**FORAGING BEHAVIOUR AND REPRODUCTIVE SEASON HABITAT SELECTION OF NORTHEAST PACIFIC PORPOISES**

by

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**A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF**

**DOCTOR OF PHILOSOPHY**

in

The Faculty of Graduate Studies

(Zoology)

THE UNIVERSITY OF BRITISH COLUMBIA

(Vancouver)

September 2011

## Abstract

Behavioural observations are fundamental to understanding and defining the habitat needs of animals. I compiled the behavioural repertoires reported for harbour (*Phocoena phocoena*) and Dall's porpoise (*Phocoenoides dalli*) by classifying the life processes of phocoenids into 12 descriptive categories. This range-wide review revealed complex sexual and social behaviours, similar foraging behaviours and breeding site fidelity, as well as differences in habitat selection between these two northern hemisphere species. I also conducted a fine-scale field study of harbour porpoise foraging behaviour at two sites in Juan de Fuca Strait (British Columbia) using point transect survey data (2007–2008), and platforms of opportunity data (1995–1996, 1998–2008) to determine the physical conditions under which harbour porpoise foraged and the extent to which they displayed specialised behaviours. I examined harbour porpoise presence, density and group sizes relative to tidal currents, tidal variation, lunar phase, lunar position, solar position, diurnality, seasonality and presence of conspecifics—and found that greater numbers of harbour porpoise occurred on the ebb current during the spring tides. Numbers of porpoise increased three-fold between April and October, when calves and high-energy behaviours were also more prevalent. To identify porpoise breeding habitat in the inland waters of southern British Columbia and northwestern Washington, I used systematically and opportunistically collected sightings of harbour and Dall's porpoise (1991–2008), and compared group sizes and frequency of occurrences for both species relative to bathymetry and tidal speeds. Overall, I found that both species selected bathymetrically differentiated habitats that were characterized by high rates of tidal mixing (with harbour porpoise preferring regions ≤100 m, and Dall's porpoise preferring 151 – 250 m). Spatial analysis identified two separate areas that may be species-specific breeding habitats—the first to be identified for either species in this region. In summary, harbour porpoise maintained stable group sizes and used tidally well-mixed foraging sites on a temporary but predictable basis. Dall's porpoise were associated with these same areas, but habitat partitioning associated with differences in bathymetry occurred in important breeding areas that may account for the coastal parapatric distribution of these two high trophic level predators.

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**Acknowledgements**

My PhD thesis is dedicated to my friends and family for encouraging me to achieve my academic aspirations; to the amazing wildlife of British Columbia for inspiring me; and to my dogs, Rainha and Spike, for teaching me the subtleties of animal behaviour.

**Chapter I – Introduction**

Ecology dates from the earliest times when humans began accumulating knowledge of natural history, and exploiting natural resources to increase their material comfort and security (Elton, 1933). However, ecological knowledge has transitioned from that which was required for the survival of early humans, to that which is now required for the survival of our planets' ecosystems. The foundations for contemporary conservation research were laid down during the mid-19$^{th}$ to mid-20$^{th}$ centuries when species identification, taxonomic classification, animal behaviour, and biological theory became increasingly popular among naturalists (*e.g.*, Humboldt and Bonpland, 1805; Allee, 1931; Gause, 1934; Hutchinson, 1959; Klopfer and MacArthur, 1961). Though these studies ranged from the ethological, to the ecological, to the psychological — they often shared a common emphasis of unraveling the mysteries of the lives of animals (Klopfer, 1962), and revealed an increasing appreciation for the complexity of animal behaviour (*e.g.*, Elton, 1927; Carpenter, 1934; Tinbergen, 1951; Sutherland, 1958; Lorenz, 1965). Understanding the behavioural repertoires of animals in an ecological context is now a cornerstone of zoological research.

Population and species survival are often directly linked to understanding the behaviours associated with the fundamental life processes of foraging, habitat selection and reproduction (Scott, 1958). As habitat for wildlife continues to be reduced or altered through human actions, research into behavioural repertoires is becoming increasingly needed to provide a solid foundation for conservation.

Knowledge of how animals select and use their habitats for foraging and reproduction is crucial for effective wildlife management. Significant progress was made in understanding the importance of species-specific habitat requirements when it was realised that some animals modify existing environmental features to their advantage. Examples include the Galapagos Islands' woodpecker finch (*Camarhynchus pallidus*) which selects particular cactus spines or twigs to use as insect probes (Millikan and Bowman, 1967), and Tanzanian chimpanzees (*Pan troglodytes*) which fashion termite probes out of branches (Goodall, 1964). Conversely, other animals are known to use existing features without modification, such as the Japanese macaques (*Macaca fuscata*) that use fresh and sea water to wash their food prior to consumption (Kawai, 1962),

bottlenose dolphins (*Tursiops* sp.) that use sponges to protect their rostra during bouts of benthic foraging (Smolker et al., 1997), and South American bowerbirds (*Ptilonorhynchus sp.*) that select twigs as construction materials and other objects including feathers, flowers and snakeskin as decorative materials in hopes of attracting mates (Borgia, 1985).  Based on this broad spectrum of taxa and behaviours, it seems likely that there are other species that use environmental features that have not yet been discovered.  As such, research that identifies the habitats associated with the fundamental life processes of particular species, and how those species interact with specific environmental features will provide ecological insights that will contribute to their conservation.

The scope of individual and group behaviours varies temporally, spatially and across taxa.  Some species exist in socially and behaviourally complex societies that remain cohesive for extended periods of time (*e.g.*, the savannah elephant, *Loxodonta africana*: Schulte, 2000; Bradshaw et al., 2005), whereas others have more solitary lives that are punctuated with temporally discrete social encounters (*e.g.*, the red-billed tropicbird, *Phaethon aethereus*: Kaufman, 1996).  There are inherent difficulties associated with studying and interpreting both individual and group behaviours, as many animals are secretive when alone, and many individuals are not readily visible to observers when animals aggregate.  These observational challenges are exacerbated in the study of cetaceans, particularly for the smallest species of cetaceans that have few surface-active displays.

Cetaceans are among the least studied and understood species.  They are also experiencing growing changes to their habitats associated with environmental degradation, displacement, risk of vessel collision, anthropogenic noise and chemical pollution (Klinowska, 1991; IUCN, 2009).  Population level impacts of anthropogenic changes remain largely unknown, but are likely exacerbated for species that occupy mostly coastal habitats, such as porpoise.

Porpoise are members of the Phocoenidae family (Gray, 1825) and are one of the least known assemblages of mammals.  They are difficult to observe in the wild because of their small size, and often (though not always) do poorly when held in captivity.  As

such, the ecological awareness of porpoise is spatially and temporally discontinuous, with differential levels of knowledge by species and geographic location.

Recent global assessment by the International Union for Conservation of Nature (IUCN) revealed that populations of the two warm-water phocoenid species, the finless porpoise (*Neophocaena phocaenoides*, Cuvier 1829) and vaquita (*Phocoena sinus*, Norris and McFarland 1958) are declining with the former considered *Vulnerable* and the latter *Critically Endangered* (IUCN, 2009). The two southern hemisphere cold-water species, the spectacled (*Phocoena dioptrica*, Lahille 1912) and Burmeister's porpoise (*Phocoena spinipinnis*, Burmeister 1865) are considered *Data Deficient*, and are classified as having an *Unknown* global conservation status (IUCN, 2009). Finally, the two northern hemisphere cold-water species, the harbour (*Phocoena phocoena*, Linnaeus 1758) and Dall's porpoise (*Phocoenoides dalli*, True 1885) are ranked as *Least Concern*, with *Unknown* global population trends (IUCN, 2009).

The southern species of porpoise have not fared well in the face of human encroachment on their habitat, and there is concern that the northern species may ultimately do no better. Range-wide research on northern species of porpoise is warranted, particularly in light of the sensitivity of harbour porpoise to human activity (Leatherwood et al., 1982; Gaskin, 1984; COSEWIC, 2003), and the questionable sustainability of the directed and incidental levels of mortality of Dall's porpoise (EIA, 2008; Hammond et al., 2008b; EIA, 2009). This is especially true in British Columbia where Dall's and harbour porpoise share the coastal waters with fisheries, recreational boaters, commercial vessel traffic, sewage and other urban runoff and development. Significant knowledge gaps exist about the habitat needs of northern hemisphere porpoise.

## Research Objectives, Hypotheses and Study Site Justification
### Objectives and Hypotheses

My research focused on the habitats and behaviours related to foraging and reproduction of the two cold-water porpoises of the North Pacific. Both the harbour and Dall's porpoise occupy the inshore waters of British Columbia throughout the year; both

have seasonal reproductive schedules with calving occurring in the summer; and both are relatively short-lived high trophic level predators that provide a prey base for top coastal predators. Despite these similarities, distinct differences exist in their life histories and habitat needs (see Chapter II).

The main objective of my dissertation was to determine how the foraging efficiency of coastal phocoenids is optimized by their habitat choice. I undertook a multi-scale study that included: 1) a 12-month field season with two marine study sites in southern British Columbia, 2) an expanded data series spanning a 13-year period in the same region, and 3) a multi-source data set encompassing 18 years of observations from a larger geographic area of coastal BC. My research was centered on a working hypothesis that coastal phocoenids in British Columbia live in relatively restricted habitats that contain oceanographic features that contribute to increased levels of tidal mixing. My study was designed to address three hypotheses related to foraging and reproductive habitat selection:

H1. Porpoise have a higher probability of occurring in and near areas of increased tidal mixing.

H2. Porpoise use localised areas of increased tidal mixing as temporary but predictable foraging arenas. Within these areas, a positive relationship should exist between the probability of occurrence and the directional tidal currents, and a negative relationship should exist on the slack tide.

H3. Porpoise densities are higher in and near tidally mixed zones during the reproductive season.


*Study Site Justification*

Little is known about the ecology of harbour and Dall's porpoise in British Columbia. I therefore sought to maximize the ecological contribution of my research by including both species in the habitat evaluation. I tested my hypotheses with a combination of systematic and opportunistic survey data, oceanographic data and oceanographic models relevant to southern British Columbia. Analysis of my observational data was biophysical and tested the relationships between porpoise

behaviour, oceanographic conditions and astronomical events. Unfortunately, logistics and declining Dall's porpoise sighting frequency limited the foraging arena work to harbour porpoise, but the reproductive habitat assessment included both species.

The inshore waters of southern British Columbia are an excellent location to study the behavioural ecology of harbour and Dall's porpoise because long-term sightings data are available, the coastal waters are logistically accessible, the oceanography is well studied (Thomson, 1981; Foreman et al., 1995; Farmer et al., 2002; Lutus, 2007), and it appears that most phocoenids have limited movements (Flaherty and Stark, 1982; Calambokidis and Barlow, 1991; Calambokidis and Baird, 1994a; Hanson et al., 1999; Chivers et al., 2002).

**Thesis Structure**

My thesis is organised into five chapters, with Chapters II – IV written as stand-alone publications, and Chapters I and V as required thesis components. Chapter I provides an introduction to my research objective, hypotheses, and my study site. Chapter II is a detailed comparative review of the behavioural ecology of harbour and Dall's porpoise using the principal classifications of Scott (1958) as a structural guide. This chapter also provides life history overviews for both species and is range-wide in scope, whereas Chapters III and IV are restricted to the inland waters of southern British Columbia. In Chapter III, I test my foraging behaviour hypothesis by examining whether harbour porpoise use specific areas of increased tidal mixing as temporary but predictable foraging arenas. In Chapter IV, I test my habitat selection hypothesis, which is again centered on the relative rates of tidal mixing, by examining both harbour and Dall's porpoise distributions during the reproductive season in southern British Columbia. Finally, Chapter V provides a summary of the major findings, associated biases and suggests directions for future work.

**Chapter II – Behavioural repertoires of the cold-water porpoises of the North Pacific**

**Introduction**

Knowing the behavioural needs of animals and how animals respond to change is an important element of conservation biology that can contribute to understanding the adaptability of species to environmental stressors. However, animal behaviours are often complex and highly varied, and typically require lengthy periods of observation to properly document. Acquiring such knowledge about cryptic or aquatic species is particularly challenging but is needed to ensure that any future behavioural shifts that may occur, do not go unnoticed as human pressures in marine ecosystems escalate.

In spite of their coastal distributions and proximity to dense human populations, the two species of cold-water porpoises that inhabit the North Pacific remain some of the least understood small cetaceans. One of the species, Dall's porpoise (*Phocoenoides dalli*), is endemic to the inshore and offshore waters of the Pacific Ocean, whereas the second, harbour porpoise (*Phocoena phocoena*), is more widespread within the neritic waters of the Northern Hemisphere. Neither species of porpoise occurs in tropical waters or in the southern hemisphere. Dall's and harbour porpoise both rely on small fish and squid for food, and have large geographic ranges with an approximate mean latitude of distribution of 55°N (Whitehead and Mann, 2000). Both species consume prey targeted by commercial fisheries, and both are subjected to incidental and intentional mortality associated with fishing throughout their ranges (Gaskin et al., 1974; Jefferson, 1988; Klinowska, 1991; Jefferson and Curry, 1994; Hammond et al., 2008b; Hammond et al., 2008a; EIA, 2009).

The available behavioural information about Dall's and harbour porpoise is spatially and temporally discontinuous. Some areas of their ranges are almost entirely devoid of data, while others have detailed historical records suggesting that some behaviours commonly associated with porpoise may no longer occur. Aspects of the natural history of harbour porpoise have been documented for centuries, which is rare among species of cetaceans that were economically unimportant (*i.e.*, Tyson, 1680; Linnaeus, 1758; Gray, 1865; Scammon, 1874; Van Beneden and Gervais, 1880; Service, 1896). Unfortunately, the scientific record for Dall's porpoise is poorer, and more

dependent on the relatively recent incidental catch or hunting records of the western Pacific (*e.g.*, True, 1885; Hepburn and Waterston, 1901; Miller, 1929; McTaggart-Cowan, 1944; Okada and Hayashi, 1951; Wilke et al., 1953; Kuroda, 1954; IWC, 1978; Walker, 1996). It is with this in mind that I have synthesized the available literature to document what is and remains to be known about the behavioural repertoires of these two porpoises.

My objectives were three-fold: 1) review what is currently known about the behaviours of Dall's and harbour porpoise, 2) identify gaps in knowledge, and 3) highlight useful research that will further contribute to their conservation. To allow the porpoise behaviours to be placed within a biological context, I begin with an overview of the life history of each species. I then present my behavioural review structured according to the nine categories identified by Scott (1958): 1) ingestive (foraging), 2) shelter-seeking (habitat selection), 3) sexual, 4) agonistic, 5) epimeletic, 6) et-epimeletic, 7) allelomimetic, 8) eliminative and 9) investigative — which I supplemented with additional categories of 10) avoidance, 11) social, and 12) rest (and sleep). To finish, I integrated the major findings with suggestions for future research directions.


**Life History**

*Harbour Porpoise*
The harbour porpoise is currently recognised as a single species with infraspecific classifications to the subspecies taxon. The three most accepted classifications are *Phocoena phocoena phocoena* in the North Atlantic, White, Barents and Kara Seas, *Phocoena phocoena vomerina* in the Pacific and *Phocoena phocoena relicta* in the Black and Azov Seas (Figure 2.1: Gaskin et al., 1974; Rosel et al., 1995; Wang et al., 1996; Read, 1999; Reeves and Notarbartolo di Sciara, 2006). In addition, Rice (1998) suggested an east-west division of the Pacific Ocean at the Aleutian Islands separating *P.p. vomerina* in the eastern North Pacific with a yet un-named subspecies in the western North Pacific (Figure 2.1).
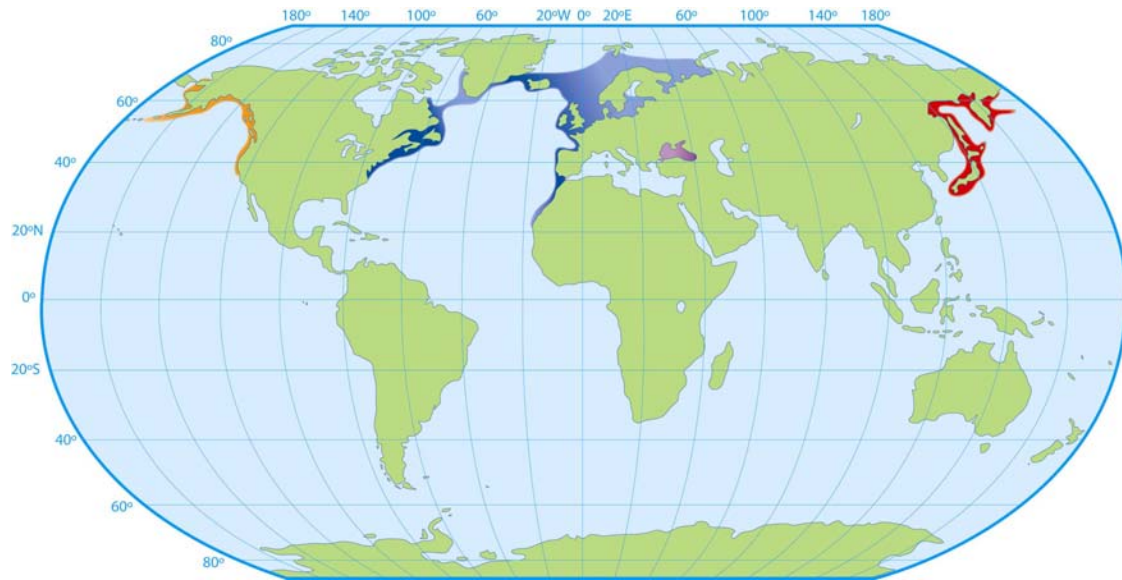
**Figure 2.1 Harbour porpoise subspecies distribution:** ***Phocoena phocoena phocoena*** **(dark blue),** ***P.p. relicta*** **(purple),** ***P.p. vomerina*** **(orange) and the proposed, but un-named western Pacific subspecies (red).**

Little phenotypic variation is observed throughout the harbour porpoise range, and although some regional differences have been found, none appear to be geographically unique (Koopman and Gaskin, 1994). Overall, this species has a counter-shaded pigmentation pattern of black to grey-brown on the dorsal surface with lighter lateral pigmentation, and white to greyish-white on the most ventral surface (Figure 2.2). Usually only the dorsal pigmentation is visible to observers due to the low profile of harbour porpoise while at the surface.

As the smallest oceanic cetacean, adult harbour porpoise range between 150 – 160 cm and 45 – 60 kg, with neonates about 70 – 90 cm and 5 kg (Møhl-Hansen, 1954; Fisher and Harrison, 1970; Gaskin et al., 1974; van Utrecht, 1978). Sexual dimorphism is evident from birth (Yurick and Gaskin, 1988), and continues throughout life to maturity at about 3 – 4 years of age when females exceed males by about 10 cm and 10 kg (Gaskin and Blair, 1977; van Utrecht, 1978; Read, 1990a; Sørensen and Kinze, 1990; Gearin et al., 1994; Lockyer, 1995; BMBF, 1997; Karakosta et al., 1999; Lockyer et al., 2001; Ólafsdóttir et al., 2002).

Harbour porpoise have been described as a promiscuous and polygynandrous species that uses sperm competition as the primary reproductive strategy (Grier and Burk,

1992; Fontaine and Barrette, 1997). The reproductive season is discrete, synchronous and seasonal, with males becoming reproductively active during the summer (Meek, 1918; Fraser, 1953). At the onset of the breeding season, the male testes increase markedly in size to account for 3 – 6% of the total body mass, exceeding mammalian body size ratio expectations by 13 times (Kenagy and Trombulak, 1986; Read, 1990b; Fontaine and Barrette, 1997). The calving interval is annual in most regions (Read, 1990b; Gaskin, 1992; Read and Hohn, 1995; Koschinski, 2002; Börjesson and Read, 2003), with the exception of California where it is considered biennial (Hohn and Brownell, 1990). Data are absent for much of the northeast Pacific so it is unknown whether all Pacific harbour porpoise adhere to this biennial schedule.

Harbour porpoise typically associate in groups of ≤10, with cow-calf pairs most easily identified (Gaskin et al., 1974; Leatherwood et al., 1982). Neonate growth is rapid (Gaskin, 1992), and the data on the timing of lactation and weaning are geographically and temporally discontinuous (Fisher and Harrison, 1970; Smith and Gaskin, 1974; Yasui and Gaskin, 1986; Smith and Read, 1992; Koschinski, 2002). Life spans can exceed 20 years, though 8 – 15 years is more common (Nielsen, 1972; Gaskin and Blair, 1977; van Utrecht, 1978; Hohn and Brownell, 1990; Gaskin et al., 1991; Gearin et al., 1994; Lockyer, 1995; Read and Hohn, 1995; Benke et al., 1998; Lockyer and Kinze, 1999; Gol'din, 2000; Lockyer et al., 2001; Ólafsdóttir et al., 2002; Rosel et al., 2003). It is not known how long weaned calves remain with their mothers, or whether related individuals have any long-term relationships. The degree of sociality is also not known, but ephemeral associations >200 animals have been documented (see sections *Ingestive Behaviour, Allelomimetic Behaviour, Rest and Sleep Behaviour* and Chapters III and IV).

Transient killer whales (*Orcinus orca*) and great white sharks (*Carcharadon carcharias*) are the harbour porpoises' main predators (Eschricht, 1862; Templeman, 1963; Arnold, 1972; Ford et al., 1998). Greenland sharks (*Læmargus microcephalus*) also eat harbour porpoise (Taylor, 1902; Williamson, 1963), but it remains unclear whether these sharks prey upon harbour porpoise or scavenge them *post-mortem*. Non-predatory, but lethal aggression directed against harbour porpoise is also demonstrated by Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) (A. Hall, pers. obs., Baird, 1998), bottlenose dolphins (*Tursiops truncatus*) (Ross and Wilson, 1996; Jepson et al.,

1997; Connor et al., 2000), and resident killer whales (A. Hall, pers. obs., Ford et al., 1998).

### *Dall's Porpoise*

Dall's porpoise are also classified as a single species, but debate exists regarding the taxonomy. Some consider them to be a single species that is phenotypically polymorphic (Ogawa, 1938; Benson and Groody, 1942; Houck, 1976; Rice, 1977; Kasuya, 1978; Shimura and Numachi, 1987; Jefferson, 1988; Escorza-Trevino et al., 2004), while others suggest there is sufficient differentiation to warrant possible classification into either subspecies or separate species (Yocom, 1946; Wilke and Kenyon, 1952; Kuroda, 1954; Tomilin, 1957; Nishiwaki, 1972; Rice, 1998; Amano and Hayano, 2007). The confusion exists because of two predominant phenotypes that are often referred to as the *truei*- and *dalli*-types, in which the main physical difference lies in the forward extent of the lateral white flank patches (Figure 2.2). Much of the described natural history is based on the *dalli*-types.

Dall's porpoise distribution includes the Sea of Japan, the Pacific waters of Japan, the Sea of Okhotsk, the Bering Sea, the Aleutian Islands, and along the western coast of North America, at least as far south as southern California, with the *truei*-types being restricted to Japanese Pacific waters, the Sea of Okhotsk, and the Kurile Islands (Figure 2.3 and Matsuura, 1943; Naguchi, 1943; Matsui and Naguchi, 1946; Wilke et al., 1953; Miller and Kellogg, 1955; Norris and Prescott, 1961; Ridgway, 1966; Klinowska, 1991). During the summer, Dall's porpoise are reported to occasionally move north into the Chukchi Sea (Sleptsov, 1961; Ridgway, 1966). The phenotype reported to move to the Chukchi was not specified, but based on what is known of migratory behaviour (see *Shelter Seeking Habitat Selection Behaviour*) it was likely the *dalli*-types.
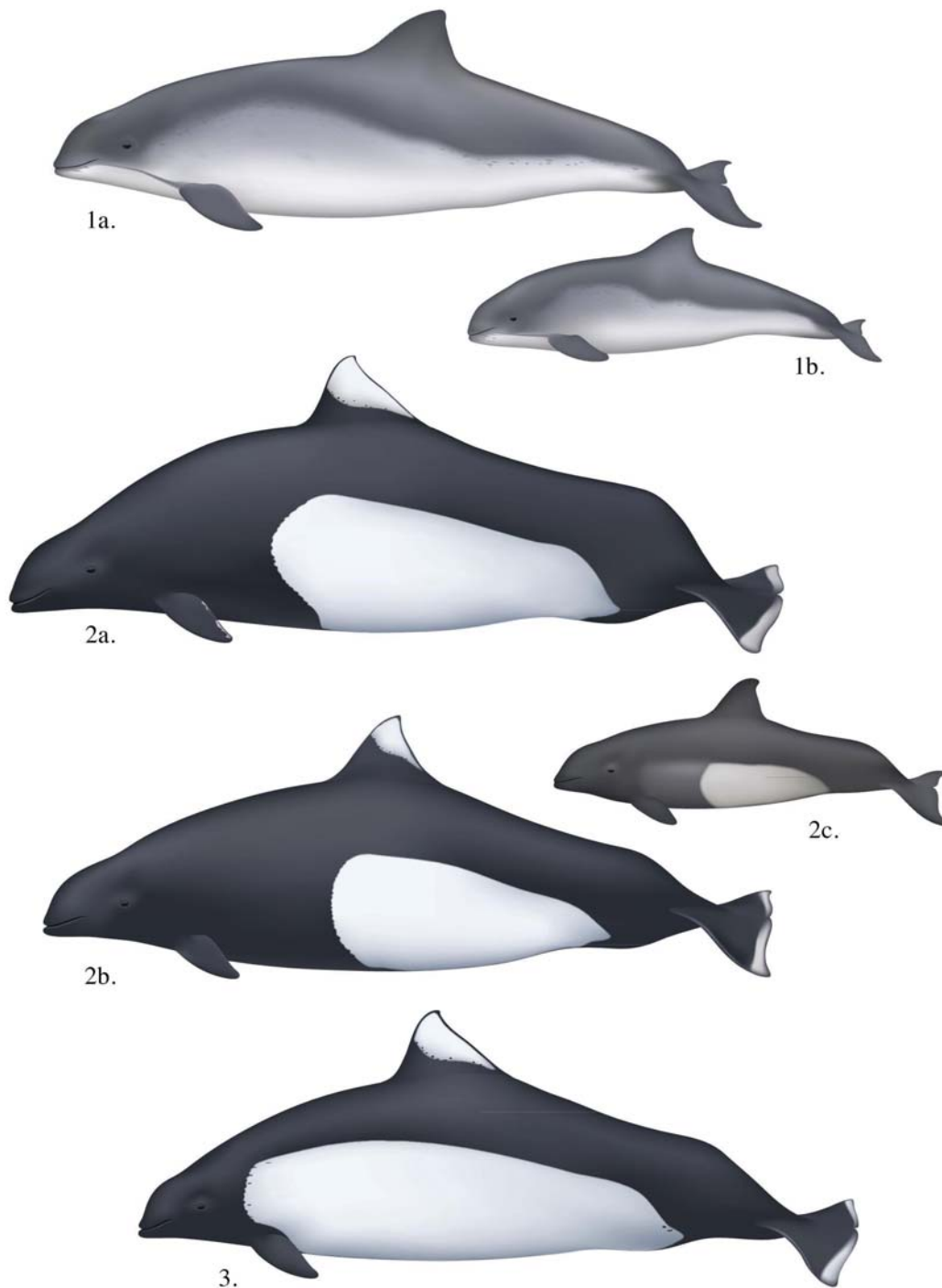
**Figure 2.2 Phenotypic variation of harbour and Dall's porpoise. 1a - mature harbour porpoise, 1b – juvenile harbour porpoise, 2a – mature male *dalli*–type Dall's porpoise, 2b – mature female *dalli*–type Dall's porpoise, 2c – juvenile Dall's porpoise, and 3 – mature male *truei*-type Dall's porpoise.**
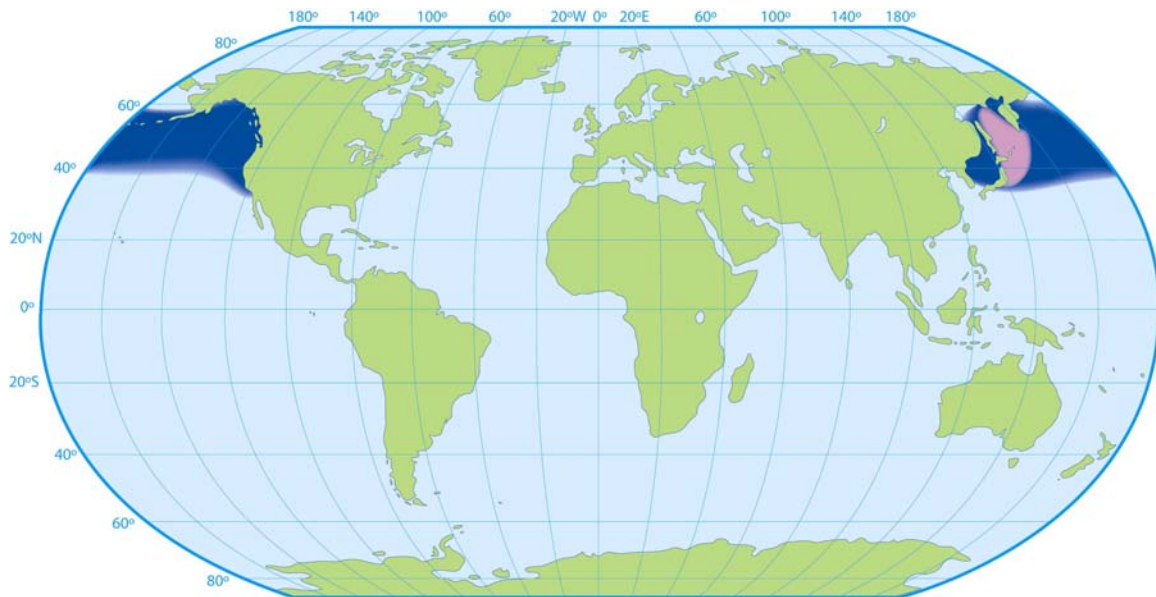
**Figure 2.3 Dall's porpoise distribution:** ***dalli*-type (blue) and *truei*-type (purple).**

The Dall's porpoise is the largest phocoenid at 210 – 220 cm and 200 kg at maturity, with neonates about 100 cm and 5.5 kg (Kasuya, 1978; Kasuya and Shiraga, 1985; Jefferson, 1988; Ferrero and Walker, 1999; Houck and Jefferson, 1999). Sexual maturity occurs at 3 – 6 years of age, when sexually dimorphic features distinguish the larger males from the smaller females (Kasuya, 1978; Newby, 1982; Kasuya and Shiraga, 1985; Jones et al., 1987; Miyazaki, 1987; Jefferson, 1989c; Ferrero and Walker, 1999; Whitehead and Mann, 2000), with the extent of the sexually dimorphic features varying geographically throughout the range (Amano and Miyazaki, 1996). Nevertheless, reproductively active males are recognisable by the pronounced dorsal and ventral keels, more canted dorsal fins, and an enlarged dorsal hump forward of the dorsal fin (Morejohn et al., 1973; Morejohn, 1979; Jefferson, 1988; Ellis, 1994; Amano and Miyazaki, 1996; Houck and Jefferson, 1999). Overall, this species lives 8 – 20 years, but animals older 10 years are rare (Walker, 1975a; Kasuya, 1978; Newby, 1982; Kasuya and Shiraga, 1985; Ferrero and Walker, 1999).

Parturition and reproductive behaviour can occur throughout the year, but most Dall's porpoise populations have a seasonal summer cycle with the females entering

oestrus within a month of parturition (Newby, 1982; Kasuya and Jones, 1984; Miller, 1987a; Ferrero and Walker, 1999). A period of delayed implantation has been suggested (Newby, 1982), but evidence supporting this has not yet been found. The monogamous or polygynous mating strategy involves seasonal male-male physical competition (Newby, 1982; Landino, 1985; Jefferson, 1989b), and the prominent secondary sexual characteristics and small testes relative to body size (Newby, 1982; Kasuya and Jones, 1984; Willis and Dill, 2007) indicate a mating strategy characterized by contest competition and low copulatory frequency (Ralls, 1977; Kenagy and Trombulak, 1986).

Physiologically, the onset of the male reproductive rut is characterised by a marked increase in testes weight, sperm production and body mass (Newby, 1982). Females may be spontaneous polyovulators, capable of ovulating several times until conception occurs (Newby, 1982). Unlike harbour porpoise, it seems that once male Dall's porpoise mate with a female, they then invest energy to prevent other males from accessing her (Willis and Dill, 2007). The calving interval ranges from 1 − 1.6 years (Okada and Hayashi, 1951; Kasuya, 1978; Kasuya and Jones, 1984), and the lactation period is estimated to range from 2 months (Loeb, 1972; Newby, 1982) to 3.5 years (Kasuya, 1978; Whitehead and Mann, 2000). It is not known how long weaned calves remain with their mothers, or whether any long-term relationships exist.

The degree of sociality of Dall's porpoise is also not well known, though group sizes typically range from 1 − 16 in oceanic populations (Miyazaki et al., 1984), and ≤6 in neritic populations (Pike and MacAskie, 1969; Hall, 1979; Bouchet et al., 1983; Dohl et al., 1983; Winans and Jones, 1988; Durban, 1994; Hall, 1996). Group size fluctuations related to behaviour or reproductive status have not yet been identified.

Transient killer whales are the only confirmed regular predators of Dall's porpoise (Rice, 1968; Pike and MacAskie, 1969; Barr and Barr, 1972; Morejohn, 1979; Newby, 1982; Taketomi, 1984; Bigg et al., 1987; Jefferson et al., 1991; Ford et al., 1998). Sharks are thought to be only occasional predators, as this porpoise's swim speed is likely prohibitive for predation by most shark species (Morejohn, 1979; Leatherwood et al., 1982).

It is clear that though both species belong to the same taxonomic family, significant similarities and differences exist within their life history parameters (Table 2.1). Furthermore, large data gaps exist for many aspects of their life histories. Once elucidated, these may further widen the life history gap between these two cold-water phocoenids.

**Table 2.1 Similarities and differences in the natural histories of northern porpoise.**

| | Harbour Porpoise | Dall's Porpoise |
|---|---|---|
| *Distribution* | | |
| Pacific Ocean | √ | √ |
| Atlantic Ocean | √ | |
| Neritic | √ | √ |
| Oceanic | | √ |
| *Size* | | |
| Adult <100kg | √ | |
| Adult >100kg | | √ |
| Neonate ~5kg | √ | √ |
| *Sexual Dimorphism* | | |
| Female > Male | √ | |
| Male > Female | | √ |
| *Reproduction* | | |
| Monogamy | | ? |
| Polygyny | | ? |
| Polygynandry | √ | |
| Sperm Competition | √ | |
| Contest Competition | | √ |
| *Longevity* | | |
| > 20 years | √ | |
| < 20 years | | √ |
| *Mean Group Size* | | |
| ≤ 10 | √ | √ |
| ≥ 10 | | √ |
| *Predators* | | |
| Killer Whales – Transient | √ | √ |
| Killer Whales – Resident | √ | |
| Sharks | √ | |
| Dolphins | √ | |

Table Key: √ – Indicates confirmed knowledge
? – Indicates uncertainty

**Behavioural Repertoires**

All aspects of an animal's ecology are influenced by its behaviour. Adaptations over time and space lend to variability within a species' behavioural repertoire. This can be more pronounced for those with broad geographical ranges. Though this wide spectrum of possibilities makes studying animal behaviour more interesting, it complicates our ability to make broad generalizations of a species behavioural ecology. Harbour and Dall's porpoise are no exception.

*Ingestive Behaviour*

Ingestive behaviours are defined as those used to acquire solid food and liquid (Scott, 1958). Much of what is known of the foraging behaviours of porpoise has been interpreted from surface observations, telemetry, and acoustics because direct underwater observation is rarely possible. Behavioural observations indicate that harbour porpoise spend approximately three-quarters of their time pursuing and consuming prey (Watson, 1976; Sekiguchi, 1995). They also suggest that Dall's porpoise consume up to 13% of their body weight in food daily (Ridgway, 1966; Crawford, 1981; Miyazaki and Kimoto, 1987; Ohizumi and Miyazaki, 1998). As with many species of cetaceans, harbour and Dall's porpoise employ several hunting strategies to facilitate prey capture. They are known to hunt independently and in cooperative groups, though the motivation for cooperative behaviours, the extent to which subsurface cooperation occurs, or the relationships among cooperating individuals remains unknown.

**Hunting Strategies.** Porpoise are known to forage in cooperative groups. Harbour porpoise for example, cooperatively chase prey in near-surface waters using zigzag patterns, straight lines and crescent formations (Prescott and Fiorelli, 1980; Taylor and Dawson, 1984), while Dall's porpoise cooperatively herd pelagic fish using a circular strategy that involves groups of porpoise encircling schools of prey and alternating between cooperatively herding and foraging (Norris and Prescott, 1961; Miyazaki et al., 1984; Miller, 1987b). As with harbour porpoise, individual Dall's porpoise also chase fish near the surface with erratic bursts of speed (Miller, 1987b). Another pattern known as 'milling' has been associated with foraging in both species (Goetz, 1983; Watson and Gaskin, 1983; Sekiguchi, 1987; Silber, 1990). Milling occurs when groups of individual porpoise surface in a non-directional pattern in close proximity to one another. Milling

behaviour may also be associated with non-cooperative foraging of several individuals hunting in the same area (Walker, 1975b), as a group resting and sleeping strategy (Morejohn, 1979), or as a surfacing pattern that is associated with subsurface cooperative foraging that has not yet been identified.

Although cooperative behaviours usually involve small groups of porpoise, much larger numbers of animals are occasionally observed. For example, several hundred harbour porpoise cooperatively herded sardines (*Sardinops caerulea*) in the surface waters of coastal California by alternating between lunge feeding and herding (Fink, 1959), while 30 – 40 harbour porpoise cooperatively herded and consumed small unidentified fish within a triangular formation in coastal Washington (A. Hall, pers. obs.). Large numbers of cooperatively foraging Dall's porpoise have not been noted.

Conversely, benthic foraging appears to be an individual behaviour in both species, though the observations are few. Individual harbour porpoise sometimes forage in the mud (Dudok van Heel, 1962b; Andersen and Dziedzic, 1964) and amongst aquatic plants (Amundin and Amundin, 1974), where they probably consume both epifauna and infauna as they can discriminate objects buried up to 10 cm in sand (Kastelein et al., 1997c). Less is known about the benthic foraging behaviours of Dall's porpoise, though Kellogg (1940) suggested that this species may forage around submerged coastal rocks based on the saddled blenny (not specified but possibly *Pholis ornata*) that were identified in stomach contents. Considering the different bathymetric preferences of the two species (Hall, 1996), it seems likely that benthic foraging is probably more important to harbour porpoise than Dall's porpoise.

