5	168	M	NR	22-Apr-2015	-	32.2	-
9	89.5	136	F	NR	27-Apr-2015	46.3	26.9	82.6
10	73	144	M	NR	27-Apr-2015	49	19	152.6
11	107	159	M	BQE	28-Apr-2015	51	25.3	68.8
12	66	148	M	BQE	28-Apr-2015	46.8	10.1	165.1
13	76.5	164	M	BQE	28-Apr-2015	47.5	14.8	62.3
14	85.5	158	M	NR	29-Apr-2015	52.3	22.7	403.3
15	93	154	F	MR	29-Apr-2015	52.2	27.8	145
16	100	158	M	BQE	29-Apr-2015	51.9	25.2	34.7
17	94.5	149	M	BQE	29-Apr-2015	46	18.7	84.4
18	88.5	142	F	NR	30-Apr-2015	45.7	34.2	201
19	102	154	F	NR	30-Apr-2015	46.8	30.8	9.6
20	109	161	M	BQE	01-May-2015	46	16.5	162.9
Mean	91.7	155	-	-	-	48.2	22.7	141.2
SD	13.6	9	-	-	-	2.8	8.5	102.9

time, we limited all our analyses between May 2nd and June 2nd (i.e., for 32 days) during which we had complete data for all 17 seals.

During the study period, we collected an average of 726.6 ± 270.9 GPS locations per seal, which corresponds to 22.7 ± 8.5 GPS locations per day. The majority of the harbour seals (n=16) stayed in the Big Qualicum area within ~70 km distance from where we captured them. Four harbour seals (20%) travelled long distances (i.e., > 70 km from their respective capture sites) and visited other areas in the Strait of Georgia such as Powell River, Malaspina Strait, Howe Sound, Gabriola Island and Indian Arm (Figure 2.2).

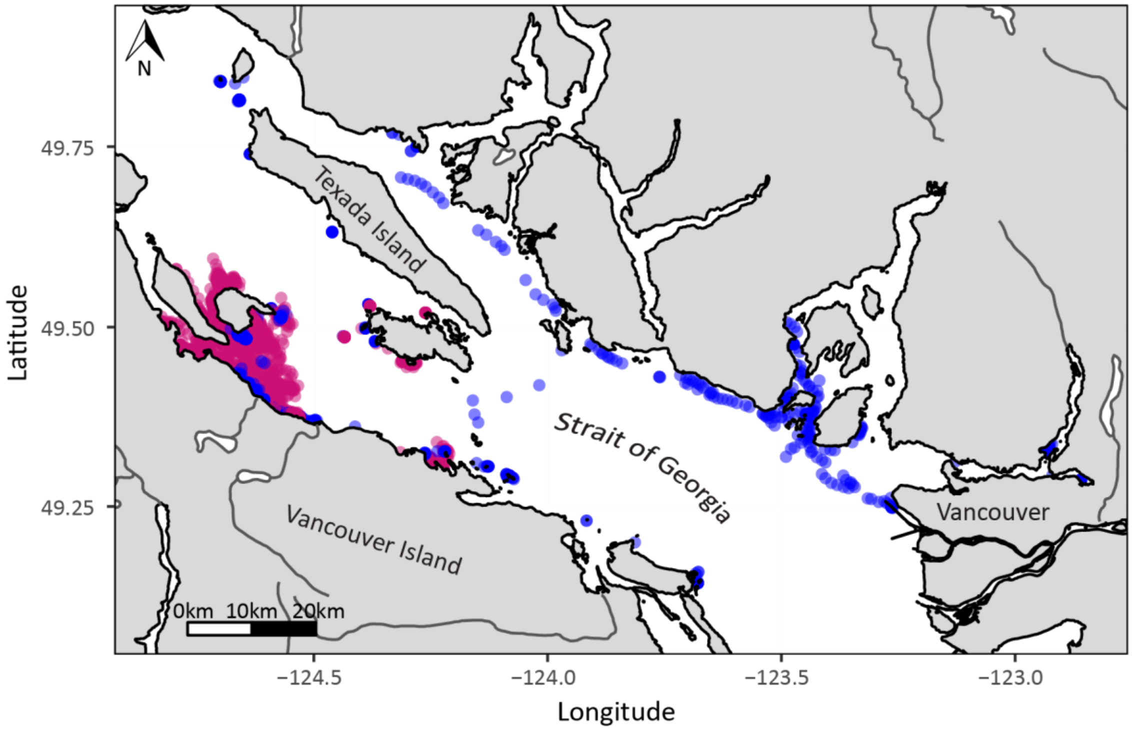

Figure 2.2: All GPS locations of all 20 harbour seals from May 2nd to June 2nd, 2015 in the Strait of Georgia, Canada. Pink dots are locations of the seals (n=16) that stayed within 70 km of their capture site and the blue dots are the locations of the ones (n=4) that travelled over 70 km from their initial capture site.

2.4.2 Total feeding intensity

Based on body accelerations, harbour seals made an average of 141.2 ± 102.9 prey chasing events (PCE) per day (Table 2.1) during the study period (from May 2nd to June 2nd). The kernel density analysis applied on the PCE locations revealed discreet patches of increasing feeding intensity within the Strait of Georgia (Figure 2.3A). Most of the feeding was located in the Big Qualicum area mainly around Hornby Island, in the Big Qualicum estuary and in the open water between them (Figure 2.3B). Additional high feeding patches were also located in other areas such as Parksville, Howe Sound and Deep Cove (Figure 2.3A).

Feeding hotspots (i.e., areas encompassing the top 30% of the kernel density estimate) occurred in three distinct patches. The first and largest feeding hotspot represented an area of 87% (4.82 km^2) of total hotspot sizes, and was located around Norris Rocks (Figure 2.3B) where there were 19328 (26%) PCEs by 11 (64.7%) distinct harbour seals (Table 2.2). These occurred throughout the water column (0-241.5 m), but were mainly between ~0-30 m and ~120-170 m (Figure 2.4). The second feeding hotspot (0.45 km^2; 8%) was located in the Big Qualicum estuary

(Figure 2.3Figure 2.3B) and included 2045 (3%) PCE by 8 (47.0%) harbour seals (Table 2.2). These PCEs ranged from the surface to 141.5 m depth but occurred primarily within the first 5 m depth (Figure 2.4). Finally, the last feeding hotspot (0.25 km^2; 4.5%) were located in the Deep Cove area (Figure 2.3C) and included 1142 (2%) PCE from 1 (5.9%) harbour seal (Table 2.2). PCEs in Deep Cove hotspot ranged from near the surface to 83 m depth, and were highly concentrated close to the surface and between 40 and 60 m depth (Figure 2.4).

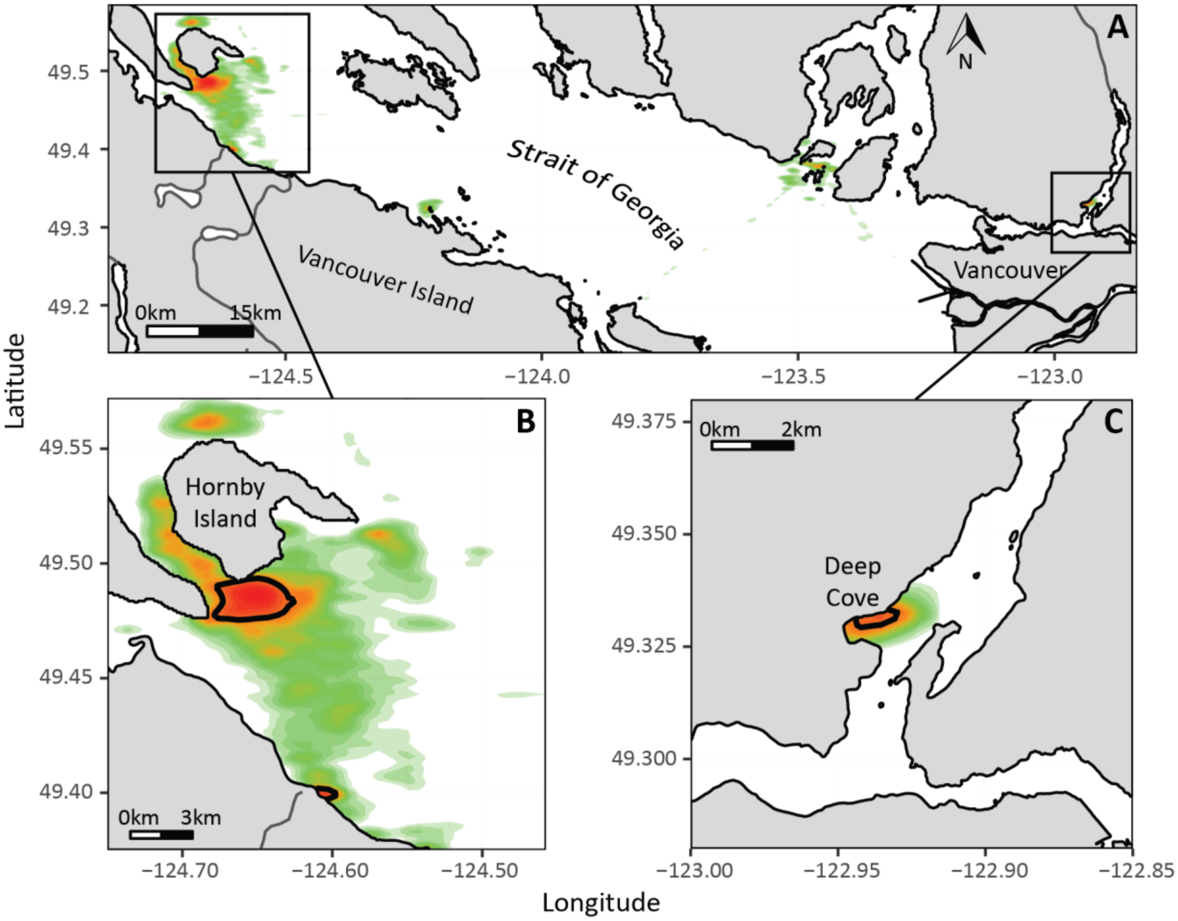

Figure 2.3: Feeding intensity maps of 17 harbour seals determined by a kernel density analysis on all prey chasing event (PCE) locations from May 2nd to June 2nd 2015 (A, B and C), and feeding hotspots (polygons with a black contour) encompassing the top 30% of the kernel density estimate (B and C). Colour scale range from green (low feeding intensity) to red (high feeding intensity). Locations shown include (A) the central part of the Strait of Georgia, (B) Big Qualicum area (blue square in A), and (C) Deep Cove (red square in A).

Table 2.2: Locations and sizes (km^2) of three feeding hotspots corresponding to the top 30% of kernel density distributions of prey chasing event (PCE) locations of 17 seals from May 2nd to June 2nd 2015. Also shown are the number of seals that fed inside each feeding hotspot (# seals), the numbers of prey chasing events (# PCE) and mean depths of their occurrence ± sd and maximum depth (PCE depth).

Hotspot	Location (long, lat)	Area (km^2)	# seal	# PCE	PCE depth (m)
Norris Rocks	49°29'05.5"N 124°39'11.5"W	4.82 (87.5%)	11 (65%)	19328 (26%)	54.5 ± 57.3 (max 241.5)
Big Q estuary	49°24'00.2"N 124°36'24.1"W	0.45 (8%)	8 (47%)	2045 (3%)	14.5 ± 38.5 (max 141.5)
Deep Cove	49°19'52.7"N 122°56'17.2"W	0.25 (4.5%)	1 (6%)	1142 (2%)	28.1 ± 18.7 (max 83.0)

2.4.3 Spatiotemporal variation in feeding intensity

A kernel density analysis of PCE locations over time during the study period revealed the temporal variation in harbour seal spatial feeding intensity synchronously to the release of coho (May 4th) and Chinook (May 14th) smolts by the Big Qualicum Hatchery (Figure 2.5). Overall, a feeding hotspot was detected around Norris Rocks during every time period. A feeding hotspot was detected in the Big Qualicum estuary during the 5 days after the release of coho smolts (May 5th to 9th; Figure 2.5). However, for the rest of the time (May 10th to June 2nd), the hotspot in the Big Qualicum estuary was no longer detected, and the associated feeding intensity decreased gradually over time (Figure 2.5). Feeding intensity in the open water between Norris Rocks and Big Qualicum estuary, and around Flora Islet was at its lowest after the release of coho smolts and then increased over time (Figure 2.5). During the last 2 time periods (May 25th to June 2nd), a feeding hotspot was detected on the northern side of Hornby Island where no feeding seemed to occur before (Figure 2.5).

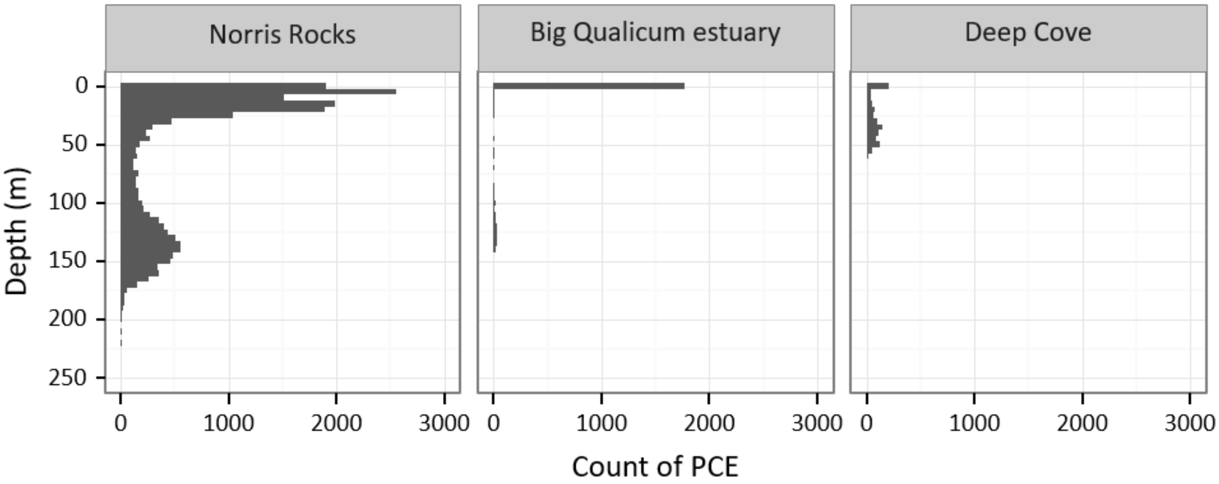

Figure 2.4: Depth distribution of all prey chasing events (PCE) by harbour seals inside three feeding hotspots (Norris Rocks, Big Qualicum estuary, and Deep Cove).

The count of the PCE detected every day in the Big Qualicum estuary indicated a large increase just after the release of coho smolts on May 5th that lasted for 4 days and then gradually decreased (Figure 2.6A). A second increase in PCE counts was also observed on May 14th in concert with the release of the chinook smolts. However, the second PCE count augmentation was smaller than the first peak by about half of its amplitude. Moreover, the second peak displayed more variance in the number of PCE between days. The daily count of seals feeding in the Big Qualicum estuary increased after the release of coho smolts from 1-2 seals to 3-5 seals and fluctuated between days until it decreased at the end of the month (~May 31st). The number of seals feeding in the estuary does not seem to vary between the coho and Chinook post-release periods (Figure 2.6B).

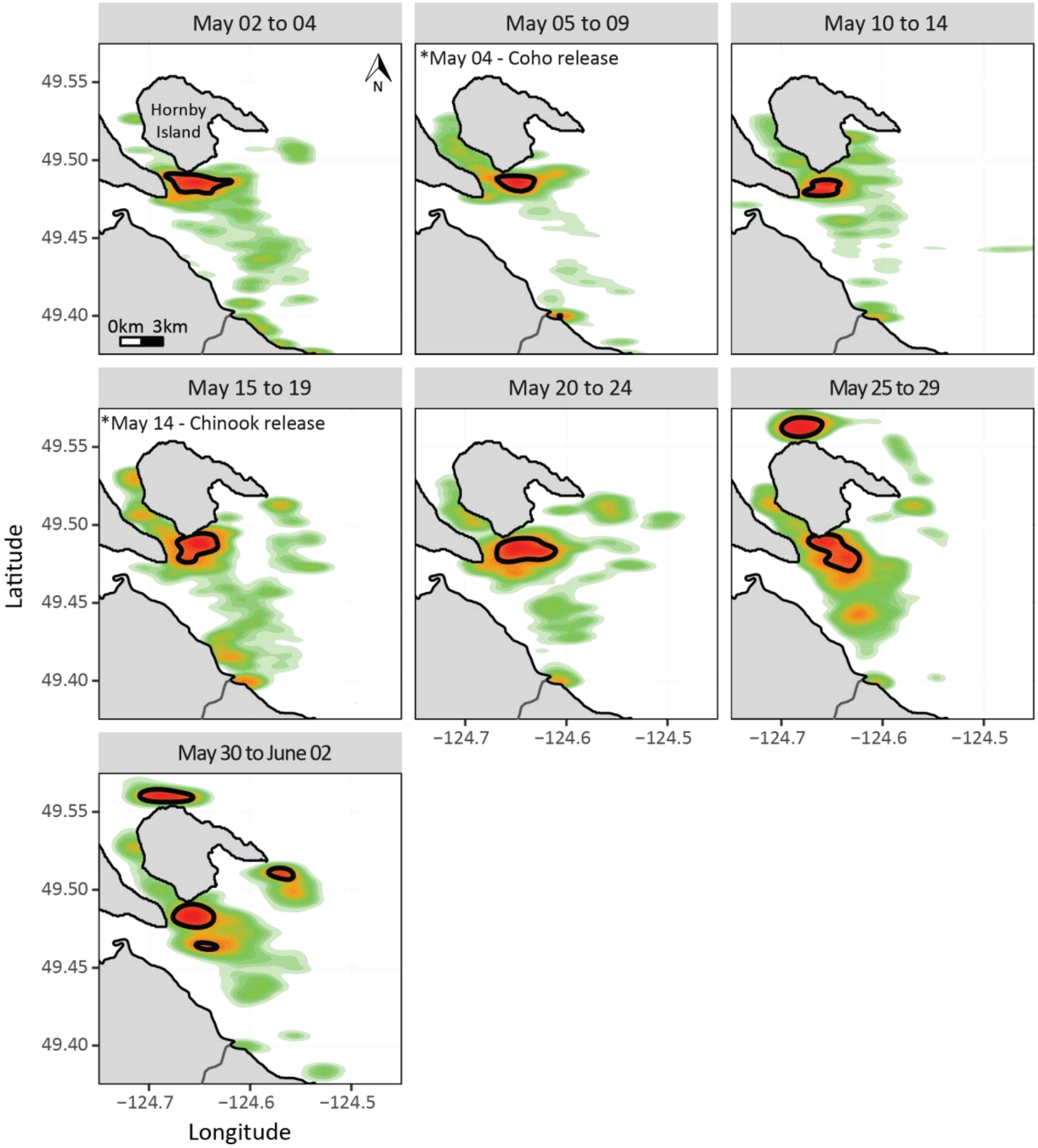

Figure 2.5: Relative feeding densities of harbour seals in the Big Qualicum area determined from a kernel density analysis on all prey chasing event (PCE) locations over the study period (May 2nd to June 2nd) during which coho (May 4th 2015) and Chinook (May 14th 2015) smolts were released from the Big Qualicum Hatchery. Colour scale range from green (low feeding intensity) to red (high feeding intensity). Feeding hotspots (i.e. areas encompassing the top 30% of the kernel density estimate) are represented by polygons with a black contour.