**Diving.** Dive depths are similar between harbour and Dall's porpoise, but dive duration differs. Both species spend most of their time in the top 10 – 20 m of the water column (Baird and Hanson, 1996; Otani et al., 1998; Otani et al., 2000; Teilmann, 2000), but can reach depths in excess of 180 m (Morejohn, 1979; Westgate et al., 1995). However, harbour porpoise tend to dive for shorter times at <2 minutes on average (Watson and Gaskin, 1983; Otani et al., 1998), than Dall's porpoise which average 2 – 4 minutes (Durban, 1994). Maximum submerged time for harbour porpoise was 10 minutes, but the animal was experimentally restrained (Kanwisher and Sundnes, 1965).

Scholander (1940) hypothesized that harbour porpoise should be able to remain submerged for as long as 12 minutes, but there is no supporting evidence. For unrestrained wild animals, the maximum dive time is likely less than or similar to the 7 minutes recorded for Dall's porpoise (Miller, 1987b).

Length and depth of dives made by harbour porpoise appear to be anticipated before the dive is commenced, as the descent rate and dive duration varies as a function of the dive depth (Otani et al., 1998). Female harbour porpoise also appear to dive longer than males, but males have faster descent and ascent rates, and dive more often than females (Westgate et al., 1995). These gender differences may be related to the different body sizes of males and females, and the resulting differences in their aerobic dive limits (see Kooyman et al., 1980; Kooyman, 1989; Westgate et al., 1995).

Dive profiles also vary according to the dive depth. Most harbour porpoise shallow dives (<20 m) are V-shaped, while most deep dives are U-shaped (Otani et al., 1998). Shallow V-shaped dives are thought to be associated with travelling, and the deeper U-shaped dives with foraging (Otani et al., 1998). Deeper foraging dives are about 3.5 times longer than travelling dives (Watson and Gaskin, 1983), and the amount of surface time does not correlate with the duration of the preceding dive (Otani et al., 1998). Harbour porpoise spend most of their time submerged (Westgate et al., 1995), though on occasion prolonged periods at the surface are noted with one of the longest recorded surface times exceeding 45 minutes (Otani et al., 1998). Most harbour porpoise dives are short at less than 2 minutes in duration (Otani et al., 1998), indicating that they likely do not reach their physiological maximum on most dives. Little is known of the dive profiles and surface time patterns of Dall's porpoise.

**Circadian Patterns.** Circadian patterns exist for both species, but are not uniform amongst all individuals within populations. For example, in Monterey Bay California, harbour porpoise foraged more in the morning and traveled and played in the afternoon (Sekiguchi, 1995), whereas in Ireland, foraging occurred on a more crepuscular schedule (Leopold et al., 1992). Resting has been noted in the afternoon in British Columbia (A. Hall, pers. obs.) and the Gulf of St. Lawrence (Hoek, 1992). Some telemetry studies indicate that harbour porpoise spend more time at the surface during the

night (Read and Gaskin, 1985; Westgate et al., 1995; Otani et al., 1998), with relative inactivity between midnight and 0600 hrs (Read and Gaskin, 1985), while others indicate that at least some animals exhibit a diel pattern by diving deeper at night than during the day (Westgate et al., 1995). Conversely, circadian patterns have not been detected in some captive harbour porpoise (Andersen and Dziedzic, 1964), or among some individuals in the Bay of Fundy (Read and Westgate, 1997).

Dall's porpoise display more defined circadian patterns as this species tends to be less active diurnally, with increasing activity levels in the late afternoon and continuing through the night and early morning (Morejohn, 1979). A captive animal was reported to be "most responsive to training at night, fairly responsive in the early morning and least responsive during the mid-day and in the afternoon" (Ridgway, 1966). Similarly, in the Sea of Japan, the ratio of stomach content weight to body weight was significantly larger before 0930 hr and declined during the day (Ohizumi and Miyazaki, 1998). This corresponds to the notion that Dall's porpoise feed on deep-sea fishes that migrate nightly to the surface (Treacy and Crawford, 1979; Boucher et al., 1980). This pattern of feeding occurs throughout much of their range (see Loeb, 1972; Crawford, 1981; Stroud et al., 1981; Miyashita and Kasuya, 1988), but is not universal. In the Sea of Okhotsk, for example, nocturnal activity is reduced and diurnal activity is increased (Walker, 1996; Amano et al., 1998). It has been suggested that these different circadian patterns reflect regional differences in the behaviour of dominant prey (Amano et al., 1998). Little is known about the differential foraging patterns of different populations for other parts of this species range.


### *Shelter-Seeking Habitat Selection Behaviour*

Knowing which habitats are required, and the characteristics that make specific areas attractive to specific species is fundamental to wildlife conservation. Habitat selection of most species tends to vary seasonally according to life processes and developmental stages. Unfortunately information about harbour and Dall's porpoise habitat selection criteria and associated behaviours is spatially and temporally discontinuous.

**Habitat Criteria.** Habitat used by harbour and Dall's porpoise likely reflects multi-scale oceanographic phenomena. Recent work in the eastern North Sea suggests that such oceanographic conditions as bathymetry and tidally-driven hydrodynamics are key factors in harbour porpoise habitat selection (Skov and Thomsen, 2008). These animals preferentially use coastal areas with upwellings, eddies, "bottleneck" zones, internal waves, fronts and geographically induced turbulence (see Chapter III and Hall, 1979; Kraus and Prescott, 1981; Gaskin and Watson, 1985; Silber, 1990; Gaskin, 1992; Johnston et al., 2005). These features are tidally driven and the spatial movements of harbour porpoise have been correlated with tidal phase from throughout their range (see Chapter III and Gaskin et al., 1975; Watson, 1976; Taylor and Dawson, 1984; Gaskin and Watson, 1985; Raum-Suryan and Harvey, 1998).

Less is known of Dall's porpoise habitat selection criteria. Neritic populations occupy regions characterized by wide straits, exposed areas, strong tidal currents, deep canyons, and depths exceeding 180 m (McTaggart-Cowan, 1944; Scheffer, 1949; Fiscus and Niggol, 1965; Pike and MacAskie, 1969; Loeb, 1972; McTaggert-Cowan, 1988; Hall, 1996). Observations in southwestern British Columbia suggest that Dall's porpoise may also select habitats with strong tidal convergence features (A. Hall, pers. obs.). As with harbour porpoise, it is likely that coastal Dall's porpoise respond to tidally generated oceanographic changes. However, the key drivers in their habitat selection remain unclear, as the fine-scale changes in habitat use of Dall's porpoise have not been examined.

In the more expansive regions of the North Pacific, the criteria used by Dall's porpoise to select their habitat appears to be associated with large-scale oceanographic phenomena. In 1977, a significant shift in the distribution of Dall's porpoise was detected in the western North Pacific when the Alaska Stream weakened and the western sub-arctic gyre south of Kamchatka strengthened (IWC, 1978; Klinowska, 1991). Animals returned to their usual habitats south of Kamchatka in the following year, when these anomalous conditions reversed (IWC, 1978; Klinowska, 1991). A spatial comparison of high-seas hunting records and by-catch locations with North Pacific oceanographic currents and atmospheric pressure systems would contribute to better understanding the ecological requirements of the pelagic Dall's porpoise populations.

**Migration.** Habitat selection relative to migratory behaviour has been noted for both species of porpoise. However, the movements of harbour porpoise are more diffuse than the clearly defined migration paths of Dall's porpoise (western North Pacific population). No migratory behaviour has been noted for either species in the eastern North Pacific.

Historically, European harbour porpoise migrated seasonally between the Baltic and North Seas (Irminger, 1846; Møhl-Hansen, 1954; Dudok van Heel, 1962b; Amundin and Amundin, 1974; Andersen, 1974; Andersen, 1982; Kinze, 1985). This migration has not been documented in recent years, but harbour porpoise are now seen year-round in areas of the Baltic Sea where they were once absent during the winter months (Andersen, 1972; Andersen, 1974; Koschinski, 2002). Conversely, harbour porpoise historically also occupied parts of the Gulf of Finland, but this is no longer the case (Määtänen, 1990). Although the causative agents of change are unclear, it is evident that something has affected the distribution and/or behaviour of harbour porpoise in the northern parts of their Atlantic range.

One possibility is that harbour porpoise respond to sea surface temperatures, as historically when the Baltic Sea froze quickly, the animals that were not able to leave died in large numbers (Irminger, 1846; Dudok van Heel, 1962a; Amundin and Amundin, 1974). If true, harbour porpoise distribution may shift northward in both the Atlantic and Pacific Oceans if ocean and global temperature continue to rise. Similarly, if predictions are correct, harbour porpoise abundances in the southern regions of their global distribution will fall as the 20 – 24°C isotherm that sets the southern limit of their range moves northward (Tolley and Rosel, 2006).

An alternative hypothesis for the cessation of migratory behaviour of Baltic harbour porpoise is that historically there were two populations in this region: one that was migratory and one that was non-migratory. The harbour porpoise observed today may be the remnants of the non-migratory population (Wang and Berggren, 1997; Huggenberger et al., 2002; Koschinski, 2002). This explanation is feasible given hunting stations set along the migration corridor could have eliminated or greatly reduced the number of migrating individuals. Huggenberger et al. (2002) suggest that the historical

catch statistics from this area be re-evaluated in light of the annual ice conditions and annual numbers harvested. In addition, historical catches of harbour porpoise prey species, changes in forage fish biomass, and incidental catch may also have influenced harbour porpoise habitat selection (see Reijnders, 1992). It seems likely that these potential influences may not be isolated, and may synergistically affect contemporary behavioural patterns.

Harbour porpoise have also been known to migrate for reproduction. Historically, harbour porpoise migrated in large numbers into the shallow waters of the Wadden and Dutch North Seas during the summer to give birth and breed (Verwey and Wolff, 1981). A similar inshore migration was reported from British waters in the early 20th century, where only males stayed after breeding (based on the sex ratios of incidentally caught specimens: Meek, 1918). A similar event was described in the Bay of Fundy, where an influx of pregnant females occurred from May to July, followed by males in July, with most animals migrating out of the bay in October to go south for the winter (Sergeant and Fisher, 1957; Neave and Wright, 1968; Gaskin, 1977). Recent radio-telemetry has not been able to detect this migratory behaviour, although the number of animals tracked was small (*n=9*: Read and Westgate, 1997).

Migratory behaviour and occupation of inshore habitats during the breeding season can vary between and within years, as shown by a 1993 summer survey in the North Sea that detected high densities of harbour porpoise occupying both inshore and offshore habitats (Hammond et al., 1995). It is difficult to hypothesize the stimuli for the apparent inter-annual variation as it is not known whether the offshore areas were occupied by reproductively active individuals, whether any sexual or age segregation was occurring, or if historically the offshore habitats were also occupied but simply undocumented. Perhaps inshore habitats are not available to all populations during the reproductive season, or offshore regions are not sufficiently well surveyed to detect subtle changes in habitat use. Additional suggestions to account for the inter-annual variability in harbour porpoise migratory behaviour include inclement weather or regional reduced prey availability (Amundin and Amundin, 1974).

In contrast to harbour porpoise, the Dall's porpoise of the western North Pacific undergo a clear and predictable migration, commencing in the early spring (Ohsumi, 1975; Walker, 1975a), with the migratory path and summer habitat selection depending on phenotype. The *dalli*-type Dall's porpoise that overwinter in the Sea of Japan migrate northward in schools during the summer to the Sea of Okhotsk and Japanese Pacific waters passing through the Tsugaru Strait (Amano and Kuramochi, 1992). Whereas the *truei*-type Dall's porpoise overwinter along the Pacific coast of Japan (Sanriku region) and migrate offshore for the summer to open water habitats between 40° – 45°N and west of 155°W (Kasuya, 1978; Miyazaki et al., 1984).

The migratory behaviour of Dall's porpoise corresponds to the reproductive season of these populations (Kasuya, 1978; Kasuya and Ogi, 1987; Miyashita and Kasuya, 1988; Amano and Kuramochi, 1992; Amano and Miyazaki, 1992; Walker, 1996; Walker, 2001). It has been suggested that the *dalli*-types that summer in the Sea of Okhotsk are sexually mature individuals that form breeding schools in their summer habitat (Amano and Kuramochi, 1992). As such, it seems likely that the migration of at least some Dall's porpoise populations is driven by reproductive parameters. It would be interesting to know if inter-annual variation exists relative to the primary prey or predators' seasonal abundance fluctuations, and if non-reproducing individuals follow these same paths.

**Non-Migratory Movements.** Non-migratory behaviour of harbour and Dall's porpoise is more difficult to define because of spatial and temporal variability and multiple putative causative stimuli. Some populations exhibit seasonal shifts in habitat selection. In the 19th century, harbour porpoise followed herring (*Clupea harengus*) schools seasonally to Norway (Eschricht, 1849 - in Amundin and Amundin, 1973-74), and seasonal movements of herring and mackerel (*Scomber scombrus*) may also explain contemporary movements of harbour porpoise in the Bay of Fundy (Gaskin, 1977). Gaskin (1992) suggested that a winter eastward and offshore movement occurs in the Gulf of St. Lawrence because access to the western regions becomes restricted by ice. Again the ice formation or sea surface temperature hypothesis may explain habitat selection behaviour, because there is a distinct lack of harbour porpoise during winter in the more northern regions of the North Atlantic (Donovan and Bjørge, 1995).

Gaskin (1992) also suggested that offshore areas such as Georges Bank that have year-round fish stocks, may provide important wintering grounds for harbour porpoise. Read et al. (1996) confirm that some Atlantic harbour porpoise occupy offshore habitats during the winter months, and hypothesized that the Gulf of Maine population disperses south for the winter to occupy the coastal shelf and slope waters of the western North Atlantic. Further confirmation of offshore winter habitat use by harbour porpoise comes from the by-catch data from drift nets set outside the 1000 m isobath in the western North Atlantic (Stenson and Reddin, 1991). Little is known of the seasonal movements and important habitats in the Pacific Ocean, but fine-scale seasonal abundance decreases have been noted in inshore regions of southern British Columbia during the winter (Hall, 2004). Research that addresses whether Pacific harbour porpoise have a corresponding offshore movement for the winter would contribute to the understanding of seasonal habitat selection behaviours in this region.

The non-migratory behaviours of Dall's porpoise appear to be opposite to that of Atlantic harbour porpoise. In the eastern North Pacific, Dall's porpoise move inshore and southward during the winter, and move offshore and northward for the summer in response to cold-water events and the seasonal movements of their principal prey species (Norris and Prescott, 1961; Loeb, 1972; Morejohn, 1979; Leatherwood et al., 1982). Dall's porpoise maintain seasonal habitats within waters that are 2.2 – 16.7°C (Leatherwood et al., 1982; Miyashita and Kasuya, 1988). In California, they have been reported to move north to about 35°N during the mid to late summer from their southerly wintering habitat near the Channel Islands, CA (34°N) (Norris and Prescott, 1961; Ridgway, 1966; Leatherwood et al., 1982). During periods of exceptionally cool water, the southerly limit extends south to 28°N off Baja California, Republic of Mexico (Morejohn, 1979; Jefferson, 1988; Houck and Jefferson, 1999). Further north, seasonal movements are suspected for Prince William Sound, Alaska, because densities are lower in the winter and spring than in the summer and fall (Hall, 1979). In British Columbia, it has been suggested that Dall's porpoise move to offshore waters for the summer (Pike and MacAskie, 1969), and recent sightings indicate an influx of animals into the Juan de Fuca Strait during the late summer and early autumn (A. Hall, pers. obs.). Though thirty years have passed since it was first suggested that the Dall's porpoise of British Columbia

seasonally shift between inshore and offshore waters (Pike and MacAskie, 1969), this aspect of their behavioural ecology has not been tested and remains unclear.

**Residency Patterns.** The residency patterns of harbour and Dall's porpoise are just beginning to be understood. It appears that these species generally reside in relatively small geographic areas (Flaherty and Stark, 1982; Calambokidis and Barlow, 1991; Gaskin, 1992; Calambokidis and Baird, 1994b; Tiedemann et al., 1996; Andersen et al., 1997; Walton, 1997; Wang and Berggren, 1997; Rosel et al., 1999; Escorza-Trevino and Dizon, 2000; Chivers et al., 2002), with males potentially moving amongst groups of females (Walton, 1997; Escorza-Trevino and Dizon, 2000). This dispersal pattern has significant conservation implications if regional populations become greatly reduced or extirpated.

It has been proposed that Dall's porpoise exhibit limited movements within their seasonal home ranges (Hall, 1981), or that they temporarily move amongst specific habitats within home ranges (Miller, 1990). This pattern may also be true of harbour porpoise. Satellite tagged animals in the Bay of Fundy maintained long periods of residency in productive areas interspersed with short periods of travel (Read and Westgate, 1997), and a radio-tracked female in Washington remained within a 65 km$^2$ area for more than 6 months (Hanson et al., 1999). High levels of inter-annual site fidelity have also been noted (Gaskin and Watson, 1985), with natal sites being important to female harbour porpoise (see *Breeding and Calving Habitats*).

It is possible that female porpoise remain in relatively small and productive areas because of the physiological limitations of their calves. Female Dall's porpoise with calves are known to select shallower waters than other Dall's porpoise, perhaps because the calves are unable to accompany their mothers into deeper regions (Durban, 1994). Alternatively, females may avoid the deeper areas because of the reproductively active and aggressive males which are maintaining breeding site fidelity (Durban, 1994). Juvenile Dall's porpoise are also consistently observed closer to shore in Monterey Bay than adults (Leatherwood et al., 1982), suggesting that the shallower regions afford young animals a survival advantage. Remaining in a smaller volume of water may require less vigilance for young porpoise to detect predators. It is also possible that this

preference for shallower habitats is related to dietary differences amongst different age and sex classes, or to some combination of these hypotheses.

The degree of dispersal and size of occupied geographic areas may well be determined by the relative productivity and levels of human disturbance within specific areas. Multi-scale studies for both species linking detailed movements of harbour and Dall's porpoise with the aforementioned factors may provide insight into the residency patterns of these species. Further research into the gender and age-specific residency patterns of harbour and Dall's porpoise are required, and much remains to be learned about the sensory cues these species use to maintain their spatial orientation within specific habitats and the stimuli that prompt movements within seasonal home ranges.

**Breeding and Calving Habitats.** Knowledge of harbour porpoise calving habitats is restricted to generalised habitat types within a few geographic areas. Historically, females in the southern North Sea brought neonates into habitats described as "knee-deep" (Beddard, 1900). Though this is no longer observed, a similar behaviour is exhibited in the western North Atlantic where females use sheltered coves to wean their calves (Watson, 1976; Gaskin, 1977). Individual females have demonstrated high levels of site fidelity in the Bay of Fundy (Watson, 1976), and in the Baltic Sea where they return to natal sites for parturition (Kinze, 1990; Sørensen and Kinze, 1990; Tiedemann et al., 1996; Andersen et al., 1997; Huggenberger et al., 2002). Since calves are believed to remain with their mothers until after the next calf is born (Klinowska, 1991), this behaviour of calving habitat site fidelity may represent a cultural transmission of knowledge along the maternal line.

Harbour porpoise are thought to mate in confined and traditional breeding areas (Koschinski, 2002) and several discrete calving habitats have been identified. In Germany, the waters near the Island of Sylt, and possibly off Amrum are thought to be calving and nursing habitats (Sonntag et al., 1999). The coastal lagoons of the Mecklenburg-Prepomerania region of the German and Polish Baltic Sea have also been identified as important (Schulze, 1996). In Denmark, calving habitats are located inside the 20 m contour in the northern part of the Little Belt, Great Belt, Sejrø Bight, around the Fyn archipelago (Sydfynske Øhav), Smålandsfarvandet and off southern Rømø

(Kinze, 1990; Sonntag et al., 1999). Other breeding and nursery areas have been suggested in the sheltered inlets and bays of western and south-western Ireland, the Shetland Islands (Evans, 1987; Leopold et al., 1992), and near Deer Island in the Bay of Fundy (Smith and Gaskin, 1983; Gaskin and Watson, 1985).

In the North Pacific Ocean, there are no known calving habitats, but areas of Prince William Sound, Glacier Bay and the Copper River estuary of Alaska have been proposed as being important for calving (Hall, 1979; Matkin and Ray, 1980; Taylor and Dawson, 1984). Information from the early 20th Century indicates young harbour porpoise were frequently observed in Goletas Channel, BC (McTaggart-Cowan, 1944), though it is uncertain whether this represents a historical or even present day calving area. Neonates have also been observed near southern Vancouver Island (see Chapters III and IV) and in Cox Lagoon, Texada Island (J. Dove, pers. comm.). These may be important calving or weaning sites.

Breeding season site fidelity is also a trait of Dall's porpoise. The *dalli*-type Dall's porpoise breed north of 45°N and in the Bering Sea, whereas the *truei*-type population breeds off the northern coast of Japan (Kasuya and Ogi, 1987). As with harbour porpoise, there are no known eastern North Pacific calving areas, but several locations are thought to be important. These include Goletas Channel, BC (McTaggart-Cowan, 1944), Johnstone Strait, BC, and the waters of Whidbey Island, WA (Jefferson, 1987; Miller, 1989). Females with near-term foetuses and neonates have also been documented in Monterey Bay, near the Channel Islands, near Santa Catalina Island, and off San Diego, CA (Norris and Prescott, 1961; Morejohn, 1979). Further north, they have been documented in the western Bering Sea (Mizue and Yoshida, 1965); in Lynn Canal, Alaska (Miller, 1929); off southern Vancouver Island, and near Moresby and Pender Islands, BC (A. Hall, pers. obs.), and off Stuart Island, WA (Durban, 1994; Willis and Dill, 2007). Other breeding and calving areas likely exist considering the expansive range of Dall's porpoise, and will require additional research to identify them.

*Sexual Behaviour*

Sexual behaviour is directly linked to the reproductive biology of a species, and consequently the fitness of individuals and species. The physical changes experienced by male Dall's and harbour porpoise (see *Life History*) likely have a profound influence on their behaviours during the reproductive season. It is also likely that porpoise exhibit more behaviours than are documented to date, since these behaviours are difficult to observe because all sexual behaviour occurs subsurface.

**Courtship.** The courtship behaviour of harbour porpoise in captivity has been described as similar to bottlenose and common dolphins (*Delphinus delphis*), and involves chasing, close approaches, pushing, swimming quickly and keeping in tactile contact for as long as several hours (Andersen and Dziedzic, 1964; Busnel and Dziedzic, 1966). Observations of captive pairs indicates that the male postures and exposes his venter while positioning above or beside the female, and touches the females' dorsal fin and lateral sides with his venter and tail (Andersen and Dziedzic, 1964; Busnel and Dziedzic, 1966). This posturing has been accompanied by low frequency (1 – 5 kHz) sounds described as 'squeaking', 'grinding' and 'blasts' (Busnel and Dziedzic, 1966). As with bottlenose dolphins, harbour porpoise also produce sounds described as pulsed yelps during courtship (Evans, 1987). Posturing has also been noted by females, and in captivity this sex has been noted to initiate sexual behaviour (Andersen and Dziedzic, 1964). Males also mouth females by gently biting the females dorsal fin and flippers (Andersen and Dziedzic, 1964). It is not known whether any of these behaviours are also exhibited in the wild, though it seems likely.

Information on wild courtship behaviours is almost completely absent from the scientific literature for harbour porpoise, and the only insight comes from the Bay of Fundy, where males accompany females and their calves during the mating season (Neave and Wright, 1968). In contrast, the limited information on Dall's porpoise courtship behaviour comes entirely from wild studies. Dall's porpoise display more conspecific aggression than harbour porpoise during courtship, with males forming strong pair bonds with individual females who are agonistically guarded from other potential mates (Willis and Dill, 2007). The role of female selection, the level of subsurface interactions, and the stimuli for female receptivity are not known. The rate of

male mating success with guarded females is also unknown.  Further investigations are required.

**Segregation by Gender and Reproductive Status.** Both harbour and Dall's porpoise exhibit segregative behaviours that reflect reproductive status and gender.  Male harbour porpoise segregate from cow-calf pairs in the Baltic and North Seas, and the northwestern Atlantic (Møhl-Hansen, 1954; Neave and Wright, 1968; Verwey, 1975; Smith and Gaskin, 1983).  This segregation may occur because females with calves have different dietary requirements than males (Recchia and Read, 1989).  Segregation by prey and habitat selection may reflect an ecological gamble by the reproductively active females to select more productive environments to meet their elevated metabolic requirements, though potentially increasing their risk to predation (Michaud, 2005).  Support for this hypothesis has been found in the Bay of Fundy (Michaud, 2005), but has not been tested in other regions.

*Post*-mating segregation of harbour porpoise has been observed in the Bay of Fundy, and among Dall's porpoise in the northwestern North Pacific and western Bering Sea (Kasuya, 1978; Klinowska, 1991).  The male harbour porpoise form groups of four or more animals in the Bay of Fundy after mating (Neave and Wright, 1968), whereas in the Baltic, male-female and mixed sex gams are observed (Møhl-Hansen, 1954).  Male Dall's porpoise find themselves segregated from the female Dall's porpoise just prior to parturition (Kasuya, 1978; Klinowska, 1991), while the reproductively active *truei*-type Dall's porpoise segregate sexually at the onset of the reproductive season (Wilke et al., 1953).

Segregative behaviour is not just limited to sexually mature animals, as age segregation also takes place in both species.  In the German North Sea, calves segregate from juvenile harbour porpoise (1 – 4 yrs) (Sonntag et al., 1999), and juvenile Dall's porpoise females segregate from mature females by occupying different habitats in the central North Pacific (Ferrero and Jones, 1986; Ferrero and Walker, 1999).  The degree to which bonds or associations are maintained amongst individuals that segregate is not understood.  It may occur in response to female energetic needs, calf dietary needs, calf safety from aggressive males, a predation reduction tactic, or some combination of all of

these options.  Insights into these possible explanations could be obtained by further analysis of the considerable number of Dall's porpoise that are intentionally or accidentally killed each year in the North Pacific (Hammond et al., 2008b).  Such information might ultimately help to lower the numbers of by-caught animals.

**Intergeneric Breeding.** There are only three records of Dall's and harbour porpoise inter-breeding.  In southern British Columbia a hybrid foetus was found within a female Dall's porpoise (Baird et al., 1998).  Subsequent work found evidence of recurring natural hybridisation between harbour and Dall's porpoise (Willis et al., 2004), though no other hybrid foetuses have been confirmed from stranded animals in this region.  There is also a report of a captive female harbour porpoise housed with three Atlantic bottlenose dolphins allowing a male dolphin to mate with her (Spotte et al., 1978).  Genetic and behavioural studies with increased sample sizes, and broader spatio-temporal frames are required where reproductive sympatry occurs to determine the geographic scope, frequency of intergeneric breeding and species-specific breeding behaviours.

### Agonistic Behaviour

Agonistic behaviour is any social behaviour related to fighting.  This includes aggressive, submissive, sub-ordinance, retreat and conciliatory behaviours (Scott and Fredericson, 1951).  Harbour porpoise are rarely observed engaged in agonistic behaviours (Andersen and Dziedzic, 1964; Amundin, 1974; Kastelein et al., 1997a; Nakahara and Takemura, 1997), but some insight comes from captive groups where male-female and male-male aggressive dominance behaviour has occurred during feeding (Andersen and Dziedzic, 1964; Busnel and Dziedzic, 1966), and with the introduction of new individuals (Amundin and Amundin, 1971; Amundin and Amundin, 1974).

Agonistic behaviours consist of rapid approaches, physical pushing, biting, and a 2 kHz signal (Andersen and Dziedzic, 1964; Busnel and Dziedzic, 1966).  Andersen and Dziedzic (1964) observed dominance behaviour at a captive feeding station in which a dominant female pressed its head against a subordinate whilst producing agonistic acoustic signals.  This resulted in the subordinate immediately vacating the feeding area (Andersen and Dziedzic, 1964).  Captive young males have also been observed to exhibit

agonistic behaviours coincident with the sexual behaviours of older animals in the tank (Andersen and Dziedzic, 1964).

Harbour porpoise also exhibit a physical threat display, in which one individual turns its snout toward another while producing rapid clicks (Nakamura et al., 1998). This results in a retreat behaviour by the other animals in the tank (Nakamura et al., 1998). Harbour porpoise are known to respond to sudden conflict by a rapid release of large air bubbles from the blowhole (Andersen and Dziedzic, 1964). This behaviour has been directed at inanimate objects and other harbour porpoise, and was interpreted as intended to frighten other individuals or as an acoustic disturbance (Andersen, 1976). This behaviour may have multiple meanings as Andersen (1976) noted it also occurred while a captive porpoise was awaiting fish from its trainer. Only one instance of aggression toward a human has been reported which involved an animal splashing its trainer with its tail flukes (Andersen, 1976). It seems likely that captive observed behaviours are not novel, and have a role in harbour porpoise society, but the extent to which they are exhibited in the wild is unknown.

In contrast to harbour porpoise, wild Dall's porpoise exhibit agonistic behaviours, especially during the reproductive season when males may lunge aggressively towards others (Durban, 1994), cow-calf pairs can be attacked (Durban, 1994), high speed chases take place, and neonates can be physically assaulted (Willis and Dill, 2007). Agonistic behaviours also occur during bow riding, when individuals physically push one another and use jaw claps to acoustically displace smaller animals (Morejohn, 1979). A threat display similar to that seen in harbour porpoise was reported with one individual orienting toward another at a 90° angle (Morejohn 1979). The recipient responded by exposing its ventral surface and opening its mouth (Morejohn, 1979). This may represent a subordinate response of submission as is seen in other animals such as wolves (*Canis lupus*) and domestic dogs (*C. l. familiaris*).

The available information on agonistic behaviours suggests that Dall's porpoise exist in a dominance mediated hierarchical social structure where young and smaller individuals submit and disperse in response to the aggressive physical and acoustic displays of larger, presumably older animals. In contrast, harbour porpoise appear to be

less aggressive and show no apparent social hierarchy. Additional observations are needed to strengthen understanding of the social structure of northern porpoise.

### *Epimeletic Behaviour*

Epimeletic behaviour occurs when one individual cares for or gives help to, another individual (Cremer et al., 2006), and can be categorized on the basis of whether it is directed towards young animals (nuturant behaviour), or towards distressed adults (succorant behaviour) (Scott, 1958). Only a few examples of epimeletic behaviour exist for either harbour or Dall's porpoise.

Reports of nurturant behaviour often involve individual females waiting near injured, captured or entangled smaller companions. This has been reported across a broad temporal frame and throughout the range of harbour porpoise. Some individuals have been known to follow fishing boats with their companions on board for over an hour (Service, 1896). Others have remained near their captured or entangled companions for several hours, and in some cases, overnight (Read and Gaskin, 1985; Hall et al., 2002).

There are also a number of reports of succorant behaviour where adult harbour porpoise remained near injured adult companions (Tomilin, 1957), and a female harbour porpoise actively tried to divert attention away from her calf while researchers attempted to capture it (Gaskin et al., 1974). Similarly, a captive porpoise displayed succorant behaviour by repeatedly swimming above another, trying to prevent the keepers from catching the deeper porpoise (Kastelein et al., 1990). The capacity of harbour porpoise to display epimeletic behaviours suggests that it likely occurs more often than is observed.

There are virtually no reports of epimeletic behaviour in Dall's porpoise, and only one report discusses a confirmed display of succorant behaviour. Norris and Prescott (1961) observed the behaviour of a group of Dall's porpoise during a capture. One Dall's porpoise followed the captured animal and only gave up its efforts when a vessel approached it (Caldwell and Caldwell, 1966). It is not known what the relationship was between these two individuals or amongst members of the larger group to which both animals belonged. The lack of recorded observations of this type of behaviour in the literature does not necessarily mean that Dall's porpoise do not exhibit epimeletic

behaviour (though they may not), and may mean that it remains to be determined how this behaviour is manifested in this species.

### *Et-Epimeletic Behaviour*

If there are reports of et-epimeletic or care-soliciting behaviour of wild or captive porpoise, they are rare and difficult to find.  It is likely that porpoise do have some type of care-soliciting behaviour, as it has been proposed that the influence of learned behaviours from the mother might be very important for harbour porpoise (Dudok van Heel, 1981).  However, documentation of this behaviour will be difficult in the wild, and should be kept in mind when conducting behavioural studies on either species.

### *Allelomimetic Behaviour*

Allelomimetic behaviour is defined as two or more animals doing the same thing with some degree of mutual stimulation (Scott, 1958).  This is sometimes referred to as contagious behaviour or behaviour that influences another to do the same thing.  Harbour and Dall's porpoise both exhibit allelomimetic behaviour in surfacing patterns, swim direction and fish herding.

The best example of allelomimetic behaviour in harbour porpoise occurred in the Gulf of St. Lawrence when ~800 harbour porpoise covering about 2 km$^2$, synchronously reduced their level of surface activity, polarized their orientations and became virtually motionless for several hours (Hoek, 1992).  A similar, but smaller scale event was documented in Washington, when four animals in about 1 km$^2$ surfaced synchronously and remained motionless for about 15 seconds (Flaherty and Stark, 1982).  The event was associated with an unexplained but distinctive odour of porpoise melon tissue (Flaherty and Stark, 1982).  This odour had not been reported elsewhere, and was possibly the smell of a minke whale (*Balaenoptera acutorostrata*).

Harbour porpoise also exhibit allelomimetic behaviours during foraging.  Gaskin (1982) described 30 – 50 harbour porpoise within a 1 km$^2$ area feeding on herring in the Bay of Fundy.  In Washington, ~30 harbour porpoise synchronously surfaced quickly in three straight lines, maintaining a school of small silvery fish in the centre of their

polygon (A. Hall, pers. obs.). Each line successively dashed through the school, then returned to continue herding (A. Hall, pers. obs.). Similarly, harbour porpoise in New Brunswick have been observed travelling in synchronized groups between foraging habitats (Gaskin and Watson, 1985).

An interesting example of Dall's porpoise allelomimetic behaviour comes from the coast of California when five adult Dall's porpoise were seen travelling single file in an easterly direction about 100 ft apart in October 1955 (Norris and Prescott, 1961). This same behaviour was observed again in December 1956, when the group consisted of about 100 adults. They were again travelling in a straight line about 100 ft apart, but the line extended for about 2 miles, with two additional groups of about 20 animals each exhibiting this same behaviour 4 – 6.5 miles seaward of the first group (Norris and Prescott, 1961). All three lines of Dall's porpoise were reported to be travelling in a southeasterly direction, moving slowly and barely breaking the surface. The authors were unable to provide an explanation.

A possible example of Dall's porpoise allelomimetic behaviour was reported by Scheffer (1950) from the offshore waters of Oregon. However, there is some uncertainty regarding the species identification, because he did not directly observe the event. Another possible example of allelomimetic behaviour comes from Alaska where seven Dall's porpoise coordinated their sounding and surfacing behaviours after researchers had attempted to capture them (Hall, 1979). The relationship amongst the animals in these examples, and the biological or ecological significance of the large group events are unknown.

### *Eliminative Behaviour*

Eliminative behaviours are those associated with the release of feces or urine (see Scott, 1958). Nothing is known about harbour or Dall's porpoise eliminative behaviours. Individuals could theoretically communicate their health or reproductive status through eliminated waste, as seen in terrestrial mammals and other small cetaceans (see Norris and Dohl, 1980). However, this aspect of porpoise behavioural ecology is difficult to ascertain, and should be kept in mind while other behavioural studies are underway.

*Investigative and Avoidance Behaviour*

Investigative behaviours are defined as any kind of sensory investigation of the environment (Scott, 1958), whereas avoidance behaviours are those that allow animals to escape from actual or potential dangers and serve as a defense against potentially harmful circumstances (McFarland, 1981). All animals show considerable variability in their investigative behaviours. For many, investigative behaviour is coupled with avoidance behaviour, and is likely a survival response. As such, avoidance behaviour is best grouped with Scott's (1958) single category of investigative behaviour as individuals must first determine the lethal potential of an object or new individual before close investigation can take place.

Both harbour and Dall's porpoise can exhibit fear of unknown or new items. Harbour porpoise avoid unknown objects (Amundin and Amundin, 1974), and often fear new items or obstacles in the captive environment (Andersen and Dziedzic, 1964; Andersen, 1976; Nakahara and Takemura, 1997). Any sudden splash, loud noise, rapid change in light levels, introduction of new individuals or sudden movements of people near the tank can elicit an avoidance response (Andersen and Dziedzic, 1964; Busnel and Dziedzic, 1966; Andersen, 1976). The harbour porpoise will increase its swim speed, and stay away from the object while swimming near the bottom of the pool (Amundin, 1974; Nakahara and Takemura, 1997). Irregular breathing patterns, including sharp exhalations, have also been noted (Andersen and Dziedzic, 1964; Nakahara and Takemura, 1997). This behaviour can last for several days, though with repeated introductions of new objects the response becomes less severe (Amundin, 1974). It is not known if wild harbour porpoise also exhibit this type of behaviour by lying on or swimming near the sea floor in the face of a new or frightening stimulus.

Avoidance or fright by harbour porpoise is also demonstrated by high speed swimming interspersed with long, flat jumps (Amundin and Amundin, 1974; Andersen, 1976). In the wild, harbour porpoise can reach speeds of 22 km/h (Walker, 1975a; Leatherwood et al., 1982) while trying to evade predators such as transient killer whales (A. Hall, pers. obs.). Avoidance or fright can also be associated with a respiratory pause of up to 1.5 minutes (Andersen, 1976), and/or a 0.4 – 1.6 second 2 kHz signal that has been likened to the bleating of a sheep (Busnel and Dziedzic, 1966). This type of alarm

or distress call has also been recognized in other small cetaceans (see Caldwell et al., 1962; Lilly, 1963).

Habituation by harbour porpoise can result in a behavioural change that advances from avoidance, to investigation, to play (Amundin, 1974). Not all porpoise respond the same way and individual variability does exist. Kastelein et al. (1997a) found no fear of new objects in their captive animals and suggested that because harbour porpoise are a coastal species they are used to encountering strange objects in their environment. Furthermore, allelomimetic behaviour may play a role, as once a toy is discovered and played with by one captive porpoise, the other porpoise in the tank are more likely to play with it (Kastelein et al., 1997a). Curiosity is reported to increase with time spent in captivity (Amundin, 1974). It seems likely that curiosity and fear responses will vary depending on how new objects and individuals are introduced.

There are few reports of Dall's porpoise displaying fright or alarm behaviours. Ridgway (1966) described a male that had been inducted into the naval training program as being nervous and irritable when exposed to new objects or situations. A putative fright or stress behaviour was reported by Walker (1975b) in which newly captive Dall's porpoise sometimes became immobile and sank for a period of time before resuming normal swimming behaviour. Some Dall's porpoise have reacted to new captive environments by throwing themselves against the walls and bottom, and refusing to swim or feed (Klinowska, 1991). Avoidance behaviours of wild Dall's porpoise are not known, but they do investigate novel objects based on their propensity to play with oceanographic equipment (see *Play* in *Social Behaviour*) and interact with allospecifics such as resident killer whales and Pacific white-sided dolphins (A. Hall, pers. obs.).