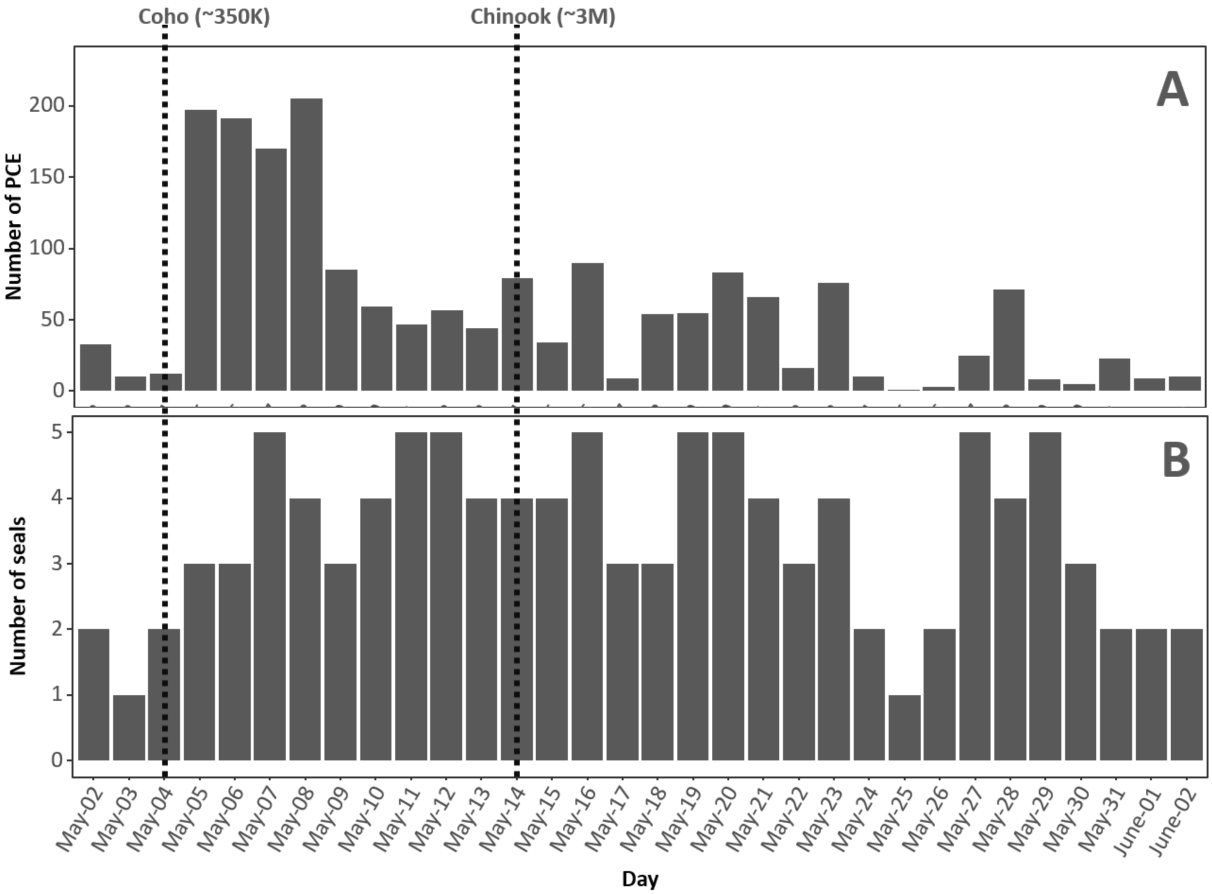

Figure 2.6: Daily (A) number of prey chasing events (PCE) and (B) number of tracked harbour seals occurring in the Big Qualicum estuary from May 2nd to June 2nd 2015. Note that the Big Qualicum Hatchery released ~350,000 coho smolts on May 4th and ~3 million Chinook smolts on May 14th.

2.5 Discussion

We collected data from 20 harbour seals and used fine-scale track reconstructions paired with body acceleration (as a proxy for feeding) to identify areas with high feeding intensities during the migrations of hatchery-reared coho and Chinook salmon smolts from the Big Qualicum River in the Strait of Georgia. We found that the majority of the tracked seals (80%) made short foraging trips (<50 km) around their main haul-out sites and stayed within the Big Qualicum area from May 2nd to June 2nd —while a smaller proportion (20%) of seals travelled long distances (>100 km) and used multiple haul-out sites located at different areas (Figure 2.2). We found high feeding intensity within the Big Qualicum area, but less feeding than expected within the estuary itself where the smolts first enter the ocean (Figure 2.3B). Contrary to our predictions, the hotspot in the estuary represented a small proportion (3%) of the total feeding intensity during the study period. Instead, most of the feeding effort (i.e., PCEs) occurred outside the estuary near Norris

Rocks —with the remainder spread around Hornby Island and in the open water between Norris Rocks and the estuary (Figure 2.3B). A second unexpected finding was that the harbour seals increased their feeding intensity in the estuary in response to the release of 350,000 coho smolts from the hatchery, but showed no change in feeding intensity in response to the release of 3 million Chinook smolts (Figure 2.6A). These findings raise questions about large-scale movement and spatial and temporal variability in feeding site fidelity.

2.5.1 Movements and feeding site fidelity

Our results show that the majority of the seals we tracked (n=16 of 20) limited their movements within the capture area in the Big Qualicum area (<50 km) where they generally used a primary haul-out site (e.g., Norris Rock and Flora Islet), but also other secondary haul-out sites (e.g., Seal Bay and Mud Bay). The rest of the seals (n=4) used the Big Qualicum area but also travelled long distances (>100 km) and used other distant areas such as the Malaspina Strait (Seal #5), Mistaken Island (Seal #13), Howe Sound (Seal #1) and Deep Cove (Seal #20). These findings are consistent with previous studies demonstrating the complexity of the harbour seal space use reflected by their high spatiotemporal variability within and between individuals (Hardee 2008; Peterson *et al.* 2012). Generally, harbour seals exhibit a high fidelity to their haul-out sites, particularly during breeding and moulting season (Yochem *et al.* 1987; Van Parijs *et al.* 2000; Härkönen & Harding 2001; Cordes & Thompson 2015), and tend to limit their movements to <50 km from these sites (Thompson & Miller 1990; Tollit *et al.* 1998; Suryan & Harvey 1998). However, many studies have shown high intra-annual variability in the large-scale movements and habitat use of small proportions of studied seal populations (Lowry *et al.* 2001; Lesage *et al.* 2004; Cordes *et al.* 2011; Peterson *et al.* 2012). Harbour seals are capable of traveling long distances (Lesage *et al.* 2004; Peterson *et al.* 2012) and using different areas and haul-out sites (Brown & Mate 1983; Thompson *et al.* 1996; Simpkins *et al.* 2003). This spatiotemporal variability has been linked to intrinsic factors such as age, body size and sex (Thompson *et al.* 1998; Burg *et al.* 1999; Lowry *et al.* 2001) as well as extrinsic factors such as seasonal prey aggregation and abundance variability (Tollit *et al.* 1998; Lesage *et al.* 2004; Small *et al.* 2005).

2.5.2 Total feeding intensity

The kernel density analysis applied on the PCE locations shows that feeding was distributed in discrete patches in the Strait of Georgia within the different areas used by the tagged harbour seals including the Big Qualicum area, around Mistaken island in the Parksville area, the Southern West part of Howe Sound, and Deep Cove (Figure 2.3A). This suggests that harbour seals usually conduct short round trips (<35 km) from their haul-out sites to forage, but that some individuals travelled long distances (>100 km) to transit from one area to another rather than round foraging trips. The largest number of PCEs were observed in the Big Qualicum area and were highest around Hornby Island (except for the eastern side of Hornby Island) and in the Big Qualicum estuary, and also spread out in the open water between the two sites. Our analysis extracted 3 distinct areas of high feeding intensity (i.e., feeding hotspots).

The first feeding hotspot was in south of Hornby Island around Norris Rocks (Figure 2.3B), the largest harbour seal haul-out site in the Big Qualicum area (Olesiuk 2010). This Norris Rocks hotspot was the largest (4.82 km^2) and included the highest percentage (26%) of total PCEs, which were conducted by 11 seals (Table 2.2). This area is mainly composed of intertidal rocky reefs and gets rapidly deep to a maximum of ~200-250 m depth away from the Norris Rocks haul-out site. The depth histogram of the PCE inside the Norris Rocks hotspot shows that feeding occurred along the water column from the surface to a maximum 241.5 m depth (Figure 2.4). However, most of the feeding occurred within the first ~40 m depth and also deeper between ~120 m and ~160 m. This suggests that harbour seals fed on a large variety of prey ranging from coastal, shallow and intertidal, pelagic and benthic prey (Thomas *et al.* 2011; Lance *et al.* 2012).

The second feeding hotspot occurred in the Big Qualicum estuary and its vicinity (Figure 2.3B). It is smaller in size (0.45 km^2) than the Norris Rocks hotspot and included fewer (3%) of PCEs (Table 2.2). In total, 8 of the 17 tagged seals fed in the estuary. Seals that fed there were most likely feeding on out-migrating smolts due to the small size of the estuary and the scarcity of other apparent alternative prey. The presence of the harbour seals there following the release of coho smolts from the hatchery suggest that they detected their arrival and preyed upon the smolts as they left the Big Qualicum River.

Salmon smolt migrations are considered as resource pulses defined as temporary events of increasing resource availability in time and space relative to the scale of their consumers (Yang *et* *al.* 2008). Harbour seals, as generalist consumers, are more likely to exploit these periodical superabundant resources because they are able to feed on other prey when pulses are absent (Ostfeld & Keesing 2000). This response can be expressed as functional and numerical responses that are synchronised with the resource pulses, and by the increase in distance travelled by consumers (Rose & Polis 1998; Middlemas *et al.* 2006; Schlacher *et al.* 2013). Previous studies have shown that harbour seals are capable of exploiting abundant resource pulses such as salmon migrations (London *et al.* 2002; Middlemas *et al.* 2006).

In contrast to our expectations, only a small fraction (3%) of the total feeding activity of the seals occurred in the Big Qualicum estuary. However, approximately half of the seals (n=8) that stayed within the Big Qualicum area made at least 1 trip to the estuary. Nevertheless, the number that regularly travelled to the river mouth each day averaged only 3.4 of the 17 seals (Figure 2.6B). These results suggest that out-migrating smolts in the Big Qualicum estuary were not a major resource prey for the overall local harbour seal population, but may have been an important source of nutrition for a small portion (>20% of the 17 tagged seals).

The Big Qualicum estuary is a relatively small estuary in the Strait of Georgia compared to others such as the Fraser River estuary, the Cowichan estuary, the Puntledge River estuary or the Campbell River estuary. Thus, our results should be carefully interpreted given that the seal behavioural responses may vary in larger estuaries characterized with different types of habitats. For instance, smolt residency time has been shown to be longer in larger sized estuaries compared to small ones — and are important areas for growth (McCabe *et al.* 1986; Bottom *et al.* 2005). These differences in smolt time residency and growth rates in estuaries are likely to impact the seal foraging behaviour.

Optimal foraging theory suggests that a predator should maximize its long-term energy gain by balancing the energy provided by the prey with the various energy, temporal and cognitive constraints associated with feeding on certain prey (Stephens & Krebs 1986). In our case, the seals feeding on smolts in small estuaries and rivers similar to the Big Qualicum would have had very low temporal and energy constraints associated with foraging in the confines of a shallow narrow river mouth. They would have avoided all energy expenditure associated with diving and time spent searching for prey, which is highly significant when foraging in the open water (Wilson *et al.* 2014; Ramasco *et al.* 2015). In rivers, harbour seals can hold their position in the water and intercept out-migration smolts in high numbers with minimal movements and hence minimum energy expenditure (Yurk & Trites 2000).

However, feeding on smolts in rivers and estuaries may present some constraints in terms of foraging efficiency. For instance, the Big Qualicum is a relatively small estuary limiting the number of seals feeding on out-migrating smolts and consequently increases intra-specific competition. Other smolt predators such as birds (Wood 1987; Ryan *et al.* 2001) are also abundant in the Big Qualicum estuary resulting in the increase of inter-specific competition as well. Although salmon smolts migrate in high number and density, their energy density (~5.04 kJ/g for coho and ~3.98 kJ/g for Chinook; Roby *et al.* 2003) is lower than other important prey in the Strait of Georgia such as Pacific herring (~5.9 kJ/g Anthony *et al.* 2000)—but are much higher than other seal prey species such as Walleye pollock (~3.5 kJ/g; Anthony *et al.* 2000). Consequently, because of the small size and intermediate energy density of the salmon smolts relatively to other prey, the seals would need to consume a large number of individual (~100 smolts per day) to reach their daily energy requirements (Howard 2009).

In addition to feeding efficiently once in the river mouth, the seals presumably need some cognitive capability to predict the migration timings if they are to take full advantage of the smolt pulses (Bell 1990; Willson & Womble 2006; Womble *et al.* 2009). How seals predict the timing of these pulses and how they assess uncertainty about it has presumable consequences on their foraging success and efficiency (Dall & Johnstone 2002) considering that the peak of the smolt pulses in small estuaries like the Big Qualicum may have a short time window of only a few days or weeks. Predators may use environmental (Real 1992) and social (Danchin *et al.* 2004) information and clues to optimize their foraging decisions such as using water temperature and lunar cycles to anticipate the downstream migration of 0-year chinook smolts (Roper & Scarnecchia 1999). Or they may simply have learned the predictable annual release timing of hatchery salmon smolts (DFO, pers. comm) compared to the high inter-annual variability in the timing of wild salmon smolt migrations (Holtby *et al.* 1989; Scheuerell *et al.* 2009). Such reduced inter-annual variability in hatchery smolt release timings would increase the abilities of seals to exploit these pulses given that pinnipeds have high learning and memory capacities that influence their future behavioural decisions even after a long time of period (Reichmuth Kastak & Schusterman 2002; Lindemann *et al.* 2006).

There were no suitable haul-out sites for harbour seals in near vicinity of the Big Qualicum estuary. Spending time ashore (i.e., either on sand and cobble beaches, rocky shelves, tidal sand and mud bars or human-made structures) is important for harbour seals during their mating and moulting periods, but also on a daily basis for resting, thermoregulation, predation avoidance, social interaction and parasite reduction (Boulva & McLaren 1979; Watts 1992, 1996; Stevik *et al.* 2002). The Big Qualicum estuary has limited haul-out space on a rocky shelf that is only available at low tide, and a cobble beach that is disturbed by humans that use a camp ground. Therefore, seals that foraged in the estuary either had to use less suitable haul-out sites or had to travel back and forth between the Big Qualcium estuary and their main haul-out sites (i.e., either Norris Rocks or Flora Islet) every 1-2 days. This constraint of frequently travelling in the open water, in addition to energitical constraints, increases the seal vulnerability to predation by killer whale (*Orcinus orca*; Ford *et al.* 1998), which presumably influences their behaviour and foraging decisions (Rattenborg *et al.* 1999; Welton *et al.* 2003).

The third and last feeding hotspot of the 17 tagged seals was located across the Strait of Georgia in Deep Cove (Figure 2.3). It was the smallest feeding hotspot (0.25 km^2) with just 2% of all PCE occuring in it. This hotspot represented the main feeding area of a single seal (seal #20) that spent relatively little time in the Big Qualicum area after it was captured. In the Deep Cove area, this seal mainly hauled-out on a pile of logs used as wave breakers for the Deep Cove marina or on log booms in the Port Moody area. These results show that, although the seal #20 transited between the Big Qualicum and the Deep Cove areas, it displayed a high foraging site fidelity in the Deep Cove area. It also shows how habour seals have a high capacity to cope with human activities and constructions. In this foraging hotspot, foraging occurred mostly between 25 and 50 m suggesting a limited and specialized diet.

2.5.3 Temporal variation of feeding hotspots

The spatial distribution of the seal feeding within the Big Qualicum area varied over the study period (i.e., from May 2nd to June 2nd; Figure 2.5). After coho smolts were released, feeding was densest in the Norris Rocks area and in the Big Qualicum estuary. However, feeding seemed to progressively move from the estuary towards the open water and areas around Hornby island such as Flora islet and its northern part where large numbers of harbour seal haul out (Olesiuk 2010). Although feeding around Norris Rocks varied in intensity between time periods, it was consistently a feeding hotspot during all the study period and thus an important feeding area for the local harbour seal population.

The number of prey chasing events in the Big Qualicum estuary showed a clear peak in feeding intensity (>150 PCE/day) on May 5th that lasted for 4 days following the release of the coho smolts from the Big Qualicum Hatchery (Figure 2.6A). After this peak, feeding intensity in the estuary dropped by about half and fluctuated between days (~48.2 ± 29.2 PCE/day) until decreasing to a very low levels (<25 PCE/day) by the end of the month. Although the number of Chinook smolts (~3 million) released from the Big Qualicum Hatchery was higher than the number of coho (~350,000), there was no corresponding peak in the foraging intensity after the release of the Chinook smolts similarly to the one after the release of the coho smolts. This suggests that harbour seals foraged on the coho smolt pulse, and did not target the Chinook smolt pulse.

The preference of the seals towards the coho smolts compared to the Chinook smolts may be explained by the size and the energy density of the smolts leaving the river. Measurements of smolts sampled before release showed that the coho smolts were bigger than the Chinook smolts. The coho smolts were in average ~12.9 cm long and weighed ~22.6 g compared to the Chinook smolts that averaged ~8.0 cm long and weighed ~5.9 g. Harbour seals may prefer prey ranging between 10–16 cm in length (Tollit *et al.* 1997), which could explain the apparent preference for coho smolts rather than Chinook smolts. In addition, the coho smolt energy density (~5.04 kJ/g) was higher than the Chinook smolts (~3.98 kJ/g) which means that in the estuary coho smolts were more energetically beneficial for harbour seals (Roby *et al.* 2003).

Prey selection theory suggests that a predator should switch from a good to a less good prey only if the good one decreases, independently to the abundance of the less good one (Stephens & Krebs 1986). Based on this theory, seals in the estuary that did not respond to the Chinook smolt release might have been finding sufficient numbers of coho smolts in the estuary to fulfil their energy requirements. Many studies have shown that prey selection in pinnipeds usually depends on the abundance of one or few key species. For instance, Californian sea lions (*Zalophus californianus*) switched to alternative prey when the abundance of 2- to 4-year-old Pacific hake decreased (Bailey & Ainley 1981) and harbour seal diet selection depended on herring and sprats abundance in the inner Moray Firth, Scotland (Tollit *et al.* 1997). Chinook smolts are considerably smaller than coho smolts when entering saltwater, and tend to spend more time in the estuary in nearshore habitats before reaching the open ocean (Myers & Horton 1982; Dumbauld *et al.* 2015). During this time, they gain body mass and store lipid, which would makes them a more energetically beneficial prey for predators later in the year. Simulation models simulations suggest that Chinook mortality rates due to seal predation peak later in the summer (July), in contrast to the coho mortality rates that are high in May-June (Nelson *et al.* unpubl. data).

Another possible explanation for the continued presence of small numbers of seals during the out-migration of Chinook is that they were targeting aggregations of other Chinook smolt predators such as the Pacific hake, spiny dogfish, river lamprey, adult Chinook salmon, lingcod and walleye Pollock (Beamish & Neville, 2001; Armstrong & Winslow 1968; Beamish *et al.* 1992; Fresh 1997; Emmett & Sampson 2007). Consistent with this possibility is the fact that feeding intensity increased in the open water next to the estuary during the Chinook migration, and occurred mainly below 70 m.

2.5.4 Limitations and biases

The main goal of our study was to have a true representation of the spatiotemporal foraging distribution and variation of the local harbour seal population during the coho and Chinook smolt out-migrations from the Big Qualicum River. To focus on the impact and behaviour of the seals towards the smolts leaving from the Big Qualicum River, we captured about half of the seals from the Big Qualicum estuary and the rest from rocky shelves in the southern part of Hornby Island (Figure 2.1). Since we did not sample individuals completely at random, our results might be biased and in this case, overestimate the behaviour of the seals that foraged more in the estuary relatively to the whole local population. Other sampling design factors could have also led to non-randomness and thus decrease accuracy in estimating the true overall population outcome. For instance, the boat rush method used to capture hauling-out seals tended to favor capturing bolder individuals because they are usually the last ones to escape into the water. Consequently, we obtained a high gender bias (15 males vs. 5 females) as males tended to stand their ground longer than females (Biro & Dingemanse 2009).

Acceleration has become a common tool to monitor and quantify distinct behaviours in free-ranging animals (Kato *et al.* 2006; Whitney *et al.* 2010; Collins *et al.* 2015). Many studies have approximated foraging success with prey capture attempts by detecting head strokes (Viviant *et al.* 2010; Volpov *et al.* 2015; Jeanniard-du-Dot *et al.* 2016). Due to logistical limitations, we ended up attaching the accelerometer to the back of the seals and we considered high body accelerations as prey chasing events, which we used to quantify foraging intensity. Using body acceleration instead of the head acceleration may lead to incorrect inferences about the number of prey consumed. It is conceivable for example that seals swimming against rivers current will hold their position in the water and use minimal movements to intercept smolts swimming by them (Yurk & Trites 2000). Moreover, harbour seals can consume small prey using suction in addition to biting feeding (Marshall *et al.* 2014). These two behaviours are likely to not be detected by the accelerometer on the animal's back and would thus under-estimate feeding attempts in the river and estuary.

Feeding events detected using acceleration are usually filtered by removing the first 3-7 m from the surface to avoid any non-feeding behaviour and minimize noise signal generated at the surface (Viviant *et al.* 2014; Guinet *et al.* 2014; Jouma'a *et al.* 2015). In our study, we could not adopt the same filtering process because all feeding events in the river and estuary were mainly close to the surface (<3 m) due to water shallowness. Thus by loosening up the filtering process, we might overestimated feeding events around haul-out sites where non-feeding events (e.g., social interactions) occur in shallow water (Davis & Renouf 1987).

One of the important and challenging elements in our study was to estimate the seal fine-scale movements in the horizontal scale, which highly depended on the number of GPS location collected. Due to logistic restrictions, we placed the GPS tags on the back of the seals instead of the head. This resulted in collecting a low number of GPS locations when the seals were at sea because they seemed to keep their back, and hence the GPS tag, submerged in the water when breathing at the surface. We used the dead reckoning method to estimate pseudo-tracks between GPS locations that we corrected with a custom algorithm based on movement environmental constraints (see Methods). Although our method was relatively easy to apply, it did not estimate the error around each estimated location. It was thus not possible to assess the accuracy and precision of PCE locations. An alternative method that allows for estimating error would have been to use state-space models (Jonsen *et al.* 2005; Patterson *et al.* 2008; Langrock *et al.* 2012). It has been applied to the dead reckoning tracks and GPS locations of humpback whales to estimate fine-scale movements and the error around it (Wensveen *et al.* 2015). This relatively new method seems to have a lot of potential for future studies, but is complex method and not straightforward to apply.

2.6 Conclusion

Overall, our results show that harbour seal predation on out-migrating smolts from the Big Qualicum River represent a small proportion of the total feeding by seals at the population scale. The major foraging area for seals in the Big Qualicum area was in the southern part of Hornby Island around Norris Rocks. The seals responded positively to the coho smolt pulse released from the Big Qualicum Hatchery by increasing their feeding intensity in the estuary. However, we did not observe any functional response to the out-migrating Chinook smolts suggesting that the seals did not feed in any significant way on them during the out migration. Our findings suggest that predator responses were not only affected by the magnitude of the resource pulses, but by other characteristics such as prey size, relative prey energy density, and availability of alternative prey. This is consistent with a similar conclusion about the foraging behaviour of harbour seals during spawning Pacific herring pulses (Thomas *et al.* 2011).

Dietary analysis indicates that predation by harbour seals on coho and Chinook smolts is likely having a substantial impact on these salmon populations (Thomas *et al.* 2016). We found significant predation by a few seals on coho smolts as they entered the estuary, but no sign of predation on Chinook smolts during our 4-week study (May 2nd and June 2nd). It is conceivable, however, that predation pressure by harbour seals on Chinook smolts is higher during the summer (July and August) rather than when the smolts leave the rivers.

Our findings bring new insights into understanding interactions between harbour seals and out-migrating coho and Chinook smolts, which is essential for developing adequate conservation actions to enhance salmon marine survival. While it has shown some general patterns of predation by the population as a whole, it has also revealed considerable variation at the level of individual foraging behaviour that might be exploited to mitigate the effect of seals on out-migrating coho and Chinook smolts. Accounting for among-individual variance may further advance understanding of predator-prey interactions and provide more efficient management decisions and strategies in a conservation context (Königson *et al.* 2013).

Chapter 3: Foraging strategies of harbour seals during salmon smolt out-migrations

3.1 Summary

Knowing where and when top predators forage—and how foraging strategies vary between individuals—contributes to understanding ecosystem processes, and helps to inform conservation actions. However, most foraging ecology studies tend to focus on populations rather than individuals; and may miss predator-prey processes that are important to wildlife management and understanding species interactions. We investigated the foraging strategies of individual harbour seals to assess the extent to which the seal populations consuming juvenile salmonids may be impeding the recovery of coho and Chinook salmon as they enter the Salish Sea (British Columbia, Canada). We tracked 17 seals—equipped with GPS loggers and Daily Diary tags—before and after thousands of coho and Chinook smolts were released from the Big Qualicum Hatchery to document and assess the temporal and spatial foraging behaviours of the seals. Comparing the foraging behaviours of smolt specialists with non-specialist seals revealed 4 different seal foraging strategies. Some seals (17.6%) only responded to the pulse of coho smolts and ignored Chinook in the river mouth, while others (17.6%) appeared to target larger fish that preyed on Chinook smolts near the river mouth. Two other groups of seals did not feed at the river mouth on the concentrated numbers of smolts, but either remained resident (53%) and fed near their main haul-out sites, or were transient (11.8%) and left the study area all together. Thus, a relatively small number of the seal population preyed on coho smolts at the river mouth during the out-migration, but none appeared to target Chinook smolts at this time of year. The spatially and temporally variable movements and feeding behaviours of the 4 groups of seals suggest a high degree of individual foraging and diet specializations—and show that only a portion of the population selectively responded to the concentrated pulse of prey as it entered the ocean.

3.2 Introduction

Interactions between prey and predators defines the structure and function of communities and trophic webs. They influence survival, size structure of prey and predator populations, as well as their growth, behavior, and distribution (Abrams 2000; Murdoch *et al.* 2003; Emmerson & Raffaelli 2004; McCauley *et al.* 2012). In marine environments, predators can directly impact prey population dynamics by removing individuals (i.e., consumption effect) through top-down or cascade processes, and they can indirectly impact the behaviours and spatial distributions of prey (i.e., risk effect) (Werner & Peacor 2003; Heithaus *et al.* 2008; Creel & Christianson 2008). Alternatively, prey availability, quantity, quality or accessibility can influence behaviours, feeding rates, energetics, and fitness of predators, and ultimately the dynamics of their populations (Robles *et al.* 1995; Menge 2000). Thus, understanding interactions between prey availability and foraging activities of marine predators can provide insights into marine ecosystem dynamics and processes that have implications for fisheries, management and conservation (Trites *et al.* 1997; Ward *et al.* 2012; Benoit-Bird *et al.* 2013; Berejikian *et al.* 2016; Estes *et al.* 2016).

The distribution of prey is spatially and temporally highly variable in marine environments (Harris *et al.* 1988; Perry *et al.* 2005; Willson & Womble 2006). In response, marine predators tend to have relatively flexible foraging behaviours and search strategies that reflect the habitat in which they forage, the type of prey they feed on, and the dynamics of prey patches they target (Georges *et al.* 2000; Benoit-Bird *et al.* 2013; Kuhn & Costa 2014; Jeanniard du Dot 2015; Thorne *et al.* 2015). Predators may also switch their typically foraging routine to exploit alternative prey that may be seasonally available, abundant, and aggregated (Willson & Womble 2006; Thomas *et al.* 2011).

A specific case of extreme variation in the spatial and temporal distribution of prey in the predator environment are resource pulses, defined as episodes of increased resource availability and characterized by high intensity, low frequency, and short duration (Yang *et al.* 2008). Optimal foraging theory (and the marginal value theorem) predicts that predators should respond to short intense prey aggregation events by maximising time in these dense patches and optimising energy gain per unit of time (Charnov 1976; Stephens & Krebs 1986) — as shown for sea otters (*Enhydra lutris*) that switch their diet to Pacific smooth lumpsuckers (*Aptocyclus ventricosus*) during decadal spawning pulses (Watt *et al.* 2000). However, too many predators taking advantage of such spatially and temporally restricted events, can lead to inter and intraspecific competition that diminishes the energetic return for each individual. How predators respond to resource pulses might impact predator survival, growth and reproduction (Boyd *et al.* 1994; O'Toole *et al.* 2015). Resource pulses are by definition short term events that animals cannot rely upon in the long-term (Yang *et al.* 2008). Understanding long-term foraging behaviours of predators and how they adjust—or do not adjust—to short- or long-term prey dynamics contributes to understanding ecosystem processes.

Intraspecific variation in foraging behaviours has been documented for a broad range of marine predators that includes seabirds (Radl & Culik 1999; Kato *et al.* 2000), toothed whales (Ford *et al.* 1998; Laidre *et al.* 2002), pinnipeds (Lea *et al.* 2002; Austin *et al.* 2004; Weise *et al.* 2010) and sea otters (Tinker *et al.* 2007). Among these species, foraging strategies typically vary between sex (Le Boeuf *et al.* 2000; Beck *et al.* 2003), age (Hastings *et al.* 2004), region (Tollit *et al.* 1998), and individuals (Villegas-Amtmann *et al.* 2008). Individual-based specialization could be an adaptation to increased intraspecific competition when resources are reduced (Glasser 1982; Schindler *et al.* 1997), and has been shown in some cases to have large ecological effects that impact spatial and temporal trophic interactions (Rall *et al.* 2011; Rudolf & Rasmussen 2013).

Harbour seals (*Phoca vitulina*) are abundant and widespread marine predators throughout the northern hemisphere oceans. They are generalist and opportunistic predators known to switch their diet and foraging behaviours as prey availability, abundance and aggregation vary seasonally and annually (Tollit *et al.* 1997; Lance & Jeffries 2007; Sharples *et al.* 2012; Wilson *et al.* 2014). Although, harbour seal diets include a large variety of fish and cephalopod species, an important proportion of their diets is usually composed of a few dominant species (Olesiuk *et al.* 1990; Tollit & Thompson 1996; Tollit *et al.* 1998; Bromaghin *et al.* 2013). For instance, harbour seals in the Salish Sea along the northeastern Pacific coast feed mainly on Pacific herring (*Clupea pallasii*), Pacific hake (*Merluccius productus*), walleye pollock (*Gadus chalcogrammus*), and salmonid species (Lance *et al.* 2012; Luxa & Acevedo-Gutiérrez 2013; Thomas 2015).

Pacific salmon species generate two annual prey pulses. The first occurs in the spring (Apr – May) when juveniles (i.e., smolts) leave rivers to reach the ocean; and the second in the fall (Sept-Nov) when adult salmonids return to their birth rivers to spawn and die (Groot & Margolis 1991). Although, many studies have shown that harbour seals take advantage of the large influx of adult salmon (Hauser *et al.* 2008; Lance *et al.* 2012), there is increasing evidence that harbour seal predation may cause significant mortality on juvenile coho, Chinook, and sockeye compared to the smaller-bodied chum and pink salmon smolts (Yurk & Trites 2000; Thomas *et al.* 2016). The level of mortality caused by harbour seals on juvenile fish leaving the rivers may be impeding the recovery of coho and Chinook salmon populations in the Salish Sea (Thomas *et al.* 2016).The objectives of our study were 1) to determine the fine-scale foraging behaviours of individual harbor seals (individual-based specialization), and how they vary spatially and temporally and 2) assess whether and how resource pulses in the form of release of high numbers of coho and Chinook smolts over few days impact foraging behaviours of individual harbor seals. We achieved this by tracking the fine-scale movements and behaviours of 20 harbour seals during, before, and following the release of thousands of coho and Chinook smolts from the Big Qualicum Hatchery. We thereby documented spatial and temporal differences in foraging strategies between seals based on their feeding intensity in the Big Qualicum estuary.

We hypothesized that harbour seals are generalist predators that readily switch their foraging behaviours to exploit seasonally abundant prey, such as salmon. Based on the presence of juvenile salmonid bones in seal scats, we expected harbour seals using haul-outs in the vicinity of Big Qualicum River to change their feeding behaviours in response to the out-migration of coho and Chinook salmon into the Salish Sea. Thus, we sought to document the extent to which harbour seals specialize in consuming juvenile salmonids, and assess the impact that this may have on coho and Chinook salmon populations.

3.3 Material and Methods

3.3.1 Animal handling and instrumentation

We undertook our study during spring 2015 in and around the Big Qualicum estuary in the central western Strait of Georgia (49° 26' 58" N, 124° 31' 43" W; Figure 2.1). Each year, the Big Qualicum Hatchery releases thousands of coho (~350,000 in May 4th, 2015) and Chinook (~3 million in May 14th, 2015) smolts into the Big Qualicum River. Many harbour seal haul-out sites, hosting over than 1000 individuals, surround the mouth of Big Qualicum River (Olesiuk 2010) and are within foraging distance (< 150 km; Hardee 2008; Peterson *et al.* 2012).

We captured 20 harbour seals within the Big Qualicum area (Figure 2.1) from April 21st to May 1st 2015, and instrumented them with a floating biologger package to their dorsal midline between their shoulders using a quick-drying epoxy glue (see Chapter 2 for more details on capture technics and animal handling procedures). The biologger packages included a Global Positioning System (GPS) satellite tag (Splash 10-F; Wildlife Computers, Redmond, WA, USA), a Daily Diary tag (Wildlife Computers, Redmond, WA, USA), and a Very High Frequency (VHF) transmitter

(MM190B; Advanced Telemetry Systems, Isanti, MN, USA). In addition to instrumentation, we recorded body mass (±0.2 kg) and length (to the nearest 0.5 cm) of each seal. All procedures applied on the harbour seals were approved by the UBC Animal Care Committee (permit # A14-0322) and Fisheries and Oceans Canada (permit # XMM 2 2015). Animal handling time for instrument deployment was < 60 minutes.

Devices were programmed to record depth at 1 sec intervals, acceleration at 16 Hz, earth's magnetic field at 8 Hz, and GPS locations every 20 min. GPS locations were recorded in May and June 2015 and were transmitted through satellite in July and August 2015. The biologger packages were positively buoyant and balanced to float with the VHF antenna upright to allow for tracking and recovery by boat after they come off during the seal annual moulting season in August-October 2015.

3.3.2 Data processing

All data processing and analyses were conducted in R (v. 3.3.2) unless otherwise mentioned. GPS locations were first filtered based on the method outlined in Austin *et al.* (2003) using a traveling speed threshold of 2.78 m/s (Lesage *et al.* 1999), and a distance threshold of 160 km. We also conducted a final visual inspection and removed all GPS locations on land. We then reconstructed the pseudotracks between each two GPS locations at a 1 sec interval using the dead reckoning method that we corrected following the steps described in Chapter 2. Each seal’s time series was portioned into either “haul-out” (i.e., resting on land) or “at-sea” state. The haul-out state began when the Daily Diary tag was dry for at least 10 min and ended up when it was wet for more than 40 sec (Russell *et al.* 2015). The seal where considered at-sea the rest of the time and at-sea trips were defined as the time interval between 2 consecutive haul-out states. We removed all at-sea trips during which seals did not conduct at least one dive during 2 hour intervals because they likely reflected seals hauling out or partially submerged in the water, or resting at the surface next to their haul-out sites. Feeding events were quantified from intense bouts of body accelerations using the Prey Chasing Event (PCE) method (see Chapter 2).

Depth readings were corrected from any drift using the automatic zero offset correction (ZOC) method from Wildlife Computers software (Instrument Helper). We used 1 hour for the maximum dive duration and 1 m for allowable surface error. We also ran a 5 sec rolling median on the depth readings to remove quick spikes that were due to Argos transmissions. Individual dives were defined as any depth exceeded 5 m and lasted more than 10 sec. Each dive was separated in 3 phases—descent, bottom and ascent. The descent phase was defined as the first section of the dive during which the descent rate is lower than 0.15 m/s and the ascent phase as the last section of dive during which the ascent rate was higher than 0.15 m/s. The bottom phase was defined as the dive section between the descent and the ascent phases. Some of the Daily Diary tags failed to record data for short time intervals (< 1 min), which we excluded and ignored in our analysis as we believe such brief gaps would not affect our results.

To describe variability in harbour seals foraging behaviour over time according to the smolt release timings, we separated the study into 4 periods: "pre-releases" (May 2nd– 4th—the 3 days before the release of coho smolts), "post coho release" (May 5nd– 14th—the 10 days between the release of coho and Chinook smolts), "post Chinook release" (May 15th– 24th—the 10 days after the release of Chinook smolts), and "post releases" (May 25th–June 2nd—the last 9 days of the study period). In addition, we investigated diurnal variation in seal foraging behaviour by delimiting days into day, dawn, dusk, and night times. We used the function `sunriset` from the R package "`maptools`" to define the time of the sunrise and sunset and the function `crepuscule` from the same package to define the beginning and end of the dawn and dusk. These times were redefined for each day and seal based on the date and the seal average GPS location. Finally, we defined the Big Qualicum estuary as the area within 500 m distance from the middle point of the estuary (9°23'55.7"N, 124°36'33.1"W).

3.3.3 Data analysis

Summary data are presented as averages ± standard deviations, unless otherwise noted. To categorize seal foraging strategies based on the intensity of their functional responses to coho and Chinook smolt releases, we quantified the intensity of each seal response by calculating the proportion of the number of PCE detected inside the Big Qualicum estuary compared to the total number of PCE. We then applied a hierarchical clustering analysis on the seal respective percentages of PCE inside the estuary to identify distinct foraging strategies. We undertook the hierarchical clustering analysis using the Euclidian distance and Ward's minimum variance method to link similar seals together. The number of significant clusters was determined by the package NbClust (Charrad *et al.* 2014) in addition to graphically examining the dendogram and plots of the inter-cluster distance against the number of clusters (McGarigal *et al.* 2000).