### Social Behaviour

Social behaviours of animals vary in complexity and significance, and scientific explanation for these behaviours often requires long-term detailed observations. It is usually more difficult to acquire behavioural observations for underwater animals, which may explain why few people have studied the social behaviours of free-ranging porpoise. Dall's porpoise are considered to be social with a fluid group structure (Houck and

Jefferson, 1999). In contrast, some have suggested that harbour porpoise are not social animals (Read and Hohn, 1995; Wells et al., 1999), while others consider them to have a rich social life (Flaherty and Stark, 1982; Klinowska, 1991; Read, 1999).

The first insights into harbour porpoise social behaviours came from a group of individuals housed together for six months in Denmark in 1963. Acoustic activity was stronger during day than night and varied with behaviours related to feeding, group hierarchical structure, courtship and reactions to new individuals (Busnel and Dziedzic, 1966; Kastelein and van Battum, 1990) (also see *Ingestive Behaviour*, *Sexual Behaviour* and *Investigative and Avoidance Behaviour*). Also the frequency of captive harbour porpoise stereotypical swim patterns declines when companions become available, suggesting a need for social contact (Kastelein et al., 1997a; Kastelein and Staal, 1997).

Splashing and breaching are considered social behaviours in wild harbour porpoise (Flaherty and Stark, 1982). These behaviours are more often observed when harbour porpoise form high-density aggregations in discrete areas during the spring, summer and fall (A. Hall, pers. obs.). The range of surface-active behaviours appears to increase as densities increase to include surfing in waves and boat wakes, and close inspection of vessels (A. Hall, pers. obs.). Although the biological meaning behind these high-density social events remains unknown, harbour porpoise appear to have well developed social behaviours set within a context of individual and group relationships. Flaherty and Stark (1982) concluded that the sociality of harbour porpoise is well developed and that strong evidence exists that individual and group relationships exist. Unfortunately, little headway has been made to understand the sociality of harbour porpoise, and even less is known about Dall's porpoise social behaviours.

**Vocal Communication.** The vocal communication of harbour porpoise includes echolocation and social clicks and click trains (Busnel et al., 1963; Busnel and Dziedzic, 1966; Schevill et al., 1969; Read, 1999), which are used in stereotypical patterns related to specific social contexts (Amundin, 1991). Recent analysis of interclick intervals (ICIs) shows that the intervals vary with feeding, approach, distress, and alarm or fright behaviour communications (Koschinski et al., 2008). Harbour porpoise have been described as compulsive echolocators when in unknown surroundings and are thought to

expand the limits of their spatial memory using stationary objects on the bottom (*e.g.,* stones) as reference points (Andersen, 1976). Whether the clicks produced by one animal learning the new environment are listened to and interpreted by other animals in the group is unknown. Nor is it known whether harbour porpoise produce whistles. Some researchers contend that they do not (Gordon and Tyack, 2001) and have deemed harbour porpoise to be less social than whistling odontocetes (Tyack, 1986), whereas others suggest that they do communicate with whistles (Verboom and Kastelein, 1995), and are more social than previously considered (Read, 1999). Bearing in mind that harbour porpoise are most often seen in groups with little distance between group members, it seems likely that harbour porpoise are social mammals, and that the full range of their vocal repertoire has simply not yet been identified.

Far less is known about the vocal communications between Dall's porpoise than between harbour porpoise. Some newly captive Dall's porpoise produce almost constant sounds, while others remain silent (Ridgway, 1966). Wild Dall's porpoise are thought to obtain environmental details through signal amplitude modulation and by varying the acoustic pulse characteristics (*e.g.,* time, duration, single or double pulses, and interpulse interval) (Awbrey et al., 1979). Dall's porpoise are considered capable of discriminating between pelagic and benthic targets among ocean clutter (Evans and Awbrey, 1984). As with harbour porpoise, it is debatable whether this species communicates with whistles, but nocturnal whistles attributed to Dall's porpoise have been reported by Alaskan fishermen (Awbrey et al., 1979). Morejohn (1979) also reported hearing squeals while Dall's porpoise were bow riding. Though whistles are not reported from captive Dall's porpoise or from other wild studies, the sample sizes from which to draw conclusions are small. Almost everything related to the vocal communications of Dall's porpoise remains to be learned.

**Play.** Play behaviours have been described as those that are associated with relieving boredom, learning and exploration (McFarland, 1981). Sometimes these behaviours are considered to be essential to learning skills that are required at later life stages (McFarland, 1981). This is considered especially true for animals that live in groups, since play can contribute to the development of social skills required for societal living (see Goodall, 2001). Harbour porpoise have been likened to bottlenose dolphins

and white-sided dolphins with respect to their ingenuity and playfulness in captive settings (Andersen and Dziedzic, 1964; Amundin and Amundin, 1974).  Although previously considered to be a non-playful species (Scheffer and Slipp, 1948), wild harbour porpoise play with salmon and eels  (Selous et al., 1906; Rae, 1965) and surf in waves (A. Hall, pers. obs., Sekiguchi, 1995), while captive harbour porpoise play with bits of seaweed, starfish (Andersen and Dziedzic, 1964), floats and knotted cotton ropes (Kastelein et al., 1997a).  Captive animals will play with food items once satiated by carrying it round the pool, dropping it to the bottom and retrieving it on the next pass (Andersen and Dziedzic, 1964).  They are known to carry these objects in their mouths, and also to balance them on their flippers, dorsal fins and tail flukes (Andersen and Dziedzic, 1964).  Playful interactions between pool mates has been observed outside the reproductive season (Andersen and Dziedzic, 1964; Nakahara and Takemura, 1997). Those animals in captivity that do not have toys can succumb to boredom and exhibit stereotypical behaviours, while individual porpoises exposed to toys can exhibit personal preferences for specific ones (Amundin, 1974).  Captive harbour porpoise have been known to play so intensively that they have injured themselves (Kastelein et al., 1997a). This need for toys in the captive environment probably indicates that harbour porpoise are used to living in interesting environments and need stimulation to maintain good health.

Wild Dall's porpoise also play, and they have been seen tugging at Nansen bottle lines, and sometimes absconding with Secchi disk lines (Morejohn, 1979).  Sub-adults occasionally engage migrating grey whales and feeding fin whales in their play behaviours (Morejohn, 1979).  Bow riding has also been described as play (Morejohn, 1979; Kasuya and Jones, 1984; Jefferson, 1991), with Dall's porpoise sometimes modifying this behaviour to include allospecifics.  Adult Dall's porpoise have been seen "snout-riding" resident killer whales (A. Hall, pers. obs.), which may have been play or a display of male strength and courage to gain the attention of females (although it is unknown whether the females considered this to be an admirable trait).

*Rest and Sleep Behaviour*

Since all mammals require periodic rest, it seems reasonable to assume that porpoise can rest or sleep in various sea conditions.  Resting, basking and logging has been observed during calm weather in Washington (Scheffer and Slipp, 1948; Flaherty and Stark, 1982), the Bay of Fundy (Gaskin et al., 1975; Hoek, 1992), British Columbia (A. Hall, pers. obs.) and Denmark (Amundin and Amundin, 1974); but has not been noted in conditions greater than Beaufort 1 (Read and Gaskin, 1985; Hanson et al., 1999). Harbour porpoise may rest while swimming, and may even experience unihemispheric sleep during V-shaped dives (Mukhametov, 1984).  It has also been theorized that harbour porpoise can devote less time to foraging and more time to resting because of the efficiency with which they can capture prey (theory of behavioural inactivity: Herbers, 1981).  There may also be a subsurface rest behaviour (Read and Gaskin, 1985; Otani et al., 1998).  The ability to rest while swimming would allow the porpoise to rest in conditions other than those at the lowest end of the Beaufort scale.

Harbour porpoise are known to select calm habitats for resting, such as the less turbulent areas of offshore waters (Read and Gaskin, 1985), or the lee of islands on a slack current (A. Hall, pers. obs.).  Foraging harbour porpoise have been noted to spend six times as long lying at the surface as travelling harbour porpoise, and calves spend 1.7 times more time lying at the surface than adults (Watson and Gaskin, 1983).  Newly captive animals and those housed a long time have been noted to remain still at the surface for periods of time during both the day and night (Andersen and Dziedzic, 1964). Motionless surface behaviour has also been observed during physiological rest and while calves are suckling (Norman and Fraser, 1938; Kellogg, 1940).  Others have suggested that porpoise observed floating on the surface may not be resting, but rather scanning for near-surface prey (Flaherty and Stark, 1982; Watson and Gaskin, 1983).  Recording echolocations and eye movements (open or closed) would help to differentiate between these possibilities.  For the captive animals, it may also reflect a response to a feeling of security, boredom (Andersen and Dziedzic, 1964) or stress.

Harbour porpoise occasionally engage in what appears to be synchronised group resting.  In southern British Columbia, three animals were observed to synchronously surface in a polarised orientation and remain motionless at the surface for over five

minutes (A. Hall, pers. obs.).  A similar but larger event occurred in the Bay of Fundy where approximately 800 animals surfaced and remained in a polarized, motionless formation for several hours (see *Allelomimetic Behaviour* and Hoek, 1992).  It was not known whether the animals were engaged in a group resting behaviour or if the synchronisation served a different function.

Little information exists on the rest and sleep behaviour of Dall's porpoise though it has been proposed that they may sleep or rest during non-directional dive patterns with periodic respirations (Morejohn, 1979).  Such dive behaviour is frequently referred to as "milling" and is often associated with foraging on mesopelagic and bathypelagic species that rise towards the surface under the cover of darkness.  It seems unlikely that sleep would occur while foraging, and that it would be more likely for Dall's porpoise to exhibit similar surface floating behaviours as harbour porpoise for both resting and nursing.  Research is needed on the resting and floating behaviours of Dall's porpoise, especially in areas with high levels of human disturbance.


**Synthesis and Future Research Directions**

The observations reported to date indicate that harbour and Dall's porpoise are distinctly different types of porpoise and display a wide spectrum of behaviours related to their respective ecologies (Table 2.2).  Both species have independent and cooperative foraging strategies, and some populations have circadian patterns that have that reflect the time of day they forage (Table 2.2).  However, the efficiency with which they hunt and the proportion of time they devote to acquiring prey remains to be determined.  Approaching vessels and the operation of echo sounders are believed to disrupt the foraging behaviour of harbour porpoise (Gaskin et al., 1975), yet this assumption and the time it takes to resume foraging have not been examined.

Both harbour and Dall's porpoise appear able to adjust their habitat selection patterns according to environmental stimuli, though Dall's porpoise may be more rigorously tied to specific migration routes, at least in the western North Pacific (Table 2.2).  Investigating environmental stimuli, as well as evaluating potential calving and mating habitats would contribute to understanding the potential importance of such areas

for the survival of populations. Understanding how porpoise select and navigate specific habitats, and determining their residency patterns may also help to reduce incidental mortality. For example, the proposed ability of harbour and possibly Dall's porpoise to maintain a mental map of their home range may lead them to reduce their echolocation rates while traversing previously learned areas, and may explain why these species are so susceptible to fishing gear entanglement. It is also important to recognize that the insights gained so far into habitat use and residency patterns have not considered any social components associated with age, reproductive status or sex. In all likelihood, movement patterns are probably driven by a synergy of stimuli. Future work aimed at evaluating acoustic and seasonal habitat use patterns will lead to greater understanding of the year-round ecology of harbour and Dall's porpoise and may help to reduce incidental mortality rates.

Human activity has the potential to disrupt porpoise and alter their distributions irrespective of the biological importance of specific habitats. A preliminary investigation into the influence of ship traffic on harbour porpoise habitat use found a negative correlation between porpoise abundance and ship densities (Herr et al., 2005). This is consistent with the hypothesis that harbour porpoise are sensitive to human activities. Harbour porpoise may respond to high levels of human activity as they would any other unfavourable environmental variable (*e.g.*, ice formation) by moving to another habitat. However, there may be fewer areas in the neritic environment devoid of human disturbance that afford harbour porpoise sufficient habitat for survival. Protecting porpoise habitat is unlikely to be a simple feat, given that harbour porpoise may move in response to sea surface temperatures, and could shift their distribution northward in response to rises in ocean temperatures associated with global warming. The distribution of Dall's porpoise is also likely to shift northward, as may seasonal patterns in migrations and habitat shifts since they also select cold temperate to sub-arctic waters.

Coarse and fine-scale evaluation of the seasonal habitat selection of both species would contribute to a greater understanding of their life histories. Identifying the stimuli for the aggregative and segregative behaviours and identifying the biophysical parameters that define the selected habitats will offer insight into many aspects of the behavioural repertoires of both species. For instance, the seasonal aggregative behaviour of harbour

porpoise might serve multiple functions including improved predator surveillance during the nearly synchronous parturition events, increasing male and female proximity during the mating season, improved opportunity for cooperative hunting during the productive spring and summer months, and opportunity for social interactions with conspecifics and related individuals. Furthermore, the apparent winter dispersal may also contribute to survival by reducing the likelihood of disease and parasite transmission to gestate females and calves, and by reducing intraspecific competition during months of reduced primary and secondary production.

Investigations into the reproductive behaviours of Dall's and harbour porpoise will provide insight into why *pre-* and *post*-zygotic reproductive barriers are, at least on occasion, incomplete. The existence of hybrids with differential viability based on sex is an important area of research as the implications for population survival are complex, especially in habitats degraded by human activity. It is interesting to note that in the 15 years since the Baird et al. (1998) report, no similar stranded foetus has been identified though carcasses of both species are recovered annually in southern British Columbia. This implies that hybridization may be a rare event, though Willis et al. (2004) estimated at least 20 putative hybrids in the region. To date, no confirmed hybrids have been recovered as stranded specimens. Furthermore, few records exist for the range of foetal and juvenile pigmentation patterns that occur in the neritic waters of the eastern North Pacific, and some putative hybrids may simply be juveniles if assessment is on colouration alone (see Morejohn et al., 1973). If intergeneric breeding behaviour is occurring on a regular basis, then the stimuli behind such a phenomenon should be investigated. Perhaps there is a shortage of male Dall's porpoise, or perhaps the male harbour porpoise are venturing beyond their usual habitats. Excursions into deeper waters by harbour porpoise have been noted to occur during the late summer (Hall, 2004). Both harbour and Dall's porpoise exhibit discrete breeding seasons, but this is undefined for many regions. The current level of understanding suggests courtship behaviours are complex, and more research is required to address these behaviours and the implications for anthropogenic disruption during the breeding season.

Direct observation should be part of all research protocols for Dall's and harbour porpoise to increase the likelihood of documenting agonistic, epimeletic, et-epimeletic,

allelomimetic, investigative, social and rest behaviours. There are clearly social components to their lives which are largely unaddressed and unknown at this time. A firm knowledge of the life history and habits of the animals is needed to ensure that sound decisions can be made about human activities that might affect the long term survival of the species (Winn and Olla, 1979). There are clear differences in these species behavioural repertoires (Table 2.2), even though harbour porpoise are often regarded as behaviourally uninteresting, while Dall's porpoise are often considered to be behaviourally limited to bow riding and high-speed surfacing by casual observers. The limited and somewhat dispersed scientific literature demonstrates to the contrary. These are behaviourally complex and interesting animals with many opportunities for zoological discovery as there are extensive gaps in our understanding of their behavioural repertoires. Research into virtually any aspect of their behavioural ecology will be a contribution, but investigations that address aspects of their foraging, habitat selection and sexual behaviours are likely to have the greatest conservation impact.

**Summary**

Understanding a species' behaviour is fundamental for effective conservation. I compiled a range-wide review of the behavioural repertoires of the northern cold-water porpoises – the harbour and Dall's porpoise. Spanning more than 150 years of literature, behaviours were classified into 12 descriptive categories including: ingestive (foraging), shelter-seeking (habitat selection), sexual, agonistic, epimeletic, et-epimeletic, allelomimetic, eliminative, investigative, avoidance, social, and rest (sleep). A variety of cooperative foraging behaviours were found for both, with dive times differing by species, and harbour porpoise gender. Habitat selection likely reflects multi-scale oceanographic phenomena, but more work needs to be done to evaluate these species habitat requirements. Breeding site fidelity was noted for both, with several harbour porpoise sites suggested as traditional breeding grounds. In the eastern North Pacific, some level of reproductive season sympatry occurs given the existence of intergeneric hybrids. Current knowledge levels indicate that both harbour and Dall's porpoise have complex sexual and social behaviours, but much remains to be learned, as these are entirely subsurface. Northern porpoise also demonstrate a suite of agonistic, avoidance,

allelomimetic, investigative and play behaviours. Harbour porpoise occasionally rest (or sleep) in large groups, but significant gaps exist in our understanding of how either species rests or sleeps, especially in turbulent sea conditions. Information on eliminative and et-epimeletic behaviours was deficient for both species, and fieldwork that includes direct observation was recommended. Integration of the behavioural literature suggested that Dall's porpoise probably exist in a dominance mediated hierarchical structure, while harbour porpoise are probably more social than is generally apparent. Nevertheless, little is known of either species social structure or group dynamics, and much remains to be discovered of the behavioural ecology of the northern cold-water porpoises.

**Table 2.2 Northern porpoises behavioural repertoire summary**

| | Harbour Porpoise | Dall's Porpoise |
|---|:---:|:---:|
| *Foraging* | | |
| Pelagic Zone | √ | √ |
| Benthic Zone | √ | ? |
| Small Cooperative Groups | √ | √ |
| Large Cooperative Groups | √ | ? |
| *Hunting Patterns* | | |
| Straight Lines | √ | |
| Zigzags | √ | |
| Crescent Formations | √ | |
| Circular Formations | | √ |
| Milling | √ | √ |
| *Mean Dive Time* | | |
| < 2 minutes | √ | |
| > 2 minutes | | √ |
| *Circadian Pattern* | | |
| Dominant Diurnal | ? | √ |
| Dominant Nocturnal | ? | √ |
| *Habitat Selection* | | |
| Migration | | √ |
| Seasonal Shifts | √ | √ |
| Residency/Home Range | ? | ? |
| Traditional Breeding Sites | √ | √ |
| Breeding Site Fidelity | √ | √ |
| *Sexual Behaviour* | | |
| Courtship Behaviours | √ | |
| Segregative Behaviour | √ | √ |
| Intergeneric | √ | √ |
| *Agonistic Behaviour* | | |
| Male-Female | √ | √ |
| Male-Male | √ | √ |
| *Epimeletic Behaviour* | | |
| Nurturant | √ | ? |
| Succorant | √ | √ |
| *Allelomimetic Behaviour* | | |
| Rest | √ | ? |
| Foraging | √ | ? |
| Travelling | ? | √ |
| *Eliminative Behaviour* | ? | ? |
| *Investigative and Avoidance* | | |
| Fear/Avoidance Response | √ | √ |
| Investigative Response | √ | √ |

|  | *Harbour Porpoise* | *Dall's Porpoise* |
|---|---|---|
| *Social Behaviour* | | |
| Echolocation | √ | √ |
| Whistles | ? | ? |
| Play | √ | √ |
| *Rest/Sleep* | | |
| At Surface | √ | ? |
| While Swimming | ? | ? |
| Subsurface | ? | ? |

Table Key: √ – indicates confirmed knowledge,
? – indicates uncertainty exists

**Chapter III  - Lunar and tidal phases influence harbour porpoise behaviour at ephemeral foraging sites**

**Introduction**

Newton (1687) was the first to suggest that celestial bodies exert a physical and measurable effect on the earths' oceans.  Today it is known that the ocean's tides result from the net difference between the gravitational forces of the sun, moon and earth, and the centrifugal forces of the earth and moon (see Thomson, 1981; Brown et al., 1989; Lalli and Parsons, 1994).  The magnitude of the tide results from interactions between the physical forces of the moon's declination, the distances between the earth, moon and sun, and the relative positions of these three celestial bodies, whereas the timing of the daily tides results from the time differences for earth and moons daily rotations (see Thomson, 1981; Brown et al., 1989; Lalli and Parsons, 1994).  Local effects of tides are further complicated by bathymetry and coastal topography (Neumann, 1981).   Given the complexity of these physical interactions, it is not surprising that explanations of tidal cycles took centuries of study.

Today, it is widely accepted that lunar and tidal cycles are inextricably linked (Thomson, 1981; Koukkari and Sothern, 2006), but controversy still exists about the biophysical connection between the movements of celestial bodies and the behaviour of organisms (Lieber and Sherin, 1972; Lieber, 1978; Barr, 2000; Lilienfeld and Arkowitz, 2009).  The debate, however, is lessened in terms of aquatic animals.   It is generally accepted that the lives of these organisms, especially those in marine environments, undulate cyclically according to astronomical events – particularly lunar movements and the corresponding tidal and nocturnal light level changes (see Gibson, 1978; Neumann, 1981; Koukkari and Sothern, 2006).

The behaviours of a variety of aquatic taxa have been found to respond to lunar cycles.  For example, some marine zooplankton adjust the bathymetric magnitude of their nocturnal migrations according to lunar phase (Blaxter, 1974; Lalli and Parsons, 1994; Benoit-Bird et al., 2009).   Similarly, densities of freshwater cladocerans (*Bosmina, Diaphanosoma, Ceriodaphnia, Daphnia*) and copepods (*Eudiaptomus* and *Mesocyclops*) in Mozambique fluctuate more than an order of magnitude throughout the lunar cycle with peaks occurring from the new to full moons (Gliwicz, 1986).  The marine palolo

worm (*Eunice viridis* Gray) of the Samoan Islands, reproduces only during the last quarter moon phase in October or November (exact timing varies by year: Caspers, 1984), and throughout northern Europe, the European eel (*Anguilla anguilla*) times its downriver migration with the moons' last quarter (Gibson, 1978). Likewise in coastal British Columbia, the onset of the freshwater migration of several salmon species (*Oncorhynchus gorbuscha*, *O. tshawytscha*, *O. nerka*) corresponds to the full moon phases (Morton and Proctor, 2001). In addition, the timing of both reproduction and peak catches correlate with full and new moon phases in a variety of forage fish, including Atlantic and Pacific herring (*Clupea harengus* and *C. pallasi*), hake (*Merluccuis merluccius*) and California grunion (*Leuresthes tenuis*) (Gibson, 1978). Such behavioural responses to lunar movements by mid and low trophic level species presumably influence the higher trophic level species.

Connections between seabird behaviour and lunar phases have been noted for over 20 years. In Kauai, the full moon lunar phase is the single most important variable affecting fallout rates of fledgling Newell's shearwaters (*Puffinus auricularis newelli*) (Tefler et al., 1987). Leach's storm-petrels (*Oceanodroma leucorhoa*) and Barau's petrels (*Pterodroma baraui*) (Watanuki, 1986) increase their colony avoidance during full moons, while streaked shearwaters (*Calonectris leucomelas*) increase their nocturnal at-sea foraging behaviours (Yamamoto et al., 2008). More recently, it was determined that seabird by-catch rates in the Japanese tuna long-line fisheries off Australia nearly quadrupled during the full moons (Brothers et al., 1999). Since, many seabirds are ecologically sympatric with marine mammals (Evans, 1982; Yen et al., 2004), similar lunar phase behavioural responses may also be expected to occur within these taxa.

Among marine mammals, variations in body mass, dive depths and colony attendance patterns of Galapagos fur seals (*Arctocephalus galapagoensis*) correspond to full moons when at-sea foraging behaviour is reduced and most animals remain nocturnally resident onshore (Trillmich and Mohren, 1981; Horning and Trillmich, 1999). Conversely in coastal British Columbia, harbour seals (*Phoca vitulina richardsi*) increase their nocturnal at-sea foraging behaviour during the spring and summer on the full moon (Watts, 1993). A similar increase has been demonstrated by spinner (*Stenella longirostris*) and dusky (*Lagenorhynchus obscurus*) dolphins off Hawaii and New

Zealand, as relative abundances thought to be related to foraging increased during the full moon (Benoit-Bird et al., 2009). Strandings may also be influenced by lunar cycles based on higher incidences of strandings by sperm whales (*Physeter macrocephalus*) on the new moons in the British Isles and on the full moons in Eastern Canada (Wright, 2005). Lunar influences on behaviour have been associated with nocturnal lunar light levels and predator-prey interactions, but no studies have yet addressed the effect of lunar phase on diurnal behaviour of marine mammals.

Harbour porpoise (*Phocoena phocoena*) are an excellent model for testing the hypothesis that lunar cycles influence diurnal behaviour, because this species requires food throughout the diel period (Kastelein et al., 1997b), and their diet includes forage fish species such as herring and hake which are influenced by lunar cycles (see above and: Smith and Gaskin, 1974; Fontaine et al., 1994; Aarefjord et al., 1995; Martin, 1996; Hall, 2004; Santos et al., 2004). Further contributing to their suitability as a model to test whether lunar cycles influence diurnal cetacean behaviour, is the ability of harbour porpoise to use bottom debris such as stones, as spatial reference points, to maintain mental maps of their captive environments (Andersen, 1976); and their tendency to live in relatively small and restricted geographic areas in the wild (Flaherty and Stark, 1982; Calambokidis and Barlow, 1991; Calambokidis and Baird, 1994a; Andersen et al., 1997; Read and Westgate, 1997; Walton, 1997; Wang and Berggren, 1997; Hanson et al., 1999; Rosel et al., 1999; Chivers et al., 2002). Thus their need to eat regularly, reliance on lunar influenced prey species, and maintenance and knowledge of relatively small home ranges suggests harbour porpoise are a good species to test the hypothesis that lunar cycles affect diurnal mammalian behaviours.

Since wild animals are likely to have the same cognitive abilities as captive animals, it seems plausible that harbour porpoise will select habitats that offer them some advantage in acquiring prey. As such, it is not unreasonable to consider that wild harbour porpoise may both recognise and make use of naturally occurring features within their selected habitats that provide access to readily available prey, and that these features serve as regularly used foraging arenas. Since at least some harbour porpoise prey are influenced by the lunar cycle, it is possible that the use of specific foraging sites may also be lunar influenced.

The effects of the lunar cycle on harbour porpoise are not known, but sightings of harbour porpoise often correspond with tidal cycles. For example, in the western Atlantic, harbour porpoise have long been known to "ride" the flood current to enter rivers and estuaries in pursuit of prey (Leighton, 1937). Spatial movements have also been associated with tidal direction, such as in the Bay of Fundy, where harbour porpoise move inshore and into shallow waters on the flood current, and move offshore on the ebb (Gaskin et al., 1975; Watson, 1976; Gaskin and Watson, 1985; Read and Gaskin, 1985). Relative abundance also increases during the flood current in this region, where harbour porpoise forage in areas of enhanced tidal vorticity resulting from island and headland wakes (Johnston et al., 2005). Off the Shetland Islands, Scotland, harbour porpoise forage near tide rips by facing into the oncoming current (Evans and Borges, 1995). In this same region, they have also been seen to move against strong tidal races and currents, with their preference for particular tidal phases varying by location (Evans, 1997; Goodwin, 2008). Off south-west Wales, harbour porpoise forage in tide races with a preference for the ebb current (Pierpoint, 2008). While, in the Pacific, increased relative densities have correlated with high tides in Alaska (Taylor and Dawson, 1984), and two hours before maximum flood currents in Washington, where their distribution coincided with tide rips and high concentrations of prey (Raum-Suryan and Harvey, 1998). Sekiguchi (1995) also found that harbour porpoise enter Monterey Bay on the flood current which was linked to 'probable-feeding'. Gaskin and Watson (1985) concluded that it was not the specific tide which was important, but rather the combined effect of the topography and tidal flow. The wide variability in tidal patterns used by harbour porpoise, suggests that they adjust to their local environmental conditions and have flexible foraging behaviours.

Further supporting the idea of foraging behaviour flexibility, are observations of harbour porpoise in Monterey Bay, California, spatially associating themselves with tidally induced internal waves (Silber, 1990). Such oceanographic features can concentrate small organisms, such as pelagic larval invertebrates and fish (Norris, 1966; Shanks, 1983; Kingsford and Choat, 1986; Shanks, 1988), and may be the key drivers that explain harbour porpoise habitat selection in the North Sea (Skov and Thomsen, 2008). Based on these observations, it is reasonable to consider that harbour porpoise

have developed a variety of foraging strategies throughout their range that make use of naturally occurring oceanographic features to help acquire prey.

The objective of my research was to determine whether localized areas of increased tidal mixing, driven by tidal flow and bottom topography, afford temporary but predictable foraging arenas for harbour porpoise, and whether their foraging behaviour was influenced by tidal or lunar phases.  I conducted my study during daylight hours at two sites in Juan de Fuca Strait, British Columbia, which were oceanographically and bathymetrically similar, and within the range of a single population.  The two study sites had mixed, predominantly diurnal tides (*i.e.,* usually one high and low tide per day, but sometimes two high and two low tides), with a diurnal inequality predominantly influenced by the moon's declination (Thomson, 1981; Davenne and Masson, 2001).  I examined whether the use of these two areas by harbour porpoise could be predicted from biophysical variables, and anticipated finding a positive relation between the relative density of harbour porpoise and increased tidal flow using surfacing behaviours and group dynamics as indicators of subsurface foraging.  My study sites were not pristine habitat, and being close to industrial shipping lanes and several marinas were subjected to high levels of traffic.  However, both sites likely represented core harbour porpoise habitat based on long-term data indicating inter- and intra-annual use of these areas by harbour porpoise (A. Hall, unpub. data, Calambokidis et al., 1997; Laake et al., 1997).  My study was the first of its kind in British Columbia, and the first overall to explore the lunar influence on the diurnal behaviour of this species.

**Methods**

Two study sites in Juan de Fuca Strait, British Columbia (Figure 3.1) were selected based on physical and biological criteria that included: 1) increased tidal mixing with eddies and shears resulting from variable geography and bathymetry (Thomson, 1981), 2) similar mean tidal velocities (Foreman et al., 1995), 3) geographic proximity, 4) accessibility by small, shore-based vessels, and 5) pre-existing data suggesting year-round use by harbour porpoise (Hall, 2004). The first study area labeled Area R (Figure 3.1) was located near the Race Rocks Ecological Reserve, BC and encompassed 73.5 km$^2$, extending from 48.343° N to 48.257° N, and 123.573° W to 123.470° W. The second labeled Area D (Figure 3.1), was located near Discovery Island, BC and encompassed 73.4 km$^2$, extending from 48.443° N to 48.357° N, and from 123.265° W to 123.162° W.

A 1.852 km X 1.852 km (1 nm X 1 nm) grid was set at right angles using True North (Figure 3.1). Transect points were designated at the nodes and labeled with alphanumeric codes (*e.g.,* R12, D22 *etc* – Figure 3.1). Those transect points on land, in water <10 m, or in US waters (*n*=7) were removed from the sampling protocol.

Survey transect points were selected randomly and surveys were completed between June 2007 and May 2008. Surveys were commenced in Beaufort ≤ 2 sea conditions, in daylight with good visibility — these conditions occurred infrequently in Juan de Fuca Strait (Appendix A1). Effort was discontinued at Beaufort ≥ 3 or when visibility declined. Data were collected in 10-minute intervals, achieving a 'snap-shot' of porpoise behaviour while reducing the likelihood of positively biasing density estimates through double counting. Using a randomized survey design further reduced this possibility. Also, the almost 2 km distance between transect points ensured that it was unlikely that a porpoise could reach the next point before the observers, since the average harbour porpoise swimming speed in this region is 2.4 km/h (Hanson et al., 1999). The probability of missing submerged porpoise was minimised since the observation interval was set to about twice the maximum harbour porpoise dive time (see *Dive Behaviour* in Chapter II and Read and Gaskin, 1985; Westgate et al., 1995; Hanson et al., 1999; Otani et al., 2000).

Data were collected on flood (incoming) and ebb (outgoing) currents, and slack water (no movement) by two experienced observers from an 8.8m 290 Sea Ray Sundancer. Data collection included: survey area, transect ID, sea state, weather, tide, scan start time, scan end time, number of porpoise, time of sighting, species, radial distance, behaviour, and the presence of calves. Visual and acoustic observational cues included splashes, dorsal fins, and the puffing sound associated with exhalation and inhalation by harbour porpoise. Surface behaviour was classified as: **SR** - slow rolling, **SRSXS** - slow rolling side by side, **FS** - fast surfacing, **BR** - breaching and **LG** - logging.

The porpoise data were compared to the direction of tidal flow (flood, ebb and slack), the relative intensity of the tidal flow (spring and neap tidal phases), lunar phase (new moon, waxing crescent, first quarter, waxing gibbous, full moon, waning gibbous, last quarter and waning crescent), and lunar position (apogee and perigee) and lunar declinational positions (equatorial, Tropic of Cancer, and Tropic of Capricorn). These variables were selected because of their contributions to the direction and intensity of tidal flow (Thomson, 1981). Seasons were defined by the solstice and equinox positions, and the harbour porpoise putative reproductive (April – October) and non-reproductive (November – March) seasons. In addition, porpoise numbers and behaviour were examined relative to the Earths perihelion and aphelion positions, even though this does not contribute to the tidal direction or intensity. Nevertheless, this physical aspect of the Earth's annual orbit was examined because little is known of the physical criteria that harbour porpoise respond to, and there was no reason to discount it. Diurnal effects were tested because circadian behavioural variations have been found in harbour porpoise foraging behaviour in other regions (see Chapter II – *Ingestive Behaviours*). Diurnal periods were defined as *am* (morning) and *pm* (afternoon). More refined or additional classifications, such as crepuscular time periods were not possible as a consequence of the weather conditions and sampling schedule.

Lunar phase, lunar position and tide were determined for each observation using Canadian Hydrographic Service Tide and Current Books Volume 5, Jtides software (Lutus, 2007) and the United States Naval Observatory data (USNO, 2008). The tide was determined by the time of the sighting, and the lunar phase and position were determined based on the date of the sighting. The fortnightly spring and neap tidal cycle was

examined in three ways: 1) ±3 days from the full/new moons and first/last quarter moons, 2) by the Victoria daily tidal height differential with spring tides defined as maxima and neap tides as minima, and 3) by daily tidal current differentials with maximum differences occurring on spring tides and minimum differences on neap tides. The Victoria tidal heights and Race Passage current data were provided by M. Foreman and R. Thomson (Institute of Ocean Sciences). The timing of the equinox, solstice, perihelion and aphelion positions were determined from data provided by the United States Naval Observatory (USNO, 2010).

Regular distance estimation calibrations were conducted using a Bushnell Yardage Pro450 laser rangefinder. Transect points were approached at speeds <10kts, to reduce the likelihood of disrupting harbour porpoise behaviours. A "sighting" was defined as an observation of a single porpoise or a group of porpoise in which the observation of one individual led to the observation of another (Hall, 2004). As with previous work in this area, single animals or groups observed independently were recorded as independent sightings (Hall, 2004). An individual or group was recorded only once, even if they remained within the radial search area for the duration of the scan. Radial distances, defined as the distance between the observer and the porpoise, were recorded as exact values, not binned values. These distances were estimated visually to either the individual, or the centre of the cluster if >1 were present. There was no predetermined distance beyond which to stop data collection, with all porpoises detected around the vessel recorded. No age or sex class was made, with the exception of cows with calves, and neonatal calves. High-density aggregations were defined as group sizes ≥15 and ≥50, which included single large groups, multiple smaller groups that were spatially and behaviourally associated with one another.

Systematic data from Survey Areas R and D were pooled for non-parametric statistical and distance analyses. For comparative purposes, the supplementary data from Areas R and D were also pooled for analysis. Both analytical data sets were limited to sea states Beaufort 0 − 2. Encounter rates and density estimates were calculated using Distance 6.0 software (Thomas et al., 2009) following the procedures and formulae described in Buckland et al. (1993). Behavioural analyses were conducted with NCSS

2000 (Hintze, 1998), and figures were produced using ArcGIS 9.1 (ESRI, 2005) and R version 2.12.2 (RDCT, 2011).

Density was estimated using the Conventional Distance Sampling (CDS) Engine:

$$D = \frac{E(n) \cdot h(0) \cdot E(s)}{2 \cdot \pi \cdot c \cdot k \cdot g_0}$$

where $D$ equals density, $E(n)$ is the expected number of animal clusters, $h(0)$ is the slope of the probability density function of distances from the point evaluated at zero distance, $E(s)$ is the mean cluster size, $c$ is the proportion of the area surveyed ($c=1$), $k$ is the number of points, and $g(0)$ is the probability of detection at the transect point (Buckland et al., 1993).
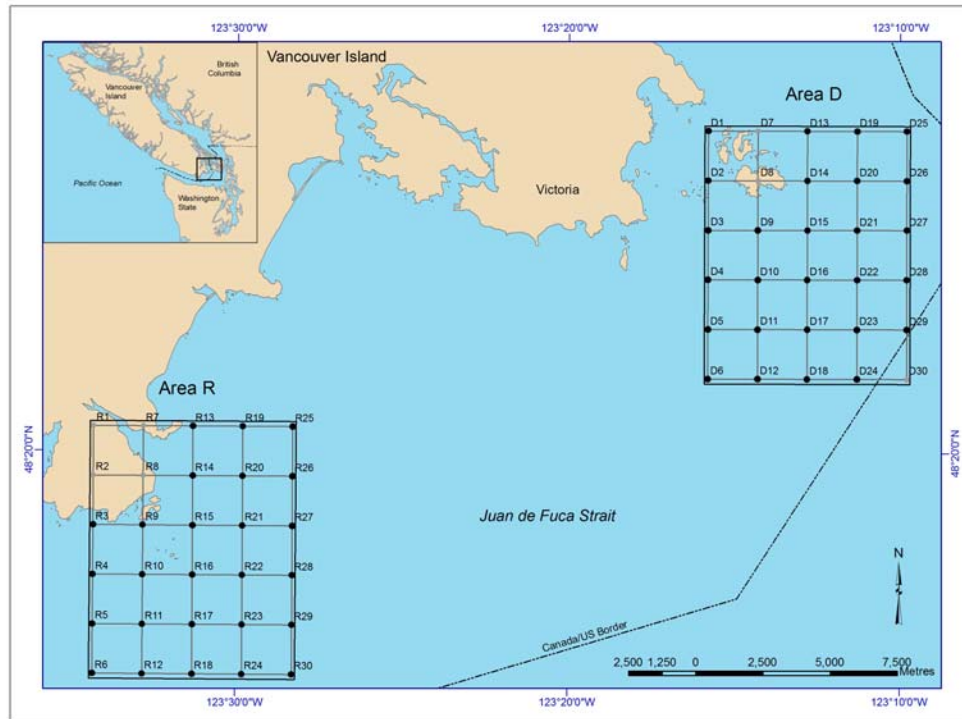


**Figure 3.1 Harbour porpoise point-transect study sites designated as Areas R, and D in the coastal waters of Southern Vancouver Island, British Columbia in Juan de Fuca Strait. The study site labels referenced local geography as Area R was near the Race Rocks Ecological Reserve, and Area D was near Discovery Island. Nodes of the intersecting grid lines designated the transect survey points and were labeled with alphanumeric codes (*i.e.,* R1, R2, D1, D2 *etc*). The grid was set 1.852 km X 1.852 km (1 nautical mile X 1 nautical mile) with the total areas of 73.5 km² (Area R), and 73.4 km² (Area D). Transect points on land, in water ≤10 metres or in US waters were excluded and are represented in grey.**

It was assumed that *g(0)=1*, or that any porpoise at zero distance was detected. However, the reality is that *g(0)* was probably *<1* because harbour porpoise have a small dorsal fin, and spend little time at the surface. Thus, harbour porpoise numbers were likely underestimated using *g(0)=1*. Although, the magnitude of this underestimate is not known, it is reasonable to assume that *g(0)* was near 1, as the data were limited to sea states Beaufort 0 – 2, and both observers were experienced in porpoise detection. In addition, the study site was in an area where harbour porpoise regularly encounter vessel traffic and the observation time was set to twice the maximum dive time (Westgate et al., 1995; see Hanson et al., 1999; Otani et al., 2000).

Observer specific correction factors were modeled with linear regression (Appendix A3), as previously done in this region (Hall, 2004), and a corrected set of distances were generated for density estimation in Distance 6.0 (Thomas et al., 2009). A global detection function, which decreased with increasing distance from the vessel was initially modeled using uniform, half-normal and hazard-rate functions (Buckland et al., 1993). Cosine, simple and hermite polynomial series expansions were tested to improve the fit. Model selection was iterative involving inspection of radial distance histograms and probability detection functions, Chi-squared goodness of fit tests, QQ plots, Kolmogorov-Smirnov and Cramér-von Mises tests, the number of parameter adjustments and Akaike's Information Criterion (AIC) scores (Buckland et al., 1993). The final model selected was a half-normal key function with a cosine adjustment. Uncorrected data were truncated at 9% or 200.0 m, and corrected data at 10% or 184.4 m.

All categorical variables were dummy coded into a binary format and processed in a stepwise regression with backward selection to identify candidate variables for inclusion in a predictive model. Candidate physical independent variables included flood current, ebb current, slack current, spring tide, neap tide, month, reproductive vs. non-reproductive months, solstice and equinox defined seasons, diurnality, and lunar phases. Two biological variables were tested in the multiple regressions to reflect the spatial distribution of the porpoise groups at each transect. A Number of Groups Index, which ranged from 0 – 1, signified whether multiple or single groups were observed at each

transect point, and an Index of Conspecifics, which also ranged from 0 – 1, was based on the observed group sizes. Developed independently of the high-density event of 20 July 2007, these indices were used as measures of social interactions, with the Number of Groups Index reflecting inter-group dynamics, and the Index of Conspecifics reflecting intra-group dynamics.

Supplementary data complemented the systematic data. These opportunistic sightings of harbour porpoise and observations of their behaviour were collected April – October over a 13-year span (1995–1996, 1998–2008) from platform of opportunity whale watch vessels operated by Inter Island Launch Ltd., out of Victoria, British Columbia in Beaufort 0 – 2 (*n*=2328), by a single observer (A. Hall). Within these data, 29 high-density aggregations were recorded in 1999 – 2004 and 2006 – 2008. Data collected included sea state, weather, tide, number of porpoise, time of sighting, species, behaviour, and presence of calves. The master data set was sub-sampled for the geographical delineations of Survey Areas R and D. These data were also coded to reflect the tidal, lunar, and seasonal conditions for each harbour porpoise sighting. Spring tides coinciding with the lunar perigee positions result in exaggerated high and low tides (Thomson, 1981), and were sampled in 1996, 1998, 1999, 2000, 2002, 2003, 2004, 2005, 2007 and 2008.

**Results**

Point transect surveys were completed 10 June 2007 – 24 May 2008 (*n=169*, Appendix A4). Numbers of adults and calves (*n=303*) fluctuated throughout the year, with peak numbers occurring in July (Figure 3.2). Effort fluctuated monthly but was highest from June – August, and in May (Figure 3.2). Sightings Per Unit Effort (SPUE) also peaked during the spring/summer periods for both age classes (Figure 3.3). The peak of non-calf SPUE in July was influenced by an unusual number of groups detected within 5.3 km$^2$ on 20 July 2007, yielding a fine-scale density estimate of ~25 porpoise/km$^2$. An order of magnitude difference existed between the annual harbour porpoise encounter rate (*n/k*) (0.11 porpoise/transect, 95%CI: 0.11, 0.12) and the 20 July 2007 encounter rate (1.03 porpoise/transect, 95%CI: 0.35, 3.08) (Appendix A5). These high density and high encounter rate values were anomalous for this region (see Hall, 2004), and were therefore removed from the annual data and not included in the following results, unless otherwise specified as high-density aggregation data. Transects conducted on 20 July 2007 were sampled prior to, and after the high-density aggregation and failed to detect another such aggregation. A second numerical non-calf SPUE peak occurred in November (Figure 3.3) when the sighting rate in the first week of surveys was relatively high, and poor weather prohibited continued effort for the remainder of the month.

Key assumptions for Distance analysis (Buckland et al., 1993) were met (Appendix A6). Data inspection indicated that no statistical difference existed in radial distance estimation by observers (Two Sample *t*-Test, *t=-0.34, d.f.=129, P=0.73*) and neither observer favoured any radial distance as no evidence of heaping was found in inspection at 2, 5, 10, 20 and 40 m increments. No evidence of evasive movement prior to detection was found, as sighting frequency decreased with increasing distance and detection was not found to be a function of group size (Appendix A6).
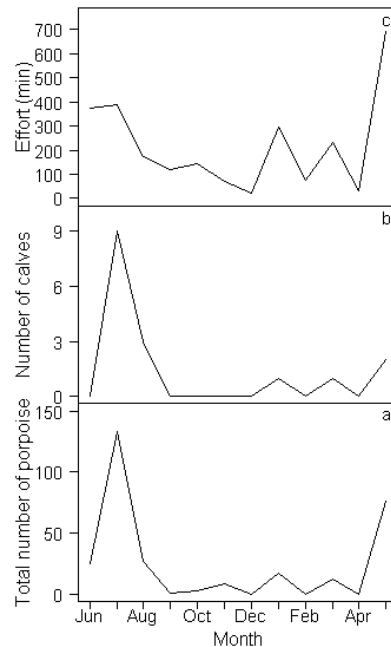
**Figure 3.2 Monthly total number of harbour porpoise (a), total number of calves (b), and total effort (min) (c) observed during the 2007–2008 point transect survey in Areas R and D in Juan de Fuca Strait, British Columbia, in Beaufort 0 – 2.**
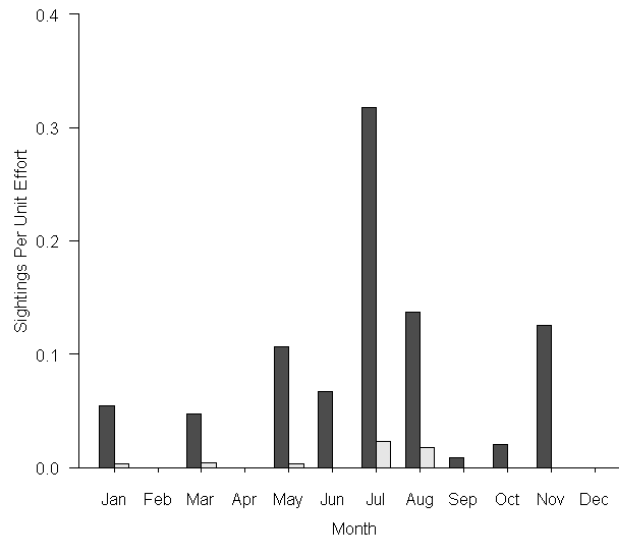


**Figure 3.3 Monthly numbers of harbour porpoise (calves and non-calves) detected per minute of observation (SPUE – Sightings Per Unit Effort) from June 2007–May 2008 in Survey Areas R and D in Juan de Fuca Strait, BC, in Beaufort 0 – 2. Non-calf sightings are in black and calf sightings are in grey. Plotted for calendar year (January – December) to show spring/summer seasonality.**

***Tidal Effect***

The 2007–2008 transect effort was significantly different on the flood, ebb and slack currents in terms of the number of transects conducted (Chi Square Test, $X^2_2=28.98, P<0.001$) and the total observation time for each tidal phase (Chi Square Test, $X^2_2=239.26, P<0.001$). The ebb current accounted for more than half of the effort (52.6%), but only a third of the sightings (35.3%). Most of the porpoise (55.1%) observed throughout the 12-month period were seen on the flood current, which only accounted for 26% of the effort. This difference was statistically significant with harbour porpoise encounter rates during flood currents greater than on the ebb or slack currents (Kruskal-Wallis One Way ANOVA *corrected for ties*, $H=14.76, d.f=2, P=0.001$), but this result was influenced by the 20 July 2007 high-density data.

In the absence of high-density data, the differential use of Areas R and D was maintained in terms of numbers (Figure 3.4) and when standardised by effort, but the ebb current encounter rate (0.12 porpoise/transect, 95% CI: 0.11, 0.14) was significantly greater than encounters with porpoise on either the flood (0.09 porpoise/transect, 95% CI: 0.09, 0.10) or slack currents (0.09 porpoise/transect, 95% CI: 0.09, 0.10) with pooled data from Survey Areas R and D (Appendix A7). This difference reflected an increase in the number of groups present (Chi Square Test, $X^2_2=67.28, P<0.001$), not an increase in the group size (Kruskal-Wallis One Way ANOVA *corrected for ties*, $H=3.79, d.f=2, P=0.14$). Similarly significantly different numbers were seen during the supplementary observations on the flood, ebb and slack currents in Survey Areas R and D (Chi Square Test, $X^2_2=380.53, P<0.001$ – Figure 3.4). Again, this was because of an increase in the number of animals observed on the ebb current (Chi Square Test, $X^2_2=170.77, P<0.001$ – Figure 3.4). Unlike the systematic data set, no difference in effort existed between tidal current phases in the supplementary data set (Chi Square Test, $X^2_2=0.97, P<0.001$).

In terms of the fortnightly spring/neap cycle (defined as ± 3 days from the full/new moons and first/last quarter moons), harbour porpoise were seen on spring and neap tides but in significantly greater numbers on the spring tides in both survey areas, in both data sets (Chi Square Test: Systematic $X^2_1=63.62, P<0.001$: Supplementary $X^2_1=74.13, P<0.001$ – Figure 3.5). The same trends held true when the spring/neap cycle was defined by the monthly tidal height differentials and when tidal height differentials

were restricted to daylight hours only (Chi Square Test: $X^2_1=12.64$, $P<0.001$, and Table 3.1). Harbour porpoise were observed more using the upper end of the tidal height differential spectrum at >1.5 m (Chi Square Test: $X^2_1=54.21$, $P<0.001$ and Appendix A8). This was not related to effort, as the sightings per unit effort (SPUE) indicated most sightings (non-zero SPUE) occurred in the higher end of the current differentials >2.5 m/s, suggesting a preference for times of increased water movement associated with the spring tides (Chi Square Test: $X^2_1=12.64$, $P<0.001$ and Appendix A8).

Transect spring tide encounter rates were 1.5 times greater than neap tide encounter rates (Spring: 0.13, 95%CI: 0.12: 0.13; Neap: 0.08, 95%CI: 0.05, 0.14), due to a greater number of groups using the study areas (Chi Square Test, $X^2_1=23.28$, $P<0.001$). No increase in group size was observed in either data set between the spring and neap tides (Systematic: Mann-Whitney U Test *corrected for ties*, $U_{neap}=594$, $U_{spring}=792$, *d.f.=85, Z=1.06, P=0.287;* Supplementary: Mann-Whitney U-Test *corrected for ties*, $U_{neap}=8598.50$, $U_{spring}=6601.50$, *d.f.=250, Z=1.78, P=0.07*). There was also no significant difference in the number of transect surveys (2007–2008) conducted on spring and neap tides (Chi Square Test, $X^2_1=4.80$, $P<0.001$), and no difference in supplementary data effort between spring and neap tides (Chi Square Test, $X^2_1=0.89$, $P<0.001$).

**Table 3.1 Maximum and minimum monthly tidal height differentials for Victoria and midpoints with the number of harbour porpoise observed below and above the tidal height differential midpoint. High-density data (20 July 2007) are excluded.**

| Month | Maximum Tide Height Differential (m) | Minimum Tide Height Differential (m) | Midpoint (m) | Number Below Midpoint (Neap Tide) | Number Above Midpoint (Spring Tide) |
|---|---|---|---|---|---|
| June | 3.13 | 1.11 | 2.12 | 20 | 5 |
| July | 2.92 | 1.04 | 1.98 | 0 | 0 |
| August | 2.51 | 1.06 | 1.79 | 0 | 27 |
| September | 2.50 | 1.07 | 1.79 | 0 | 1 |
| October | 2.93 | 1.07 | 2.00 | 3 | 0 |
| November | 3.27 | 1.13 | 2.20 | 9 | 0 |
| December | 3.30 | 1.27 | 2.29 | 0 | 0 |
| January | 3.00 | 1.12 | 2.06 | 2 | 15 |
| February | 2.48 | 1.07 | 1.77 | 0 | 0 |
| March | 2.25 | 1.01 | 1.63 | 2 | 10 |
| April | 2.63 | 0.96 | 1.80 | 0 | 0 |
| May | 3.09 | 0.99 | 2.04 | 10 | 29 |
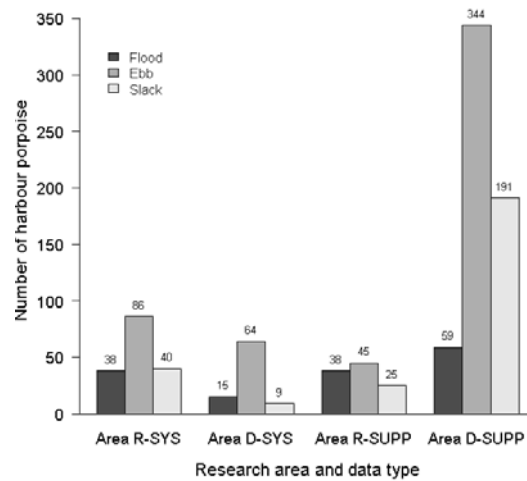
**Figure 3.4 Total number of harbour porpoise detected on flood, ebb and slack currents in Juan de Fuca Strait, British Columbia, excluding the high density groups (n≥15), with the greatest numbers detected on the ebb current. Systematic data (SYS) from June 2007 – May 2008 were compared to the supplementary platform of opportunity data (SUPP) spanning 13 years (1995–1996, 1998–2008) in Survey Areas R and D. High-density groups were removed from both data sets for comparison of regular group size occurrences. The total number is indicated above the bars.**
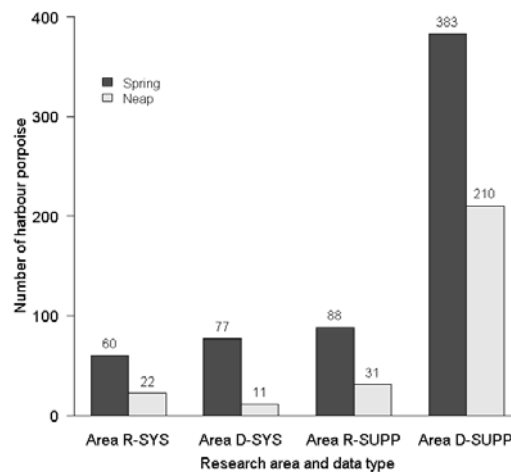


**Figure 3.5 Total number of harbour porpoise observed on the spring and neap tidal cycles in Survey Areas R and D in Juan de Fuca Strait, British Columbia with more animals observed on the spring tide in each data set and both survey areas. Systematic point transect data (SYS) from June 2007 – May 2008 were compared to supplementary (SUPP) platform of opportunity data from 1995–1996, 1998–2008. High-density groups (n≥15) were removed from both data sets for comparison of regular group size occurrences. The total number is indicated above the histogram bars.**

*Lunar Effects*

Numbers of animals observed during the 2007–2008 survey varied under different lunar conditions. Nearly half of all animals (48.8%) were detected during the syzygy conditions of the new or full moons (Figure 3.6), with statistically more being seen on the new moon (Chi Square Test, $X^2_1=13.12$, $P<0.001$). In contrast, <1% were observed during quadrature conditions on the first and last quarter moons (Figure 3.6). Animals were also observed under the waxing and waning crescent, and waxing and waning gibbous lunar phases (50%), with the majority (36%) of these sightings occurring before and after the full moon *(i.e.,* waxing and waning gibbous moons).

When lunar phase effort was taken into account, this syzygy versus quadrature difference was still statistically significant (Chi Square Test, $X^2_1=80.00$, $P<0.001$), with density at syzygy (7.25 porpoise/km, 95%CI: 5.42, 9.70) an order of magnitude greater than at quadrature (0.74 porpoise/km, 95%CI: 0.55, 0.99 – Appendix A9). Correspondingly, the supplementary data showed a greater proportion of harbour porpoise using Survey Areas R and D on new and full moons, than on the quarters (Figure 3.6). Again, this syzygy versus quadrature difference was significant (Chi Square Test: $X^2_1= 86.40$, $P<0.001$).

The proportions of harbour porpoise foraging in Survey Areas R and D did not vary according to whether the moon was in a perigee or apogee position, in either the systematic or supplementary data sets (Chi Square Test: Systematic: $X^2_1=0.03$, $P<0.001$; Supplementary: $X^2_1=6.16$, $P<0.001$).

No difference was observed in the number of animals present on spring tides that coincided with the lunar perigee position in either the systematic or supplementary data sets (Mann-Whitney U Test *corrected for ties*, Systematic: (all): $U_{spring}=226.5$, $U_{perigean\_spring}=286.5$, d.f.=64, Z=0.6, P=0.55, (note: the 20 July 2007 high density aggregation occurred on a neap tide so stratification was not necessary); Supplementary: (all data): $U_{spring}=1487$, $U_{perigean\_spring}=1373$, d.f.=150, Z=0.3, P=0.77; Supplementary (high density stratified): $U_{spring}=1170$, $U_{perigean\_spring}=1015$, d.f.=132, Z=0.5, P=0.62; Supplementary (high density only): $U_{spring}=32$, $U_{perigean\_spring}=12$, d.f. = 16, Z=1.1, P=0.28).
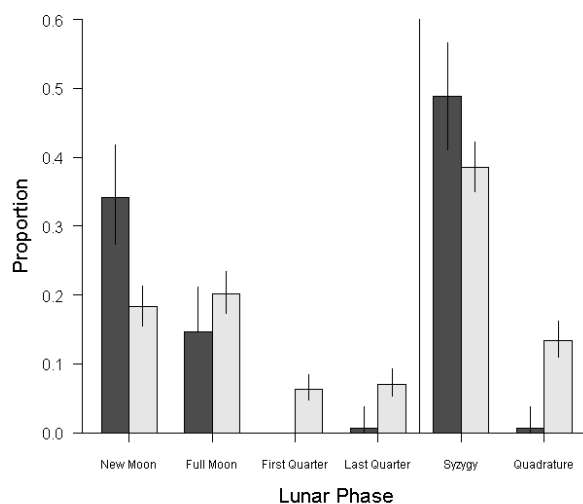
**Figure 3.6 Proportion of harbour porpoise observed in Survey Areas R and D during the 2007–2008 systematic point transect survey (*n=170*), and the 1995–1996, 1998–2008 platform of opportunity supplementary data collection (*n=711*), with high densities removed (*n≥15*). Sightings data were classed by six lunar conditions with the new moon, full moon, first quarter, and last quarter presented separately from the syzygy and quadrature conditions. Syzygy occurs during either the full or new moon when the moon, earth and sun are in alignment, while quadrature occurs on the first and last quarter when the moon, sun and earth are at right angles. Systematic point transect data are in black and supplementary platform of opportunity data are in grey, with 95% confidence intervals.**

Group sizes and numbers of individuals did not change according to the declination of the moon. There was no difference in the group sizes using the study areas whether the moon was in tropic or equatorial positions, *i.e.,* the moon over the Tropic of Cancer (greatest northerly declination), Tropic of Capricorn (greatest southerly declination) or the equator (Mann-Whitney U Test *corrected for ties*, Systematic (high denisty stratified) $U_{non-equitorial} = 341$, $U_{equitorial}=572$, *d.f.=92, Z=1.46,P=0.14*; Supplementary (all data) $U_{non-equitorial} =1775.5$, $U_{equitorial}=1590.5$, *d.f.=115, Z=0.51, P=0.61;* Supplementary (high density stratified) $U_{non-equitorial} =1343$, $U_{equitorial}=1209$, *d.f.=100, Z=0.50, P=0.65*) and there was also no difference in the numbers of animals observed under these conditions (Chi Square Test, Systematic $X^2_1=0.25$, *P<0.001*; Supplementary: $X^2_1=1.32$, *P<0.001*).

*Diurnality*

No diurnal effect was found. Equal numbers of sightings occurred in the morning and afternoon, and group sizes did not vary (Mann-Whitney U Test *corrected for ties*, $U_{am}=1698.5$, $U_{pm}=1361.5$, *d.f.*=122, Z=0.99, P=0.32). There was no difference between the *am* and *pm* effort in the systematic survey (Chi Square Test, $X^2_1=1.75$, P<0.001); no difference was found in the number of animals observed before (*am*) and after (*pm*) 1200 in the supplementary data set (Chi Square Test, $X^2_1=0.11$, P<0.001), though the effort was greater in the afternoon (Chi Square Test, $X^2_1=104.14$, P<0.001).

*Seasonality*

Seasonality was tested for in several ways. No significant difference was observed with either the number of harbour porpoise, or the number groups observed using the study areas during the Summer and Winter Solstice months versus the Spring and Autumn Equinox months during the transect survey (Mann-Whitney U Test *corrected for ties*, $U_{solstice}=37.5$, $U_{equinox}=81.5$, *d.f.*=22, Z=1.55, P=0.12: Chi Square Test, $X^2_1=3.79$, P<0.001). In the supplementary data, there was also no difference in the number of observations of harbour porpoise (Chi Square Test, $X^2_1=5.23$, P<0.001), or the group sizes (Mann-Whitney U Test *corrected for ties*, $U_{solstice}=590$, $U_{equinox}=510$, *d.f.*=67, Z=0.50, P=0.62). Effort did not differ significantly for either data set (Chi Square Test: Systematic: $X^2_1=0.50$, P<0.001, Supplementary: $X^2_1=4.89$, P<0.001).

Due to uneven sampling effort in winter and summer, it was not possible to determine whether the Earths' perihelion and aphelion positions influenced harbour porpoise behaviour in either data set. However, it was interesting to note that in 2007 the aphelion occurred on 7 July (USNO, 2010), and almost 2 weeks later the high-density aggregation of 20 July 2007 was detected in the systematic survey. Also, the greatest winter (Oct 2007 – Feb 2008) concentration of harbour porpoise observed in the transect survey occurred on 18 January 2008, which was about 2 weeks after the perihelion event of 3 January 2008 (USNO, 2010). In the 1995–1996, 1998–2008 supplementary data set, 63% of the June and July high-density events occurred within about 2 weeks of the July aphelion (USNO, 2010).

However, Figure 3.2 indicates that more harbour porpoise were observed during the summer months than the winter months, and statistically significant greater numbers were observed during April – October (Chi Square Test, $X^2_2=52.78$, $P<0.001$).  Again, there was no change in the group sizes (Mann-Whitney U Test *corrected for ties*, $U_{Apr-Oct}=774$, $U_{Nov-Mar}=1028$, $d.f.=121$, $Z=0.98$ $p=0.33$).  As expected, differential effort was exerted in the seven-month April – October timeframe, than in the five-month November – March timeframe.  However, encounter rate statistical differences were detectable with more animals observed per unit of time from April – October (Mann-Whitney U Test *corrected for ties*, $U_{Apr-Oct}=5475.5$, $U_{Nov-Mar}=3996.5$, $d.f.=210$, $Z=2.02$, $P=0.04$).  Within this spring and summer timeframe, the months of August, September and October were statistically different from April, May, June and July (high density data removed: Kruskal-Wallis *corrected for ties*, $H=40.37$, $d.f.=11$, $p=0.00$, MCP Z Test with a Bonferroni Correction, August, September, October $Z>3.36$, $P<0.0008$).  The April – October density estimate was more than double (9.79 porpoise/km, 95% CI: 7.23, 13.26) than the November – March estimate (3.91 porpoise/km, 95% CI: 2.92, 5.23, and Appendix A9).  Effects of biological seasonality could not be determined for the supplementary data due to an absence of winter data.

### *Integration*

Multiple regression analysis of the candidate physical and biological/social variables revealed that habitat selected by foraging harbour porpoise in Survey Areas R and D could be predicted by three key physical variables and two biological/social variables.  These included the direction of the ebb current, time of year (*i.e.,* April – October), syzygy conditions (*i.e.,* new and full moons), and the Index of Conspecifics and the Number of Groups Index.  The final relationship ($R^2 = 0.94$) was:

$$\log NP = \left[-0.69 + 0.01(E) + 0.05(AO) + 0.03(FN) + 1.33(IC) + 0.04(NG)\right]$$

where *NP* is the total number of porpoise, *E* is ebb current, *AO* is the April-October timeframe, *FN* is the Full or New Moons (*i.e.,* syzygy conditions), *IC* is the Index of Conspecifics, and *NG* is the Number of Groups Index.  Model fit was reduced with the removal of the biological/social indices (without Number of Groups Index $R^2=0.86$;

without Index of Conspecifics $R^2=0.13$), and as expected the relative importance of the physical variables changed as the model changed (Appendix A19).

*High Density Aggregations*

The single high-density aggregation observed during the 2007–2008 systematic survey on 20 July 2007 occurred on a flood current during a neap tidal phase, after the new moon on a waxing crescent equatorial moon. However, 29 high-density aggregations recorded in the supplementary data set (1995–1996, 1998–2008) occurred most frequently on the ebb current; though the greatest mean group size and the greatest total estimate were observed on the slack current. Inter-annually, high-density aggregations occurred most frequently in May, and the largest mean group sizes were also observed in May (Figure 3.7). High-density aggregations were also rare events as they accounted for only 5.4% of all observations (1995–1996, 1998–2008).

No statistical difference in the occurrence of harbour porpoise high-density aggregations was observed on the spring and neap tides (Chi Square Test, $X^2_1=1.69$, $P<0.001$), but greater numbers of porpoise were observed on the spring tides (Chi Square Test, $X^2_1=296.48$, $P<0.001$).

Overall, more harbour porpoise high-density aggregations occurred when the moon was at syzygy (48%) than at quadrature (14%), and greater numbers of porpoise were observed during the new and full moons (*i.e.,* syzygy) (Chi Square Test, $X^2_1=567.20$, $P<0.001$).

There was no statistical difference as to whether the moon was at apogee or perigee (Chi Square Test, $X^2_1=6.16$, $P<0.001$) or whether the moon was in tropic or equatorial positions (Chi Square Test, $X^2_1=1.32$, $P<0.001$). Spatially, the high-density groups observed within Survey Areas R and D during the 2007–2008 systematic surveys and the 1995–1996, 1998–2008 opportunistic surveys were clustered. The highest densities (>200 porpoise) occurred within 10.3 km$^2$ in Area D, and all occurred within 34.3 km$^2$ in Survey Area D, and 24 km$^2$ in Survey Area R (Figure 3.8).
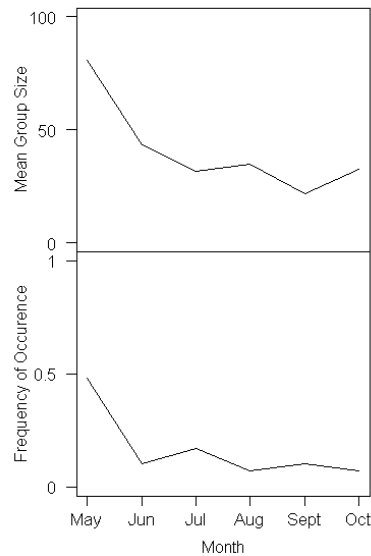
**Figure 3.7 Frequency of occurrence of harbour porpoise high-density aggregations detected in Survey Areas R and D during opportunistic data collection from whale watch vessels in Juan de Fuca Strait, BC. Observations were made from April to October in 1995–1996, 1998–2008. Data limited to sea states Beaufort 0 – 2.**
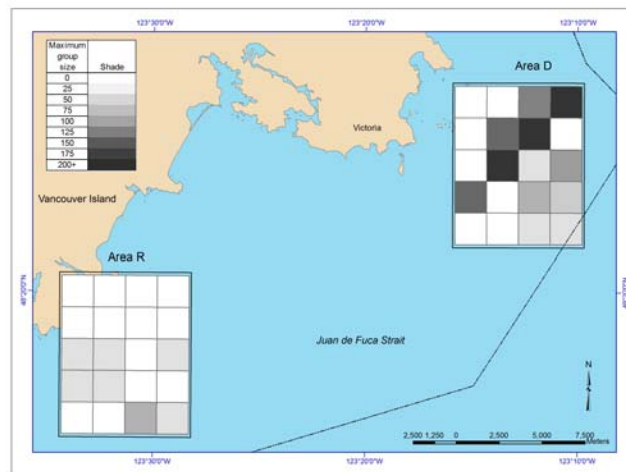


**Figure 3.8 High-density aggregations, in sea states Beaufort 0 – 2, of harbour porpoise within Survey Areas R and D for the 2007–2008 point transect surveys and the 1995–1996, 1998–2008 opportunistic surveys in Juan de Fuca Strait. The grid is 1.852 km X 1.852 km (1nm X 1nm).**

*Calves*

Calves were sighted 15 times during the 2007–2008 transect surveys (March, *n* = 1; May, *n* = 2, July, *n* = 9; August, *n* = 3), with an additional possible cow-calf pair in January. The calves were seen alone and as part of small groups ≤5. Most of the calf sightings (60%) occurred during the high-density aggregation of 20 July 2007, with 47% detected at one transect point alone (Appendix A10).

During the opportunistic surveys, calves were detected 32 times between 1995–1996, and 1998–2008 (Appendix A10). Again, they were seen as single animals and in small groups, with 79% occurring in groups ≤5. Calves were detected May – October, with 47% detected in July and August (Appendix A10). Detection on tidal current phases varied with 50% occurring on the ebb, 19% on the flood and 31% on slack currents, but statistical evaluation was not conducted due to the small sample size (*n=32* – Appendix A10).

*Surface Behaviour*

During the 2007–2008 survey, harbour porpoise were in the presence of conspecifics in 87% of the sightings. A significant difference existed in the number of observations of single groups to the number of multiple groups present at any transect point, with multiple groups most common (Chi Square Test, $X^2_1=27.60$, $P<0.001$).

Animals that were synchronously slow rolling at the surface (**SRSXS**) were in significantly larger groups than animals observed to be surfacing independently of conspecifics (**SR**) (Mann-Whitney U Test *corrected for ties*, $U_{SR}=389.5$, $U_{SRSXSr}=3012.5$, *d.f.=47, Z=7.37, P=0.00*). No relationship was found between the flood, ebb and slack currents and the independent behaviour (Kruskal-Wallis *corrected for ties*, *H=3.26, d.f.=2, P=0.20*), but the synchronous surfacing behaviour (**SRSXS**) occurred more frequently during the flood currents (Kruskal-Wallis *corrected for ties, H=12.97,d.f.=2, P=0.00*, Kruskal-Wallis Multiple Comparison Test with Bonferroni correction, $Z_{flood-ebb}=2.80$, $P=0.005$, $Z_{flood-slack}=3.15$, $P=0.002$).

Qualitatively, foraging porpoise demonstrated two behavioural patterns that were associated with small-scale fronts and spatially restricted areas of tidal upwelling. Animals that were positioned within upwellings slow rolled (**SR**) independent of other

animals at the surface and showed very little lateral movement, while those in areas of horizontal water flow, displayed fast surfacing (*FS*) behaviours as they moved from quiescent into disrupted waters. Synchronised foraging behaviour was documented with groups of harbour porpoise positioning themselves across a channel facing into the oncoming current. The animals maintained their relative spatial positioning as they progressed into the current covering approximately a 300 m$^2$ area. The group submerged after a series of 8–10 ventilations, and resurfaced at a location posterior to the last ventilation. Behavioural synchrony was observed between group members, and this pattern continued for over an hour.

Lastly, logging behaviour was only observed in areas with little water flow (*i.e.,* slack water or in the leeward waters of islands). Synchronised logging behaviour was observed on one occasion with three animals sequentially maintaining a motionless posture at the surface. After several minutes the group returned to a synchronised slow rolling, side-by-side (**SRSXS**) behaviour.

**Discussion**

The data show that the foraging behaviour of harbour porpoise in Juan de Fuca Strait (BC) is affected by tidal and lunar cycles. Increased relative densities of porpoise were predictable in the study areas as a function of the ebb current, the occurrence of new or full moons (*i.e.,* often associated with the spring tide), and the time of year (*i.e.,* April–October). In terms of the lunar phase, harbour porpoise occurred more frequently during the new moon over the full moon, but both of these lunar phases together (*i.e.,* syzygy) appeared to have a greater effect on foraging than either the first or last quarter moons (*i.e.,* quadrature). Including the presence of conspecifics and the number of groups index improved the predictive ability of the integrative model suggesting there is a social component to the foraging behaviour of harbour porpoise in tidally well-mixed areas, and may suggest a cooperative strategy for either prey capture or predator surveillance during bouts of feeding. The results of my study suggest that groups of harbour porpoise adjust their spatial positioning over fine-scales in response to ephemeral physical stimuli.

In contrast to my findings, Flaherty and Stark (1982) failed to find a relationship between tidal cycles and the numbers, behaviours, or group sizes of harbour porpoise in nearby Washington. Similarly, Baird and Guenther (1991) also failed to find an association between the presence of porpoise and areas of high tidal current flow. The failures of these studies to find such differences may be related to the large scales of their respective study areas. Flaherty and Stark (1982) observed harbour porpoise over 1459 km$^2$, and Baird and Guenther examined all of the inland waters of southern British Columbia. The disparity between my findings and these other studies provides further support that harbour porpoise adjust their behaviour over fine-scales. For studies that aim to address behavioural responses of porpoises, scales relative to individuals rather than a populations' potential geographic distribution may be more appropriate.

Gaskin (1992) stated that harbour porpoise distribution is linked to the distribution of the pelagic schooling fish upon which they prey. In the western Atlantic, harbour porpoise concentrate in habitats containing pelagic fish "bottleneck" zones, where the probability of contact between the porpoise and the fish is greatest (Kraus and Prescott, 1981; Gaskin, 1992). Atlantic harbour porpoise have also been known to select areas with strong topographic upwellings which increased the availability of herring

(Graham, 1933; Forrester, 1958; Jovellanos and Gaskin, 1983; Gaskin, 1992). Such fine-scale habitat adjustments provides additional support that harbour porpoise have the ability to know the physical features of their local environments as suggested by Andersen (1976), and that they likely maximise their foraging efficiency through behavioural adjustments over time and space. Behavioural adjustments such as these likely influence both harbour porpoise intra- and inter-group dynamics. Although the relationship between and within groups remains unknown, there is likely an important social component to foraging given that harbour porpoise were most often seen in groups, and that social variables improved the predictive integrative model. Furthermore, physical variables alone were insufficient to predict porpoise numbers well. More refined predictive models will likely also need to include other factors that are currently unaccounted for. These may include factors such as the presence and spatial orientation of prey species; the within water column physical structures, such as fronts and upwellings, that are generated on different tidal phases and tidal velocities; or the past presence of predators within some defined lag time.

In my study areas, groups of foraging harbour porpoise remained in spatially restricted areas by facing into the oncoming currents, then synchronously allowing the current to carry them subsurface to their initial starting positions. Each group surfaced in unison, and the pattern repeated itself over and over. Facing into the oncoming currents or topographically generated upwellings may effectively increase the probability of harbour porpoise encountering prey items. Figuratively this can be envisioned in the same way that a conveyor belt is used to transport items. The oncoming oceanographic currents may effectively "deliver" prey items to the waiting harbour porpoise. This "Conveyor Belt Hypothesis" is consistent with my behavioural observations, and the findings of harbour porpoise positioning in fish bottleneck zones and areas of high herring densities in the western Atlantic (see above).

Testing the conveyor belt hypothesis will require further study. One means of testing it would be to compare the physical properties of the water column in study areas R and D on the flood, ebb and slack currents during the spring and neap tidal phases. Examination of the spatial positioning of subsurface currents, fronts, upwellings and downwellings relative to prey species aggregations, and harbour porpoise subsurface

behaviours would also be useful for testing this hypothesis. Given that the ebb currents during the spring tidal cycle should maximally concentrate harbour porpoise prey either in currents, eddies or fronts, the relative spatial positioning of harbour porpoise under these conditions should lend to maximising the species encounter rates and subsequently harbour porpoise foraging efficiency. If this is the case, then the ebb current during the spring tidal cycle must confer the most advantageous "conveyor belt" of prey items to harbour porpoise. The year-round and inter-annual presence of harbour porpoise in the study areas suggests that this type of ephemeral foraging arena may be central to harbour porpoise habitat selection in coastal British Columbia.

The possibility of harbour porpoise using the physical features to optimize their foraging efficiency is further supported by the tidal asymmetry that exists in some parts of southern British Columbia, and the interactions between ocean currents and pelagic species found in other regions. Harbour porpoise may target the ebb currents because they are stronger than flood currents along the shoreline of southern Vancouver Island, and these currents are further enhanced by the net outward flow of the surface waters resulting from the estuarine circulation (Thomson, 1981; Thomson et al., 2007). These stronger outgoing currents lead to greater deflection from bottom topography and generate stronger upwellings and tidal rips (R. Thomson, pers. comm.). Such oceanographic features can contribute to temporary concentrations of zooplankton and small fish, such as herring, sand lance (*Ammodytes hexapterus*) and capelin (*Mallotus villosus*), which are consumed by harbour porpoise (Hunt et al., 1998; Lavoie et al., 2000; Simard et al., 2002; Cotté and Simard, 2005). It may be that harbour porpoise exploit these physical oceanographic conditions to maximise their chances of encountering prey items.

Based on relative densities of harbour porpoise, my study sites were used most heavily from April to October — the putative reproductive season. The presence of cow-calf pairs in the study areas may indicate that these foraging habitats also hold an inter-generational significance to harbour porpoise, as this species is considered to breed in traditional areas (Koschinski, 2002), and several Atlantic calving and nursing habitats have already been identified (Smith and Gaskin, 1983; Gaskin and Watson, 1985; Evans, 1987; Sørensen and Kinze, 1990; Leopold et al., 1992; Schulze, 1996; Sonntag et al.,

1999).  Additional work on this topic will help determine the presence of harbour porpoise calving and nursing habitats in British Columbia.