We compared the different seal clusters in their foraging behaviours using some common variables describing their horizontal movements, feeding, and diving behaviours (Tremblay & Cherel 2000; Kuhn & Costa 2014). These variables were transformed when applicable using either a log or square root transformation for non-normal data or an arcsine transformation for proportion data. An ANOVA was performed to compare the mean of the variables that were summarized for each seal for the whole study period such as time in haul-out (%), PCE rate (PCE/h), dive rate (dive/hour), maximum diving depth (m), and the intra-depth zone index (IDZ; %). The IDZ is an index on the consistency in dive depths between two consecutive dives (Tremblay & Cherel 2003). The IDZ is the proportion of time that dive depths ranged within ±10% of the previous dive depth.

Linear mixed effects models (LME) with the seal clusters as fixed effect and the seal ids as random effects were used to determine whether seal clusters differed for the variables that were summarized by dive or trip. These variables included dive mean depth (m), dive max depth (m), dive duration (min), dive bottom phase duration (min), dive descent and ascent rates (m/s), trip duration (hour), trip maximum distance (km), and trip horizontal speed (km/hour). We compared the LME models to the null model (i.e., without any fixed effect), and considered the best models to have AICc lower by at least 2 from the null model AICc (Burnham & Anderson 2002). In cases where the seal clusters were found to be statistically different, we used a *post hoc* Tukey HSD multiple comparison tests (`multcomp package`) to determine more specifically which clusters differed (Bretz *et al.* 2002).

We extracted when and where PCEs were the densest (i.e., areas of high feeding intensities) to investigate spatial and temporal differences in foraging behaviours between seal clusters. We then created feeding density maps for each seal cluster to highlight geographical differences in feeding intensities over time. We also considered the intensity of seal feeding events as a function of depth and time of day. Finally, we extracted the diurnal patterns of the seal feeding densities inside the Big Qualicum estuary over the duration of the study. We calculated all feeding densities using a kernel density analysis on either PCE locations (i.e., longitude and latitude), PCE depths (m), or times and dates — and used the package `ks` (Duong 2007) to estimate the kernel density distribution with an unconstrained bandwidth matrix (Wand & Jones 1993) and a smoothed cross-validation bandwidth selector (Hall *et al.* 1992).

3.4 Results

We captured and equipped 20 harbour seals (15 males and 5 females) with biologgers from April 21st to May 1st, 2015. The average mass of all harbour seals was 91.7 ± 13.6 kg and the standard length was 155 ± 9 cm. During the moulting season (i.e., August-October 2015), we recovered 19 of the 20 biologgers deployed, and succeeded in downloading data from 17 of them. Data could not be obtained from 2 of the devices. GPS locations were recorded from May 1st to July 1st, and averaged 22.7 ± 8.5 locations seal^{-1}d^{-1}. The Daily Diary tags recorded and archived data for an average of 48.2 ± 2.8 d (Table 3.1). Due to inconsistency between devices in deployment time intervals, we limited our analyses to the period May 2nd to June 2nd, 2015 (i.e., for 32 days) during which we had full data for all 17 seals.

Table 3.1: Deployment summary, morphometric measurements, and basic spatial, feeding and diving data from 15 male (M) and 5 female (F) harbour seals in the Strait of Georgia during the study period (May 2nd to June 2nd, 2015). Capture sites include Big Qualicum Estuary (BQE; 49°23'57''N, 124°36'31''W), Norris Rocks (NR; 49°23'57"N, 124°36'31"W), Maude Reef (MR; 49°29'57"N, 124°41'03"W) and Flora Islet (FI; 49°30'48"N, 124°34'12"W).

Seal ID	Capture site	Deployment date	Sex	Length (cm)	Mass (kg)	# of GPS	# of PCE	#. of dives
1	BQE	21-Apr-2015	M	165	91	118	10697	3958
2	BQE	21-Apr-2015	M	148	75.5	887	2645	917
3	BQE	22-Apr-2015	F	142	78.5	1229	994	1470
4	NR	22-Apr-2015	M	162	81.5	664	7168	2008
5	NR	22-Apr-2015	M	163	93	417	-	-
6	NR	22-Apr-2015	M	164	103	926	4998	2855
7	FI	01-May-2015	M	168	110	558	-	-
8	NR	22-Apr-2015	M	168	117.5	1032	-	-
9	NR	27-Apr-2015	F	136	89.5	861	2643	1578
10	NR	27-Apr-2015	M	144	73	609	4882	1616
11	BQE	28-Apr-2015	M	159	107	811	2203	1309
12	BQE	28-Apr-2015	M	148	66	322	5282	2126
13	BQE	28-Apr-2015	M	164	76.5	473	1995	1884
14	NR	29-Apr-2015	M	158	85.5	725	12907	3247
15	MR	29-Apr-2015	F	154	93	888	4639	4202
16	BQE	29-Apr-2015	M	158	100	805	1110	2883
17	BQE	29-Apr-2015	M	149	94.5	598	2702	1148
18	NR	30-Apr-2015	F	142	88.5	1095	6431	2488
19	NR	30-Apr-2015	F	154	102	986	306	257
20	BQE	01-May-2015	M	161	109	529	5214	3339
AVG	-	-	-	155.4	91.7	726.7	4518.6	2193.2
SD	-	-	-	9.3	13.6	270.9	3294.4	1062.6

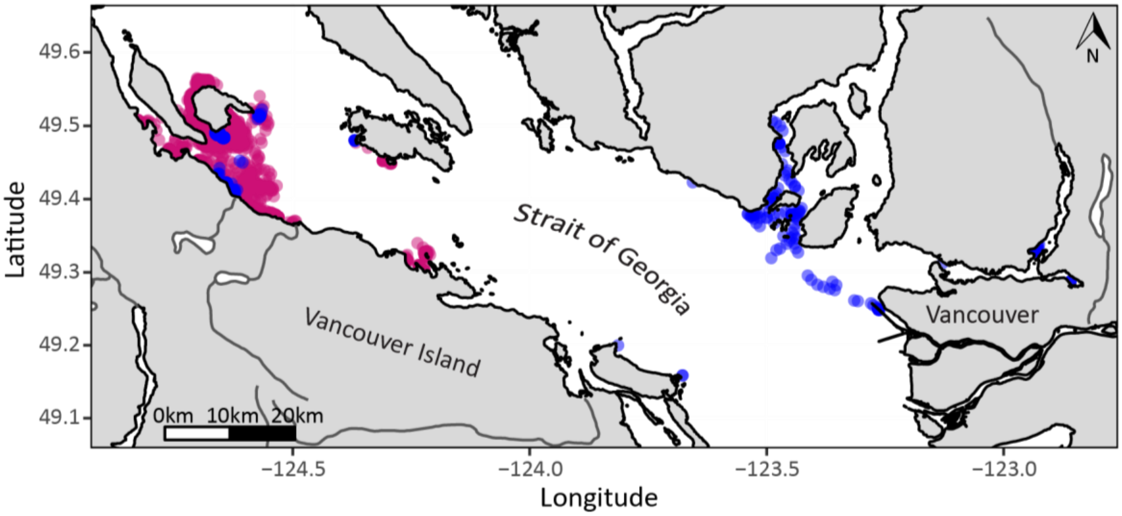

Figure 3.1: GPS locations of all 17 harbour seals that recorded Daily Diary data from May 2nd to June 2nd, 2015 in the Strait of Georgia, Canada. Pink dots are locations of the seals that stayed within 70 km of their capture site (n=15 seals) and the blue dots are the locations of the ones that travelled over 70 km from their initial capture site (n=2).

Among the 17 seals from which we recovered GPS locations and Daily Diary data, 15 seals stayed within the Big Qualicum area (< 70 km from capture sites) during the study, and 2 seals traveled long distances and used different areas in the Strait of Georgia such as Howe Sound and Deep Cove (Figure 3.1).

3.4.1 *In-estuary foraging strategies*

Over 32 days (i.e., from May 2nd to June 2nd, 2015), we detected an average of 2,193 ± 1,063 PCE seal^{-1}. The Big Qualicum estuary accounted for 2.4% of total PCEs and was used by 8 of the 17 harbour seals (i.e., 47% of the tracked seals). On average, seals made 4.2 ± 7.8 % of their PCE's inside the Big Qualicum estuary. However, not all seals entered the estuary. Excluding those seals that did not enter the estuary results in the average estuary bound seal (n=8) having 9.0 ± 9.5 % of their PCE's (range: 0.1 to 28.4 %) occurring in the Big Qualicum estuary.

The hierarchical cluster analysis on the percentage of PCE inside the Big Qualicum estuary indicated that individuals could be classified into 4 distinct groups (Figure C-1). However, since the first group with the highest PCE percentage had only one individual, we decided to combine it with the second seal resulting in a group of 3 individuals. We created a new group called "Transient seals" with the 2 seals that left the Big Qualicum area and used different areas in the Strait of

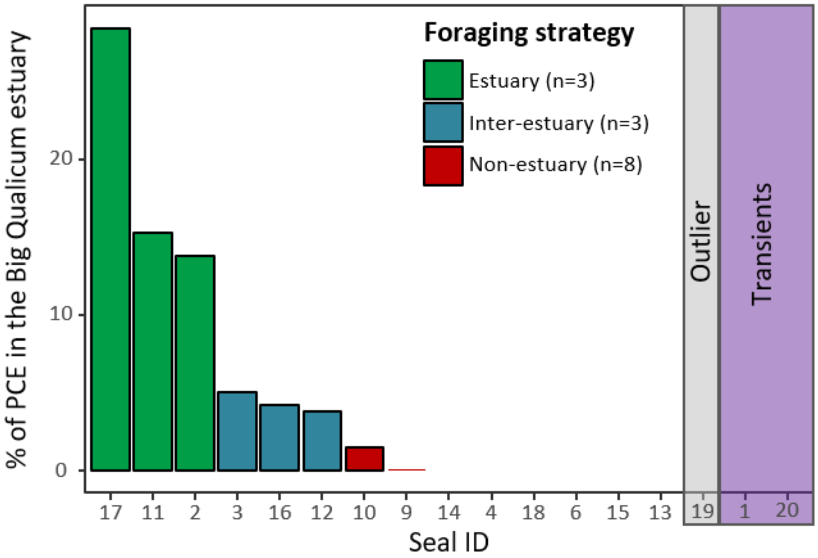

Figure 3.2: Percentage of Prey Chasing Events (PCE) inside the Big Qualicum estuary for 17 tracked harbour seals. The seals were grouped into 3 in-estuary foraging strategies based on their percentage of PCE using a hierarchical clustering analysis (see Methods). Estuary seals had the highest percentages of PCE in the Big Qualicum estuary (Green; n=3), Intermediate estuary seals had low percentages of PCE (Blue; n=3), and Non-estuary seals had minimal or null percentages of PCE (Red; n=8). Among the Non-estuary seals, Seal #19 was excluded from analysis due to uncommon behaviour, and Seals #1 and #20 were grouped into a distinct cluster because they used different areas in the Strait of Georgia (e.g., Howe Sound and Deep Cove).

Georgia. Transient seals were more likely to exhibit different foraging behaviours and strategies compared to Big Qualicum resident seals due to their differences in space and habitat use (Tollit *et al.* 1998). Therefore, our analysis resulted in 4 groups: “Estuary”, “Intermediate estuary”, “Non-estuary”, and “Transient” seals. We considered these 4 groups to have distinct foraging strategies based on their predation pressure towards salmon smolts leaving the Big Qualicum River, as well as differences in their large-scale spatial distributions.

Estuary seals (n=3) had the highest PCE percentages inside the Big Qualicum (19.2 ± 8.1 %) and increased their feeding intensity to 48.2 ± 13.1 % PCE (range: 36.8 to 62.6 %) after the release of coho smolts by the Big Qualicum Hatchery (Figure 3.2 and Figure 3.3). Although, seals #17 and # 11 fed in the estuary during all 4 time periods, Seal #2 fed there exclusively during the post-coho release period (Figure 3.3). Intermediate estuary seals (n=3) had relatively low percentages of PCE (4.4 ± 0.6 %) in the Big Qualicum estuary and seemed to have the highest PCE percentages during the post-Chinook release period (10.0 ± 3.9 %; Figure 3.2 and Figure 3.3). However, Seal #16 seemed to feed with low and constant intensity inside the Big Qualicum estuary starting from the release of coho smolts (Figure 3.3). Non-estuary (n=8) and transient (n=2) seals had very low (< 1.5 %) or null percentages of PCE inside the Big Qualicum estuary (Figure 3.2).

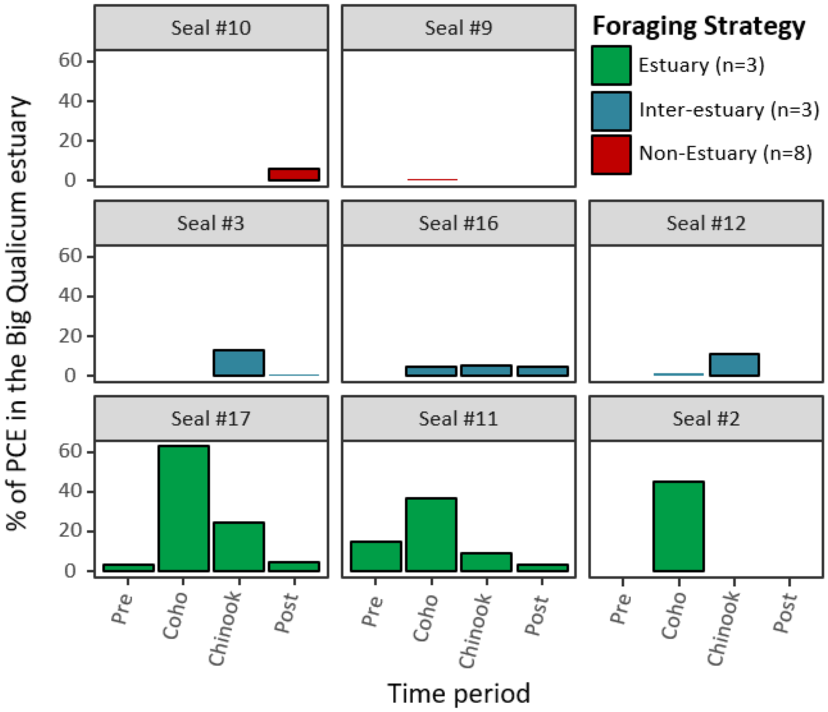

Figure 3.3: Percentage of Prey Chasing Events (PCE) inside the Big Qualicum estuary for 8 harbour seals during the different time periods. Only seals with at least 1 PCE inside the Big Qualicum estuary are presented. Time period includes: Pre (May 2nd-4th)—3 days before the release of coho smolts; Coho (May 5th-14th)—10 days between the release of coho and Chinook smolts; Chinook (May 15th–24th)—10 days after the release of Chinook smolts; and Post (May 24th–June 2nd)—10 days at the end of the study period. Three in-estuary foraging strategies were identified using a hierarchical clustering analysis based on their percentages of PCE inside the Big Qualicum estuary. Estuary seals had the highest percentages of PCE's in the Big Qualicum estuary (Green; n=3), Intermediate estuary seals had low percentages of PCE (Blue; n=3), and Non-estuary seals had minimal or null percentages of PCE (Red; n=8).

3.4.2 Foraging strategies: movement and diving behaviour variation

When exploring the diving behaviour and the spatial distribution of the 17 harbour seals, we found that Seal #19 exhibited uncommon behaviour in comparison to other seals. Seal #19 had a very low activity intensity by limiting its movements to a very restricted area around Norris Rocks and diving in average 2.8 ± 3.9 dive/day for the first 27 days (87% of the time) of the study period (Figure D-1). Seal #19 conducted diving trips only for the last 4 days of the study. Therefore, we considered Seal #19 behaviour as an outlier and excluded it from our analysis.

We did not find any difference in mass ($F_{3,12} = 1.04$, $P = 0.41$) and length ($F_{3,12} = 0.92$, $P = 0.46$) between seal foraging clusters. However, transient seals seemed to be within the heaviest and largest seals tracked. Male seals were longer ($F_{1,15} = 7.52$, $P = 0.01$) than females but not heavier ($F_{1,15} = 0.06$, $P = 0.80$). Overall, tracked seals conducted on average 24.6 ± 7.3 trip seal^{-1} that lasted 19.9 ± 13.5 h. During the study period they conducted in average 2193.2 ± 1062 dive day^{-1} at an average of 46.1 ± 48.6 m depth (max = 355.0 m). Dive duration was 5.7 ± 2.6 min (max = 41.7 min) and duration of the bottom phase was 4.0 ± 2.3 min (max 40.0 min) representing on average 69.5 ± 21.1 % of total dive duration. Among all behavioural variables that we extracted from the data of the tracked seals, we found differences between the seal foraging clusters for only the dive ($F_{3,12} = 5.42$, $P = 0.01$) and PCE ($F_{3,12} = 3.63$, $P = 0.04$) rates. The seals that fed inside the Big Qualicum estuary (i.e., estuary and intermediate estuary seals) had lower dive and PCE rates than other seals (i.e., non-estuary and transient seals).

3.4.3 Foraging strategies: spatiotemporal feeding variation

Harbour seals grouped into the 3 foraging strategies resident in the Big Qualicum area (i.e., estuary, intermediate estuary, and non-estuary seals) exhibited different foraging behaviours in space and time. During the study period, estuary seals had their highest feeding densities near the Big Qualicum estuary, around Flora Islet, and their lowest density in the open water between the two locations (Figure 3.4). High feeding intensities occurred either at ~100-160 m depth during the night or mid-day, or in shallow waters (<10 m depth) mainly during the night (Figure 3.5). After the release of the coho smolts by the Big Qualicum Hatchery, the estuary seals fed mainly in or close to the Big Qualicum estuary in shallow waters (Figure 3.4). Within the Big Qualicum estuary, estuary seals had their highest feeding intensity at dusk, which decreased through night and was low during the day (Figure 3.6). After the coho were released, the feeding density of the estuary seals gradually decreased inside the Big Qualicum estuary while increasing around Flora Islet and in the open water between Flora Islet and the Big Qualicum estuary (Figure 3.4). Estuary seals also increased their feeding density at depth (~100-160 m) during night and mid-day, which remained consistent during the post-release period. In addition to feeding at depth, estuary seals exhibited high feeding density in shallow waters at mid-day, dawn and dusk, and night time during the Chinook release (Figure 3.5).

Intermediate estuary seals fed mainly in the open water between Norris Rocks and the Big Qualicum estuary, and in the vicinity of the Big Qualicum estuary. Their open water feeding was scattered in different dense patches (Figure 3.4). Intermediate seal feeding was dispersed throughout the water column (~ 0 to 180 m depth) and throughout the day. Nonetheless, feeding

Table 3.2: Feeding and movement summary (AVG ± SD) of 17 tagged harbour seals regrouped by their foraging strategies from May 2nd to June 2nd, 2015. Foraging strategies were defined using a hierarchical cluster analysis on the percentage of Prey Chasing Events (PCE) of each seal inside the Big Qualicum estuary and their large-scale spatial distribution. Seal #19 (*italicized*) was considered as an outlier due to its unusual diving behaviour and was excluded from the variable summaries of the non-estuary seals.