The increase in density during the putative reproductive season suggests that a link may exist between harbour porpoise reproductive biology and the availability of prey in the study sites.  It may be that this is a factor in these sites being used as calving grounds.  The observation that 47% of all calves detected were observed on one day in July provides support for this idea.  However, it may also be that females use the study sites to maximize their foraging efficiency during lactation, and that females bring their calves to foraging arenas with greatest probability of prey contact for weaning and calf prey capture practice.  Males may also maximize their chances of encountering receptive females by aggregating in foraging arenas that females regularly use.  The reproductive season is energetically the most expensive season for all age classes and sexes.  Thus, tidally well-mixed sites may simply afford the greatest energetic return for the metabolic investment of calving, mating, and ontogenetic growth of neonates during specific oceanographic and lunar conditions.

The occurrence of high-density aggregations also corresponded with the putative reproductive season (April – October), which is when prey aggregations were seen near the surface, and high-energy behaviours and vocal communications were greatest (A. Hall, unpub. data).  This suggests that the April – October time frame is a socially and biologically important time of year for harbour porpoise in Juan de Fuca Strait.  Although the function(s) of the high-density aggregations remains unknown, it seems plausible based on the timing and field observations, that my study areas may be energetically, socially and reproductively important for the harbour porpoise of southern British Columbia.

Overall, the social dynamics of harbour porpoise group sizes appeared to be relatively stable during my 13 years of observations, as group size fluctuations were not detected.  However, I recognise that much remains to be learned about the relationship between surface and sub-surface behaviours of harbour porpoise.  Intra-group surfacing synchrony appeared to regularly occur between group members, which may be indicative of cooperative foraging, or other allelomimetic behaviours (see Chapter II).  Synchrony

may also be a means to maintain visual cohesion among family units, or reflect collective unihemispheric sleep patterns (Otani et al., 1998; Lyamin et al., 2008) or some other social function. Harbour porpoise engaged in the synchronous slow rolling surfacing behavioural pattern (*SRSXS*) were in statistically larger groups than other surface behaviours. The notion that this behaviour may be exhibited during unihemispheric sleep seems highly possible as these groups appeared to remain in the same spatial positioning relative to group members and geographic location. However, it is also possible that this surface positioning is exhibited in multiple behavioural states and may be part of foraging, intra-group communication, or even predator surveillance strategies.

As with other behaviours, it may be that logging also serves more than one function to harbour porpoise. It is also likely that harbour porpoise evolved more than one resting behaviour, given that logging at the surface only seems possible in calm conditions and appears to occur for only short periods (see Results and Scheffer and Slipp, 1948; Andersen and Dziedzic, 1964; Amundin and Amundin, 1974; Gaskin et al., 1975; Flaherty and Stark, 1982; Hanson et al., 1999). It has also been suggested that logging behaviour may form part of a foraging strategy that involves visual or acoustic scanning of the waters just below the surface (Flaherty and Stark, 1982). It is possible that this behaviour may occur during sleep, foraging, lactation, social communication, predator surveillance, or other behaviours not yet identified. Furthermore, harbour porpoise probably log at the surface more often than is reported, as this behaviour is one of the most difficult to identify. Documentation of logging requires the calmest sea conditions, a well-formed search image for stationary porpoise, and the good fortune to be in the right place at the right time. It is also possible that the standard line transect survey method often used (*e.g.*, Calambokidis et al., 1993; Hammond et al., 1995; Polacheck, 1995; Hall, 2004) may put observers at a disadvantage to document this particular behaviour if porpoise respond to moving vessels by diving. Definitive assessments of the relationship between surface and subsurface behaviours are complicated by a complete lack of knowledge of the latter. Future observational studies that make use of stationary observers, such as point transect or land-based studies may provide further details on this and other poorly understood surface behaviours.

My findings are likely only a first step in understanding the fine-scale foraging behaviours of harbour porpoise. For instance, in addition to foraging in tidally well-mixed areas, harbour porpoise must employ additional foraging strategies to meet their need to eat regularly (Kanwisher and Sundnes, 1965; Kastelein and Staal, 1997; Kastelein et al., 1997d; Koopman, 1998). One means to achieve this would be to feed upon prey with less ephemeral aggregations that could be found more reliably. Since captive harbour porpoise are able to discriminate objects buried in sand (Kastelein et al., 1997c), one such source may be those prey that are associated with the benthos. In southern British Columbia, benthic foraging may include inshore regions as has been found in other areas (Dudok van Heel, 1962b; Andersen and Dziedzic, 1964; Koopman, 1998), but may also include offshore zones as well.

In the more offshore zones of Juan de Fuca and Georgia Straits, massive submarine sand dunes have been identified that are within the bathymetric range of harbour porpoise (Mosher and Thomson, 2000; Mosher and Thomson, 2002). The significance of these sandy benthic habitats to local populations of sand lance is being evaluated (SAPSLIE, 2009). If these submarine structures are found to be important sand lance habitat, they could also serve as another seasonally important foraging arena, since this forage fish is seasonally consumed by the harbour porpoise of this region (Hall, 2004). As work on harbour porpoise diet continues, greater insight into the possible additional foraging arenas of harbour porpoise will become clearer.

In addition to diurnal studies, the nocturnal component to foraging must be elucidated. Recent work in the North Sea indicated that nocturnal feeding behaviours are important for harbour porpoise (Todd et al., 2009). Nocturnal foraging may well be important in my Study Areas R and D as well. I conducted my observations during daylight hours, but suspect that my study animals could have employed different foraging strategies at night. Nocturnal behavioural changes may be a simple function of the spring/neap tidal cycle, but could also be influenced by colour given that the moonlight colour index changes with lunar phase (*i.e.*, the full moon spectrum is bluer and the quarter moon phases are redder: Gehrels et al., 1964; Kopal, 1969). Knowing the changes in prey species composition and relative abundance in these tidally well-mixed areas under differing oceanographic, lunar and diel conditions will undoubtedly provide

greater insight into the different foraging strategies, arenas and behaviours of harbour porpoise.

The behavioural ecology of harbour porpoise appears to be integrally linked to and ambient oceanographic and lunar conditions. My observations have shown that harbour porpoise use ephemeral well-mixed foraging sites on a temporary but predictable basis. The prime conditions for harbour porpoise to forage in these tidally well-mixed sites can be related to the ebb current on a spring tidal phase, which is associated with the new and full moons. This use of a particular current is consistent with what has been shown in other regions (see above), but the link between harbour porpoise foraging behaviour and lunar phase has not been previously documented. A better understanding of the relationships between harbour porpoise behaviours, oceanographic features and lunar conditions will come as additional research is undertaken.

My study is the first to find a relationship between the lunar phase and harbour porpoise behaviour, as well as to show that lunar phases influence the diurnal behaviour of a cetacean. My study is also the first to demonstrate that point transects are an effective method to evaluate small cetacean behaviour on a fine spatial scale. These findings raise many interesting questions about the physical and biological stimuli that porpoise respond to, such as whether the diurnal porpoise behaviours are directly connected nocturnal events, or whether the nocturnal and diurnal behaviours are independent from one another. My research also points to the need to better understand the sociality of the species and the social stimuli that contribute to the movements and behaviours of harbour porpoise in particular habitats in the breeding and non-breeding seasons.

Much remains to be learned about the ecology and behaviour of harbour porpoise in British Columbia. Most notable is the need to better understand the extent of cooperation amongst foraging individuals, and physical oceanographic and lunar cycle influences on the productivity and assemblages of prey species sought by harbour porpoise. Further documenting benthic and pelagic foraging behaviours as well as logging, and other putative resting or foraging behaviours, will also significantly contribute to understanding the life history and physiological needs harbour porpoise.

Such research is needed to properly manage and ensure the long-term conservation of this cryptic and poorly understood species.

**Summary**

Harbour porpoise's need to eat regularly and their consumption of a broad spectrum of prey species suggests that harbour porpoise have specialised foraging strategies. I sought to determine the physical conditions under which harbour porpoise foraged and the extent to which they display specialised behaviours. Counts and behavioural data were collected in Juan de Fuca Strait, British Columbia over 12 months (2007–2008) using a distance-based point transect survey; and were augmented with 13 years of supplementary data (1995–1996, 1998–2008). Presence and relative numbers of harbour porpoise were examined in light of tidal phase, tidal variation, lunar phase, lunar position, solar position, diurnality and seasonality. Harbour porpoise used the study areas on a predictable basis with greater numbers occurring on the ebb currents. Harbour porpoise numbers also increased on the fortnightly spring tides when encounter rates were 1.5 times higher compared to neap tides; and a three-fold increase occurred during the putative breeding season (April – October). These data show that harbour porpoise in southern British Columbia moved as groups and used tidally well-mixed foraging sites on temporary but predictable bases. The porpoise showed highly specialised foraging strategies that occur at relatively fine spatial scales.

**Chapter IV – Seasonal breeding habitats of Dall's and harbour porpoise in the inside waters of southern British Columbia and northern Washington**

**Introduction**

Most animals have preferred localities where they spend the majority of their lives (Scott, 1958). Such places are suited to the animal's particular physiological requirements or breeding habits (Elton, 1927), and are usually centred on the habitats used by neonates and juveniles (Scott, 1958). Knowledge gained by an animal through early life experiences about preferred habitats may transfer from one generation to the next when breeding site fidelity exists, and may contribute to the long-term survival of populations. Identifying reproductive habitats is therefore one of the greatest contributions that can be made for wildlife conservation.

Distinguishing the breeding sites of aquatic mammals is difficult because their reproductive habitats vary widely by species and geography. Habitat selection for some historically exploited species are well known, such as for the grey whale (*Eschrichtius robustus*) and northern fur seal (*Callorhinus ursinus*) (Scammon, 1874; Beddard, 1900; Atkinson, 1988; Goddard, 1997). However, the connections between habitat use and biological processes are not as clear for many other species of marine mammals, particularly those that have had little or no economic, entertainment or food value. Most species of porpoise fall into this category.

The relationships between porpoise life history, behaviour and habitat selection are poorly understood. Limited observations throughout the ranges of the two northern species — the harbour (*Phocoena phocoena*) and Dall's porpoise (*Phocoenoides dalli*) — have identified some site fidelity to potential traditional breeding areas (Smith and Gaskin, 1983; Gaskin and Watson, 1985; Evans, 1987; Kasuya and Ogi, 1987; Kinze, 1990; Leopold et al., 1992; Schulze, 1996; Sonntag et al., 1999; Koschinski, 2002). Both species have large distributional ranges and presumably have more traditional breeding sites than are currently recognised. Nowhere is this more likely to be true than in the eastern North Pacific Ocean, where harbour and Dall's porpoise often occur in parapatric distributions (Hall, 1996; Calambokidis et al., 1997; Tynan et al., 2005).

Reproductive habitats for harbour or Dall's porpoise have yet to be identified in the eastern North Pacific, although several sites have been proposed, including Prince William Sound, Glacier Bay and the Copper River estuary of Alaska for harbour porpoise (Hall, 1979; Matkin and Ray, 1980; Taylor and Dawson, 1984) and Johnstone Strait, British Columbia (BC), and the waters of Whidbey Island, Washington (WA), for Dall's porpoise (Jefferson, 1987; Miller, 1989). In addition, the presence of Dall's, harbour and hybrid porpoise in the coastal waters of British Columbia and Washington suggests some distributional overlap during the reproductive season of harbour and Dall's porpoise (see Baird et al., 1998; Willis et al., 2004).

The reproductive season for harbour and Dall's porpoise has not been defined in British Columbia or Washington. Elsewhere in the North Pacific and North Atlantic, the presence of newborns in the spring and early summer, followed by reproductive behaviours and reproductively associated physiological changes in the mid summer to early autumn, have been consistently observed (Meek, 1918; Okada and Hayashi, 1951; Fraser, 1953; Fisher and Harrison, 1970; Gaskin et al., 1984; Kasuya and Jones, 1984; Jefferson, 1989b; Jefferson, 1989a; Lockyer, 1995; Fontaine and Barrette, 1997; Ferrero and Walker, 1999; Neimanis et al., 2000; Halldórsson and Víkingsson, 2003). It therefore seems reasonable to consider that the reproductive season in southern British Columbia and northern Washington follows a similar pattern of parturition in the spring and early summer, followed by a period of mating in the summer through to early autumn.

It is one thing to determine when breeding and parturition likely occur, and another to know where it occurs and what features of the environment define the breeding habitats of either harbour or Dall's porpoise. Aggregations of prey promoted by the physical environment are believed to explain the distribution of some cetaceans (Baumgartner, 1997; Moore et al., 2002; Simard et al., 2002; Cotté and Simard, 2005), although avoiding predators such as sharks and killer whales (*Orcinus orca*) also likely plays a role, especially for smaller cetaceans (Heithaus, 2001a; Heithaus, 2001b; Heithaus and Dill, 2002). Harbour and Dall's porpoise probably also select habitats that contain reliable food sources to meet their relatively high metabolic needs (Ridgway, 1966; Koopman, 1994; Kastelein et al., 1997b; Kastelein et al., 1997d). This may be

particularly true during the reproductive season which is energetically expensive for both species (Fisher and Harrison, 1970; Kasuya, 1978; Newby, 1982; Gaskin et al., 1984; Lockyer, 1995; Fontaine and Barrette, 1997). It therefore seems likely that the reproductively important habitats of harbour and Dall's porpoise in southern British Columbia and northern Washington should correlate with areas of high prey abundance associated with high levels of tidal mixing (see Chapter III).

The goal of my study was to identify potential breeding sites of Dall's and harbour porpoise in southern British Columbia and northern Washington by determining whether the frequency of occurrences of adults, calves and high-density aggregations were related to season, bathymetry and relative tidal flow rates. My study spanned 18 years (1991–2008) and spatially encompassed the inshore, coastal waters of southern British Columbia and northern Washington from the western entrance of Juan de Fuca Strait to the northern reaches of the Strait of Georgia (Figure 4.1). Dall's and harbour porpoise have been systematically and opportunistically recorded in this area since 1991. Hybrids have also been identified here (indicating mating activity between harbour and Dall's porpoise - Baird et al., 1998; Willis et al., 2004), as has male Dall's porpoise rutting behaviour (Willis and Dill, 2007). There have also been significant numbers of stranded gestate harbour and Dall's porpoise, neonates and reproductively active males recovered during the spring, summer and autumn months (A. Hall unpub. data and Hall, 2004). Collectively, these observations indicate that breeding has been occurring somewhere within this large geographic region, and suggest that analysis of observational data may identify the breeding season and sites, as well as identify the physical features that define reproductive areas of Dall's and harbour porpoise in British Columbia.

**Methods**

Requests for harbour and Dall's porpoise sightings were made to local researchers, the public and cetacean sightings networks in British Columbia and Washington through formal data requests, email messages and public presentations. The responses culminated in an 18-year multi-source data set that included: **1.** Aerial line transect survey data (NMFS, 2006); **2.** Small vessel line transect survey data (Hall, 1996; Hall, 2004); **3.** Platform of Opportunity (POP) data collected from whale watch boats operated by Inter Island Launch Ltd., out of Victoria, British Columbia; and **4.** Supplementary harbour and Dall's porpoise sightings data provided by the British Columbia Cetacean Sightings Network (BCCSN, 2005), and independent researchers and observers throughout coastal British Columbia (Appendix A11).

Four nested study areas were defined within the inshore waters of southern British Columbia and northwestern Washington (Figure 4.1) based on biophysical criteria that included the availability of: **1.** Bathymetric data (Foreman et al., 2008); **2.** Tidal speed data (Foreman et al., 2008); and **3.** Harbour and Dall's porpoise data. The largest study site (Study Area A - Figure 4.1) encompassed 37,648 km$^2$ of British Columbia and Washington coastal waters and extended from the western entrance of Juan de Fuca Strait to northern Georgia Strait. Three smaller study areas were defined within the geographical bound of Study Area A (Figure 4.1), and were labeled as Study Areas B, (4892 km$^2$), C (567 km$^2$) and D (200 km$^2$). The broad spectrum of depths and tidal speeds found throughout southern British Columbia and northern Washington (see Thomson, 1981; Thomson, 1994; Foreman et al., 2008) made the study areas ideal for evaluating the relationship between habitat selection by harbour and Dall's porpoise and bathymetry and the relative rates of water movement.

The available data were collected using different techniques and observers. Study Area A included systematic aerial line transect data, using a distance-based sampling protocol (Buckland et al., 1993) collected by the National Marine Fisheries Service of the United States (NMFS) in the inland waters of Washington and British Columbia during August 2002 and August 2003 (NMFS, 2006). Study Area A also included supplementary harbour and Dall's porpoise sightings data from British Columbia and Washington waters, provided by the BCCSN and independent researchers. Study Area B

included opportunistic sightings from the platform of opportunity whale watch boats from BC and Washington waters. In contrast, Study Areas C and D included sightings of harbour and Dall's porpoise from independent systematic line transects conducted only in British Columbia waters (Hall, 1996; Hall, 2004).

Data from Areas C and D were evaluated together because sample sizes from Study Area D were prohibitively small, and both sets of data were collected during vessel line transects by the same observer (Hall, 1996; Hall, 2004). Harbour and Dall's porpoise sightings data were analysed as Study Area A, B, C and D, and as geographically pooled sets.

All sightings of harbour and Dall's porpoise included locations, species, dates, times, group sizes and sea states. The platform of opportunity whale watch data also included weather, behaviour, presence of calves and hybrids. Hybrid identification was based on physical characteristics and behaviour which included grey pigmentation, a lack of the typical black and white colour pattern with Dall's porpoise body profile and surfacing behaviours (Morejohn et al., 1973; Kasuya, 1978; Jefferson, 1987). Calves were defined as neonates with fetal folds still evident, small animals in close proximity to a larger animal exhibiting synchronous surface behaviours (*i.e.,* a cow-calf pair), and individuals that were exhibiting non-synchronous behaviours but were smaller than the other porpoise in the group. All calves were assumed to be <6 months of age. All other porpoise were defined as adults, with no gender differentiation, except for females in cow-calf pairs. High-density aggregations were defined as group sizes ≥15 and ≥50, which included single large groups, and multiple smaller groups that were spatially and behaviourally associated with one another.

All latitude and longitude values were converted to decimal degrees to create an ordered pair (*x,y*) of spatial coordinates for use within a Geographical Information System (GIS) with latitude and longitude represented by the *y* and *x* coordinates, respectively. All data were assigned a unique numerical record identification and were coded according to sampling method (*i.e., Systematic* or *Opportunistic*), and were stratified and coded to reflect the putative breeding (April – October) and non-breeding seasons (November – March). Finally, the BCCSN data contained additional coded

information reflecting the species identification confidence and the sightings location accuracy. Locations or species identification coded as *inaccurate, incomplete,* or *possible* were removed from the analytical data set, leaving only those harbour and Dall's porpoise sightings coded as *certain* for species identification and *accurate to within 1 km* for the spatial reference.

All observers were assumed to accurately estimate group sizes since harbour and Dall's porpoise typically occur in groups <10 in southern British Columbia and northwestern Washington. Any harbour or Dall's porpoise groups that were reported as a range (*e.g.,* 4 – 6) were converted to the range average (*e.g.,* 5), and all harbour and Dall's porpoise data were refined to only include individuals or groups observed in sea states ≤ Beaufort 2.
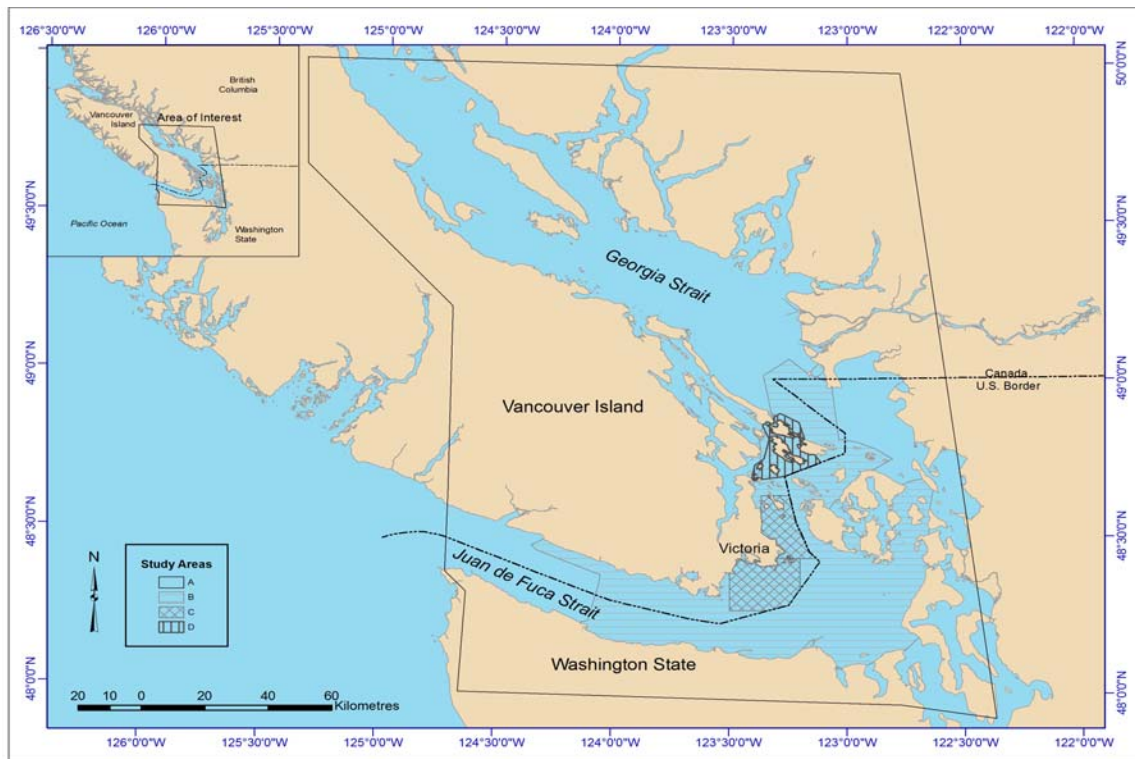


**Figure 4.1 Four nested study areas in southern British Columbia and northern Washington inland waters. Study Area A included the waters from Juan de Fuca to Strait of Georgia. Study Area B included the area encompassed by the platform of opportunity whale watch vessels and included eastern Juan de Fuca Strait and southern Strait of Georgia and connecting waters. Study Area C was located adjacent to the shoreline of southeastern Vancouver Island and Study Area D was within the southern Gulf Islands of British Columbia.**

The aerial and vessel line transect sightings data were effort corrected to reflect the number of porpoise observed per kilometre travelled on each transect. In other words, the sightings data were standardised by the length of the transect line to provide a measure of the relative density of porpoise at each sightings location. The whale watch platform of opportunity data were effort corrected by the kilometres travelled by area, and the extent of the water area covered by the whale watch vessels was divided into a series of contiguous polygons based on the geographic references recorded in field logbooks (Appendix A17). The course of travel for each whale watch trip was also approximated from the field logbooks. Each course was divided into a series of transit legs to reflect the position and distance travelled within each polygon, and the polygons were scored based on the number of transit legs intersecting with the polygon. The average distance travelled per transit leg per polygon was calculated and the cumulative number of kilometres of effort per polygon was determined. From this, the relative effort per polygon was calculated. A polygon-specific effort correction factor was then applied to each harbour and Dall's porpoise data point to generate a corrected sighting value. The per-polygon effort correction for sightings was based on the assumption that the actual harbour and Dall's porpoise data points reflected each species' preferred habitat within that polygon. Both corrected and uncorrected sightings data were evaluated in the inferential and spatial analyses.

The BCCSN and the independent researchers and observer sightings data could not be effort corrected due to the non-systematic nature of data collection, and a lack of additional data from which to determine the relative amounts of regional effort exerted to collect the harbour and Dall's porpoise sightings.

All spatial data were referenced to the North American Datum 1983 (NAD 83), UTM Zone 10, Central Meridian -123°, using a Transverse Mercator projection. The *x, y, z* bathymetric and tidal speed point data (Foreman et al., 2008) were interpolated using Triangular Irregular Network (TIN) to create a continuous raster surface. Raster surfaces were interpolated for the tidal speed data on a 500 m X 500 m grid, and for the bathymetric data on a 250 m X 250 m grid. Bathymetric and tidal speed point values were extracted for each harbour and Dall's porpoise data point in Study Areas A, B, C and D from the raster surfaces in ArcGIS 9.1 (ESRI, 2005). Tidal speeds were grouped

into 12 incremental classes to assess the frequency of occurrence of harbour and Dall's porpoise relative to each tidal speed class in each study area. Bathymetric values were grouped into 50 m incremental classes to assess porpoise frequency of occurrence relative to each depth class in each study area. Pooled assessments were also conducted.

Spatial patterns were evaluated for uncorrected data and effort corrected data for Study Areas A, B, C and D, and using pooled data. Distributional patterns of each harbour and Dall's porpoise sightings data set in each study area were evaluated using average nearest neighbour analysis. Spatial autocorrelation was evaluated using the Moran's $I$ statistic with an inverse distance function. Cluster and hot spot analyses were evaluated with the Anselin Moran's $I$ and the Getis-Ord $G_i^*$ statistics with inverse distance functions and a fixed distance band threshold of 3000 m. All spatial analyses used the Euclidean distance measurement method.

Reproductively important areas were first evaluated by determining whether patterns of harbour and Dall's porpoise group sizes were statistically significant throughout each of the study areas using the Anselin Local Moran's $I$. This analysis was run for both harbour and Dall's porpoise in all study areas, except for Dall's porpoise in Study Area A (aerial survey) and Study Areas C and D (vessel survey) due to small sample sizes. Harbour and Dall's porpoise clustering patterns were evaluated for uncorrected, effort corrected and high-density stratified data. The high-density data were evaluated at group sizes ≥15 and ≥50 for both species in each study area and for pooled data. The Getis-Ord $G_i^*$ statistic was used to evaluate whether hot or cold spots of groups of either high or low group size values existed for either species in each study area and for pooled data. This evaluation was run for each species in each study area, except for Dall's porpoise in Study Area A (aerial survey) and Study Areas C and D (vessel survey) due to the small sample sizes.

All spatial conversions, analyses and maps were prepared using ArcGIS 9.1 software (ESRI, 2005). All non-spatial statistical analyses were conducted using NCSS software (Hintze, 1998), and statistical figures were generated in the software R version 2.12.2 (RDCT, 2011).

**Results**

*Data Collation and Summary*

The cumulative data (1991–2008) consisted of 2800 harbour and Dall's porpoise groups totaling 11,458 individuals sighted in Beaufort 0 – 2 sea conditions, within the bounds of Study Area A. Data from April – October (spring to fall), when births and copulations were expected to occur, accounted for 94% of these data in terms of the number of sightings and the number of animals observed. Harbour porpoise sightings made up the majority (66%) of the April – October sightings, while Dall's porpoise made up the majority (57%) of the November – March sightings. The November – March data were not analysed any further due to the sparsity of winter sightings from within the four nested study areas.

Animals identified as hybrid porpoises (*n*=43) only occurred from April to October, and were associated with a small number of Dall's porpoise groups. The highest frequency of hybrid occurrence was June – September with the highest peak in July (Figure 4.2).
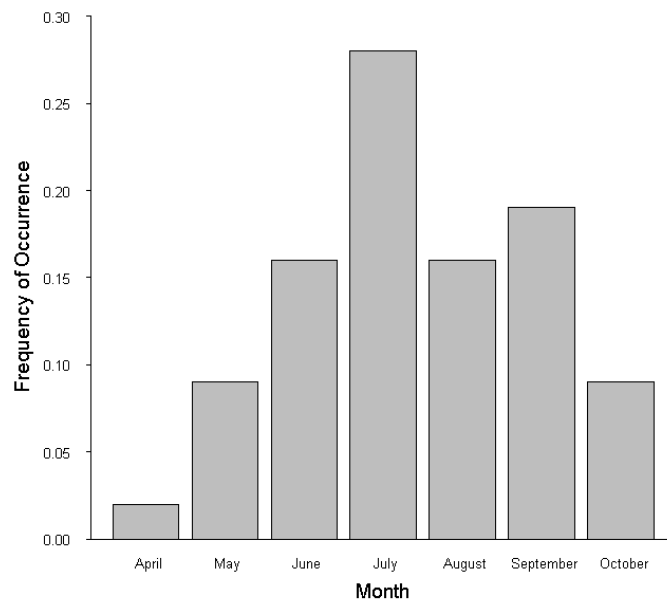


**Figure 4.2 Monthly frequency of occurrence of 43 hybrid porpoises in Study Area B from April-October (1995–1996, 1998–2008). Peak numbers of hybrids were observed from July through September.**

**Table 4.1 Monthly frequency of occurrence of harbour and Dall's porpoise calf sightings and high densities from April – October in Study Area A (1991–2008) with all data sets presented. Pooled monthly frequencies for both species are also presented.**

| Month | Harbour Porpoise Calves | Dall's Porpoise Calves | Pooled Calves | Harbour Porpoise High Densities | Dall's Porpoise High Densities | Pooled High Densities |
|---|---|---|---|---|---|---|
| April | 0.01 | 0.06 | 0.03 | 0.03 | 0.13 | 0.08 |
| May | 0.09 | 0.11 | 0.09 | 0.29 | 0.23 | 0.26 |
| June | 0.15 | 0.12 | 0.14 | 0.17 | 0.16 | 0.16 |
| July | 0.22 | 0.20 | 0.22 | 0.19 | 0.08 | 0.13 |
| August | 0.28 | 0.29 | 0.28 | 0.03 | 0.08 | 0.06 |
| September | 0.17 | 0.18 | 0.17 | 0.12 | 0.20 | 0.16 |
| October | 0.08 | 0.03 | 0.06 | 0.17 | 0.13 | 0.15 |
| **Total Counted** | **125** | **65** | **190** | **58** | **51** | **109** |

The highest frequency of occurrence of harbour and Dall's porpoise calves seen from April to October ($n=190$) was from June – September, with peaks for both species in July and August (Table 4.1). Conversely, the harbour and Dall's porpoise high-density aggregations that occurred from April to October ($n=109$) displayed a bimodal distribution with the range of months differing slightly between the two species.

Harbour porpoise high densities peaked from May – July, and again during September – October (Table 4.1). Dall's porpoise high densities peaked from April – June, and again during September – October (Table 4.1). Pooled high densities of both species also showed a bimodal distribution of May – July and September – October (Table 4.1).

Collated data from Study Areas A, B, C and D differed in terms of the number years of observation, effort, total number of harbour and Dall's porpoise sightings and total number of animals (Table 4.2). The cumulative recorded effort from all areas was 156,424 km in sea states Beaufort $\leq 2$ (Table 4.2). Areas A and B had the greatest number of sightings and porpoise, and Area B had the greatest effort (Table 4.2). However, the actual effort exceeded the reported values in Table 4.2, because the effort was not documented for the harbour and Dall's porpoise sightings data in Study Area A (BCCSN/OTHER).

Harbour porpoise outnumbered Dall's porpoise in the number of sightings and the number of animals in Study Area A (Table 4.2). Overall, porpoise group sizes observed during the 2002 and 2003 aerial surveys did not significantly differ (Mann-Whitney U Test *corrected for ties*, $U_{2002}=46686.5$, $U_{2003}=52953.5$, *d.f.=617, Z=1.53, P=0.127*). Significantly more porpoise were observed in 2003 compared to 2002 (Chi Square Test, $X^2_1=61.17$, *P<0.001*), but effort corrections for each species negated this statistical difference (harbour porpoise: Mann-Whitney U Test *corrected for ties*, $U_{2002}=48624$, $U_{2003}=51016$, *d.f.=639, Z=0.52, P=0.60*: Dall's porpoise: Mann-Whitney U Test *corrected for ties*, $U_{2002}=87$, $U_{2003}=121$, *d.f.=27, Z=0.72, P=0.47*). This meant that the 2002 and 2003 aerial survey data from Study Area A could be pooled by species for analysis.

In Study Area B, the annual number of hours of observation did not differ between years (Chi Square Test, $X^2_{12}=24.12$, *P<0.001*), but the annual numbers of kilometres traveled were different (Chi Square Test, $X^2_{12}=4275.80$, *P<0.001*). The total number of harbour and Dall's porpoise observed each year in Study Area B also differed significantly (Chi Square Test: Harbour porpoise - $X^2_{12}=623.00$, *P<0.001,* Dall's porpoise - $X^2_{12}=644.90$, *P<0.001*). No inter-annual variation was detected in harbour porpoise group sizes in Study Area B (Kruskal-Wallis *corrected for ties*, *H=15.3, d.f.=12, p=0.23*), but Dall's porpoise group sizes differed significantly from year to year (Kruskal-Wallis *corrected for ties*, *H=34.9, d.f.=12, p=0.001*).

In terms of the effort corrected data similar numbers of harbour porpoise were observed regionally (per kilometre) within Study Area C (Mann-Whitney U Test *corrected for ties*, $U_{CNorth}=2042.5$, $U_{CSouth}=2313.5$, *d.f.=130, Z=0.94, P=0.347*), and inter-annually (Mann-Whitney U Test *corrected for ties*, $U_{2001}=1720.5$, $U_{2002}=1410.5$, *d.f.=130, Z=0.72, P=0.47*). This meant that harbour porpoise data from Study Area C could be pooled regionally and inter-annually. The small numbers of Dall's porpoise observed in Study Area C resulted in them being pooled with Study Area D data, which alone were also too small for independent evaluation. The pooled data set consisted of 49 Dall's porpoise in 13 groups (Table 4.2).

**Table 4.2 Harbour and Dall's porpoise data summaries showing data source, years of observation, effort and number of harbour and Dall's porpoise sightings and animals by Study Area. Data only include sightings in sea states Beaufort 0 – 2, collected April – October from Study Areas A, B, and C and D in the inshore waters of southern British Columbia and northwestern Washington.**

| Study Area | Data Source | Years of Observation | Effort, km | Harbour Porpoise | | Dall's Porpoise | |
|---|---|---|---|---|---|---|---|
| | | | | Number of sightings | Number of animals | Number of sightings | Number of animals |
| A | Aerial Survey | 2002-2003 | 6471 | 600 | 1000 | 27 | 57 |
| A | BCCSN/ OTHER | 1991 - 2006 | — | 424 | 1023 | 197 | 534 |
| B | Platform of Opportunity | 1995-1996, 1998-2008 | 147,107 | 735 | 4765 | 712 | 3853 |
| C and D | Vessel Survey | 1995, 2001-2002 | 2846 | 92 | 177 | 13 | 49 |
| **Total** | **All** | **1991-2008** | **156,424** | **1851** | **6965** | **949** | **4493** |

Inter-annual evaluation of the BCCSN/OTHER data from Study Area A indicated that group sizes of harbour porpoise did not significantly vary between years (Kruskal-Wallis *corrected for ties*, *H=7.69, d.f.=8, p=0.46*), in contrast to the differences in group sizes of Dall's porpoise which did vary from year to year (Kruskal-Wallis *corrected for ties*, *H=14.90, d.f.=11, p=0.04*).

*Temporal Trends*

The effort corrected Study Area B data provided an opportunity to compare temporal trends. The 1995–2008 time series showed opposite overall trajectories for harbour and Dall's porpoise per annum sightings per unit effort (SPUE).
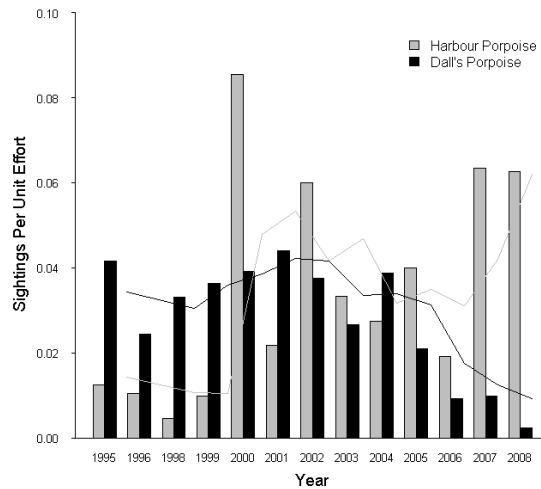
**Figure 4.3 Sightings per unit effort (SPUE) of total numbers of harbour and Dall's porpoise per kilometre travelled on whale watch Platforms of Opportunity from April – October (1995–1996, and 1998–2008). Data are limited Beaufort 0 – 2 in Study Area B. A two-year running average is overlaid for each species to show the overall SPUE trajectories over time in southern British Columbia and northwestern Washington. Harbour porpoise are represented in grey and Dall's porpoise are represented in black.**

Two-year moving average trend lines indicated an increasing SPUE for harbour porpoise and a decreasing SPUE for Dall's porpoise (Figure 4.3). Temporal variation could not be calculated from the other data sets due to the temporal limitations of the aerial and transect surveys (Table 4.2), and the inability to effort correct the BCCSN/OTHER dataset. These three data sets were considered as "snap-shots" of harbour and Dall's porpoise numbers and habitat use.

### *Tidal Speed Analysis*

Study Area A aerial line transect data showed significant differences in the tidal speeds selected by harbour and Dall's porpoise (Mann-Whitney U Test *corrected for ties*, $U_{Dall's}=10973$, $U_{Harbour}=5227$, *d.f.=34.63, Z=3.12, P=0.002*). Intra-species differences were also detected as the number of harbour and Dall's porpoise observed in different tidal speed classes was significantly different (Chi Square Test: Harbour porpoise - $X^2_{11}=611.74$, *P<0.001*; Dall's porpoise - $X^2_{11}=97.74$, *P<0.001*).

The same trend was found in the Study Area A BCCSN/OTHER data, as an inter-species difference existed in the tidal speeds selected by each species (Mann-Whitney U

Test *corrected for ties*, $U_{Dall's}=4569$, $U_{Harbour}=14637$, d.f.$=149.16$, $Z=7.31$, $P=0.00$), and the tidal speed classes selected by harbour and Dall's porpoise (Chi Square Test: Harbour porpoise - $X^2_{11}=980.87$, $P<0.001$; Dall's porpoise - $X^2_{11}=1410.46$, $P<0.001$), with a preference for the higher tidal speed classes by harbour porpoise and a preference for the lower end of the range by Dall's porpoise (Tables 4.3 and 4.4).

In comparison to Study Area A, the tidal speeds used by harbour and Dall's porpoise did not significantly differ between harbour and Dall's porpoise in Study Area B (Mann-Whitney U Test *corrected for ties*, $U_{Dall's}=257764$, $U_{Harbour}=265556$, d.f.$=1445$, $Z=0.49$, $P=0.62$).  However, evaluating each species independently indicated that neither species used all classes equally, and both occurred more frequently in the higher end of the tidal speed spectrum (Tables 4.3 and 4.4: Chi Square Test: Harbour porpoise - $X^2_{11}=2340.81$, $P<0.001$; Dall's porpoise - $X^2_{11}=4940.65$, $P<0.001$).

The pooled vessel transect data from Study Areas C and D also showed an inter-species difference between harbour and Dall's porpoise different tidal speed selection (Mann-Whitney U Test *corrected for ties*, $U_{Dall's}=474$, $U_{Harbour}=2100$, d.f.$=13.47$, $Z=3.82$, $P=0.00$), as well as intra-species differences with neither species using all tidal classes equally (Chi Square Test: Harbour porpoise - $X^2_{11}=933.55$, $P<0.001$; Dall's porpoise - $X^2_{11}=71.61$, $P<0.001$), with the highest frequency of occurrences in the mid range of the tidal speed spectrum (Tables 4.3 and 4.4).

Although harbour and Dall's porpoise were found in all tidal classes (Tables 4.3 and 4.4), harbour porpoise most often occurred in rates of $0.5 - 2.0$ m/s compared to Dall's porpoise in waters of $0.5 - 0.8$ m/s (Figure 4.4).  These apparent preferences were statistically different (Chi Square Test: Harbour porpoise - $X^2_{11}=2188.56$, $P<0.001$; Dall's porpoise - $X^2_{11}=3883.01$, $P<0.001$).

**Table 4.3 Harbour porpoise frequency of occurrence in 12 incremental tidal speed classes. Data are presented from Study Areas A, B and C and D. Pooled data from across all study areas within the bounds of Study Area A are also presented.**

| Tidal Speed Class (m/s) | Study Area A (Aerial Survey, *n=1000*) | Study Area A (BCCSN/ OTHER, *n=1023*) | Study Area B (POP, *n=4765*) | Study Area C and D (Vessel Survey, *n=177*) | Study Area A Pooled (*n=6965*) |
|---|---|---|---|---|---|
| 0 – 0.10 | 0.15 | 0.07 | 0.00 | 0.00 | 0.03 |
| 0.11 – 0.20 | 0.08 | 0.07 | 0.03 | 0.02 | 0.04 |
| 0.21 – 0.30 | 0.21 | 0.07 | 0.02 | 0.02 | 0.05 |
| 0.31 – 0.40 | 0.12 | 0.16 | 0.06 | 0.02 | 0.07 |
| 0.41 – 0.50 | 0.11 | 0.04 | 0.06 | 0.06 | 0.06 |
| 0.51 – 0.60 | 0.13 | 0.04 | 0.14 | 0.07 | 0.12 |
| 0.61 – 0.70 | 0.10 | 0.05 | 0.14 | 0.14 | 0.13 |
| 0.71 – 0.80 | 0.08 | 0.47 | 0.14 | 0.46 | 0.18 |
| 0.81 – 0.90 | 0.01 | 0.02 | 0.15 | 0.10 | 0.12 |
| 0.91 – 1.00 | 0.00 | 0.00 | 0.12 | 0.07 | 0.09 |
| 1.01 – 2.00 | 0.00 | 0.00 | 0.14 | 0.03 | 0.10 |
| >2.01 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| **All Speeds** | **1.00** | **1.00** | **1.00** | **1.00** | **1.00** |

**Table 4.4 Dall's porpoise frequency of occurrence in 12 incremental tidal speed classes. Data are presented from Study Areas A, B and C and D. Pooled data from across all study areas within the bounds of Study Area A are also presented.**

| Tidal Speed Class (m/s) | Study Area A (Aerial Survey, *n=57*) | Study Area A (BCCSN/ OTHER, *n=534*) | Study Area B (POP, *n=3853*) | Study Area C and D (Vessel Survey, *n=49*) | Study Area A Pooled (*n=4493*) |
|---|---|---|---|---|---|
| 0 – 0.10 | 0.00 | 0.38 | 0.01 | 0.02 | 0.05 |
| 0.11 – 0.20 | 0.00 | 0.37 | 0.01 | 0.00 | 0.05 |
| 0.21 – 0.30 | 0.25 | 0.14 | 0.02 | 0.30 | 0.04 |
| 0.31 – 0.40 | 0.04 | 0.01 | 0.03 | 0.09 | 0.03 |
| 0.41 – 0.50 | 0.12 | 0.01 | 0.10 | 0.22 | 0.09 |
| 0.51 – 0.60 | 0.33 | 0.01 | 0.24 | 0.02 | 0.21 |
| 0.61 – 0.70 | 0.18 | 0.03 | 0.28 | 0.06 | 0.24 |
| 0.71 – 0.80 | 0.09 | 0.03 | 0.20 | 0.22 | 0.18 |
| 0.81 – 0.90 | 0.00 | 0.01 | 0.08 | 0.06 | 0.06 |
| 0.91 – 1.00 | 0.00 | 0.01 | 0.03 | 0.00 | 0.03 |
| 1.01 – 2.00 | 0.00 | 0.00 | 0.03 | 0.00 | 0.02 |
| >2.01 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| **All Speeds** | **1.00** | **1.00** | **1.00** | **1.00** | **1.00** |
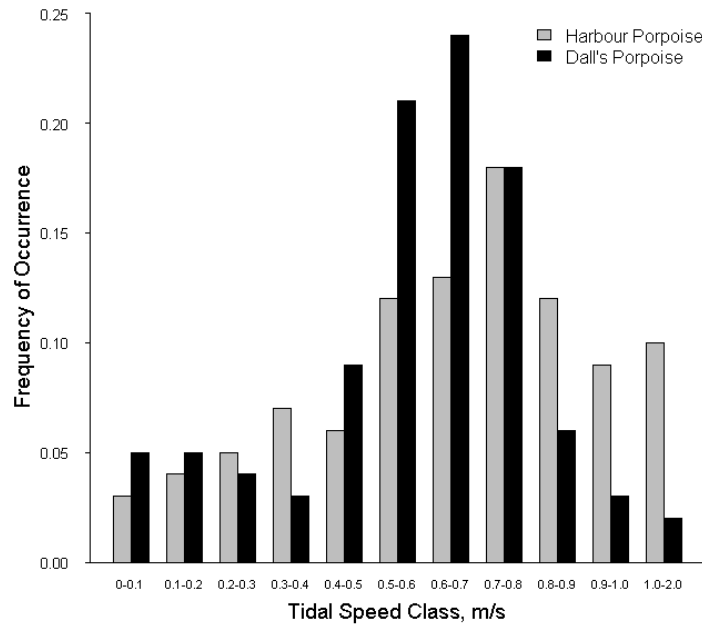
**Figure 4.4 Frequency of occurrence of harbour and Dall's porpoise in incremental tidal speed classes (m/s). Data were pooled from all data sets across Study Areas A, B, and C and D in southern British Columbia and northwestern Washington. Harbour porpoise are represented in grey and Dall's porpoise are represented in black.**

### *Bathymetric Differentiation*

The aerial surveys in Study Area A indicated that harbour and Dall's porpoise used significantly different depth ranges (Mann-Whitney U Test *corrected for ties*, $U_{Dall's}=11690$, $U_{Harbour}=4510$, d.f.$=28.76$, $Z=3.90$, $P=0.001$). Both species were most often found in water up to 250 m depth, but harbour porpoise were often in areas $\leq$100 m (49%), whereas Dall's porpoise most frequently occupied the 101 – 300 m range (66% - Tables 4.5 and 4.6). These depth class differences were statistically significant (Chi Square Test: Harbour porpoise - $X^2_7=835.60$, $P<0.001$; Dall's porpoise - $X^2_7=835.60$, $P<0.001$).

The non-systematic BCCSN/OTHER Study Area A data also showed that harbour and Dall's porpoise used waters with significantly different depths (Mann-Whitney U Test *corrected for ties*, $U_{Dall's}=15153$, $U_{Harbour}=4053$, d.f.$=293$, $Z=8.06$, $P=0.000$). Harbour porpoise were most frequently reported in water $\leq$100 m deep (81%), whereas

Dall's porpoise occurred most frequently in deeper water >150 m (73%). Again, these depth class differences were statistically significant (Chi Square Test: Harbour porpoise - $X^2_7=1194.52, P<0.001$; Dall's porpoise - $X^2_7=361.18, P<0.001$).

In Study Area B harbour and Dall's porpoise also used significantly different depths (Mann-Whitney U Test *corrected for ties*, $U_{Dall's}=416505$, $U_{Harbour}=106814.5$, *d.f.=1195, Z=19.49, P=0.000*). As in Study Area A, harbour porpoise were most frequently encountered in water ≤100 m (78%), whereas Dall's porpoise were most frequently in water >150 m (57%), though the 51 – 150 m range was also well represented (Tables 4.5 and 4.6). The Study Area B depth class differences were also statistically significant (Chi Square Test: Harbour porpoise - $X^2_7=1406.87, P<0.001$; Dall's porpoise - $X^2_7=2128.31, P<0.001$).

In Study Areas C and D, most harbour porpoise (95%) and Dall's porpoise (56%) were in water ≤150m (Tables 4.5 and 4.6). However, the Dall's porpoise sample size was small (Table 4.2), and may not accurately represent the bathymetric habitat use in this region. The depth class difference observed for harbour porpoise was statistically significant (Chi Square Test: $X^2_7=1400.32, P<0.001$), but could not be evaluated for the small numbers of Dall's porpoise observed.

Evaluating the pooled frequency of occurrences in 50 m depth classes of all Study Areas (A, B, C and D) showed that harbour and Dall's porpoise occurred across all depths, except the deepest at >350 m (Tables 4.5 and 4.6). It also showed a bathymetric habitat preference by harbour porpoise of ≤100 m (74%), whereas Dall's porpoise appeared to prefer water from 51 – 300 m (93%), with the highest frequencies from 151 – 250 m (Tables 4.5 and 4.6, Figure 4.5). Again these bathymetric differences were statistically significant (Chi Square Test: Harbour porpoise - $X^2_7=15197.45, P<0.001$; Dall's porpoise - $X^2_7=2013.76, P<0.001$).
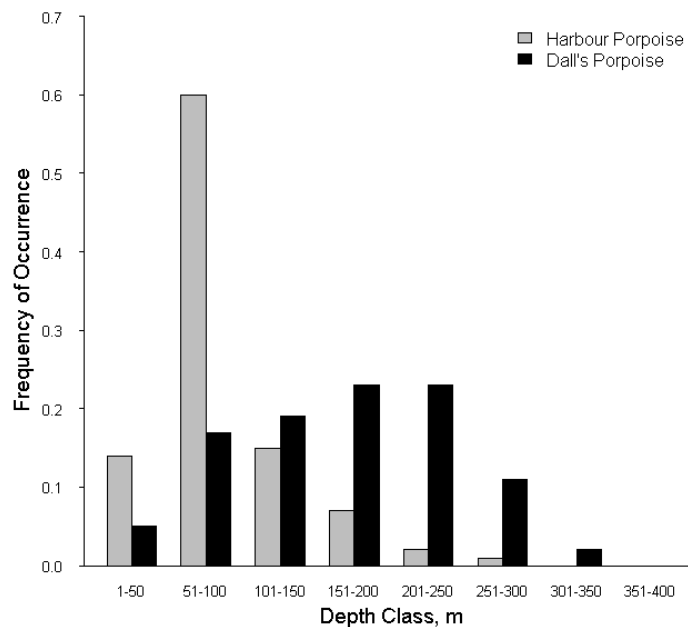
**Figure 4.5 Frequency of occurrence of harbour and Dall's porpoise in 50 metre depth classes. Data are pooled from all data sets across Study Areas A, B and C and D in southern British Columbia and northwestern Washington. Harbour porpoise are represented in grey and Dall's porpoise are represented in black. Sample sizes are presented in Tables 4.5 and 4.6.**

**Table 4.5 Frequency of occurrence of harbour porpoise in 50 metre depth classes. Data from Study Areas A, B, C and D in the coastal waters southern British Columbia and northwestern Washington are presented independently and pooled (April–October: 1991–2008).**

| Depth (m) | Study Area A (Aerial Survey *n=1000*) | Study Area A (BCCSN/ OTHER *n=1023*) | Study Area B (POP *n=4765*) | Study Area C and D (Vessel Survey *n=177*) | Study Area A Pooled (*n=6965*) |
|---|---|---|---|---|---|
| 0 – 50 | 0.17 | 0.14 | 0.13 | 0.11 | 0.14 |
| 51 - 100 | 0.32 | 0.67 | 0.65 | 0.70 | 0.60 |
| 101 - 150 | 0.24 | 0.09 | 0.14 | 0.14 | 0.15 |
| 151 - 200 | 0.19 | 0.03 | 0.06 | 0.04 | 0.07 |
| 210 - 250 | 0.05 | 0.02 | 0.02 | 0.02 | 0.02 |
| 251 - 300 | 0.02 | 0.01 | 0.00 | 0.00 | 0.01 |
| 301 - 350 | 0.02 | 0.02 | 0.00 | 0.00 | 0.00 |
| >350 | 0.00 | 0.02 | 0.00 | 0.00 | 0.00 |
| **All Depths** | **1.00** | **1.00** | **1.00** | **1.00** | **1.00** |

**Table 4.6 Frequency of occurrences of Dall's porpoise in 50 metre depth classes in Study Areas A, B, C and D in the coastal waters of southern British Columbia and northwestern Washington. Pooled data from across all study areas are also presented (April–October: 1991–2008).**

| Depth (m) | Study Area A (Aerial Survey, *n=57*) | Study Area A (BCCSN/ OTHER, *n=534*) | Study Area B (POP, *n=3853*) | Study Area C and D (Vessel Survey, *n=49*) | Study Area A Pooled (*n=4493*) |
|---|---|---|---|---|---|
| 0 – 50 | 0.00 | 0.02 | 0.05 | 0.21 | 0.05 |
| 51 - 100 | 0.33 | 0.08 | 0.19 | 0.14 | 0.17 |
| 101 - 150 | 0.10 | 0.18 | 0.19 | 0.21 | 0.19 |
| 151 - 200 | 0.34 | 0.17 | 0.24 | 0.07 | 0.23 |
| 210 - 250 | 0.12 | 0.22 | 0.23 | 0.21 | 0.23 |
| 251 - 300 | 0.10 | 0.15 | 0.10 | 0.14 | 0.11 |
| 301 - 350 | 0.00 | 0.19 | 0.00 | 0.00 | 0.02 |
| >350 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| **All Depths** | **1.00** | **1.00** | **1.00** | **1.00** | **1.00** |

*Spatial Analysis*

The calculated nearest neighbour ratios (*NNR*) mostly negative *Z* scores and mean distances determined in the average nearest neighbour analysis indicated that harbour and Dall's porpoise groups were generally clustered on scales of <1000 m (Tables 4.7 and 4.8). Exceptions to this scale of clustering occurred for harbour porpoise in Study Area A (aerial survey and BCCSN/OTHER), which was the largest study area. Dall's porpoise were also found to have larger scales of clustering in Study Area A (aerial survey) and a dispersed distribution in Study Areas C and D. However, the Dall's porpoise results might reflect the small sample sizes in Study Areas A, C and D (Table 4.1).

There was no evidence of statistically significant spatial autocorrelation for either harbour or Dall's porpoise in any study area (Tables 4.9 and 4.10). However, the resolution of the data required that a minimum distance of 3 km be used as a threshold value for spatial pattern analyses. Positive Moran's *I* values indicated a weakly clustered pattern for both species in all data sets at 3 km, with the exception of the harbour porpoise in Study Areas C and D. However, this 3 km weakly clustered pattern was not statistically significant in any study area (Tables 4.9 and 4.10).

**Table 4.7 Average nearest neighbour statistic values for harbour porpoise in Study Areas A, B, and C and D combined (April – October).  Values for the pooled data set are also presented.  All data come from southern British Columbia and northwestern Washington (1991–2008).**

| Study Area | Data Source | *NNR* | *Z* | *P* | Mean Distance (m) | Distribution |
|---|---|---|---|---|---|---|
| A | Aerial Survey | 0.34 | -30.57 | 0.00 | 1395.6 | Clustered |
| A | BCCSN/ OTHER | 0.45 | -10.34 | 0.00 | 3322.4 | Clustered |
| B | Platform of Opportunity | 0.46 | -27.49 | 0.00 | 754.9 | Clustered |
| C and D | Vessel Survey | 0.46 | -14.64 | 0.00 | 628.2 | Clustered |
| A | Pooled | 0.31 | -53.72 | 0.00 | 771.6 | Clustered |

**Table 4.8 Average nearest neighbour statistic values for Dall's porpoise in Study Areas A, B, and C and D combined.  Values for the pooled data set are also presented.  All data come from southern British Columbia and northwestern Washington from April – October (1991–2008).**

| Study Area | Data Source | *NNR* | *Z* | *P* | Mean Distance (m) | Distribution |
|---|---|---|---|---|---|---|
| A | Aerial Survey | 0.65 | -3.47 | 0.00 | 4970.11 | Clustered |
| A | BCCSN/ OTHER | 0.21 | -21.18 | 0.00 | 789.57 | Clustered |
| B | Platform of Opportunity | 0.48 | -26.64 | 0.00 | 624.00 | Clustered |
| C and D | Vessel Survey | 1.54 | 3.76 | 0.00 | 6289.02 | Dispersed |
| A | Pooled | 0.24 | -44.99 | 0.00 | 658.65 | Clustered |

**Table 4.9 Moran's *I* statistic values for harbour porpoise in Study Areas A, B, and C and D combined. Values for the pooled data set are also presented. All data come from southern British Columbia and northwestern Washington from April – October (1991–2008).**

| Study Area | Data Source | *I* | *Z* | *P* |
|---|---|---|---|---|
| A | Aerial Survey | 0.32 | 1.52 | 0.13 |
| A | BCCSN OTHER | 0.01 | 0.15 | 0.88 |
| B | Platform of Opportunity | 0.02 | 0.14 | 0.89 |
| C and D | Vessel Survey | -0.04 | -0.04 | 0.96 |
| A | Pooled | 0.01 | 0.50 | 0.62 |

**Table 4.10 Moran's *I* statistic values for Dall's porpoise in Study Areas A, B, and C and D (April – October). Values for the pooled data set are also presented. All data come from southern British Columbia and northwestern Washington (1991–2008).**

| Study Area | Data Source | *I* | *Z* | *P* |
|---|---|---|---|---|
| A | Aerial Survey | 0.26 | 1.01 | 0.31 |
| A | BCCSN OTHER | 0.15 | 0.63 | 0.53 |
| B | Platform of Opportunity | 0.11 | 0.79 | 0.43 |
| C and D | Vessel Survey | 0.16 | 0.85 | 0.39 |
| A | Pooled | 0.13 | 1.15 | 0.25 |

### Reproductively Important Areas

Statistically significant groups of harbour porpoise were identified southeast of Victoria in Juan de Fuca Strait, while significant groups of Dall's porpoise occurred in mid and northern Haro Strait (identified using Anselin Local Moran's *I* statistic, Figure 4.6, Appendices A13 and A14). One additional Dall's porpoise group occurred within the significant group area identified for harbour porpoise, and another single location for Dall's porpoise was identified southwest of Victoria (Figure 4.6).

The same general areas were identified in the Getis-Ord $G_i^*$ hot spot analysis, which identified one statistically significant harbour porpoise hot spot southeast of Victoria in eastern Juan de Fuca Strait, and one in northern Haro Strait for Dall's porpoise (Figure 4.7, Appendices A15 and A16). In addition, two smaller sites were also identified for harbour porpoise near the Canada-US border in southern Georgia Strait, and farther to the southeast in US waters in Juan de Fuca Strait, and one additional smaller site was identified for Dall's porpoise southeast of the harbour porpoise hot spot in Juan de Fuca Strait (Figure 4.7).

The majority of the statistically significant points were encompassed with ellipses to represent the April – October important hot spot habitat areas for each species (Figure 4.7). The harbour porpoise hot spot encompassed 150 km$^2$ and the Dall's porpoise hot spot encompassed 175 km$^2$. These two areas accounted for 0.40% and 0.45%, respectively, of the total area of Study Area A.

The hot spots (Figure 4.7) also encompassed 41% and 49% of the 1991–2008 reported harbour and Dall's porpoise calf sightings, respectively (see Appendix A17 for a map of the calf sightings), and 67% and 57% of the harbour and Dall's porpoise high-density aggregations ≥15, respectively (see Appendix A18 for maps of the high-density locations). Stratifying the high-density aggregations to group sizes ≥50 resulted in 74% of the harbour porpoise and 100% of the Dall's porpoise high-density groups being encompassed by the hot spot ellipses (see Appendix A18 for maps of the high-density locations).
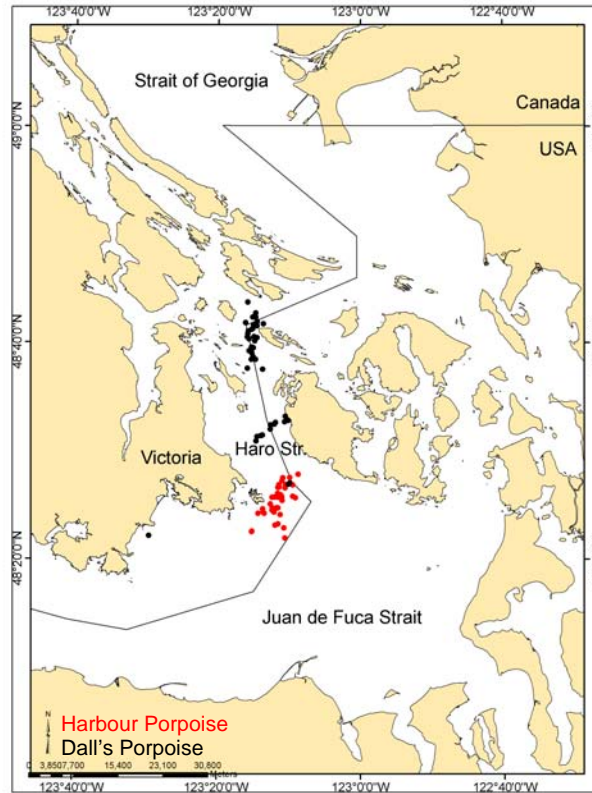
**Figure 4.6 Statistically significant harbour and Dall's porpoise group size clusters identified through Anselin Local Moran's *I* analysis of pooled data from Study Areas A, B, and C and D (1991–2008). Important areas for harbour porpoise identified southeast of Victoria, BC, and for Dall's porpoise in mid to north Haro Strait in both US and Canadian waters. Two other Dall's porpoise sites were found southeast and southwest of Victoria. Dall's porpoise are represented in black, and harbour porpoise are represented in red.**

Similarities existed between the bathymetric and tidal speed habitat selections found within the harbour and Dall's porpoise hotspots and with the individual study area evaluations for each species. The harbour porpoise in the Juan de Fuca Strait hot spot were found over waters ranging from 1.0 – 150.0 m (Figure 4.8). The median depth in the Juan de Fuca Strait hot spot for harbour porpoise was 69 m (95% CI: 67.6, 70.0). In contrast, the Dall's porpoise hot spot occurred over deeper waters in Haro Strait ranging from 51.0 – 350.0 m (Figure 4.8). The median Dall's porpoise depth in the Haro Strait hot spot was 228.2 m (95% CI: 218.8, 236.6).
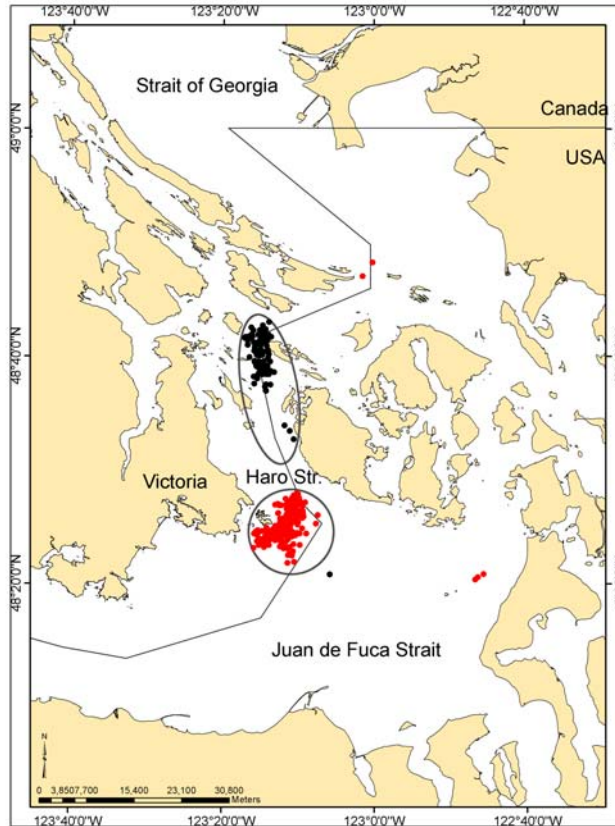
**Figure 4.7 Harbour and Dall's porpoise hot spots identified through Getis-Ord $G_i^*$ statistical analysis of April – October pooled data from Study Areas A, B, C and D. Ellipses encircle the majority of the hot spot data points for harbour and Dall's porpoise. The harbour porpoise hot spot is in Juan de Fuca Strait, and the Dall's porpoise hot spot is the mid to northern reaches of Haro Strait. Harbour porpoise are represented in red and Dall's porpoise are represented in black.**

In terms of the hot spot tidal speeds, harbour porpoise were mostly in a range of 0.4 – 2.0 m/s (Figure 4.9), with a median tidal speed of 0.89m/s (95% CI: 0.85 – 0.92). The Dall's porpoise in the Haro Strait hot spot occupied a narrower range of tidal speeds than the harbour porpoise in the Juan de Fuca hot spot with a range of 0.3 – 1.0 m/s (Figure 4.9). The Dall's porpoise median tidal speed was 0.67 m/s (95%CI: 0.65 – 0.68). The bathymetric and tidal speeds differences between harbour and Dall's porpoise in the two hot spot ellipses were statistically significant (bathymetric: Mann-Whitney U Test *corrected for ties*, $U_{Dall's}=26638$, $U_{Harbour}=254$, *d.f.=119, Z=14.73, P=0.000*: tidal speed: Mann-Whitney U Test *corrected for ties*, $U_{Dall's}=5099$, $U_{Harbour}=21793$, *d.f.=275, Z=9.32, P=0.000*).
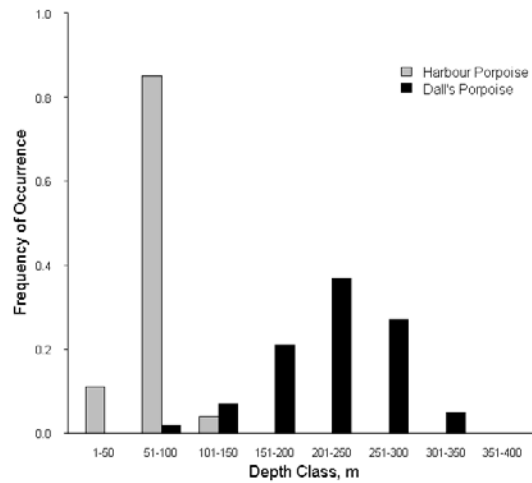
**Figure 4.8 Hot spot bathymetric frequency of occurrences for harbour and Dall's porpoise (April – October). Data from Study Areas A, B, C and D yielded a bathymetric differentiation with harbour porpoise over shallower waters and Dall's porpoise over deeper waters. Harbour porpoise are represented in grey, and Dall's porpoise are represented in black.**
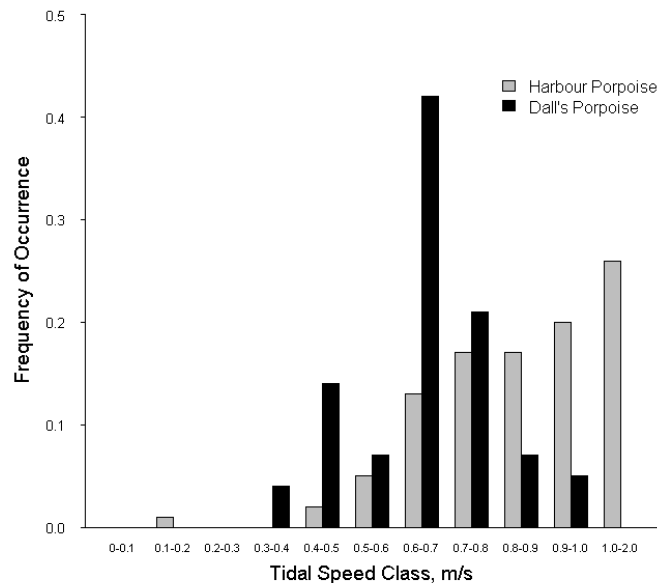


**Figure 4.9 Harbour and Dall's porpoise hot spot tidal speed class frequency of occurrences for harbour and Dall's porpoise pooled data from Study Areas A, B, C and D (April – October). Harbour porpoise are represented in grey, and Dall's porpoise are represented in black.**

**Discussion**

The systematic and opportunistic sightings of porpoise (1991–2008) show that harbour and Dall's porpoise breed in the inshore waters of southern British Columbia and northwestern Washington from April to October, and winter in these same waters from November to March. It is interesting that these two ecologically similar species seem to co-exist in the inland waters of southern British Columbia and northern Washington despite similar seasonal reproductive schedules and habitat tidal speed preferences. Segregation between harbour and Dall's porpoise in this region appears to be related to habitat partitioning by water depth.

*Seasonality*

The number of porpoise peaked twice during the breeding season. The first peak from May – July appears to be related to parturition based on the increases in numbers of calves counted throughout July and August; while the second peak in numbers from September – October might be related to mating or some other phenomena. Assuming a gestational period of 10 – 11 months (Møhl-Hansen, 1954; Fisher and Harrison, 1970; Kasuya, 1978; Newby, 1982; Read, 1990b; Sørensen and Kinze, 1990) would mean that copulations should have occurred from July to October the previous year. Unfortunately, no sub-surface copulatory behaviour was observed and there are no data on foetal growth and adult physiological changes (*i.e.,* testes growth and regression, and ovulatory schedules) to better define the parturition and mating timelines for southern British Columbia and northern Washington.

The data were insufficient to determine the significance of the inshore waters to harbour and Dall's porpoise during November – March. However, the presence of both species in these waters during the winter months suggests that this area continues to be important to them. Harbour porpoise have been confirmed using the inshore waters of southern BC throughout the year (see Chapter III and Hall, 2004), but more work is needed to evaluate the biological and ecological significance of these waters, as well as the importance of the hot spot habitats during the winter to harbour and Dall's porpoise.

Although the numbers of harbour and Dall's porpoise varied from year to year (1991–2008), the frequency of Dall's porpoise sightings in southern British Columbia

and northern Washington has declined since 2002. In contrast, the group sizes of harbour porpoise in this region exhibited inter-annual stability, and the number of groups appeared to have increased from 2005 until observations concluded in 2008. Continued data collection will shed light on whether the decline of Dall's porpoise and increase of harbour porpoise is part of a larger cyclical pattern, or whether the patterns identified in this study are indicative of generalised population trends. Similar Dall's porpoise declines are suspected for Monterey Bay, CA, and parts of southeast Alaska (T. Jefferson, pers. comm.).

The frequency of porpoises identified as hybrids also peaked in July, which was consistent with the peak in sighting of harbour porpoise and Dall's porpoise calves. However, the visually identified hybrids may have been misclassified, given that juvenile Dall's porpoise have displayed grey pigmentation in other parts of their range (Morejohn et al., 1973). This indeed appears to be the case based on the declining frequency of hybrid porpoise towards the autumn months when juvenile Dall's porpoise with grey colouration would transition to the typical black and white colours (Morejohn et al., 1973; Kasuya, 1982). Genetic analysis of the supposed hybrids will be required to confirm whether hybrid porpoise do occur most frequently in the mid-summer or whether some are phenotypic variants of juvenile Dall's porpoise.

### Reproductively Important Habitats

Approximately 38,000 km$^2$ of inland waters were surveyed for porpoise in southern British Columbia and northern Washington. However, significant numbers were found only in <1% of the total area. Spatial analysis revealed two relatively small hot spots — one for harbour porpoise and a second for Dall's porpoise (Figure 4.7). Both hot spots contained calves and adults suggesting that they constitute breeding areas for harbour and Dall's porpoise, and may have ecological implications for population survival.

Recent sightings in 2010 and 2011, following completion of my data collection, confirmed that both hot spots continued to be used by harbour and Dall's porpoise cow-calf pairs, and may continue to be important beyond the breeding season as a winter nursery area for Dall's porpoise cows and calves (Figures 4.10 and 4.11). Inter-annual

winter and summer evaluations of these porpoise hot spot habitats will contribute to better understanding the seasonal and inter-generational importance to the harbour and Dall's porpoise of southern British Columbia and northern Washington.

**Figure 4.10 A cow-calf Dall's porpoise pair in northern Haro Strait within the identified hot spot habitat. Photograph taken January 2011.**

**Figure 4.11 Neonate harbour porpoise in the identified eastern Juan de Fuca hot spot. Photograph taken October 2010.**

The association of harbour and Dall's porpoise with high tidal speeds suggests porpoise select productive habitats. This is consistent with the suggestion by Michaud (2005) that female harbour porpoise select highly productive habitats during the reproductive months. It may be that female harbour porpoise choose productive habitats to satisfy their energetic needs during parturition, lactation and mating. Female Dall's porpoise may also select reproductive season habitats that satisfy not only their needs, but the needs of their young calves as well.

In the North Atlantic, harbour porpoise are also considered to be scarce in areas without coastal fronts or topographically generated upwellings (Gaskin, 1992). Instead increased numbers of harbour porpoise have been associated with seasonal prey species abundance increases, occupation of sheltered habitats during calving season, and a seasonal increase in energetic demand related to calving, lactation and/or seasonal migrations (Lockyer, 1987; Bernard and Hohn, 1989; Recchia and Read, 1989; Weir et al., 2007). Studies evaluating changes in prey species abundance and distribution relative to the different tidal speed classes may prove useful in better understanding why the porpoises of southern British Columbia and northern Washington are associated with high tidal speeds during the reproductive season.

It may be that it is not the relative rates of water flow that determine the presence of porpoise, but rather the aggregations of zooplankton and small fish at the interfaces of currents (*i.e.,* fronts) that attract weaning calves and reproductively active adults. It is also possible that tidal speeds and bathymetric preferences during the reproductive season of harbour and Dall's porpoise reflects speeds that maximise the likelihood of encountering desired prey, and the depths at which vertical trapping of prey species occurs because the topographic depth is less than biological maximum of the porpoises' prey species. Considering that the eastern Juan de Fuca Strait hot spot for harbour porpoise is also a year-round foraging arena for this species (see Chapter III), as well as the fact that groups of cow-calf pairs cooperatively forage in this same area (A. Hall pers. obs.), it seems likely that both hot spots serve multi-purposes for both species which continue to feed throughout the breeding season.

Areas with high tidal flow may also be an important foraging arena for weaned juveniles as they transition from zooplankton and small fish to the adult fish and squid diets (Smith and Read, 1992; Aarefjord et al., 1995; Gannon et al., 1998; Börjesson et al., 2003; Víkingsson et al., 2003; Santos et al., 2004). It is unknown whether Dall's porpoise transition from milk to an adult diet on zooplankton and small fish, but preliminary information from the Bering Sea suggest they may (Mizue and Yoshida, 1965; Ohizumi et al., 2003). Fine-scale behavioural and dietary studies in southern British Columbia and northern Haro Strait will help further define the significance of the high tidal flow areas for all age classes and sexes.

*Habitat Selection and Partitioning*

The observed regional decline of Dall's porpoise cannot be related to a BC population-wide decline – although there may well have been one. Attempts to count porpoise in BC coastal waters have only recently been started (Laake et al., 1997; Williams and Thomas, 2007; Ford et al., 2010), but are insufficient to establish the geographic bounds and large-scale movement patterns of Dall's porpoise. In the western Atlantic, harbour porpoise are known to shift habitats in response to changes in the abundance of prey species (Kenney et al., 1996), and in the western Pacific, Dall's porpoise are known to respond to large-scale oceanographic phenomena (IWC, 1978; Klinowska, 1991). This suggests that the residency of Dall's porpoise in inshore waters may be dictated by offshore oceanographic or atmospheric conditions. The aerial survey data of Study Area A showed the coastal waters of southern British Columbia and northwestern Washington were essentially unoccupied by Dall's porpoise in August 2002 and 2003 (NMFS, 2006). Unfortunately, it is impossible to know whether the Dall's porpoise of southern British Columbia and northwestern Washington declined or shifted habitats due to the temporal lags between distributional studies and the lack of offshore data.

Though harbour and Dall's porpoise were found overall to select similar tidal speeds, the bathymetric differentiation may provide enough habitat specificity and niche breadth dissimilarity to permit some degree of co-existence and niche partitioning between these two high trophic level coastal predators. Furthermore, this bathymetric differentiation may reduce competition and allow these two species to co-exist in these

relatively small areas in spite of overlapping prey species (Scheffer, 1953; Fink, 1959; Morejohn, 1979; Simenstad et al., 1979; Stroud et al., 1981; Gearin and Johnson, 1990; Walker et al., 1998; Hall, 2004). The largely parapatric distribution in this region may simply be a function of the physical properties of the coastal topography and the habitat selection differences that preclude harbour and Dall's porpoise from inter-specific competition. Similar habitat partitioning of bottlenose dolphins (*Tursiops truncatus*), Risso's dolphins (*Grampus griseus*), dwarf sperm whales (*Kogia sima*) and pantropical spotted dolphins (*Stenella attenuata*) has also been associated with bathymetry in Gulf of Mexico (Baumgartner, 1997; Davis et al., 1998). This supports Schoener's (1986) concept that spatial segregation is primarily achieved through differential habitat use. Further ecological study will help in understanding the trophic and competitive interactions that occur in southern British Columbia and northern Washington.

### *Future Work*

My findings are only the first step in evaluating the habitat needs of harbour and Dall's porpoise in British Columbia and Washington. Additional fine-scale surveys that document cow-calf pairs and reproductive behaviours are required to validate whether the reproductively important areas are habitats for calving, mating or weaning. Further evaluation of other potential sites that have similar bathymetric and tidal speed values may also provide insight into whether other similar important reproductive habitats exist for harbour and Dall's porpoise in the coastal waters of the eastern North Pacific or whether the inshore waters of southern BC and northern Washington are unique.

The geographic range of harbour and Dall's porpoise is extensive in British Columbia and Washington. To put my findings in context, the geographic boundaries of populations need to be established to evaluate the regional importance of the identified important areas. For instance, if there is only one reproductive hot spot per population, then the conservation importance of the identified sites will be elevated. There is also the possibility that males move amongst reproductive sites where females are philopatric (Escorza-Trevino and Dizon, 2000; Chivers et al., 2002). The possibility that females primarily inhabit the reproductive season habitats, may be indicative of a female dominated society, as is seen in some other social mammals (*e.g.,* Gould et al., 2003). This potential link between females and the reproductive season habitats provides support

for the idea that females depend more on their immediate environment during the reproductive season than males (Kastelein et al., 1997b), and that they must be close to a reliable food supply in order to metabolically support parturition, lactation and mating. Female harbour porpoise are also thought to use the months between lactation as a time to store extra energy (Kastelein et al., 1997d). If true, female harbour porpoise may exhibit longer residency patterns in highly productive areas than males. Further support for this possibility comes from the notion that solitary males have wider-ranging foraging behaviours than females (Gaskin et al., 1975). The sociality of harbour and Dall's porpoise needs to be evaluated to help put these findings in context.