Foraging strategy	Seal ID (sex)	Mass (kg)	Length (cm)	PCE rate (PCE/hour)	Time in haul-out (%)	Trip duration (h)	Max distance (km)	Transit rate (km/h)
Estuary	17 (M)	94.5	149	4	12.4	35.2±19.3	7.0±2.8	2.6±0.5
	11 (M)	107	159	3.6	21.2	19.1±6.2	8.1±4.0	2.9±0.8
	02 (M)	75.5	148	5.4	36.4	13.5±6.5	2.5±3.2	1.0±0.3
	AVG ± SD	92.3±15.9	152.0±6.1	4.4±0.9	23.4±12.1	20.3±13.2	5.6±4.3	2.1±1.0
	CV (%)	17.2	4	21.5	51.9	65.1	77.1	49.9
Intermediate estuary	03 (F)	78.5	142	1.5	13.8	21.9±15.0	6.0±3.7	2.8±0.5
	16 (M)	100	158	1.6	12.2	21.4±8.7	7.3±2.9	2.7±0.5
	12 (M)	66	148	7.6	9.7	27.1±15.3	6.8±3.8	1.8±0.8
	AVG ± SD	81.5±17.2	149.3±8.1	3.6±3.5	11.9±2.1	23.2±13.0	6.8±3.4	2.5±0.7
	CV (%)	21.1	5.4	97.3	17.4	56	50.7	29.3
Non-estuary	10 (M)	73	144	8.7	27.3	17.0±8.0	3.7±3.7	1.9±0.5
	09 (F)	89.5	136	4	14.8	23.0±15.9	7.3±3.5	2.5±0.7
	14 (M)	85.5	158	20.9	19.5	21.0±19.4	2.8±2.6	1.9±0.5
	04 (M)	81.5	162	11.9	21.6	16.3±8.8	3.4±4.5	2.2±0.8
	18 (F)	88.5	142	9.8	14.5	17.6±8.2	3.0±1.4	1.9±0.4
	06 (M)	103	164	8.2	20.9	15.6±4.2	4.5±1.3	1.7±0.3
	15 (F)	93	154	7.1	14.5	17.3±14.5	3.3±2.2	0.6±0.2
	13 (M)	76.5	164	3.3	21.8	19.1±6.1	2.5±1.0	1.4±0.4
	19 (F)	*102*	*154*	*0.5*	*24.1*	*17.7±4.9*	*2.8±1.3*	*1.8±0.8*
	AVG ± SD	86.3±9.5	153.0±11.0	9.2 ± 5.5	19.4±4.6	18.0±11.3	3.6±3.0	1.7±0.7
	CV (%)	11	7.2	59.4	23.5	63	82.2	42.3
Transient	01 (M)	91	165	17	18.2	28.9±30.8	10.9±7.0	1.2±1.0
	20 (M)	109	161	8.6	21.3	20.3±10.6	13.1±29.1	2.0±1.3
	AVG ± SD	100.0±12.7	163.0±2.8	12.8 ± 5.9	19.7±2.1	23.8±21.3	12.3±23.0	1.7±1.3
	CV (%)	12.7	1.7	46.4	10.9	89.6	187	73.8

Table 3.3: Diving summary (AVG ± SD) of 17 tagged harbour seals grouped by their foraging strategies from May 2nd to June 2nd, 2015. Foraging strategies were defined using a hierarchical cluster analysis on the percentage of Prey Chasing Events (PCE) of each seal inside the Big Qualicum estuary and their large-scale spatial distribution. Seal #19 (*italicized*) was considered as an outlier due to its diving behaviour and was excluded from the variable summaries of the non-estuary seals. IDZ is the intra-depth zone index.

Foraging strategy	Seal ID (sex)	Dive rate (dive/hour)	Dive depth (m)	Max dive depth (m)	Dive duration (min)	Bottom time (min)	Descent rate (m/s)	Ascent rate (m/s)	IDZ (%)
Estuary	17 (M)	1.7	81.4±59.4	264	6.0±2.2	3.2±1.8	1.0±0.4	0.8±0.3	40.6
	11 (M)	2.2	54.3±50.8	234	7.3±3.1	5.2±2.6	0.8±0.3	0.6±0.2	34.5
	02 (M)	1.9	73.1±60.8	225	6.6±3.6	4.3±3.3	0.9±0.5	0.7±0.5	44.6
	AVG ± SD	1.9±0.2	68.6±57.9	241.0±20.4	6.6±3.1	4.3±2.7	0.9±0.4	0.7±0.4	39.3±48.9
	CV (%)	12	84.3	8.5	46	63.5	44.8	51.9	124.2
Intermediate estuary	03 (F)	2.2	72.4±52.5	229	6.4±2.4	3.7±1.8	0.8±0.3	0.7±0.3	46.9
	16 (M)	4.3	33.4±36.8	200	6.0±2.7	4.6±2.3	0.7±0.3	0.6±0.3	61
	12 (M)	3.1	65.8±51.5	205	4.7±1.8	2.8±1.6	1.1±0.4	0.9±0.3	42.7
	AVG ± SD	3.2±1.0	52.9±49.1	211.3±15.5	5.7±2.5	3.8±2.1	0.8±0.4	0.7±0.3	51.8±50.0
	CV (%)	32.4	92.8	7.3	43.8	56.1	44.3	42.6	96.4
Non-estuary	10 (M)	2.9	67.0±61.1	206	5.5±2.3	3.4±2.1	0.9±0.5	0.8±0.3	45.9
	09 (F)	2.4	77.2±60.6	324.5	7.7±2.5	4.5±2.3	0.7±0.2	0.6±0.3	55.1
	14 (M)	5.3	15.4±8.9	102.5	4.3±2.2	3.6±2.2	0.7±0.3	0.7±0.3	44.7
	04 (M)	3.3	82.5±63.8	324.5	6.1±2.7	3.3±2.0	1.0±0.5	0.7±0.3	43.3
	18 (F)	3.8	20.8±23.5	153	4.8±2.0	3.7±1.8	0.6±0.2	0.6±0.2	37.5
	06 (M)	4.7	35.1±31.4	163	5.0±2.3	3.4±1.9	0.6±0.3	0.6±0.3	34.8
	15 (F)	6.4	13.0±9.2	88.5	5.0±2.1	4.3±2.1	0.6±0.3	0.6±0.2	51.9
	13 (M)	3.1	44.7±36.8	150	6.5±3.3	4.8±2.8	0.7±0.4	0.7±0.3	30
	19 (F)	*0.4*	*36.5±40.2*	*164.5*	*6.3±2.2*	*4.5±1.8*	*0.5±0.2*	*0.6±0.2*	*33.9*
	AVG ± SD	4.0±1.4	37.1±45.0	189.0±91.1	5.4±2.6	3.9±2.2	0.7±0.4	0.6±0.3	43.3±49.5
	CV (%)	33.9	121.3	48.2	47.9	56.3	50.1	44	114.5
Transient	01 (M)	6.3	65.5±48.6	355	6.8±2.7	4.5±2.6	0.9±0.4	0.8±0.3	51.7
	20 (M)	5.5	42.0±42.5	312.5	5.8±2.4	4.1±2.4	0.8±0.3	0.6±0.3	43.4
	AVG ± SD	5.9±0.6	54.7±47.4	333.8±30.1	6.3±2.6	4.3±2.5	0.8±0.3	0.7±0.3	47.9±50.0
	CV (%)	9.3	86.6	9	41.3	57.3	39.4	38.5	104.4

was mainly shallow (~ 0 to 30 m depth) at night, and deep (~ 90 to 150 m depth) during the day (Figure 3.5). Overall, variability in the spatial feeding distribution of the intermediate seals was low during the different periods. However, during the post-chinook period, the intensity of feeding seemed to decrease in the open water, and increase in the Big Qualicum estuary vicinity (Figure 3.4). In contrast, variability in feeding depths and diurnal patterns of the intermediate seals was relatively high between periods.

Before the coho and Chinook were released, the intermediate seals fed mainly during the day and at depth (~ 90 to 150 m depth). However, following the smolt release, they tended to feed in shallow waters (mostly at night) in addition to feeding at depth. Intermediate seal feeding occurred mainly during the day for the pre-releases and the post-Chinook release periods, and at night and afternoon for the post-coho release period—and at night and morning for the post-releases period (Figure 3.5). When intermediate estuary seals fed inside the Big Qualicum estuary during the post-Chinook period, they fed throughout 24 hours, but had the highest feeding intensities during the daytime (~ May 18th to 22nd) and around dusk (~ May 21st to 25th; Figure 3.6).

Non-estuary seals had their core feeding areas around Norris Rocks and along the west shore of Hornby Island. Although, non-estuary seal feeding was relatively consistent in space between periods, they expended their feeding to Flora Islet and North of Hornby Island vicinities (Figure 3.4). Non-estuary seals had a nocturnal feeding pattern along the water column, but was denser in the sallow area (~ 0 to 50 m depth) which was also consistent through all periods (Figure 3.5).

Finally, transient seals included the 2 seals that left the Big Qualicum estuary and used other areas in the Strait of Georgia. Seal #1 was in the Howe Sound area and Seal #20 was in the Deep Cove area. The transient seals seemed to have consistent feeding depths (~ 90 to 120 m depth) along the day time. However, they exhibited shallow (~ 0 to 20 m depth) intense feeding at late night/dawn during the pre-release period and dusk/early night during the post-Chinook release period. They also had scattered intense feeding patches at mid-depth (~ 50 m depth) throughout the daytime during the post-coho release period (Figure 3.5).

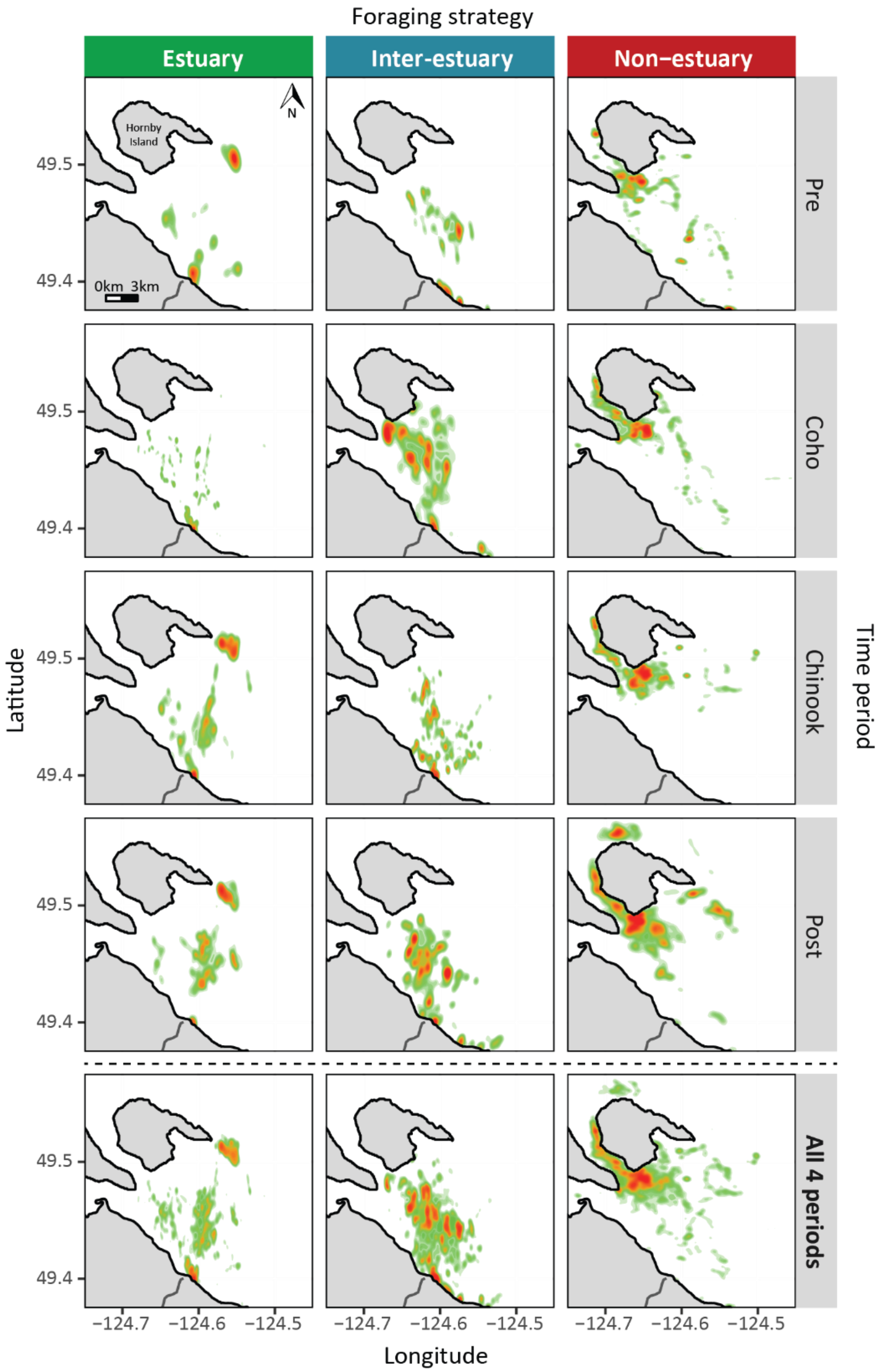

Figure 3.4: Feeding density maps of harbour seals grouped by foraging strategies in the Big Qualicum area determined from a kernel density analysis on all Prey Chasing Event (PCE) locations over 4 study periods (Pre-Release, Coho Release, Chinook Release, Post-Release). Estuary seals (n=3) had the highest percentages of PCE's in the Big Qualicum estuary, Intermediate estuary seals (n=3) had low percentages of PCE, and Non-estuary (n=8) seals had minimal or null percentages of PCE. Time periods include: Pre (May 2nd-4th)—3 days before the release of coho smolts; Coho (May 5th-14th)—10 days between the release of coho and Chinook smolts; Chinook (May 15th–24th)—10 days after the release of Chinook smolts; and Post (May 25th–June 2nd)—9 days at the end of the study period. Colour scale range from green (low feeding density) to red (high feeding density).

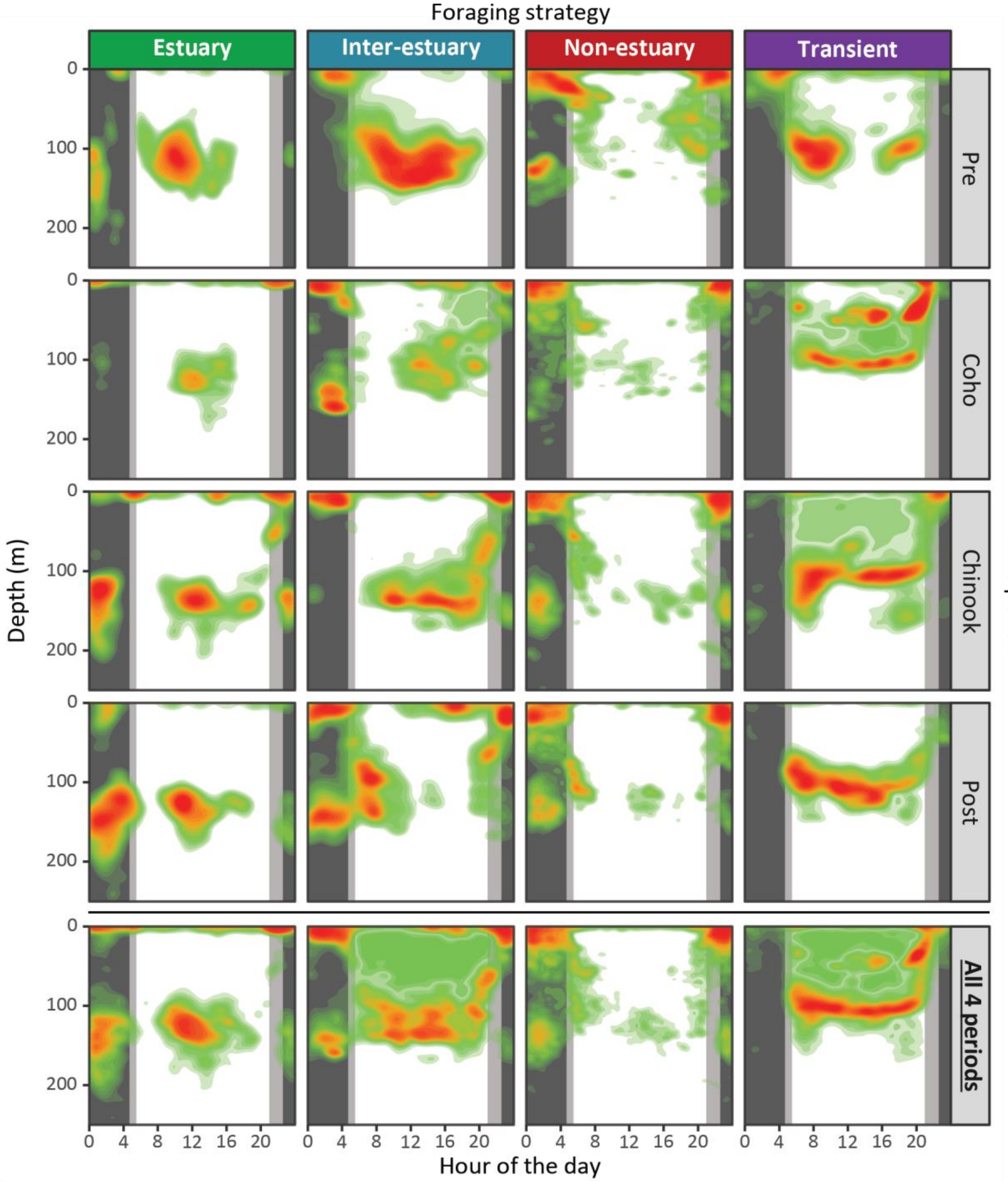

Figure 3.5: Feeding density of harbour seals grouped by foraging strategies determined from a kernel density analysis on depth and time of day (i.e., 24 hours) of all Prey Chasing Events (PCE) over 4 study periods (Pre-Release, Coho Release, Chinook Release, Post-Release). Estuary seals (n=3) had the highest percentages of PCE in the Big Qualicum estuary, Intermediate estuary seals (n=3) had low percentages of PCE, and Non-estuary (n=8) seals had minimal or null percentages of PCE's. The transient seals (n=2) were non-estuary seals that did not stay in the Big Qualicum area. Time periods includes Pre (May 2nd-4th)—3 days before the release of coho smolts; Coho (May 5th-14th)—10 days between the release of coho and Chinook smolts; Chinook (May 15th–24th)—10 days after the release of Chinook smolts; and Post (May 25th–June 2nd)—9 days at the end of the study period. Colour scale ranges from green (low feeding density) to red (high feeding density). Mean day (white), dawn (light grey), dusk (light grey), and night (dark grey) hours are delimited by background shading.

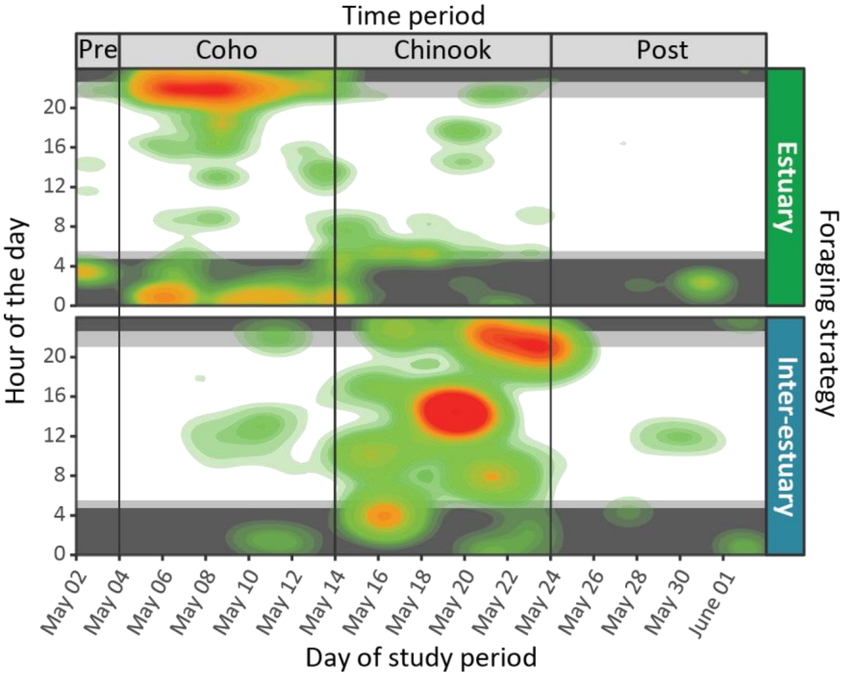

Figure 3.6: Feeding density of harbour seals grouped by foraging strategies determined from a kernel density analysis on the day and the time of all Prey Chasing Event (PCE) inside the Big Qualicum estuary. Estuary seals (n=3) had the highest percentages and intermediate estuary seals (n=3) had low percentages of PCE in the Big Qualicum estuary. Time periods include: Pre (May 2nd-4th)—3 days before the release of coho smolts; Coho (May 5th–14th)—10 days between the release of coho and Chinook smolts; Chinook (May 15th–24th)—10 days after the release of Chinook smolts; and Post (May 25th–June 2nd)—9 days at the end of the study period. Colour scale ranges from green (low feeding density) to red (high feeding density). Mean day (white), dawn (light grey), dusk (light grey), and night (dark grey) hours are delimited by background shading.

3.5 Discussion

We combined fine-scale movement tracks with body accelerations (as proxy for feeding) to identify foraging strategies used by 17 harbour seals during out-migrations of hatchery-released coho and Chinook salmon smolts from the Big Qualicum River in the Strait of Georgia. We identified 4 groups of seals with differing foraging strategies—of which one group (the "estuary seals", n = 3) fed on outmigrating coho smolts at dusk and night in the estuary, and a second group (the "intermediate estuary seals", n = 3) had few prey chasing events in the estuary after the release of Chinook smolts. The third group of seals (the "non-estuary seals", n = 9) stayed close to their haul-outs and fed in nearshore and deep waters, while the fourth group (the "transient seals", n=2) left the study area and travelled >100 km to feed and rest in others areas of the Strait of Georgia. These findings raise questions about the spatiotemporal variability in foraging behaviours within and among these foraging strategies.

3.5.1 In-estuary foraging strategies

Harbour seals are generalist and opportunistic predators feeding on large variety of prey (Lance *et al.* 2012), and thus, are likely to alter their daily, seasonal, or annual foraging behaviours to take advantage of abundant resource pulses such as outmigrating salmon smolts (Yang *et al.* 2008; Thomas *et al.* 2016). Among the 9 seals that fed in the Big Qualicum estuary, the estuary seal cluster (n = 3) regrouped the seals that had the highest PCE percentage (19.2 ± 8.1 %) inside the estuary (Figure 3.2). The feeding of the estuary seals occurred mostly after the release of coho smolts (48.2 ± 13.1 % PCE) and decreased over time to low percentages (11.1 ± 12.2 % PCE) during the Chinook smolt out-migration (Figure 3.3). These results suggest that estuary seals likely took advantage on coho, but not on the pulse of Chinook smolts.

The selection of coho over Chinook smolts by the estuary seals may be explained by the size and the energy density of the two species of smolts. When released from the estuary, the hatchery coho smolts (mean mass ~22.6 g and mean length ~12.9 cm) were heavier and larger than the Chinook smolts (mean mass ~5.9 g and mean length ~8.0 cm). Others have reported that harbour seals in other systems are more likely to choose prey ranging between 10 and 16 cm (Tollit *et al.* 1997), which is consistent with the selection we observed of coho over Chinook smolts. The energy density of coho smolts leaving rivers (~5.04 kJ/g) has also been shown to be higher than Chinook smolts (~3.98 kJ/g ; Roby *et al.* 2003). Thus, coho smolts seemed to be more profitable prey for harbour seals based on their larger size and higher energy density—even though Chinook smolts were numerically more abundant.

Feeding of the estuary seals in the Big Qualicum estuary during the coho out-migration happened mostly at dusk and night with the highest intensity at dusk (Figure 3.6). This is consistent with salmon smolts actively swimming at night when migrating downstream, which has been suggested as an antipredator behaviour that counters their vulnerability during the day (McDonald 1960). Dusk is likely to be the most efficient time window for seals to hunt salmon smolts because luminosity is low enough for the smolts to initiate their migration and high enough for the seals to be able to detect them (Wilson *et al.* 2014).

The estuary seals (17.6% of the population) specialized in feeding on coho, but not on Chinook smolts in the Big Qualicum estuary. This group feed most intensively at dusk and night during the 7 days that followed the release of coho smolts. The presence of this group of seals in the river mouth is consistent with the tendency of other small proportions of harbour seal populations specializing in feeding on salmon in rivers and estuaries (Wright *et al.* 2007; Graham *et al.* 2011).

Intermediate estuary seals (n = 3) fed in the estuary at low percentages (4.4 ± 0.6 %) during the Chinook smolt out-migration period (Figure 3.2). However, it seems unlikely that these individuals were feeding on outmigrating Chinook smolts. First, there was no functional response to the 3 million Chinook smolts compared to the presence of 350,000 coho smolts. Second, the highest feeding intensity of the intermediate estuary seals occurred 4 days after the release of the Chinook smolts compared to the estuary seals that fed intensively less than a day after the release of the coho smolts (Figure 3.6). Finally, the intermediate estuary seals fed in the estuary during all hours of the day, but at higher intensities during the day (~12:00-16:00), late day and dusk (~19:00-22:00), and late night and dawn (~4:00-5:00).

As previously mentioned, salmon smolts initiate their migrations in rivers and estuaries at night (McDonald 1960), which does not align with the intermediate estuary seals feeding more during the day. Instead, the low intensity and the delayed feeding response of the intermediate estuary seal feeding suggest an indirect response to the release of Chinook smolts (Yang *et al.* 2008). In other words, the seals may not have been actually directly feeding on the Chinook smolts themselves—but on other larger fish that were preying on Chinook smolts. Many prey species consumed by harbour seals (Lance *et al.* 2012; Thomas 2015) are known to feed on outmigrating salmon smolts. These include the Pacific hake, spiny dogfish, river lamprey, adult Chinook salmon, lingcod and walleye pollock (Beamish & Neville; Armstrong & Winslow 1968; Beamish *et al.* 1992; Fresh 1997; Emmett & Sampson 2007).

Our assessment of predation by seals on outmigrating smolts might underestimate their impact because of how we reconstructed seal tracks and estimated feeding events (i.e., PCE—a proxy for seal feeding intensity). First, the relatively small area of the Big Qualicum estuary and the method we used to correct dead reckoning tracks does not allow for estimating the error associated with each location. Second, some real feeding events might not have been detected by the accelerometer located on the seal backs rather than on the seal heads. This could occur for example if the seals swam against the water current and used only head movements to intercept dense schools of smolts. Similarly, some harbour seals might have used suction in addition to biting (Marshall *et al.* 2014) to capture small, slow moving prey, which would have little body acceleration and make these feeding events undetectable.

3.5.2 Foraging strategies: movement and diving behaviour variation

In contrast to the resident animals (i.e., estuary, intermediate estuary, and non-estuary seals) that stayed within the Big Qualicum area (< 30 km from capture sites), 2 of the captured animals travelled >100 km from the capture sites and were deemed transient seals (n=2; 11.7%). Long distant movements of small numbers of seals have been previously observed in the Salish Sea (Peterson *et al.* 2012) and in other ecosystems as well (Lowry *et al.* 2001; Lesage *et al.* 2004; Cunningham *et al.* 2009; Vincent *et al.* 2010). These seals typically haul-out at multiple sites, but tend to make short foraging trips near them (Hardee 2008; Peterson *et al.* 2012). The transient seals were all males, and although we did not find a significant difference in mass and length between the foraging strategies, the transient seals were among the largest individuals tracked (Table 2). Other studies have reported males tending to travel further than females (Lowry *et al.* 2001; Lesage *et al.* 2004; Peterson *et al.* 2012).

Aside from feeding areas, the only variables that distinguished the 4 types of foraging strategies were differences in rates of dives and prey chasing events (Table 3.2 & Table 3.3). The two groups of seals that fed in the Big Qualicum estuary (i.e., estuary and intermediate estuary seals) had lower dive rates than the seals that fed outside (i.e., non-estuary and transient seals). The estuary and intermediate estuary seals did not dive when in the river and estuary (~ 3-5 m), which is consistent with previously observed predation on outmigrating smolts (Yurk & Trites 2000). Due to their foraging strategies, these seals dove less frequently, and thus, presumably could have reduced their foraging effort to target salmon smolts that tend to swim close to the surface (Dawley *et al.* 1986).

Estuary and intermediate estuary seals had lower rates of prey chasing events (PCE) than non-estuary and transient seals, which we did not expected. The seals targeting smolts in the estuary presumably captured more individual fish to meet their daily metabolic energy requirements (Thomas *et al.* 2016) than the seals outside the estuary that captured larger prey such as adult Chinook salmon, Pacific herring, Pacific hake, and walleye pollock. Thus, the burst changes in accelerometry we quantified to estimate prey chasing events should have been higher in the estuary. Instead, it appears that the accelerometer on the seal back may not have captured the more passive hunting technics used to capture (i.e., yielding higher rate of false negative PCE).

It is also possible that the number of PCE's detected varies between prey types whereby small prey such as smolts results in a single PCE detection, and larger prey such as an adult salmon result in multiple PCEs. Longer chasing times to capture a large prey could result in multiple high accelerations that translate into multiple PCEs. Prey in open water are likely more difficult for seals to capture than prey in constraint habitats (e.g., rivers and estuaries), and could therefore result in more unsuccessful capture attempts. Finally, extra PCEs (i.e., higher rates of false positive PCE) could also occur if larger prey require a longer active handling phase.

3.5.3 Foraging strategies: spatiotemporal feeding variation

Within the Big Qualicum area, the 3 resident groups of seals showed considerable spatial and temporal separation in their feeding habitats (Figure 3.4). Estuary seals fed mostly in the river mouth during the coho out-migration and also around Flora Islet—as well as less intensively in the open water between these 2 locations. In contrast, non-estuary seals concentrated their feeding in south and west areas of Hornby Island mostly in the Norris Rocks area (Figure 3.4)—while the intermediate estuary seals used roughly the space between the estuary and the non-estuary seals feeding habitats. The habitat used by this intermediate group therefore overlapped with the one used by the other two groups of seals. However, intermediate estuary seals fed close to Norris Rocks while the estuary seals fed in the estuary during the coho release period—and later moved to the estuary during the chinook release period while the estuary seals moved to the open water and Flora Islet.

In addition to feeding locations, diving depths and feeding times of day differed between the 4 foraging strategies (Figure 3.5). Estuary and non-estuary seals seemed to feed at specific and consistent depths and times of day—although estuary seals shifted from deep daytime feeding to shallow feeding at dusk and nighttime during the coho release period. Overall, estuary seals fed between ~100–200 m depth at mid-day and night, except during the coho release period—whereas, the non-estuary seals fed at night mostly within the first 50 m depth, but at lower intensity along the water column reaching ~180 m depth. Conversely, the feeding behaviour of intermediate seals seemed to be more variable over time. These intermediate seals were shallow and nighttime feeders (< 50 m) similar to the non-estuary seals—as well as deep (~ 100 to 200 m) daytime and nighttime feeders similar to the estuary seals (Figure 3.5).

The spatial and temporal variability seen among the 4 foraging strategies suggests that the groups of seals are targeting different types of prey. Many studies have shown differences in seal diets that correspond to among-individual differences in feeding habitats (Tollit *et al.* 1998; Hastings *et al.* 2004; Lance *et al.* 2012; Wilson *et al.* 2014). The spatial composition of prey species tend to reflect physical factors such as bathymetry, temperature, salinity, current and sea-bed sediment type that influences primary and secondary production (Gray 1974; Lough *et al.* 1989; Gray & Otway 1994; Perry *et al.* 1994). In our study, estuary and intermediate estuary seals fed in the Big Qualicum estuary that is characterized by sandy and soft bottom—whereas the non-estuary seals fed mainly along Hornby Island that is characterized by a mix of sandy and rocky bottoms. Seals targeting different prey types are known to exhibit different foraging behaviours (e.g., diving depths, diurnal patterns, etc.), which are usually associated with differences in sex, age, and region (Thompson *et al.* 1998; Hastings *et al.* 2004; Wilson *et al.* 2014).

By comparing the spatiotemporal feeding variability between all seal foraging strategies, our analysis suggests that estuary, non-estuary, and transient seals were specialist predators compared to the intermediate estuary seals that were generalist predators. Estuary seals specialized on feeding on coho smolts in the Big Qualicum estuary, as well as on prey located in deep and open waters. However, the distinct feeding hotspots found at mid-day and nighttime suggest that the seals targeted different prey types. Non-estuary seals mainly fed at night on near-shore prey within the first 50 m depth, but also fed at lower intensity at deep depths (~ 100–180 m). Transient seals on the other hand tended to feed more at depth during the day (~ 90–120 m) suggesting that they targeted a specific prey type. Estuary, non-estuary, and transient seals seemed to be consistent in their depths and daytime feeding hotspots—whereas intermediate estuary seals seemed to be more variable in the depths and times of day they fed. Thus, the generalist intermediate estuary seals likely targeted a wider range of prey that overlapped with those taken by estuary and non-estuary seals.

3.5.4 Why multiple foraging strategies?

Foraging and dietary specializations are widespread in the animal kingdom (Bolnick *et al.* 2003) as shown in marine species as sea otters (Tinker *et al.* 2007), marine birds (Tremblay & Cherel 2000; Camprasse *et al.* 2017), odontocetes (Ford *et al.* 1998), and otariids (Lea *et al.* 2002; Villegas-Amtmann *et al.* 2008; Kernaléguen *et al.* 2015). Some intra-species niche variation is likely affected by sexual dimorphisms (Temeles *et al.* 2000), ontogenetic shifts (Polis 1984), and discrete morphological group differences (Smith & Skúlason 1996)—as well as by individual specializations (Bolnick *et al.* 2003). In our study, we were restricted to capturing adult sized harbour seals >60 kg (Olesiuk 1993), and ultimately caught and tracked mostly adult males. Given, the low sexual dimorphism of harbour seals compared to other pinniped species (Staniland 2005), and the small sample size of females, it seems most likely that the different foraging strategies we uncovered reflect individual specializations.

Individual specialization could be promoted by ecological factors such as predation and intra- and inter-specific competition (Araújo *et al.* 2011). For instance, sea otters showed high individual diet specialization in a resource-poor area (Tinker *et al.* 2008) compared to a resource-rich area where no diet specialization occurred between individuals (Bentall 2005).

The community composition of the Salish Sea ecosystem has changed dramatically in recent decades due to changes in the physical environment (Beamish *et al.* 1999; Gower 2002; Masson & Cummins 2007), fishing and harvesting regulations (DFO 2002; Olesiuk 2010; Carretta *et al.* 2011), and salmon enhancement initiatives (Beamish *et al.* 2008; Labelle 2009). In Puget Sound (the southern portion of the Salish Seas), the ecosystem has shifted from high-energy forage fish such as Pacific herring and surf smelt to low-energy prey such as sticklebacks and jellyfish (Greene *et al.* 2015). Harbour seal diets in the Salish Sea have been dominated by Pacific herring and Pacific hake (Olesiuk 1993; Lance *et al.* 2012), which either have high inter-annual variability in numbers or have declined (DFO 2009, 2012; Preikshot *et al.* 2013). Such diminution and variability in these key prey species may amplify variability among foraging behaviours and diet compositions of individual harbour seals. Thus, estuary seals may specialize in eating outmigrating coho smolts because their preferred prey (i.e., more profitable prey such as Pacific herring and Pacific hake) are not as available as before or may be less predictable among years. The millions of salmon smolts released by hatcheries in the Salish Sea as part of the Pacific Salmon Enhancement Program (Labelle 2009), might favour specialisation of seals feeding on smolts. These salmon smolts are released annually in large numbers at predictable times, and would provide energy to harbour seals at minimal foraging costs (Yurk & Trites 2000).

Although, intra-species variance in foraging behaviours is mostly driven by extrinsic factors such as competition, predation, or social interactions, the process that drives an individual to adopt a certain foraging strategy or to select one combination of prey over another is more intrinsic to individuals (Bolnick *et al.* 2003). Optimal foraging theory predicts an individual should choose among available prey to maximize energy gain and reproductive success (Stephens & Krebs 1986). However, individuals in any given habitat are unlikely to perceive and evaluate prey value in the same way due to behavioural, morphological, and physiological trade-offs that in turn result in fundamental differences among them in foraging niches (Bolnick *et al.* 2003). An individual that adopts a specific foraging strategy would expand its ability to perform that strategy while losing the ability to efficiently employ an alternative strategy. Multiple foraging trade-offs have been found in predators related to prey recognition and searching (Bernays 1998; Bernays & Funk 1999), prey capture and handling (Robinson 2000), and prey digestion (Burrows & Hughes 1991).

Personalities is another individual factor that could lead to the creation and maintenance of different foraging niches (Réale *et al.* 2007; Toscano *et al.* 2016). Individuals with different personalities might access different resources due to differences in their foraging activity (Sweeney *et al.* 2013), foraging spatial distribution (Cote *et al.* 2010; Quinn *et al.* 2011), foraging social interactions (Briffa *et al.* 2015), predation risk (Griffen *et al.* 2012), or physiological traits (Careau *et al.* 2008; Biro & Stamps 2010). Bolder individual are likely to be more risk averse than shy individuals which make them using area of high predation risk and a larger range of dispersal hosting different prey compositions (Clobert *et al.* 2009; Griffen *et al.* 2012). Thus, differences in harbour seal personalities might explain some of the apparent individual specialization in diet compositions and foraging strategies.

3.6 Conclusion

In summary, we found 4 harbour seal foraging strategies from which only one group (3 seals; 17.6%) seemed to specialize on consuming outmigrating coho at the mouth of the Big Qualicum River. This group of seals showed a preference for coho smolts, but did not target the subsequent migration of Chinook smolts into the ocean. The 4 documented foraging strategies differed spatially and temporally, suggesting they reflect different degrees of individual specializations to capture different species of prey.

Individual specialization has implications for management and conservation. In our case, only a small proportion of harbour seal population targeted coho smolts in river mouths, which means that survival of coho smolts could be increased by preventing a few individual predators from accessing the smolts rather than taking actions against the remaining larger population of seals that feeds on alternative prey. Such action was taken in the Baltic Sea where damage to salmon traps was reduced by implementing a selective culling program targeting grey seals that had specialized on exploiting salmon trap fisheries (Königson *et al.* 2013). Although there is a tendency to assume homogeneity of diets and foraging behaviours of predator populations, our study and others point to individual specialization that have implications for modelling food webs, competition, and predator-prey interactions (Bolnick *et al.* 2003), as well as decisions and actions to conserve and manage wildlife populations (Graham *et al.* 2011).