The reproductive season has been referred to as the most interesting season (Amundin and Amundin, 1974), and is critical for population survival. My study was based on the assumption that the observed adult harbour and Dall's porpoise were reproductively active. Behavioural research that focuses on subsurface behaviours, including physical interactions and acoustic communications which are likely important components of sexual behaviour (see Chapter II) will help further understand the biological importance of the identified hot spots to harbour and Dall's porpoise in British Columbia and Washington. Additionally, the nocturnal and sub-surface behaviours, including copulatory behaviour of harbour and Dall's porpoise also need to be evaluated, as my study was limited to observations from the surface during daylight hours only.

There are currently more questions than there are answers about the reproduction of harbour and Dall's porpoise. Most important is the need to understand the boundaries and biological significance of mating, calving and nursery habitats in regions that overlap with human activity. The near shore environments are exposed to a potential wide range of habitat pressures that stem from proximity to human developments (Evans, 2002). This is particularly true for my study area as this region is heavily influenced by a variety of maritime activities including shipping, naval exercises (torpedo testing and live-fire ammunition ranges), recreational and commercial fishing, passenger and cargo transportation, wildlife viewing, and sewage outfalls — to list just a few. Identifying the spatial overlap between reproductive areas and commercial net fisheries may also help reduce the incidental mortality of harbour and Dall's porpoise as calves and cow-calf pairs are known to become entangled (Hall et al., 2002). The extent to which these, and

other human activities, influences the life history and ecology of harbour and Dall's porpoise are unknown. Recognising the importance of breeding season habitats, and continued monitoring and research are required for the conservation of these small coastal mammals.

**Summary**

Systematic and opportunistic sightings of harbour and Dall's porpoise (1991–2008) were analysed to identify reproductively important habitat in the inland waters of southern British Columbia and northwestern Washington. Group sizes and frequency of occurrences were compared for Dall's and harbour porpoise relative to bathymetry and tidal speeds. Both species occurred over a variety of depths, with harbour porpoise preferring regions ≤100 m, and Dall's porpoise preferring 151 – 250 m water depths. Both species occurred in tidally active waters that were at the upper end of the tidal speed spectrum ≥0.5 m/s, and both species displayed clustered distributions over relatively fine scales of <1000 m. Porpoise were not evenly distributed across the inside waters, but showed preferences for two small core areas in eastern Juan de Fuca Strait and northern Haro Strait (one for harbour porpoise and a second for Dall's porpoise). The presence of inter-annual harbour and Dall's sightings, calves and high densities suggest these two hot spots may be important breeding sites for harbour and Dall's porpoise in this region of the eastern North Pacific.

**Chapter V – Conclusions**

The main goal of my research was to investigate whether areas of increased tidal mixing serve as ephemeral foraging arenas for harbour porpoise, and whether these areas correlate with habitat selected by harbour or Dall's porpoise during the reproductive season. I addressed the foraging arena question with a multi-scale study that included direct observation of harbour porpoise numbers and behaviour in two study sites in Juan de Fuca Strait, British Columbia over a 12-month period in 2007–2008, and in an expanded time series that I collected over 13 years (1995–1996, 1998–2008). The reproductive season habitat selection question was evaluated using a multi-source data set that encompassed 18 years of field observations. The reproductive habitat evaluation had a broadened geographical scope from the foraging arena study, and extended from the western entrance of Juan de Fuca Strait to the northern reaches of Georgia Strait, BC, encompassing 37,648 km$^2$ of coastline. The reproductive habitat selection evaluation was based on bathymetry, tidal speeds, and relative porpoise frequencies, high-density aggregations and presence of calves. The two physical oceanographic features were deemed important because they related directly to ocean productivity, porpoises need for a regular and reliable food source, and because these features are likely recognised by the porpoises.

As outlined in the following sections, my findings were based on a variety of analytical processes that included inferential statistics, spatial statistics and distance-based modeling. My work relied heavily on direct field behavioural observations and counts of animals, and has led to a new understanding of the physical oceanographic features present in the habitat selected by porpoises within the coastal environment of British Columbia throughout the year and during the reproductive season. My research has also led to a greater understanding of how harbour porpoise likely optimize their foraging efficiency. Finally, my work has provided the first description of reproductively important habitats for both harbour and Dall's porpoise in southern British Columbia and northwestern Washington. Throughout my evaluations, I highlighted the need to continue field studies to fill in spatial and temporal gaps in our understanding of harbour and Dall's porpoise ecology.

**Summary of Findings**

In Chapter II, I reviewed more than 150 years of literature to synthesize the available data and identify data gaps related to the behavioural repertoires of harbour and Dall's porpoise. I used a framework of 12 behavioural categories that included: ingestive (foraging), shelter-seeking (habitat selection), sexual, agonistic, epimeletic, et-epimeletic, allelomimetic, eliminative, investigative (Scott, 1958), rest (sleep), play and avoidance behaviours. I found that a wide range of behaviours related to the ecologies of harbour and Dall's porpoise have been documented, but that significant regional and categorical deficiencies exist. Overall, more research has been conducted in the North Atlantic than the North Pacific for harbour porpoise, with the eastern North Pacific almost devoid of behavioural data for many categories. Similar geographic heterogeneity exists for Dall's porpoise with more known for the western North Pacific populations than for eastern North Pacific populations. In the latter case, the information base was regionally disparate, with more data coming from the waters of California than anywhere else in the eastern North Pacific. It was also clear that the tendency for reporting behavioural observations and interesting anecdotes in the formal literature has declined in recent years.

Similarities and differences between the two northern porpoise species were compared. Foraging behaviours differed by species, and also by gender for harbour porpoise. Little is known of the dive profiles of Dall's porpoise. For both harbour and Dall's porpoise, the year-round habitat selection likely reflects multi-scale oceanographic phenomena, but more work needs to be done to develop models that can predict large-scale habitat selection. However, breeding site fidelity was noted for both species, with several areas in the North Atlantic, Baltic Sea and western North Pacific already proposed as porpoise breeding grounds. Current knowledge indicates that harbour and Dall's porpoise have complex sexual, social, agonistic, avoidance, allelomimetic, investigative and play behaviours, but that much remains to be learned — especially for the Dall's porpoise. Information on eliminative and et-epimeletic behaviours is deficient for both species.

Future research efforts that should make significant contributions to knowledge and conservation of harbour and Dall's porpoise include further evaluation of foraging

behaviours, regional circadian patterns, residency patterns and fine-scale habitat selection criteria.  These key ecological aspects will likely contribute to reducing regional incidental mortality, and will assist in evaluating the impacts of anthropogenic activities on harbour and Dall's porpoise.  Continued field studies that include direct observations will be important for answering specific ecological questions, rather than relying on the presently discontinuous data.  Also the reporting of opportunistic behavioural observations should be encouraged in the primary literature as these notes can contribute to more rigorous behavioural studies.  With regard to northern porpoise, many opportunities for zoological discovery exist, however studies that address habitat and behavioural questions related to foraging and reproduction will likely have the strongest conservation impact.

In Chapter III, I conducted a fine-scale behavioural study to determine the physical conditions under which harbour porpoise foraged, and the extent to which they display specialised behaviours.  I evaluated whether harbour porpoise used areas of high tidal mixing as temporary, but predictable foraging arenas.  This was based on the underlying premise that harbour porpoise likely exploit naturally occurring features within their home ranges that contribute to the optimisation of prey encounter rates.

I established two oceanographically and bathymetrically similar study sites in Juan de Fuca Strait, British Columbia.  I collected numerical and behavioural harbour porpoise data over 12 months (2007–2008) using a distance-based point transect sampling protocol (Buckland et al., 1993).  These data were augmented with 13 years of supplementary data (1995–1996, 1998–2008) collected from platform of opportunity whale watch boats in the same study areas.

Analyses were limited to only data collected in Beaufort 0 – 2 sea conditions. The point transect data were used to model harbour porpoise encounter rates and density using Distance 6.0 computer software (Thomas et al., 2009).  Presence and relative numbers of harbour porpoise were examined in light of tidal phase, tidal variation, lunar phase, lunar position, solar position, diurnality and seasonality.  Harbour porpoise used the study areas on a predictable basis with greater numbers occurring on the ebb (out-going) currents.  Harbour porpoise numbers also increased on the fortnightly spring tides

associated with the new and full moons, when encounter rates were 1.5 times higher than on the neap tides (first and last quarter moons). Harbour porpoise were also present in greater numbers during the putative reproductive season (April – October), when a three-fold density increase was observed. These numerical increases were due to an increase in the number of groups using the study areas, not an increase in the harbour porpoise group sizes.

High-density aggregations of harbour porpoise and calves were recorded in the systematic and supplementary data sets. The high-density aggregations occurred most frequently on the ebb current, and on the spring tidal phase associated with the new and full moons. Half of the high-density events occurred in May, though they were detected May through October. Overall, an average per annum frequency of 0.9% was calculated, suggesting these aggregations are rare events. The largest events (≥200 porpoise) were spatially clustered to within 10 km$^2$. Observations of calves were also associated with high-density aggregation events, with the highest frequencies of calf detection in July and August in both data sets.

Harbour porpoise were observed to be relatively social, with 87% of all sightings in the presence of conspecifics. Behavioural state differences were observed among group sizes, with larger cohesive groups exhibiting synchronous surfacing and submergences. I hypothesized that this may represent a rest behaviour involving neural unihemispheric sleep. Also, I recorded several foraging patterns that involved different spatial patterns relative to water flow. Fast surfacing behaviours occurred only when animals were crossing small-scale tidally generated fronts, moving from quiescent water into turbulent water. Synchronised behaviours were observed when groups of harbour porpoise remained in spatially restricted areas by facing into the oncoming currents. The porpoise then synchronously allowed the current to carry them subsurface to their initial starting positions. Each group surfaced in unison, and the pattern repeated itself over and over. This behaviour may represent a foraging technique that effectively increases the probability of harbour porpoise encountering prey items. From these observations, I developed the "Conveyor Belt Hypothesis" which requires field-testing for verification. Overall, my data show that harbour porpoise in southern British Columbia moved as groups and used tidally well-mixed foraging sites on a temporary but predictable basis.

The porpoise also showed highly specialised foraging strategies that occur at relatively fine spatial scales.

In Chapter IV, I collated a multi-source data set of harbour and Dall's porpoise field sightings that spanned 18 years (1991–2008). I evaluated whether the timing of the breeding season in southern British Columbia and northern Washington is similar to other populations. I also considered the April – October timeframe and whether the habitat selection of harbour and Dall's porpoise during this time was spatially associated with areas of high tidal speeds. This work was based on findings of Chapter III, and the notion that like harbour porpoise, Dall's porpoise probably also have to remain near a regular and reliable food source, as they are not tolerant to periods of food shortages. I hypothesized that the habitat selection of harbour and Dall's porpoise during the breeding season (April – October) will spatially correlate with regions that contain productive areas that are associated with high rates of tidal mixing.

I established four nested study areas that encompassed 37,648 km$^2$ of coastal waters and extended from the western entrance of Juan de Fuca Strait to northern Georgia Strait. Data were collated from systematic aerial line transect surveys, systematic vessel line transect surveys, and platform of opportunity whale watch vessels. These three data sources provided enough additional information to allow the data to be effort corrected. A non-effort corrected data set provided by coastal researchers and the British Columbia Cetacean Sightings Network supplemented these data.

Analyses were limited to data collected between April and October (1991–2008) in sea states Beaufort 0 – 2. I used a series of inferential and spatial statistics to evaluate temporal and spatial patterns relative to bathymetry and rates of water movement. Counts of porpoise group sizes and frequency of occurrences were compared for each species relative to bathymetry and tidal speeds. The bathymetric and tidal speed physical data were extracted from a previously developed coast-wide tidal model (Foreman et al., 2008).

A temporal comparison between harbour and Dall's porpoise in southern British Columbia revealed a decline in encounter rates and group sizes of Dall's porpoise between 1995 and 2008. Conversely, the sighting rate of harbour porpoise increased in

this same time frame, though group sizes remained constant. Spatially, both species used a wide range of depths, but the highest frequencies of harbour porpoise were regions ≤100 m, whereas the highest frequencies of Dall's porpoise were in regions with ranges of 151 – 250 m. Both species exhibited similar tidal speed preferences, with harbour porpoise occurring most often in waters moving 0.5 – 2.0 m/s and Dall's porpoise in waters moving 0.4 – 0.8 m/s.

Spatial analyses determined that both species occurred in clustered distributions over relatively fine scales of less than about 1 km. Spatial pattern analysis of harbour and Dall's porpoise inter-annual group size data revealed two statistically significant locations in eastern Juan de Fuca Strait and northern Haro Strait. These sites were proximal and tidally similar, but were bathymetrically dissimilar. Spatially, these sites coincided with the majority of high-density aggregations for both species and a high proportion of the calf sightings. As a result, the eastern Juan de Fuca and northern Haro Strait sites were suggested to be important breeding habitats for harbour and Dall's porpoise.

**Evaluation of Research Hypotheses**

My study addressed three hypotheses related to foraging and reproductive season habitat selection.

***Hypothesis 1: Porpoise have a higher probability of occurring in and near areas of increased tidal mixing.***

The results of Chapters III and IV supported this hypothesis. In Chapter III, I used tidal speeds (Foreman et al., 2008) as a proxy for levels of tidal mixing to help establish my study sites. I found that the relationship between the occurrence of harbour porpoise and relative rates of tidal mixing was dependent on the direction of tidal current, fortnightly lunar schedule of full and new moons which generate the spring tidal phase, the time of year, and the presence of conspecifics. In Chapter IV, I used the same tidal model, but over a larger spatial and temporal scale. I found that harbour porpoise numbers were positively correlated with tidal speeds of 0.5 – 2.0 m/s, while Dall's porpoise numbers were positively correlated with tidal speeds of 0.4 – 0.8 m/s.

*Hypothesis 2: Porpoise use localised areas of increased tidal mixing as temporary but predictable foraging arenas.*

Originally I had intended to test this hypothesis by comparing harbour and Dall's porpoise foraging behaviour. However, the sighting rate of Dall's porpoise in the 2007–2008 survey was insufficient for analysis. Nevertheless, this hypothesis was supported by the findings in Chapter III, at least with regard to harbour porpoise.

Two independent data sets in two survey areas indicated that harbour porpoise preferentially used the tidally well-mixed sites on the ebb current during the spring tidal phase associated with the full and new moons. Results were inconsistent as to whether greater numbers were observed on the full or new moon lunar phase, but showed a significant increase when analysed together (*i.e.,* syzygy alignment) as a result of an increase in the number of foraging porpoise rather than an increase in the sizes of the groups observed. An increase in sample sizes under each of these lunar conditions may present a definitive answer as to whether harbour porpoise prefer to forage on the new or full moon.

As discussed in Chapter III, the oceanographic conditions selected by the porpoise appear to be consistent with visual foraging behaviour and an optimization of prey encounter rates. It also appeared that these conditions lent to specialised cooperative hunting strategies. The use of the tidally well-mixed foraging arenas was both temporary and predictable based on tidal direction, lunar conditions, time of year and presence of conspecifics.

*Hypothesis 3: Porpoise densities are higher in and near tidally mixed zones during the breeding season.*

The results of Chapters III and IV supported this hypothesis. In Chapter III, I found that during the breeding season (April – October), the density of harbour porpoise more than doubled from the non-breeding portion of the year (November – March). Calves were mostly observed in the study areas in May, July and August and the peak harbour porpoise sighting rates were in August, September and October, which

corresponds to the breeding season. While in Chapter IV, I determined that the breeding season occurred from April to October based on the timing of calves and high-density aggregation events. I also found that harbour and Dall's porpoise associated with areas of high tidal mixing and were most often found in waters with mid to high tidal speeds.

**Potential Caveats**

The review of Dall's and harbour porpoise behavioural repertoires was limited to literature in English, French and a few German publications. It is likely that other aspects of these species behaviours are recorded in other languages. In particular, I suspect there is information in the Russian literature that was unavailable to me. This is especially likely for historical accounts. Collaboration with other behavioural zoologists from throughout these species distributions will almost certainly lead to greater insight.

The sampling method (*i.e.,* point transect) used in Chapter III may be questioned since the standard method of assessing harbour porpoise and other cetaceans is line transects. However, there is merit in using point transects when the goal is to systematically document behaviours for statistical analysis. Also, there is some question as to whether harbour porpoise avoid moving vessels (Barlow, 1988). If this is the case, it can pose analytical problems in line transect analysis but may have been overcome by using point transects.

Additionally, weather conditions often pose problems in most cetacean fieldwork. This is particularly true for porpoise due to the small size of the animals and the general lack of surface-active displays. Also, differential day lengths of winter versus summer in the mid-latitudes reduced the time available for winter data collection. The only way to overcome these inherent difficulties is to have multi-year studies to effectively increase the time available for data collection in each season. Telemetry may also help offset these limitations, however this data collection technique is not free of problems either.

I was not able to include any prey biomass data for either study area because these data were unavailable due to the fine-scale nature of my work, and a general deficiency of porpoise diet data in British Columbia. This could have provided additional insight into understanding the driving forces behind when and why harbour porpoise used the

tidally well-mixed foraging arenas. However, this may not be a significant limitation of the study since Baumgartner (1997) suggested that the aggregation of prey species is promoted by the physical environment, and my evaluation focussed on the physical environment.

The data collection method used in Chapter IV was not ideal as it relied on a variety of sources, observers and data collection techniques. Consistency amongst species identification and group size estimation may be questioned. However, I believe these problems were overcome by refining the data as discussed in Chapter IV. Ideally, time and resources would have been available to provide long-term systematic sightings data for both harbour and Dall's porpoise. Considering the scale of the British Columbia coastline and costs involved, it seems unlikely that this type of data is a reality. As such, making use of the available data to make ecological inferences is the next best option. Combining scientifically collected data with local knowledge can be a useful approach and the use of volunteer observers and platforms of opportunity is increasingly recognised as important for the long-term monitoring of cetaceans (Leaper et al., 1997; Evans and Hammond, 2004; MacLeod et al., 2004; Weir et al., 2007). These sources have proven useful in my research, and should not be overlooked in future studies.


**Future Research**

Fieldwork that incorporates visual, acoustic and prey sampling will offer greater insight into the relationships between the surface, subsurface and circadian behaviour patterns of harbour and Dall's porpoise. Also, determination of group structure and fluidity is key to understanding the sociality of both species. In addition, efforts to understand the seasonal habitat selection of neritic and pelagic populations will provide critical information for conservation efforts that aim to reduce incidental mortality and reduce anthropogenic stressors. Concurrent with this should be an evaluation of harbour porpoise winter habitat use, especially in offshore areas. This could be conducted as part of other winter research or shipping that occurs in offshore regions, and should be a key research priority in areas where offshore anthropogenic activities such as petrochemical

drilling or wind farm installation is either occurring or planned since these activities can change habitat quality (Evans, 2002; Carstensen et al., 2006).

Evaluation of environmental stimuli, including prey species biomass distributions, will aid in understanding present day habitat selections as well as potentially providing a basis for predicting future habitat use. It would also be interesting to know if harbour porpoise inshore habitat use has changed in response to coastal developments or increasing coastal human populations. This may be helpful in predicting the amount of remaining suitable habitat that exists, as well as providing a basis for an index of potential future distribution and available habitat. This is key for reducing anthropogenic stressors and will provide critical information for the prediction of important habitats in the face of changing ocean conditions (see Evans, 2002).

Research that serves to establish protected areas should also be conducted. Nature reserves that protect harbour porpoise have already been established in the Wadden, Baltic, North, Celtic, and Irish Seas; and in the North Atlantic (Hoyt, 2005). The high levels of human activity in southern BC may preclude status as a Marine Biosphere Reserve under the United Nations Educational Scientific and Cultural Organization (UNESCO), but the criteria for some level of protection for should be evaluated, as it is clear that harbour and Dall's porpoise inter-annually use the waters of southern British Columbia and northwestern Washington during the biologically important reproductive season, and the winter months may be just as important to cow-calf pairs. At a minimum, the proposed breeding grounds need to be verified, and wildlife viewing guidelines relevant to harbour and Dall's porpoise and net fishery management plans should be updated to reflect these findings. The findings of Chapters III and IV will also be helpful for coastal emergency response protocols for catastrophic events, such as oil spills. If such an event spatially and temporally overlaps with either species calving or mating seasons in eastern Juan de Fuca or northern Haro Strait, the effects could be numerically devastating to the populations over the long-term if the traditional habitats are degraded or destroyed.

Long-term monitoring of the identified hot spots, as well as identification of others with similar qualities will prove useful in determining their future importance. I

look forward to future synthesis of distributional data to help answer behavioural ecological questions relevant to the conservation of harbour and Dall's porpoise. Multidisciplinary work that evaluates cetacean behaviour, oceanographic conditions, and prey species seasonal biomass distribution and habitat preferences will contribute to an overall understanding of the physical and biological dynamics of neritic ecosystems. Long-term conservation of both species also requires communication and cooperation with fisheries and wildlife tourism managers.

To conclude, my research was the first to examine the links between porpoise behaviour and celestial events, the first to demonstrate that point transects offer a useful technique for cetacean behavioural studies, and was the first to identify reproductive habitats and the reproductive season (April to October) in British Columbia and Washington. It is becoming clear that it is not the preference for a particular tide or current that is important for coastal porpoises, but rather the effects these conditions have on the physical environment. Areas of high tidal mixing clearly play an important role in harbour porpoise foraging activities, and are a factor in habitat selection throughout the April to October reproductive season for harbour and Dall's porpoise. My results contributed to a greater understanding of the habitat use and behaviour of harbour and Dall's porpoise in British Columbia, and may contribute to addressing similar questions elsewhere in their range.

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**Appendix A – Supplementary Porpoise Survey and Analysis Information**

**A1 Wind Speed at Race Rocks 10 June 2007 – 24 May 2008.**

These data are presented as an estimate of the rarity of the occurrence of suitable weather conditions for surveying for harbour porpoise in Juan de Fuca Strait. To provide an accurate estimate of the actual number of days with suitable conditions would require cross-referencing hourly wind speed data, with hourly rainfall and fog conditions with sunrise and sunset data. These data are provided simply as a general indicator of the wind conditions in and near Survey Areas R and D. Maximum wind speed data for the Race Rocks weather station were obtained from the National Climate Data and Information Archive (www.climate.weatheroffice.gc.ca).

**Table A1.1 Monthly average maximum wind gusts and number of days with Beaufort 2 (11 km/h) conditions at Race Rocks. July, October and November had incomplete data sets and are indicated with an asterisk in the table (*).**

| Month | Monthly Average Wind Gust (km/h) | Number of days with Beaufort 2 maximum | Proportion of possible survey days based on wind data alone |
|---|---|---|---|
| June 2007 | 51.05 | 2 | 0.10 |
| July 2007 | 41.84* | 4* | 0.13* |
| August 2007 | 44.58 | 7 | 0.23 |
| September 2007 | 42.45 | 4 | 0.13 |
| October 2007 | 14.80* | 20* | 0.65* |
| November 2007 | 21.52* | 18* | 0.60* |
| December 2007 | 60.87 | 1 | 0.03 |
| January 2008 | 55.42 | 3 | 0.10 |
| February 2008 | 43.14 | 6 | 0.21 |
| March 2008 | 49.03 | 6 | 0.19 |
| April 2008 | 46.57 | 5 | 0.17 |
| May 2008 | 44.88 | 4 | 0.17 |

## A2 Group Size vs. Detection Distance

The size of most harbour porpoise groups detected during the 2007–2008 point transect survey were ≤5. Figure A3.1 shows that the sizes of the groups detected declined with distance. No animals were detected beyond 400 m, and most were within 250 m of the vessel. All large groups were detected within 250 m, and of the groups ≤5, the proportion sighted declined with increasing distance.
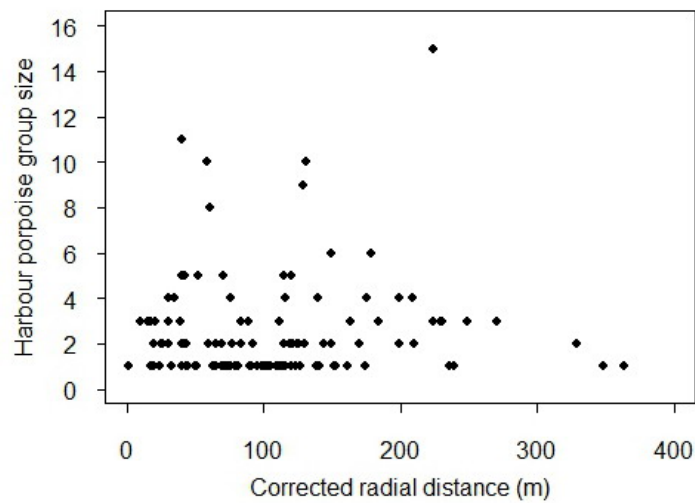


**Figure A2.1 Harbour porpoise group size as a function of increasing distance from the survey vessel.**

**A3 Observer Specific Correction Factors**

      The relationship between the actual and estimated distances between the observer and a life-size model porpoise fin was determined to correct the visual distances estimated by each observer (see Hall, 2004). Linear regression best fit the data, though power, logarithmic, polynomial, exponential and moving average trend lines functions were tested. The best-fit line equations were used to correct the field distance estimates for each observer. Observer 1 was Chris Hall, and Observer 2 was Anna Hall. The Observer 1 correction equation was: $y = 0.99x + 0.16$, $R^2 = 0.94$, and the Observer 2 correction equation was: $y = 0.99x - 0.69$, $R^2 = 0.95$. A 1:1 estimated to actual distance relationship was also plotted using a dashed line for comparison (Figure A1.1).
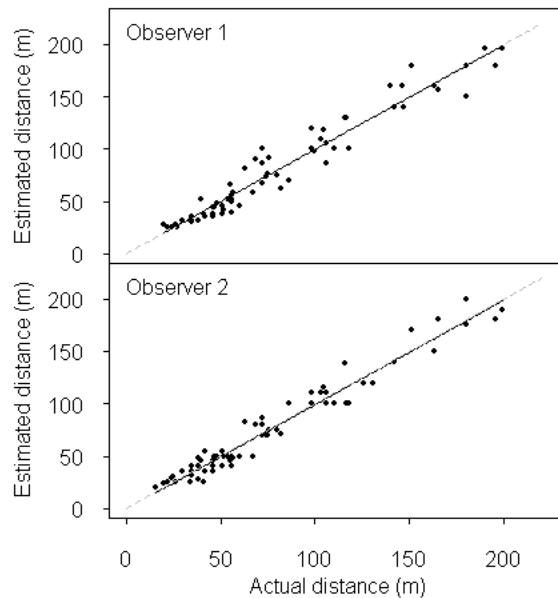


**Figure A3.1 Observer specific correction factors.**

## A4 Point Transect Sightings Summary

**Table A4.1 Harbour (Pp) and Dall's porpoise (Pd) sightings summary at each transect point surveyed from 10 June 2007 – 24 May 2008**

| Area | Date | Species | Transect Point | Group Size |
|------|------|---------|----------------|------------|
| D | 10-Jun-07 | | D1 | 0 |
| D | 10-Jun-07 | | D6 | 0 |
| D | 10-Jun-07 | | D3 | 0 |
| D | 10-Jun-07 | | D7 | 0 |
| D | 10-Jun-07 | | D4 | 0 |
| D | 10-Jun-07 | | D2 | 0 |
| D | 10-Jun-07 | | D5 | 0 |
| D | 10-Jun-07 | | D1 | 0 |
| D | 12-Jun-07 | | D4 | 0 |
| D | 12-Jun-07 | Pp | D15 | 3 |
| D | 12-Jun-07 | Pp | D21 | 1 |
| D | 12-Jun-07 | | D26 | 0 |
| D | 12-Jun-07 | | D25 | 0 |
| R | 24-Jun-07 | Pp | R23 | 1 |
| R | 24-Jun-07 | Pp | R23 | 1 |
| R | 24-Jun-07 | | R17 | 0 |
| R | 24-Jun-07 | | R11 | 0 |
| R | 24-Jun-07 | | R5 | 0 |
| R | 24-Jun-07 | | R17 | 0 |
| R | 24-Jun-07 | | R10 | 0 |
| R | 24-Jun-07 | | R4 | 0 |
| R | 24-Jun-07 | Pp | R16 | 2 |
| R | 24-Jun-07 | Pp | R16 | 2 |
| R | 24-Jun-07 | Pp | R16 | 1 |
| R | 24-Jun-07 | Pp | R16 | 1 |
| R | 24-Jun-07 | Pp | R16 | 1 |
| R | 24-Jun-07 | Pp | R16 | 1 |
| R | 24-Jun-07 | Pp | R16 | 1 |
| R | 24-Jun-07 | Pp | R16 | 1 |
| R | 24-Jun-07 | Pp | R16 | 1 |
| R | 24-Jun-07 | Pp | R17 | 4 |
| R | 24-Jun-07 | Pp | R17 | 2 |
| R | 24-Jun-07 | Pp | R17 | 1 |
| R | 30-Jun-07 | | R6 | 0 |
| R | 30-Jun-07 | Pp | R12 | 1 |
| R | 30-Jun-07 | | R17 | 0 |
| R | 30-Jun-07 | | R21 | 0 |
| R | 30-Jun-07 | | R13 | 0 |
| R | 30-Jun-07 | | R25 | 0 |

| Area | Date | Species | Transect Point | Group Size |
|------|------|---------|----------------|------------|
| R | 20-Jul-07 | | R4 | 0 |
| R | 20-Jul-07 | Pp | R5 | 2 |
| R | 20-Jul-07 | Pp | R5 | 1 |
| R | 20-Jul-07 | Pp | R5 | 3 |
| R | 20-Jul-07 | Pp | R10 | 3 |
| R | 20-Jul-07 | Pp | R10 | 1 |
| R | 20-Jul-07 | Pp | R10 | 3 |
| R | 20-Jul-07 | Pp | R10 | 4 |
| R | 20-Jul-07 | Pp | R10 | 8 |
| R | 20-Jul-07 | Pp | R10 | 15 |
| R | 20-Jul-07 | Pp | R10 | 1 |
| R | 20-Jul-07 | Pp | R10 | 2 |
| R | 20-Jul-07 | Pp | R10 | 4 |
| R | 20-Jul-07 | Pp | R10 | 2 |
| R | 20-Jul-07 | Pp | R10 | 6 |
| R | 20-Jul-07 | Pp | R10 | 4 |
| R | 20-Jul-07 | Pp | R10 | 10 |
| R | 20-Jul-07 | Pp | R10 | 3 |
| R | 20-Jul-07 | Pp | R10 | 5 |
| R | 20-Jul-07 | Pp | R10 | 9 |
| R | 20-Jul-07 | Pp | R10 | 10 |
| R | 20-Jul-07 | Pp | R10 | 3 |
| R | 20-Jul-07 | Pp | R10 | 3 |
| R | 20-Jul-07 | Pp | R10 | 4 |
| R | 20-Jul-07 | Pp | R10 | 4 |
| R | 20-Jul-07 | Pp | R17 | 1 |
| R | 20-Jul-07 | Pp | R17 | 1 |
| R | 20-Jul-07 | Pp | R17 | 1 |
| R | 20-Jul-07 | Pp | R17 | 1 |
| R | 20-Jul-07 | Pp | R17 | 2 |
| R | 20-Jul-07 | Pp | R28 | 3 |
| R | 20-Jul-07 | Pp | R28 | 1 |
| R | 20-Jul-07 | Pp | R28 | 1 |
| R | 20-Jul-07 | Pp | R28 | 1 |
| R | 20-Jul-07 | Pp | R28 | 5 |
| R | 20-Jul-07 | Pp | R28 | 5 |
| R | 20-Jul-07 | Pp | R28 | 1 |
| R | 20-Jul-07 | | R15 | 0 |
| D | 12-Aug-07 | | D6 | 0 |
| D | 12-Aug-07 | Pp | D5 | 2 |
| D | 12-Aug-07 | Pp | D11 | 1 |
| D | 12-Aug-07 | Pp | D11 | 1 |
| D | 12-Aug-07 | | D4 | 0 |
| D | 12-Aug-07 | Pp | D3 | 2 |

| Area | Date | Species | Transect Point | Group Size |
|---|---|---|---|---|
| D | 12-Aug-07 | Pp | D3 | 3 |
| D | 12-Aug-07 | Pp | D19 | 2 |
| D | 12-Aug-07 | Pp | D19 | 1 |
| D | 12-Aug-07 | Pp | D19 | 2 |
| D | 12-Aug-07 | Pp | D27 | 5 |
| D | 12-Aug-07 | | D22 | 0 |
| R | 27-Aug-07 | Pp | R15 | 1 |
| R | 27-Aug-07 | Pp | R15 | 1 |
| R | 27-Aug-07 | | R14 | 0 |
| R | 27-Aug-07 | Pp | R13 | 1 |
| R | 27-Aug-07 | Pp | R13 | 3 |
| R | 27-Aug-07 | Pp | R13 | 1 |
| R | 27-Aug-07 | Pp | R13 | 1 |
| D | 03-Sep-07 | | D5 | 0 |
| D | 03-Sep-07 | | D10 | 0 |
| D | 03-Sep-07 | | D16 | 0 |
| D | 03-Sep-07 | | D23 | 0 |
| D | 03-Sep-07 | | D21 | 0 |
| D | 03-Sep-07 | | D27 | 0 |
| D | 03-Sep-07 | Pp | D28 | 1 |
| R | 24-Sep-07 | | R13 | 0 |
| R | 24-Sep-07 | Pd | R29 | 3 |
| R | 24-Sep-07 | | R24 | 0 |
| R | 24-Sep-07 | | R18 | 0 |
| R | 24-Sep-07 | | R17 | 0 |
| R | 24-Sep-07 | | R3 | 0 |
| R | 12-Oct-07 | | R27 | 0 |
| R | 12-Oct-07 | | R21 | 0 |
| R | 12-Oct-07 | | R28 | 0 |
| R | 12-Oct-07 | | R29 | 0 |
| R | 12-Oct-07 | | R23 | 0 |
| R | 12-Oct-07 | | R17 | 0 |
| R | 12-Oct-07 | Pp | R5 | 3 |
| R | 14-Oct-07 | | R19 | 0 |
| R | 14-Oct-07 | | R14 | 0 |
| R | 14-Oct-07 | | R10 | 0 |
| R | 14-Oct-07 | | R5 | 0 |
| R | 14-Oct-07 | | R11 | 0 |
| R | 14-Oct-07 | | R23 | 0 |
| R | 14-Oct-07 | | R28 | 0 |
| R | 14-Oct-07 | | R21 | 0 |
| R | 06-Nov-07 | | R20 | 0 |
| R | 06-Nov-07 | | R27 | 0 |
| R | 06-Nov-07 | | R21 | 0 |

| Area | Date | Species | Transect Point | Group Size |
|------|------|---------|----------------|------------|
| R | 06-Nov-07 | Pp | R28 | 3 |
| R | 06-Nov-07 | Pp | R12 | 2 |
| R | 06-Nov-07 | Pd | R12 | 3 |
| R | 06-Nov-07 | Pp | R4 | 4 |
| R | 08-Dec-07 | | R15 | 0 |
| R | 08-Dec-07 | | R5 | 0 |
| R | 06-Jan-08 | | R19 | 0 |
| R | 06-Jan-08 | | R20 | 0 |
| R | 18-Jan-08 | | R3 | 0 |
| R | 18-Jan-08 | | R5 | 0 |
| R | 18-Jan-08 | | R14 | 0 |
| R | 18-Jan-08 | Pp | R15 | 2 |
| R | 18-Jan-08 | Pp | R15 | 2 |
| R | 18-Jan-08 | Pp | R15 | 5 |
| R | 18-Jan-08 | | R21 | 0 |
| R | 18-Jan-08 | Pp | R20 | 2 |
| R | 18-Jan-08 | Pp | R13 | 2 |
| R | 18-Jan-08 | Pp | R13 | 1 |
| R | 18-Jan-08 | Pp | R13 | 1 |
| R | 23-Jan-08 | | R14 | 0 |
| R | 26-Jan-08 | | R15 | 0 |
| R | 26-Jan-08 | | R21 | 0 |
| R | 26-Jan-08 | | R28 | 0 |
| R | 26-Jan-08 | | R22 | 0 |
| R | 26-Jan-08 | | R17 | 0 |
| R | 26-Jan-08 | | R18 | 0 |
| R | 26-Jan-08 | | R12 | 0 |
| R | 26-Jan-08 | | R10 | 0 |
| R | 28-Jan-08 | Pp | R13 | 2 |
| R | 28-Jan-08 | | R28 | 0 |
| R | 28-Jan-08 | | R29 | 0 |
| R | 28-Jan-08 | | R15 | 0 |
| R | 28-Jan-08 | | R10 | 0 |
| R | 28-Jan-08 | | R11 | 0 |
| R | 28-Jan-08 | | R4 | 0 |
| R | 28-Jan-08 | | R14 | 0 |
| R | 04-Feb-08 | | R29 | 0 |
| R | 04-Feb-08 | | R17 | 0 |
| R | 04-Feb-08 | | R10 | 0 |
| R | 04-Feb-08 | Pd | R4 | 3 |
| R | 04-Feb-08 | | R14 | 0 |
| R | 26-Feb-08 | | R26 | 0 |
| R | 26-Feb-08 | | R21 | 0 |
| R | 29-Feb-08 | | R25 | 0 |

| Area | Date | Species | Transect Point | Group Size |
|---|---|---|---|---|
| R | 06-Mar-08 | Pp | R10 | 2 |
| R | 06-Mar-08 | | R4 | 0 |
| R | 12-Mar-08 | | D3 | 0 |
| D | 12-Mar-08 | | D26 | 0 |
| D | 12-Mar-08 | Pd | D28 | 2 |
| D | 12-Mar-08 | Pd | D28 | 4 |
| D | 12-Mar-08 | Pd | D28 | 3 |
| D | 12-Mar-08 | Pd | D28 | 1 |
| D | 12-Mar-08 | Pp | D28 | 3 |
| D | 12-Mar-08 | Pp | D28 | 2 |
| D | 12-Mar-08 | Pp | D28 | 2 |
| D | 12-Mar-08 | | D22 | 0 |
| D | 12-Mar-08 | | D18 | 0 |
| D | 12-Mar-08 | Pp | D12 | 2 |
| D | 12-Mar-08 | Pp | D11 | 1 |
| R | 30-Mar-08 | | R26 | 0 |
| R | 30-Mar-08 | | R20 | 0 |
| R | 30-Mar-08 | | R21 | 0 |
| R | 30-Mar-08 | | R22 | 0 |
| R | 30-Mar-08 | | R10 | 0 |
| R | 30-Mar-08 | | R4 | 0 |
| R | 30-Mar-08 | | R3 | 0 |
| D | 30-Mar-08 | | R13 | 0 |
| R | 07-Apr-08 | | R19 | 0 |
| R | 07-Apr-08 | | R21 | 0 |
| R | 07-Apr-08 | | R15 | 0 |
| D | 04-May-08 | | D3 | 0 |
| D | 04-May-08 | Pp | D25 | 1 |
| D | 04-May-08 | | D13 | 0 |
| D | 04-May-08 | | D15 | 0 |
| D | 04-May-08 | Pp | D10 | 4 |
| D | 04-May-08 | Pp | D10 | 6 |
| D | 04-May-08 | Pp | D5 | 4 |
| D | 04-May-08 | Pp | D5 | 3 |
| D | 04-May-08 | Pp | D5 | 11 |
| D | 04-May-08 | Pp | D5 | 5 |
| D | 04-May-08 | Pp | D5 | 3 |
| R | 18-May-08 | Pp | R25 | 2 |
| R | 18-May-08 | Pp | R25 | 3 |
| R | 18-May-08 | Pp | R21 | 2 |
| R | 18-May-08 | | R22 | 0 |
| R | 18-May-08 | | R29 | 0 |
| R | 18-May-08 | | R10 | 0 |
| R | 18-May-08 | Pp | R3 | 3 |

| Area | Date | Species | Transect Point | Group Size |
|------|------|---------|----------------|------------|
| R | 18-May-08 | | R14 | 0 |
| R | 19-May-08 | Pp | R19 | 1 |
| R | 19-May-08 | Pp | R19 | 1 |
| R | 19-May-08 | Pp | R19 | 1 |
| R | 19-May-08 | Pp | R27 | 1 |
| R | 19-May-08 | | R22 | 0 |
| R | 19-May-08 | Pp | R23 | 1 |
| R | 19-May-08 | Pp | R23 | 1 |
| R | 19-May-08 | | R17 | 0 |
| R | 19-May-08 | | R10 | 0 |
| R | 19-May-08 | | R15 | 0 |
| R | 23-May-08 | | R4 | 0 |
| R | 23-May-08 | | R11 | 0 |
| R | 23-May-08 | | R24 | 0 |
| R | 23-May-08 | | R23 | 0 |
| R | 23-May-08 | Pp | R21 | 1 |
| R | 23-May-08 | Pp | R21 | 2 |
| R | 23-May-08 | Pp | R21 | 3 |
| R | 23-May-08 | | R26 | 0 |
| R | 23-May-08 | | R25 | 0 |
| R | 23-May-08 | | R19 | 0 |
| D | 24-May-08 | | D20 | 0 |
| D | 24-May-08 | | D21 | 0 |
| D | 24-May-08 | | D22 | 0 |
| D | 24-May-08 | | D17 | 0 |
| D | 24-May-08 | Pp | D11 | 1 |
| D | 24-May-08 | Pp | D11 | 1 |
| D | 24-May-08 | Pp | D11 | 1 |
| D | 24-May-08 | Pp | D11 | 1 |
| D | 24-May-08 | Pp | D11 | 1 |
| D | 24-May-08 | Pp | D11 | 1 |
| D | 24-May-08 | Pp | D11 | 2 |
| D | 24-May-08 | Pp | D11 | 1 |
| D | 24-May-08 | Pp | D11 | 1 |
| D | 24-May-08 | Pp | D11 | 1 |
| D | 24-May-08 | Pp | D11 | 1 |
| D | 24-May-08 | Pp | D11 | 1 |
| D | 24-May-08 | Pp | D5 | 2 |
| D | 24-May-08 | Pp | D5 | 1 |
| D | 24-May-08 | Pp | D5 | 1 |

**A5 Annual and High Density Aggregation Encounter Rates**

As presented in Chapter III, an order of magnitude difference existed between the annual and high-density aggregation (20 July 2007) encounter rates (porpoise/transect) (Figure A5.1). The 95% confidence intervals indicate that these differences are statistically significant.
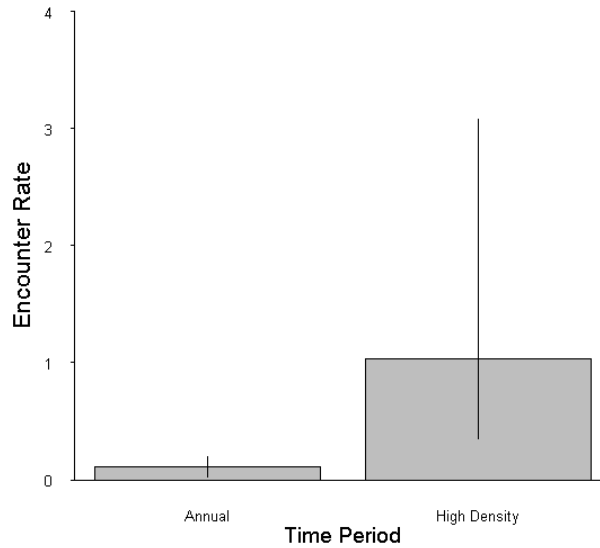


**Figure A5.1 Annual and high-density harbour porpoise encounter rates (porpoise/transect) determined from the June 2007 – May 2008 point transect in Study Areas R and D.**

**A6 Key Assumptions of Distance Analysis**

Density estimation in Distance 6.0 (Thomas et al., 2009) requires satisfying three key assumption. These are:

1) all objects of interest are detected with certainty;

2) all objects are detected at the initial location; and,

3) measurements are exact (Buckland et al., 1993).