Chapter 4: Research conclusions

The goal of my study was to understand how out-migrating coho and Chinook salmon smolts (i.e., juvenile fish) impact harbour seal foraging behaviour in the Strait of Georgia. I achieved this by mapping the feeding distribution of 20 tracked seals in space and time to identify areas of high feeding intensity (i.e., feeding “hotspots”). I then looked at differences in the foraging strategies used by individual seals relative to the timing of the salmon smolt out-migrations. The 20 harbour seals were equipped with biologgers near Big Qualicum River where thousands of coho and Chinook smolts are released annually by the Big Qualicum Hatchery. From the data obtained from the seals, I was able to reconstruct their fine-scale movements and identify feeding events derived from the seal body accelerations. Overall, I used the geographical location, depth and time of the seal feeding events to differentiate individual strategies and estimate their potential impact on the coho and Chinook smolts when leaving the Big Qualicum river mouth.

I found that the majority of the seals I tracked fed in the Big Qualicum area. In fact, 80% of the seals remained during the study period. The other 20% of the seals traveled long distances and used other areas in the Strait of Georgia such as Howe Sound and Deep Cove. Within the Big Qualicum area, the largest feeding hotspot was near Norris Rocks, the most important harbour seal haul-out site in that area (Olesiuk 2010). I also found that the Big Qualicum estuary was a feeding hotspot for the local harbour seal population. Although, 8 seals fed in the estuary, only 3% of total feeding occurred there. I found that only few seal individuals (n=3) were specialized in feeding on coho, but not on Chinook smolts. This specialization on coho was reflected by increased feeding intensity in the Big Qualicum estuary after the release of the coho smolts.

In addition to the coho smolt specialist feeders, I also observed another group of seals in the Big Qualicum estuary (n=3) that seemed to react to the Chinook smolt release. However, due to the timing and low intensity of feeding, and a delay in their functional response, I believe that their apparent response to the Chinook smolt pulse was likely an indirect response. This means that this group of seals were likely targeting other fish predators of Chinook smolts rather than the smolts themselves.

In addition to the seals that seemed to respond to the presence of salmon smolts, I noted two other feeding patterns suggestive of feeding on deep-water species. Thus, I concluded that seals in my study area employed different foraging strategies (i.e., fed at different locations, depths and times of the day), suggesting 4 individual foraging and diet specializations.

4.1 Summary of findings

By tracking harbour seal movements in the Strait of Georgia, I found that the majority of the tracked seals (80%) stayed within the Big Qualicum area, where we captured them, and made short foraging trips (< 30 km) around their main haul-out sites. The other smaller proportion (20%) of seals travelled long distances (>100 km) and used multiple haul-out sites at different areas such as Howe Sound and Deep Cove. My results are consistent with previous studies that described the general spatial distribution and space use of harbour seal populations. Harbour seals are considered a non-migratory species that is faithful to their main haul-out sites, particularly during breeding and moulting seasons (Yochem *et al.* 1987; Van Parijs *et al.* 2000; Härkönen & Harding 2001; Cordes & Thompson 2015). Nonetheless, a small portion of harbour seal populations are known to travel long distances (> 100 km) to reach and use other areas and haul out sites (Thompson *et al.* 1996; Lowry *et al.* 2001; Simpkins *et al.* 2003; Lesage *et al.* 2004; Peterson *et al.* 2012). These differences between the movements of individual seals have been attributed to multiple factors such as the preferential use of certain habitats, the spatiotemporal changes in prey density, competition, predation risk, and even to their personalities (Tollit *et al.* 1997; Brown *et al.* 1999; Bolnick *et al.* 2003; Chapman *et al.* 2011).

My results showed that the Big Qualicum estuary was a feeding hotspot for the local harbour seal population during the salmon smolt out-migrations. Harbour seals are generalist and opportunistic predators that feed on a large variety of prey (Middlemas *et al.* 2006; Lance & Jeffries 2007; Thomas *et al.* 2011). Therefore, harbour seals likely take advantage of these temporary resource pulses. Earlier studies have also observed similar behaviour in harbour seals during salmon smolt out-migrations (Yurk & Trites 2000), as well as during adult returns (London *et al.* 2002; Middlemas *et al.* 2006). However, feeding in the Big Qualicum estuary related to smolt migrations represented only 3% of all the total feeding events I detected. This result is consistent with the percentage of coho (2.9 %) and Chinook (2.9 %) smolts that Thomas *et al.* (2016) found in harbour seal scats in the Strait of Georgia. Although, salmon smolts represent a small proportion of the seal diet, Thomas (2015) suggested that when converted to a number of individuals, these small percentages could account for millions of smolts consumed in a single month.

Although 8 seals (47%) fed in the Big Qualicum estuary, I found that only 3 seals (17.6 %) targeted coho and not Chinook smolts by increasing their feeding intensity in the Big Qualicum estuary during the 4 days following the release of the coho smolts from the Big Qualicum Hatchery. The fact that harbour seals fed more on coho smolts compared to Chinook in the spring is consistent with an analysis of seal scats that found seals in the Strait of Georgia consumed coho smolts mainly from April to July, and Chinook smolts in June-July (Thomas *et al.* 2016). There is strong evidence that harbour seals start feeding on coho smolts as soon as they leave rivers whereas they target Chinook smolts later during the summer.

The reason why harbour seal target coho over Chinook smolts during early out-migration could be due to the size and the energy density of the smolts. When leaving the Big Qualicum Hatchery, coho smolts are larger in size and have higher energy density than Chinook smolts (see Discussions in Chapters 2 & 3 for more details). In addition, the size of coho smolts (~12.6 cm) is within the range of 10-16 cm length that is thought to be the preferred prey range for harbour seals, whereas Chinook smolts were <10 cm (Tollit *et al.* 1997).

From the spatiotemporal distribution of harbour seal feeding, I showed that harbour seals adopted distinct foraging behaviours and strategies. I found 4 foraging strategies that varied in their feeding patterns inside the Big Qualicum estuary as well as their global spatial distribution in the Strait of Georgia. These seal groups fed in different geographical locations, depths and times, which suggest that they targeted different prey (Tollit *et al.* 1997, 1998; Luxa & Acevedo-Gutiérrez 2013). Differences in foraging behaviours have been reported in harbour seals (Tollit *et al.* 1998; Hastings *et al.* 2004; Wilson *et al.* 2014) in addition to many other marine predators (Ford *et al.* 1998; Lea *et al.* 2002; Tinker *et al.* 2007; Villegas-Amtmann *et al.* 2008; Camprasse *et al.* 2017). Usually these differences in foraging behaviours can be explained by sex and age (Thompson *et al.* 1998; Hastings *et al.* 2004). However, all of the individuals we captured were adults, and the proportion of females were small relative to the males, which prevented testing for differences due to age or sex. I therefore hypothesise that the differences I observed in foraging strategies were likely due to individual specialisation and preferences (Bolnick *et al.* 2003).

4.2 Strengths and weaknesses

As with all research, my thesis research had its strengths and limitations. Although, others have recorded the movements and foraging behaviours of harbour seals in the Salish Sea (Hardee 2008; Olesiuk 2010; Thomas *et al.* 2011; London *et al.* 2012; Peterson *et al.* 2012; Ward *et al.* 2012; Wilson *et al.* 2014; Berejikian *et al.* 2016), my research is the only one that has tracked seals at a very fine-scale (every second) and combined seal locations, depths and body accelerations to determine feeding behaviours.

In my study, I used acceleration of the seal's body as a proxy for feeding events. Over the past decade, accelerometry has become increasingly used to analyse specific animal behaviours (Brown *et al.* 2013). A number of studies have used head-mounted accelerometers to identify prey capture attempts in multiple marine species (Viviant *et al.* 2010; Gallon *et al.* 2013; Volpov *et al.* 2015), and is accepted to being a more accurate means to identify foraging behaviours than other traditional methods. These traditional methods typically infer animal foraging from either dive data or location data.

Inferring foraging from only dive and location data can be misleading given that harbour seals are generalist predators and display a variety of foraging behaviours (Tollit *et al.* 1998; Wilson *et al.* 2014). For instance, it was shown that many pinniped species including harbour seals often rest at depth while at sea (Crocker *et al.* 1997; Watanabe *et al.* 2015). This behaviour, when resting on the bottom, could result in a U-shaped dive that is usually considered to be a foraging dives, and would therefore overestimate the overall foraging behaviour (Lesage *et al.* 1999; Baechler *et al.* 2002). Moreover, in the Salish Sea, harbour seals often move into shallow habitats such as rivers and estuaries where they feed near the surface (Yurk & Trites 2000). In this case, diving data would underestimate foraging because the animals are not diving.

Location data have been also used to infer foraging behaviours of other marine species (Le Boeuf *et al.* 2000; Fauchald & Tveraa 2003; Ramasco *et al.* 2015). Typically, animal movements are separated using horizontal speed and bearing into two categories such as *directed and fast travel*, and *resident behaviour* that has slower speeds and higher tortuosity (Boyd 1996; Le Boeuf *et al.* 2000). Such local and slow movements are attributed to area-restricted search (ARS) representing foraging effort within a prey patch (Fauchald & Tveraa 2003; Barraquand & Benhamou 2008). Multiple methods have been developed to identify these ARS such as the first-passage time (Fauchald & Tveraa 2003), the fractal landscape (Tremblay *et al.* 2007), the resident time (Barraquand & Benhamou 2008), and state-space models (Patterson *et al.* 2008). All of these methods have different strengths and limitations (review in Carter *et al.* 2016) but all of them simplify animal trips in two discrete behaviours, i.e., travelling and foraging (Jonsen *et al.* 2005; Breed *et al.* 2009). Therefore, using only location data to generate ARS would overestimated the foraging activity of our harbour seals because they frequently rested at the surface and at depth (Thompson *et al.* 1991; Boyd 1996; Crocker *et al.* 1997; Russell *et al.* 2015; Watanabe *et al.* 2015).

Some studies have combined location and diving data using state-space models to separate resting from foraging states, and improve activity budget estimates. In fact, combining horizontal and vertical movements has shown that harbour seals rest at the surface during >10% of their time at sea (Russell *et al.* 2015). However, these modelling approaches assume that animals forage and capture prey only at depth and do not consider that predators could target prey relatively close or right at the surface. In my study, I found that only a few harbour seals were specialized to take advantage of outmigrating salmon smolts by increasing their feeding intensity in water <3 m deep (depending on tide height) in the Big Qualicum River.

Although accelerometry is probably the best means to identify particular animal behaviours in the wild, it has some limitations. Accelerometry methods require recording acceleration at very high rates (from ~ 8 to 32 Hz) which drains batteries and results in large amounts of data. Therefore, deploying accelerometers is highly restricted to short time period and whether or not they can be recovered afterwards to download the data.

Estimating feeding events using body acceleration could be biased in different ways depending where a seal forages and on what type of prey it targets. First, high acceleration bouts could be detected and considered as feeding events when an animal is actually conducting non-feeding behaviours. For example, the social interactions of harbour seals with their conspecifics around haul out sites could be misinterpreted as feeding events. In addition, not all feeding events detected by acceleration are successful feeding events. Predators often miss their prey, which could vary according to the prey type and the experience and ability of the predator. For instance, feeding on schools of salmon smolts in shallow and restrained rivers is technically easier for a seal to be more successful compared to a school of Pacific herring in the open water. Therefore, missed capture attempts could be different within and among individual predators.

In addition to overestimating feeding events, there are situations where the acceleration algorithm may not be able to detect real feeding events and will hence underestimate feeding events. In my study, I had to attach the accelerometer on the back of the seals and not on their head. The majority of previous accelerometry studies have tested the detection of feeding events while the accelerometer was mounted on the animal head (Viviant *et al.* 2010; Jouma'a *et al.* 2015; Volpov *et al.* 2015). However, a few studies using two accelerometers (mounted on the head and the back of the animals) found that detection of prey capture attempts from the back is proportional to the one from the head, but with some underestimation (T. Jeanniard du Dot & C. Guinet, pers. comm.). In my study, seals that fed the most in the Big Qualicum River and estuary might swim against the river current and stabilize their bodies in the way that minimized movements while intercepting outmigrating smolts (Yurk & Trites 2000). Moreover, harbour seals can consume prey using suction in addition to biting feeding (Marshall *et al.* 2014). These two foraging tactics will result in minimal body acceleration, and will thus likely miss detecting some prey consumptions. Therefore, feeding on smolts in rivers may be underestimated compared to feeding in other habitats such as shorelines and open waters.

The main goal of my study was to accurately quantify the foraging behaviour of the local harbour seal population during the coho and Chinook smolt out-migrations from the Big Qualicum River. To achieve this, and to make sure that I had enough data from seals feeding in the Big Qualicum river mouth, I tried to capture half of the seals from the Big Qualicum estuary, and the other half from rocky haul out sites around the estuary. My results showed that not all seals move to the estuary to take advantage of the outmigrating smolts. However, I may have overestimated the proportion of seals feeding on smolts in the estuary because I did not randomly sample individuals in space. Avoiding this bias would have required capturing individuals at each haul out site in proportion to their estimated abundance recorded from past surveys (Olesiuk 2010).

An important challenge when working with wild animals is to have a balanced sample size between sexes, ages and other visible morphs in order to represent all behavioural variance in the population. Usually, the major limitation to achieving this goal is related to logistical and financial considerations. In my study, I sampled more males (n = 15) than females (n = 5) which decreases confidence in accurately describing the behaviours of the whole population. It is well know that adult males harbour seals may exhibit different foraging behaviours and strategies than juveniles and adult females (Thompson *et al.* 1998; Hastings *et al.* 2004). Our tendency to select males over females for tracking was due in large part to our requirement that the size and weight of the biologgers not adversely affect the movements and behaviours of our study animals. We therefore followed the recommended standard to restrict the weight of the devices to < 1-2% of the animal body weight (Sutton & Benson 2003; Wilson *et al.* 2004), which resulted in taking adult males because they tended to be > 60 kg (Olesiuk 1993).

A second factor that resulted in capturing more males than females was due to the capture methods I used. Most of the seals in my study were captured using the boat rush method, which consisted of rushing with a boat towards a harbour seal haul out site, jumping from the boat and capturing a seal as fast as possible using a hoop net. Many individual seals escaped into water before we reached the haul out site, and many of these escaping seals might have been females. Although there is no clear evidence about this specific behaviour, bolder individuals such as older males may be more readily captured than shier individuals (Biro & Dingemanse 2009). This might explain the sexual bias in my sample size since males tend to be bolder than females and less inclined than females to escape earlier when the boat rushed towards the haul out site.

4.3 Future research

My study contributed to understanding harbour seal foraging behaviour during salmon smolt pulses. However, there are many other aspects of foraging behaviour that could have been explored by combining telemetry and diet data together. My study described foraging behaviour of the seal population at a very fine-scale, and did not have additional information about what type of prey they fed on, and where and when that predation occurred. Intensive harbour seal scat collections should be conducted while biologgers are recording fine-scale information about the seal foraging behaviours to make better inferences about the prey the seals are consuming and where and when that predation occurs.

Other future research could spatially and temporally survey available prey in the Big Qualicum area. Although this is logistically and financially challenging to achieve, there are a number of benefits to doing so, such as knowing what seals do not eat in addition to knowing what they actually consume. This information would yield a better understanding of predator-prey interactions, and the concepts related to diet selection and optimal foraging theory that affect population dynamics and community structure. Fully understanding interactions between seals and salmons requires investigating all interactions between seals and all other available prey.

In my study, the positioning of the devices on the animal bodies had significant implications for my analyses. Logistical considerations meant that I had to attach my GPS tags and accelerometers to the animal backs. As a result, I had fewer GPS locations than I expected and probably missed multiple feeding events when the body movement was minimal. I therefore recommend that GPS tags be attached on top of the animal's head to increase the probability of getting a GPS location at every surfacing. I also suggest attaching accelerometers to the head of the animal, or on the necks if the head is not an option. Integrating GPS tags and accelerometers into the same device may resolve this constraint. However, it may limit battery lifespans and results in larger devices that ultimately affect diving performance.

In this study, we mainly captured individual seals in the Big Qualicum estuary and in the southern part of Hornby Island. However, a survey of the Big Qualicum area showed many other abundant harbour seal haul out sites within foraging distance from the Big Qualicum estuary (Hardee 2008; Olesiuk 2010). Thus, I recommend spreading the capture design across the different haul out sites available in the Big Qualicum area. For instance, there are multiple sites located on the southern part of Lasqueti Island that could be considered. An additional sampling design consideration when capturing seals from different haul out site is the relative abundance of seals using each site. This would mean for example that the number of seals captured from high abundant haul out sites such as Norris Rocks should be proportionally larger than other lower abundant sites such as Big Qualicum estuary.

Finally, logistic constraints in my study meant tracking harbour seals only 3 days before the release of coho smolts, which was insufficient to properly document harbour seal foraging behaviour when no salmon smolt pulses occurred. Recording feeding behaviours a few weeks before the release of the smolts would give a more thorough comparison of harbour seal behaviours before and after the smolt releases.

4.4 Application and importance of research

Past dietary studies have yielded valuable insights about harbour seal diet composition in the Salish Sea, as well as how it changes spatially and temporally (Lance & Jeffries 2007; Thomas *et al.* 2016). They have shown when and at what proportion harbour seals are consuming salmon species either during their out-migrations when smolts leave rivers to reach the ocean or when adults return to their birth rivers to spawn (Thomas *et al.* 2016). Although the proportion of salmon smolts consumed is relatively small in the harbour seal total diet, it was suggested that predation of harbour seal on coho and Chinook smolts is likely having a substantial impact on these salmon populations. However, little attention has been given to understanding where, when and how this predation occurs, and more importantly, whether or not individual harbour seals vary in their rates of predation on coho and Chinook smolts. Thus, the tracking I undertook of fine-scale movements and foraging behaviours of harbour seals during the out-migrations of salmon smolts has direct implications in the conservation and enhancement of coho and Chinook populations in the Salish Sea.

In Chapter 2, I used the tracked harbour seal feeding events to identify areas of high feeding intensity. My results showed that harbour seals responded to coho smolt pulse released from the Big Qualicum Hatchery by increasing their feeding intensity in the estuary. However, there was not any clear functional response to the out-migrating Chinook smolts suggesting that the seals did not consume them at a significant rate. Although, the overall feeding intensity in the estuary was relatively small compared to the total feeding events, I found that harbour seals targeted coho smolts and not Chinook when they left the river. My findings therefore bring new insights into understanding interactions between harbour seals and out-migrating coho and Chinook smolts, which is essential for developing adequate conservation actions to enhance salmon marine survivals.

In Chapter 3, I quantified harbour seal general foraging behaviour to identify various foraging strategies among seals that are consistent with individual foraging and diet specialization. I found predation on out-migrating coho smolts in river mouths is a specialized behaviour of a small group of seals. Thus, my study provides new information about harbour seal predation that could be used to conserve coho salmon populations through targeted actions on a sub-group of the harbour seal population.

In conclusion, I sought to increase knowledge about harbour seal foraging behaviour in the Salish Sea. Harbour seals are one of most abundant predators, and are known to have an important impact on the Salish Sea ecosystem structure and dynamics (Olesiuk 1993; Thomas *et al.* 2011; Lance *et al.* 2012; Ward *et al.* 2012). Thus, my findings about variability in harbour seal foraging behaviours can be used to improve ecosystem models, and further the conservation and management of salmon populations.

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Appendices

Appendix A - Biologger package

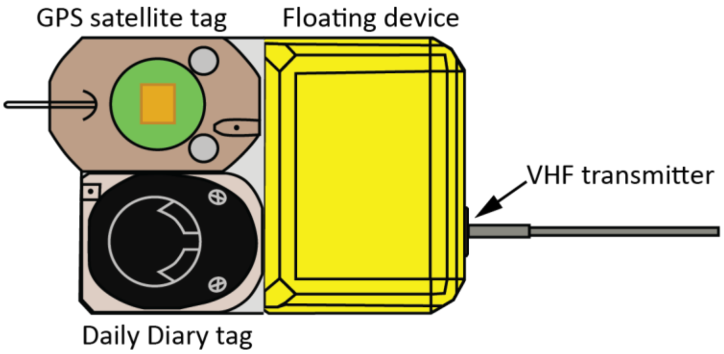

Figure A-1: The biologger package used to equip harbour seals. It includes a Global Positioning System (GPS) satellite tag (Splash 10-F; Wildlife Computers, Redmond, WA, USA), a Daily Diary tag (Wildlife Computers, Redmond, WA, USA), a Very High Frequency (VHF) transmitter (MM190B; Advanced Telemetry Systems, Isanti, MN, USA), and a floating device for recovery.

Appendix B - Bathymetry maps

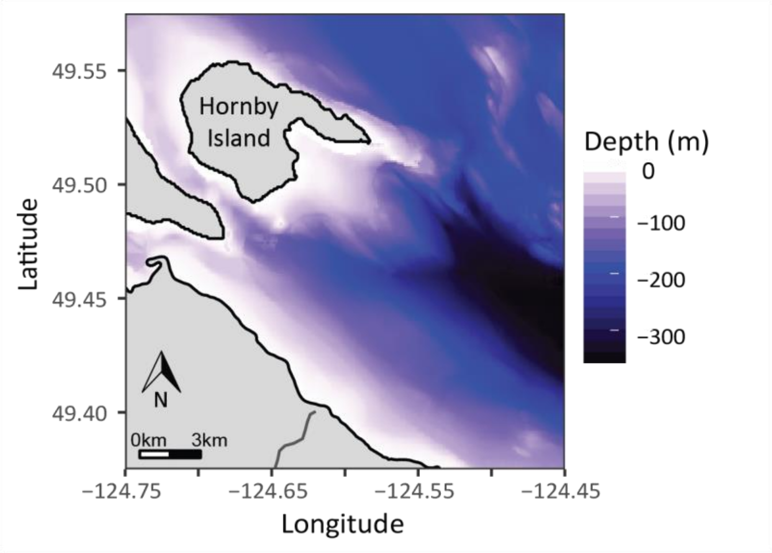

Figure B-1: Bathymetry depth (m) of the Big Qualicum area.

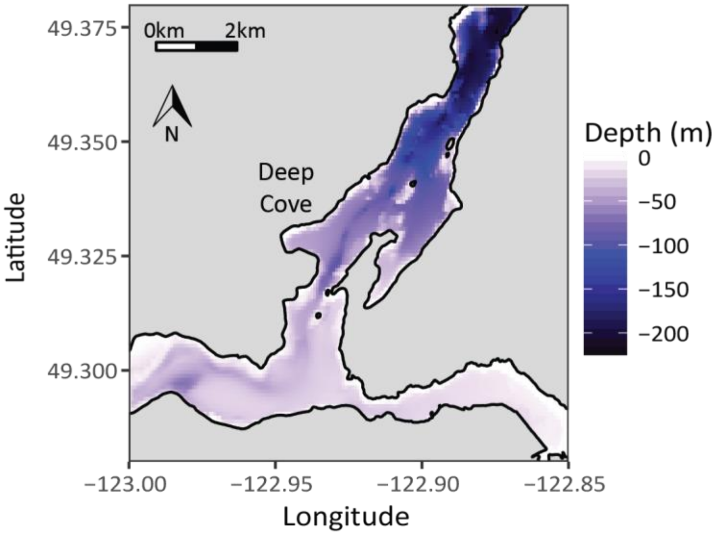

Figure B-2: Bathymetry depth (m) the the Deep Cove area.

Appendix C - Foraging strategies (Hierarchical cluster analysis)

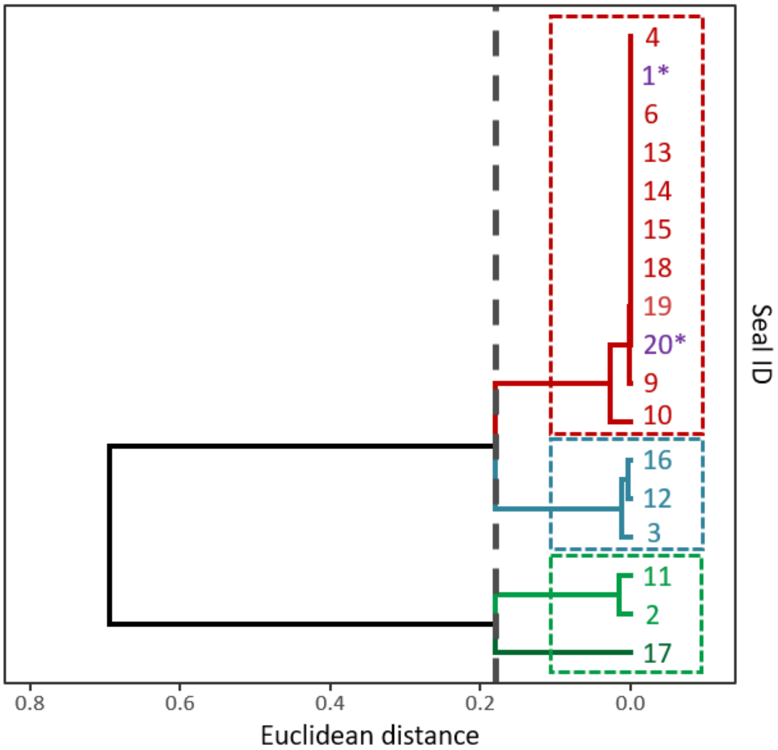

Figure C-1: Dendogram of hierarchical cluster analysis used to detect grouping in feeding intensity in the Big Qualicum estuary among individual harbour seals. Although, the hierarchical cluster analysis suggested 4 groups, we grouped Seals #2, #11 and #17. The green cluster is the estuary seals with high percentages of PCE in the estuary, the red cluster is the intermediate seals with low percentages of PCE in the estuary, and the red cluster is the non-estuary seals with very low or none of percentages in the estuary. Although Seals #1 and #20 were also non-estuary seals, we combined them in a distinct group because they left the Big Qualicum area and used other areas in the Strait of Georgia (i.e., Howe Sound and Deep Cove).

Appendix D - Activity intensity (Seal #19)

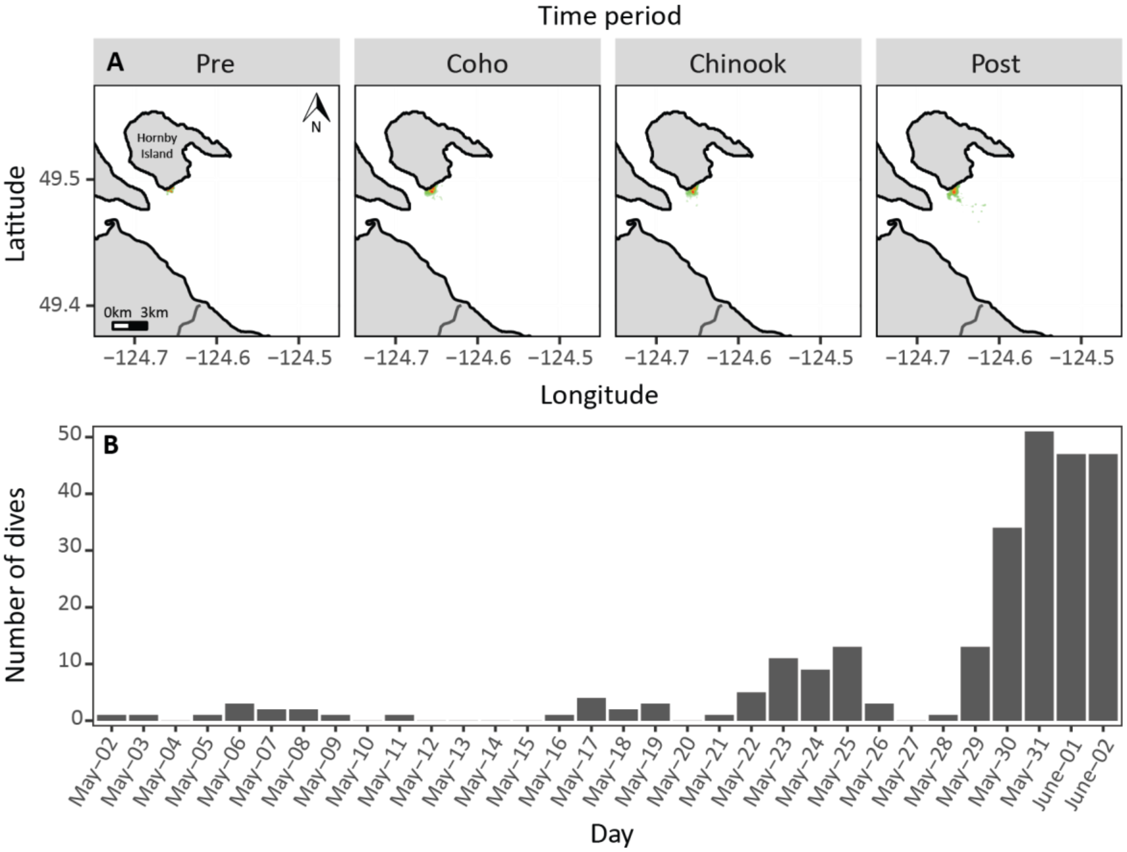

Figure D-1: Spatial distribution and diving intensity of Seal #19 from May 2nd to June 2nd, 2015 in the Strait of Georgia. (A) Areas used by Seal #19 during the 4 study periods. Colour scale ranges from green (low feeding density) to red (high feeding density). Time includes: Pre (May 2nd-4th)—3 days before the release of coho smolts; Coho (May 5th 14th)—10 days between the release of coho and Chinook smolts; Chinook (May 15th–24th)—10 days after the release of Chinook smolts; and Post (May 25th–June 2nd)—9 days at the end of the study period. (B) Number of dives may by Seal #19 for each day of the study period.

Appendix E - Foraging depth and time

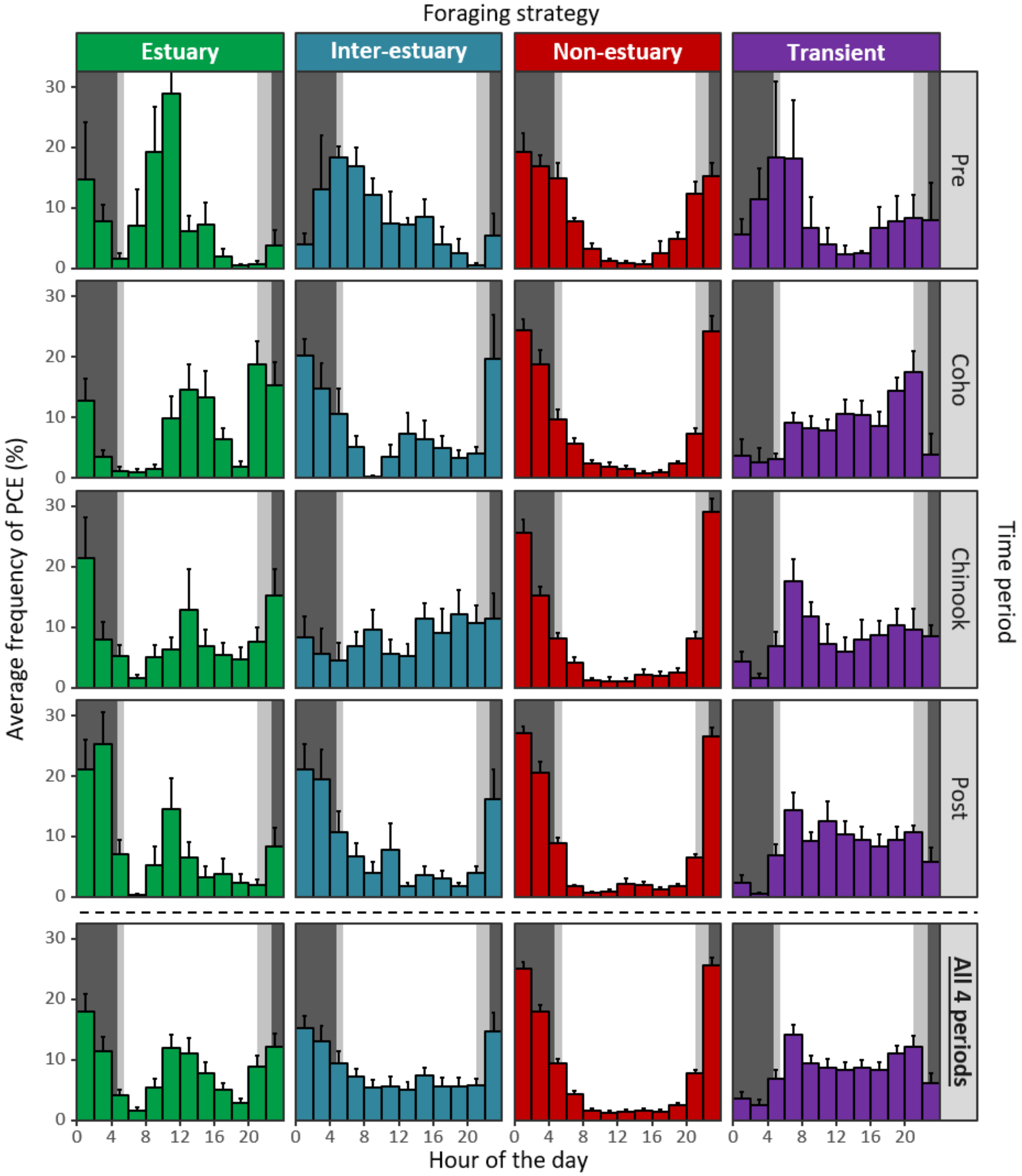

Figure E-1: Average frequency of Prey Chasing Events (PCE) per day (% ± SE) for each 2 hour interval over 4 study periods (Pre-Release, Coho Release, Chinook Release, Post-Release). Estuary seals (n=3) had the highest percentages of PCE in the Big Qualicum estuary, Intermediate estuary seals (n=3) had low percentages of PCE, and Non-estuary (n=8) seals had minimal or null percentages of PCE's. The transient seals (n=2) were non-estuary seals that did not stay in the Big Qualicum area. Time periods includes Pre (May 2nd-4th)—3 days before the release of coho smolts; Coho (May 5th 14th)—10 days between the release of coho and Chinook smolts; Chinook (May 15th–24th)—10 days after the release of Chinook smolts; and Post (May 25th–June 2nd)—9 days at the end of the study period. Mean day (white), dawn (light grey), dusk (light grey), and night (dark grey) hours are delimited by background shading.

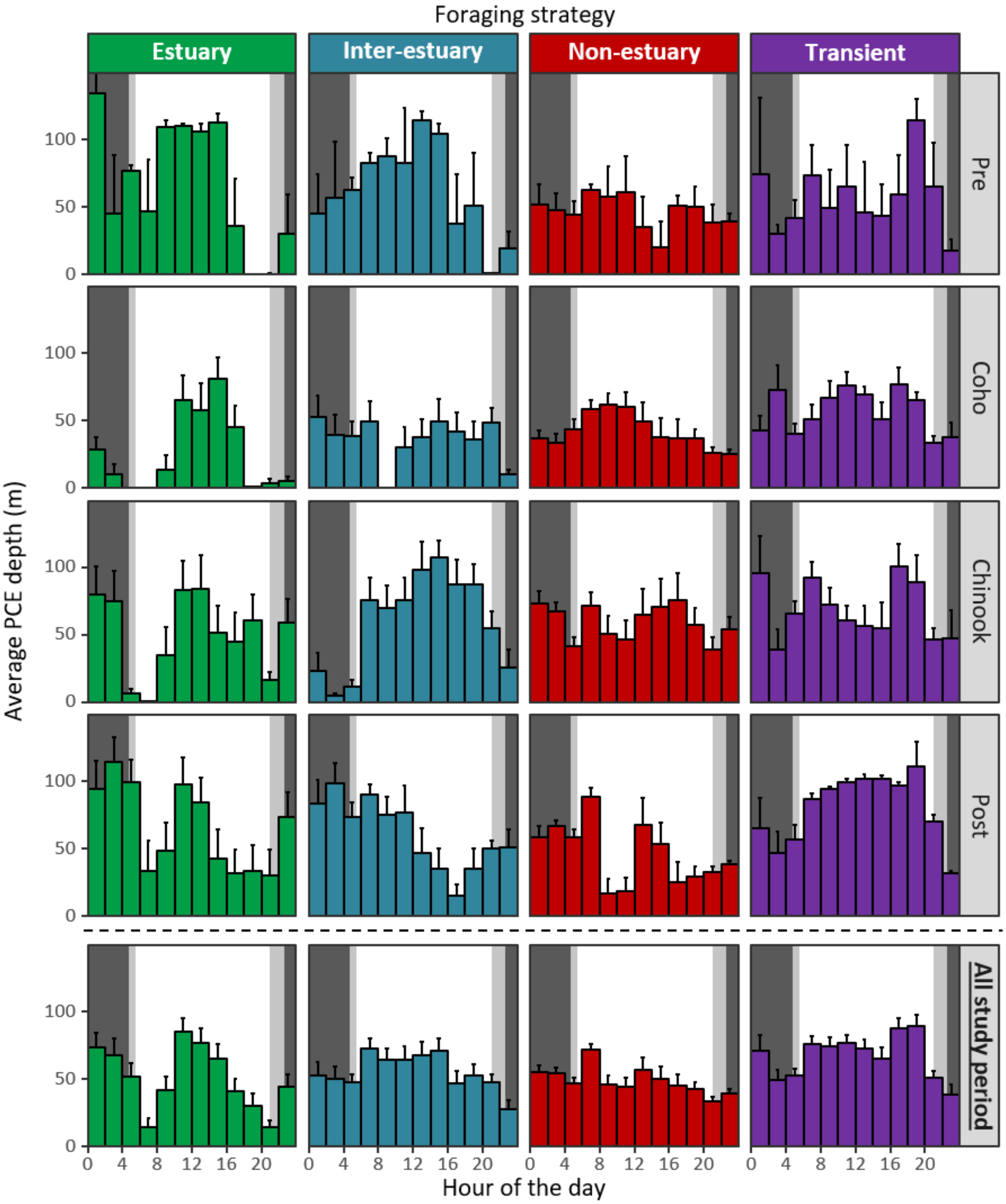

Figure E-2: Average depth of Prey Chasing Events (PCE) per day (AVG ± SE) for each 2 hour interval over 4 study periods (Pre-Release, Coho Release, Chinook Release, Post-Release). Estuary seals (n=3) had the highest percentages of PCE in the Big Qualicum estuary, Intermediate estuary seals (n=3) had low percentages of PCE, and Non-estuary (n=8) seals had minimal or null percentages of PCE's. The transient seals (n=2) were non-estuary seals that did not stay in the Big Qualicum area. Time periods includes Pre (May 2nd-4th)—3 days before the release of coho smolts; Coho (May 5th 14th)—10 days between the release of coho and Chinook smolts; Chinook (May 15th–24th)—10 days after the release of Chinook smolts; and Post (May 25th–June 2nd)—9 days at the end of the study period. Mean day (white), dawn (light grey), dusk (light grey), and night (dark grey) hours are delimited by background shading.