Assumption #1 was met by using the same two observers with extensive experience observing wild small cetaceans throughout the study. Any species identifications, which were uncertain due to lighting conditions, angle of the animal, or any other condition were excluded.

Assumption #2 was met based on the negative relationship between the frequency of harbour porpoise sightings and increasing distance from the vessel (Figure A6.1). A slight increase in harbour porpoise frequency of occurrence existed from 0-40 m and 41-80 m (Figure A6.2). This was expected because a point transect can be considered a line transect of zero length, and is a generalization of the traditional circular plot surveys (Buckland et al., 1993). In this type of transect, the key measurement is defined as the radial distance, $r_i$, from the random point to the object of interest, which is searched within area. As such, the initial increase in sighting frequency is expected because as the radius increases there will be an initial increase in sighting frequency to some distance at which it will begin to decline (Buckland et al., 1993).

This unimodal pattern is evident is evident in Figure A6.1. A spike in the frequency of sighting would have been observed closer to the vessel, if the porpoise had been attracted to the vessel, and there would have been a frequency of occurrence spike farther away from the vessel had the animals been evading the vessel. Neither of these patterns was observed in the data suggesting that Assumption #2 was satisfied.

Assumption #3 was satisfied by using experienced observers with formal training in distance estimation at sea. Additionally, regular visual distance calibrations were conducted on each survey, and an observer specific distance correction factor was calculated for each observer.
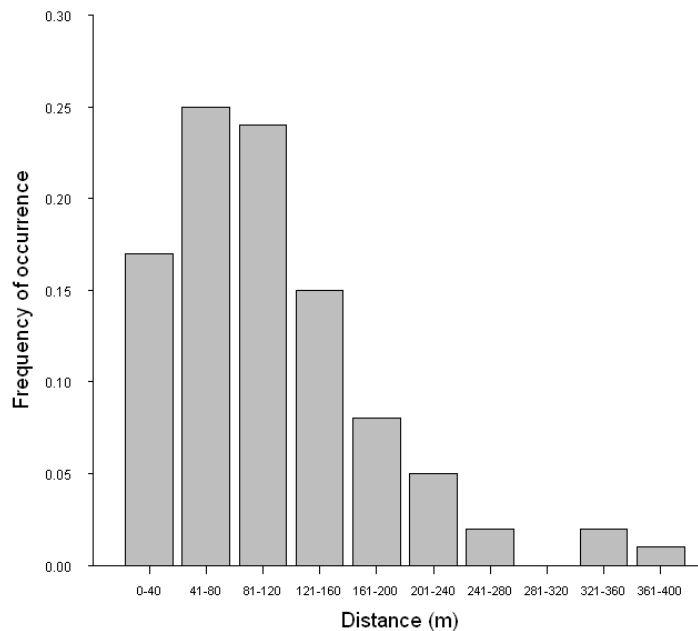
**Figure A6.1 Harbour porpoise sighting declining frequency of occurrence with increasing distance from vessel.**

The distribution of data in Figure A3.1 indicates little variability in the distance estimation of either observer, though both observers had increasing variability with distance. This was to be expected as the ability to accurately estimate the distance to objects, which are further away, diminishes with increasing distance. To further satisfy this assumption, I truncated the data as recommended such that the farthest 5 − 10% of data were eliminated from the distance analysis (see Buckland et al., 1993).

## A7 Harbour Porpoise Current Encounter Rates

The number of harbour porpoise detected at each transect was greater on the ebb, than the flood or slack currents when the data were analysed without the high-density data of 20 July 2007. The ebb current encounter rate (porpoise/transect) was statistically significant when compared to the flood and slack current encounter rates.
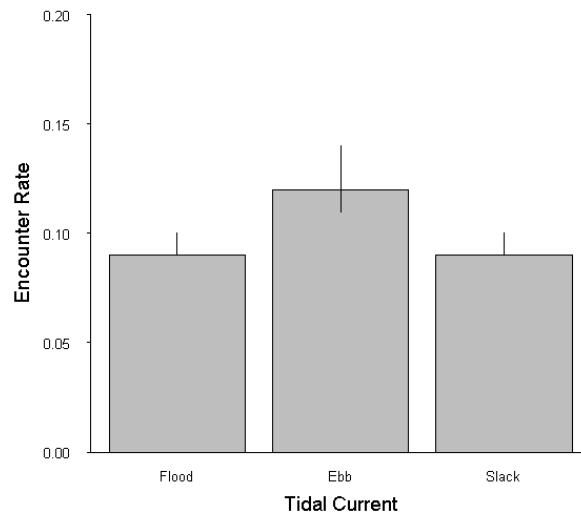


**Figure A7.1 Harbour porpoise encounter rate (porpoise/transect) on the flood, ebb and slack currents. Data from the 2007 – 2008 point transect survey in areas R and D in Juan de Fuca Strait are presented without the high-density data of 20 July 2007.**

**A8 Tidal Height and Current Differentials**

The tidal height differential was determined using the maximum and minimum tidal heights at Victoria – data provided by M. Foreman (Institute of Ocean Sciences). Figure A8.1 shows that harbour porpoise were detected on the spring (maximum tidal height differentials) and neap (minimum tidal height differentials) during the 2007 – 2008 point transect survey with statistically more porpoise were observed in survey areas R and D during the spring tides (see Chapter III – Results).

Figure A8.2 shows the tidal height differential during daylight hours only, as surveys were only conducted during the day with harbour porpoise numbers. Statistically more porpoise were observed during the daylight with tidal height differentials $\geq 1.5$ (see Chapter III - Results).

Figure A8.3 shows that harbour porpoise detected during the 2007 – 2008 point transect survey in Survey Areas R and D were detected during times of greatest water movement, using current data for Race Passage. Most sightings occurred with currents between $2.0 – 3.0$ m/s. This was statistically significant (see Chapter III – Results).
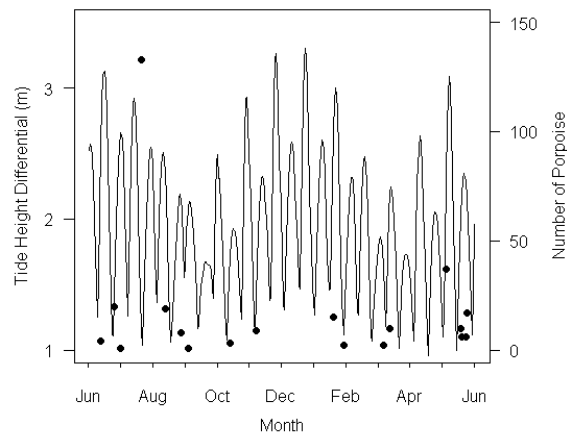


**Figure A8.1 Tidal height differential and number of harbour porpoise observed per month during the June 2007 – May 2008 point transect survey. Spring tides occur when the tide height differential is greatest and neap tides occur when the tide height differential is smallest.**
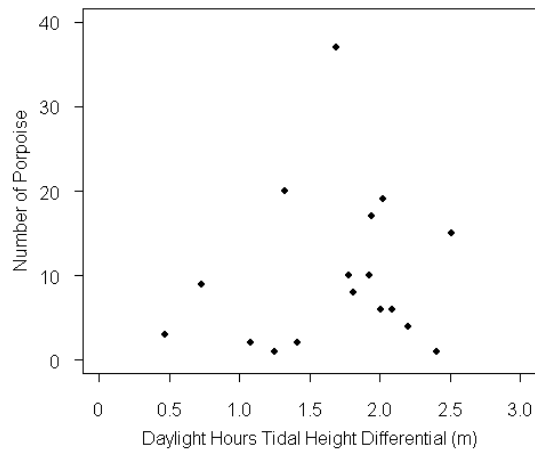
**Figure A8.2 Tidal height differential at Victoria in daylight hours only with harbour porpoise observed during the 2007 – 2008 point transect survey in Survey Areas R and D in Juan de Fuca Strait.**
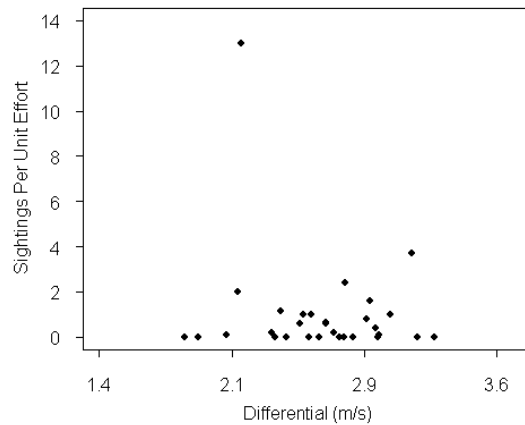


**Figure A8.3 Harbour porpoise point transect (2007 – 2008) sightings per unit effort (porpoise/min) with current differential (m/s) for Race Passage.  The harbour porpoise SPUE data indicate a preference for current differentials in the higher end of the spectrum (≥2.5m/s) associated with the spring tide.  Zero values occur from 1.85 – 3.17 m/s.**

**A9 Harbour Porpoise Densities.**

Harbour porpoise densities calculated in Distance 6.0 (Thomas et al., 2009) for syzygy, quadrature, breeding, and non-breeding time periods indicate that statistical differences exist based on lunar phase (*i.e.,* syzygy vs. quadrature) and time of year (*i.e.,* breeding vs. non-breeding).  See Chapter III Results for exact density and confidence limit values, and for statistical results.
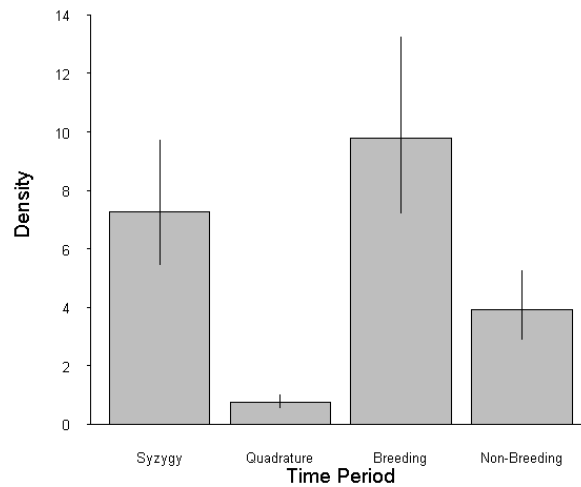


**Figure A9.1 Harbour porpoise density (porpoise/km) in Study Areas R and D pooled at syzygy and quadrature lunar conditions and during the breeding (April – October) and non-breeding (November – March) time periods.  95% Confidence Intervals are plotted for each set of data.**

**A10 Systematic and Supplementary Harbour Porpoise Calf Sightings**

      Almost half (47%) of all harbour porpoise calves observed during the 2007–2008 transect survey were detected at point transect R17, and most (93%) were detected between May and August (Table A10.1). Similarly, most calves were detected during the supplementary observations from May – September, with the highest frequency (47%) in July and August (Table A10.2). The majority of these calves were detected on the ebb tide, with fewer detected on the flood than the slack tide (Table A10.3).

**Table A10.1 Harbour porpoise groups with calves with counts and proportion of total classified by transect point.**

| Date | Point Transect ID | Total Observed | Proportion of Total |
|---|---|---|---|
| 4 May 2008 | D5 | 1 | 0.07 |
| 12 August 2007 | D19 | 2 | 0.13 |
| 4 May 2008 | D25 | 1 | 0.07 |
| 12 August 2007 | D27 | 1 | 0.07 |
| 20 July 2007 | R10 | 6 | 0.40 |
| 6 March 2008 | R10 | 1 | 0.07 |
| 27 August 2007 | R15 | 1 | 0.07 |
| 20 July 2007 | R17 | 1 | 0.07 |
| 20 July 2007 | R28 | 1 | 0.07 |

**Table A10.2 Frequency of occurrence of harbour porpoise groups with calves in the supplementary data set (1995–1996, 1998–2008).**

| Month | Number of Groups with Calves | Frequency |
|---|---|---|
| May | 5 | 0.16 |
| June | 5 | 0.16 |
| July | 8 | 0.25 |
| August | 7 | 0.22 |
| September | 6 | 0.19 |
| October | 1 | 0.03 |

**Table A10.3 Harbour porpoise groups with calves on flood, ebb and slack currents with counts and frequency of occurrence from the supplementary data set (1995–1996, 1998–2008).**

| Current | Number of Harbour Porpoise Groups with Calves | Frequency |
|---|---|---|
| Flood | 6 | 0.19 |
| Ebb | 16 | 0.50 |
| Slack | 10 | 0.31 |

**A11 List of Additional Observers and Researchers**

1. Jeff Laake – National Marine Mammal Laboratory, Alaska Fisheries Science Center/NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115-6349, USA.

2. Russell Markel – University of British, Department of Zoology, #2370-6270 University Blvd., Vancouver, B.C., V6T 1Z4, Canada.

3. Jim Borrowman – Stubbs Island Whale Watching, PO Box 2-2, Telegraph Cove, British Columbia, V0N 3J0, Canada.

4. Dom Tollitt – Sea Mammal Research Unit, Scottish Oceans Institute, University of St. Andrews, St. Andrews, Fife, KY16 8LB, Scotland, UK.

5. Frances Robertson – University of British, Department of Zoology, Marine Mammal Research Unit, Fisheries Centre, Room 247, AERL, 2202 Main Mall, University of British Columbia, Vancouver, B.C. Canada, V6T 1Z4, Canada.

6. Volker Deeke – Sea Mammal Research Unit, Scottish Oceans Institute, University of St. Andrews, St. Andrews, Fife, KY16 8LB, Scotland, UK.

7. Alison Keple – University of British, Department of Zoology, Marine Mammal Research Unit, Fisheries Centre, Room 247, AERL, 2202 Main Mall, University of British Columbia, Vancouver, B.C., V6T 1Z4, Canada.

**A12 Platform of Opportunity Effort Correction Polygons**

   The area covered by the whale watching boats was divided into a series of contiguous polygons. These polygons were used to correct the sightings data by the effort exerted in each polygon, as is described in Chapter IV Methods section.



**Figure A12.1 Effort polygons for area covered by platform of opportunity whale watch vessels (1995–1996, 1998–2008).**

## A13 Harbour Porpoise Anselin Local Moran's I Analysis Results

Anselin Local Moran's *I* analysis of harbour porpoise group size data was conducted in ArcGIS9.1 (ESRI, 2005). Only statistically significant results ($\alpha=0.05$) were presented (Table A13.1). These data correspond with those presented in Figure 4.6.

**Table A13.1 Local Moran's *I, Z* scores and *P* Values from spatial cluster and outlier analysis of harbour porpoise group sizes.**

| Group Size | Local Moran's Index | Z Score | P Value |
|:---:|:---:|:---:|:---:|
| 13 | 0.03 | 2.95 | 0.00 |
| 13 | 0.02 | 3.06 | 0.00 |
| 25 | 0.10 | 4.69 | 0.00 |
| 250 | 0.66 | 49.68 | 0.00 |
| 100 | 0.14 | 16.15 | 0.00 |
| 15 | 0.04 | 2.78 | 0.01 |
| 50 | 0.16 | 12.66 | 0.00 |
| 150 | 0.39 | 50.27 | 0.00 |
| 200 | 0.50 | 54.09 | 0.00 |
| 15 | 0.04 | 3.93 | 0.00 |
| 10 | 0.02 | 2.24 | 0.03 |
| 85 | 0.19 | 9.92 | 0.00 |
| 13 | 0.05 | 3.23 | 0.00 |
| 20 | 0.09 | 5.80 | 0.00 |
| 30 | 0.02 | 4.23 | 0.00 |
| 13 | 0.02 | 4.28 | 0.00 |
| 45 | 0.10 | 4.77 | 0.00 |
| 45 | 0.07 | 12.40 | 0.00 |
| 20 | 0.09 | 7.52 | 0.00 |
| 25 | 0.05 | 6.80 | 0.00 |
| 100 | 0.25 | 14.99 | 0.00 |
| 20 | 0.04 | 4.11 | 0.00 |
| 55 | 0.15 | 6.65 | 0.00 |
| 20 | 0.07 | 5.88 | 0.00 |
| 10 | 0.02 | 2.10 | 0.04 |
| 25 | 0.02 | 2.73 | 0.01 |
| 20 | 0.02 | 2.30 | 0.02 |
| 100 | 0.05 | 6.44 | 0.00 |
| 25 | 0.08 | 5.41 | 0.00 |
| 35 | 0.10 | 4.52 | 0.00 |
| 75 | 0.10 | 20.98 | 0.00 |
| 11 | 0.02 | 2.24 | 0.02 |
| 30 | 0.08 | 7.90 | 0.00 |
| 50 | 0.02 | 4.23 | 0.00 |
| 40 | 0.07 | 7.92 | 0.00 |
| 150 | 0.02 | 8.21 | 0.00 |
| 200 | 0.11 | 13.61 | 0.00 |

## A14 Dall's Porpoise Anselin Local Moran's *I* Analysis Results

Anselin Local Moran's *I* analysis of Dall's porpoise group size data was conducted in ArcGIS9.1 (ESRI, 2005). Results in Table A14.1 correspond with those presented in Figure 4.6, and are significant ($\alpha$=0.05).

**Table A14.1 Local Moran's *I, Z* scores and *P* Values from spatial cluster and outlier analysis of harbour porpoise group size data.**

| Group Size | Local Moran's Index | Z Score | P Value |
|:---:|:---:|:---:|:---:|
| 11 | 0.02 | 2.61 | 0.01 |
| 9 | 0.01 | 2.55 | 0.01 |
| 9 | 0.02 | 2.89 | 0.00 |
| 13 | 0.03 | 3.92 | 0.00 |
| 25 | 0.01 | 4.80 | 0.00 |
| 10 | 0.01 | 2.67 | 0.01 |
| 20 | 0.00 | 3.25 | 0.00 |
| 10 | 0.01 | 2.89 | 0.00 |
| 18 | 0.03 | 5.32 | 0.00 |
| 15 | 0.02 | 2.52 | 0.01 |
| 25 | 0.04 | 5.55 | 0.00 |
| 25 | 0.11 | 12.72 | 0.00 |
| 10 | 0.02 | 3.41 | 0.00 |
| 25 | 0.03 | 9.28 | 0.00 |
| 25 | 0.14 | 13.43 | 0.00 |
| 10 | 0.00 | 2.26 | 0.02 |
| 18 | 0.03 | 4.00 | 0.00 |
| 20 | 0.05 | 7.20 | 0.00 |
| 45 | 0.03 | 10.06 | 0.00 |
| 40 | 0.10 | 14.18 | 0.00 |
| 10 | 0.03 | 3.35 | 0.00 |
| 18 | 0.02 | 4.93 | 0.00 |
| 25 | 0.04 | 16.97 | 0.00 |
| 35 | 0.28 | 31.21 | 0.00 |
| 38 | 0.18 | 19.35 | 0.00 |
| 30 | 0.02 | 3.33 | 0.00 |
| 80 | 0.33 | 52.72 | 0.00 |
| 40 | 0.34 | 27.90 | 0.00 |
| 45 | 0.07 | 7.96 | 0.00 |
| 13 | 0.02 | 3.25 | 0.00 |
| 10 | 0.03 | 4.17 | 0.00 |
| 13 | 0.02 | 2.98 | 0.00 |
| 25 | 0.14 | 15.50 | 0.00 |
| 10 | 0.02 | 2.64 | 0.01 |
| 20 | 0.02 | 5.58 | 0.00 |
| 20 | 0.02 | 6.32 | 0.00 |
| 10 | 0.02 | 2.58 | 0.01 |

| Dall's Porpoise Group Size | Local Moran's Index | Z Score | P Value |
|---|---|---|---|
| 10 | 0.02 | 2.37 | 0.02 |
| 10 | 0.02 | 2.71 | 0.01 |
| 10 | 0.02 | 3.38 | 0.00 |
| 20 | 0.18 | 6.99 | 0.00 |
| 12 | 0.02 | 2.41 | 0.02 |
| 20 | 0.03 | 5.23 | 0.00 |
| 13 | 0.14 | 5.21 | 0.00 |

## A15 Harbour Porpoise Getis-Ord $G_i^*$ Analysis Results

Harbour porpoise Getis-Ord $G_i^*$ hot spot analysis was conducted in ArcGIS9.1 (ESRI, 2005). Results in Table A15.1 correspond with Figure 4.7. The $G_i^*$ statistic is the Getis-Ord $Z$ score value, and the $GiP$ Value is the Getis-Ord $P$ value ($\alpha$=0.05).

**Table A15.1 Harbour porpoise Getis-Ord $G_i^*$ statistics.**

| Group Size | $G_iZ$ Score | *GiP* Value |
|---|---|---|
| 2 | 7.37 | 0.00 |
| 2 | 7.28 | 0.00 |
| 4 | 7.11 | 0.00 |
| 250 | 7.09 | 0.00 |
| 3 | 7.07 | 0.00 |
| 2 | 7.06 | 0.00 |
| 2 | 7.05 | 0.00 |
| 3 | 7.03 | 0.00 |
| 1 | 7.02 | 0.00 |
| 8 | 7.02 | 0.00 |
| 1 | 7.00 | 0.00 |
| 75 | 6.93 | 0.00 |
| 13 | 6.89 | 0.00 |
| 1 | 6.85 | 0.00 |
| 4 | 6.84 | 0.00 |
| 13 | 6.84 | 0.00 |
| 2 | 6.82 | 0.00 |
| 3 | 6.79 | 0.00 |
| 3 | 6.79 | 0.00 |
| 5 | 6.79 | 0.00 |
| 3 | 6.77 | 0.00 |
| 3 | 6.77 | 0.00 |
| 2 | 6.76 | 0.00 |
| 2 | 6.75 | 0.00 |
| 2 | 6.73 | 0.00 |
| 30 | 6.73 | 0.00 |
| 2 | 6.73 | 0.00 |
| 7 | 6.73 | 0.00 |
| 1 | 6.73 | 0.00 |
| 2 | 6.72 | 0.00 |
| 3 | 6.71 | 0.00 |
| 1 | 6.70 | 0.00 |
| 20 | 6.68 | 0.00 |
| 3 | 6.67 | 0.00 |
| 4 | 6.66 | 0.00 |
| 4 | 6.66 | 0.00 |
| 3 | 6.66 | 0.00 |
| 1 | 6.66 | 0.00 |

| Group Size | *Gi* Z Score | *Gi* P Value |
| --- | --- | --- |
| 2 | 6.63 | 0.00 |
| 2 | 6.61 | 0.00 |
| 15 | 6.59 | 0.00 |
| 2 | 6.59 | 0.00 |
| 6 | 6.59 | 0.00 |
| 5 | 6.56 | 0.00 |
| 1 | 6.56 | 0.00 |
| 2 | 6.55 | 0.00 |
| 50 | 6.54 | 0.00 |
| 3 | 6.51 | 0.00 |
| 7 | 6.51 | 0.00 |
| 2 | 6.48 | 0.00 |
| 2 | 6.46 | 0.00 |
| 1 | 6.45 | 0.00 |
| 5 | 6.39 | 0.00 |
| 15 | 6.37 | 0.00 |
| 3 | 6.34 | 0.00 |
| 1 | 6.34 | 0.00 |
| 3 | 6.31 | 0.00 |
| 2 | 6.28 | 0.00 |
| 3 | 6.28 | 0.00 |
| 4 | 6.28 | 0.00 |
| 3 | 6.28 | 0.00 |
| 8 | 6.28 | 0.00 |
| 5 | 6.28 | 0.00 |
| 2 | 6.24 | 0.00 |
| 1 | 6.20 | 0.00 |
| 2 | 6.20 | 0.00 |
| 1 | 6.19 | 0.00 |
| 200 | 6.16 | 0.00 |
| 2 | 6.15 | 0.00 |
| 2 | 6.15 | 0.00 |
| 10 | 6.15 | 0.00 |
| 1 | 6.12 | 0.00 |
| 8 | 6.11 | 0.00 |
| 25 | 6.10 | 0.00 |
| 5 | 6.09 | 0.00 |
| 1 | 6.09 | 0.00 |
| 3 | 6.07 | 0.00 |
| 4 | 6.07 | 0.00 |
| 1 | 6.04 | 0.00 |
| 1 | 6.04 | 0.00 |
| 2 | 6.03 | 0.00 |
| 1 | 6.02 | 0.00 |
| 1 | 5.99 | 0.00 |
| 6 | 5.98 | 0.00 |

| Group Size | *Gi* Z Score | *Gi* P Value |
|---|---|---|
| 20 | 5.96 | 0.00 |
| 55 | 5.94 | 0.00 |
| 3 | 5.92 | 0.00 |
| 1 | 5.92 | 0.00 |
| 2 | 5.88 | 0.00 |
| 2 | 5.84 | 0.00 |
| 2 | 5.84 | 0.00 |
| 10 | 5.83 | 0.00 |
| 1 | 5.82 | 0.00 |
| 6 | 5.82 | 0.00 |
| 1 | 5.82 | 0.00 |
| 3 | 5.78 | 0.00 |
| 2 | 5.77 | 0.00 |
| 100 | 5.74 | 0.00 |
| 2 | 5.70 | 0.00 |
| 1 | 5.65 | 0.00 |
| 1 | 5.62 | 0.00 |
| 1 | 5.61 | 0.00 |
| 20 | 5.59 | 0.00 |
| 3 | 5.58 | 0.00 |
| 3 | 5.57 | 0.00 |
| 1 | 5.54 | 0.00 |
| 6 | 5.53 | 0.00 |
| 5 | 5.46 | 0.00 |
| 4 | 5.46 | 0.00 |
| 13 | 5.40 | 0.00 |
| 5 | 5.39 | 0.00 |
| 2 | 5.38 | 0.00 |
| 3 | 5.38 | 0.00 |
| 2 | 5.38 | 0.00 |
| 5 | 5.38 | 0.00 |
| 3 | 5.35 | 0.00 |
| 150 | 5.34 | 0.00 |
| 5 | 5.33 | 0.00 |
| 2 | 5.31 | 0.00 |
| 85 | 5.31 | 0.00 |
| 5 | 5.27 | 0.00 |
| 2 | 5.22 | 0.00 |
| 11 | 5.22 | 0.00 |
| 20 | 5.19 | 0.00 |
| 7 | 5.18 | 0.00 |
| 1 | 5.18 | 0.00 |
| 2 | 5.13 | 0.00 |
| 2 | 5.13 | 0.00 |
| 3 | 5.13 | 0.00 |
| 3 | 5.13 | 0.00 |

| Group Size | *Gi* Z Score | *Gi* P Value |
| --- | --- | --- |
| 3 | 5.13 | 0.00 |
| 3 | 5.06 | 0.00 |
| 1 | 5.04 | 0.00 |
| 45 | 5.04 | 0.00 |
| 1 | 5.01 | 0.00 |
| 1 | 5.00 | 0.00 |
| 1 | 4.99 | 0.00 |
| 2 | 4.99 | 0.00 |
| 1 | 4.97 | 0.00 |
| 1 | 4.95 | 0.00 |
| 125 | 4.94 | 0.00 |
| 2 | 4.93 | 0.00 |
| 3 | 4.91 | 0.00 |
| 2 | 4.91 | 0.00 |
| 5 | 4.89 | 0.00 |
| 1 | 4.89 | 0.00 |
| 25 | 4.88 | 0.00 |
| 5 | 4.86 | 0.00 |
| 100 | 4.86 | 0.00 |
| 1 | 4.86 | 0.00 |
| 1 | 4.78 | 0.00 |
| 5 | 4.76 | 0.00 |
| 20 | 4.76 | 0.00 |
| 38 | 4.76 | 0.00 |
| 1 | 4.73 | 0.00 |
| 10 | 4.73 | 0.00 |
| 1 | 4.71 | 0.00 |
| 1 | 4.71 | 0.00 |
| 30 | 4.71 | 0.00 |
| 2 | 4.70 | 0.00 |
| 1 | 4.70 | 0.00 |
| 2 | 4.70 | 0.00 |
| 11 | 4.70 | 0.00 |
| 2 | 4.69 | 0.00 |
| 50 | 4.69 | 0.00 |
| 3 | 4.68 | 0.00 |
| 4 | 4.66 | 0.00 |
| 4 | 4.63 | 0.00 |
| 35 | 4.63 | 0.00 |
| 5 | 4.63 | 0.00 |
| 2 | 4.59 | 0.00 |
| 2 | 4.57 | 0.00 |
| 1 | 4.57 | 0.00 |
| 5 | 4.52 | 0.00 |
| 1 | 4.41 | 0.00 |
| 1 | 4.36 | 0.00 |

| Group Size | *Gi* Z Score | *Gi* P Value |
|---|---|---|
| 2 | 4.28 | 0.00 |
| 1 | 4.25 | 0.00 |
| 1 | 4.02 | 0.00 |
| 2 | 3.93 | 0.00 |
| 1 | 3.88 | 0.00 |
| 2 | 3.87 | 0.00 |
| 3 | 3.87 | 0.00 |
| 3 | 3.86 | 0.00 |
| 1 | 3.82 | 0.00 |
| 3 | 3.82 | 0.00 |
| 1 | 3.79 | 0.00 |
| 1 | 3.76 | 0.00 |
| 1 | 3.75 | 0.00 |
| 30 | 3.73 | 0.00 |
| 5 | 3.71 | 0.00 |
| 2 | 3.69 | 0.00 |
| 200 | 3.69 | 0.00 |
| 13 | 3.68 | 0.00 |
| 4 | 3.68 | 0.00 |
| 4 | 3.64 | 0.00 |
| 1 | 3.52 | 0.00 |
| 2 | 3.50 | 0.00 |
| 1 | 3.44 | 0.00 |
| 1 | 3.42 | 0.00 |
| 2 | 3.39 | 0.00 |
| 1 | 3.38 | 0.00 |
| 6 | 3.37 | 0.00 |
| 1 | 3.37 | 0.00 |
| 3 | 3.36 | 0.00 |
| 4 | 3.32 | 0.00 |
| 40 | 3.31 | 0.00 |
| 2 | 3.31 | 0.00 |
| 150 | 3.23 | 0.00 |
| 20 | 3.23 | 0.00 |
| 3 | 3.19 | 0.00 |
| 1 | 3.19 | 0.00 |
| 5 | 3.16 | 0.00 |
| 5 | 3.15 | 0.00 |
| 3 | 3.12 | 0.00 |
| 2 | 3.09 | 0.00 |
| 1 | 3.09 | 0.00 |
| 1 | 3.08 | 0.00 |
| 25 | 3.07 | 0.00 |
| 1 | 3.04 | 0.00 |
| 2 | 3.02 | 0.00 |
| 1 | 2.99 | 0.00 |

| Group Size | *Gi* Z Score | *Gi* P Value |
|---|---|---|
| 1 | 2.97 | 0.00 |
| 1 | 2.95 | 0.00 |
| 2 | 2.94 | 0.00 |
| 10 | 2.94 | 0.00 |
| 1 | 2.93 | 0.00 |
| 2 | 2.92 | 0.00 |
| 1 | 2.92 | 0.00 |
| 5 | 2.91 | 0.00 |
| 2 | 2.91 | 0.00 |
| 6 | 2.90 | 0.00 |
| 6 | 2.90 | 0.00 |
| 6 | 2.90 | 0.00 |
| 2 | 2.89 | 0.00 |
| 2 | 2.87 | 0.00 |
| 5 | 2.87 | 0.00 |
| 100 | 2.87 | 0.00 |
| 100 | 2.86 | 0.00 |
| 1 | 2.83 | 0.00 |
| 5 | 2.83 | 0.00 |
| 1 | 2.81 | 0.00 |
| 4 | 2.80 | 0.01 |
| 1 | 2.80 | 0.01 |
| 4 | 2.74 | 0.01 |
| 6 | 2.74 | 0.01 |
| 2 | 2.72 | 0.01 |
| 1 | 2.68 | 0.01 |
| 1 | 2.64 | 0.01 |
| 1 | 2.59 | 0.01 |
| 3 | 2.59 | 0.01 |
| 1 | 2.57 | 0.01 |
| 5 | 2.56 | 0.01 |
| 3 | 2.55 | 0.01 |
| 1 | 2.55 | 0.01 |
| 1 | 2.54 | 0.01 |
| 3 | 2.54 | 0.01 |
| 1 | 2.54 | 0.01 |
| 2 | 2.52 | 0.01 |
| 1 | 2.52 | 0.01 |
| 1 | 2.52 | 0.01 |
| 1 | 2.51 | 0.01 |

# A16 Dall's Porpoise Getis-Ord $G_i^*$ Analysis Results

Getis-Ord $G_i^*$ Dall's porpoise hot spot analysis was conducted in ArcGIS9.1 (ESRI, 2005). Table A16.1 results correspond with those in Figure 4.7. The $G_i^*$ statistic is the Getis-Ord Z score value, and the *GiP* Value is the Getis-Ord *P* value ($\alpha$=0.05).

**Table A16.1 Dall's porpoise Getis-Ord $G_i^*$ statistics.**

| Group Size | *Gi* Z Score | *Gi P* Value |
|:---:|:---:|:---:|
| 25 | 5.42 | 0.00 |
| 3 | 5.25 | 0.00 |
| 10 | 5.18 | 0.00 |
| 2 | 5.04 | 0.00 |
| 80 | 5.00 | 0.00 |
| 2 | 4.99 | 0.00 |
| 4 | 4.98 | 0.00 |
| 7 | 4.93 | 0.00 |
| 1 | 4.90 | 0.00 |
| 13 | 4.89 | 0.00 |
| 40 | 4.88 | 0.00 |
| 6 | 4.88 | 0.00 |
| 2 | 4.88 | 0.00 |
| 2 | 4.85 | 0.00 |
| 2 | 4.83 | 0.00 |
| 3 | 4.81 | 0.00 |
| 3 | 4.81 | 0.00 |
| 5 | 4.80 | 0.00 |
| 2 | 4.79 | 0.00 |
| 25 | 4.78 | 0.00 |
| 20 | 4.77 | 0.00 |
| 4 | 4.73 | 0.00 |
| 2 | 4.72 | 0.00 |
| 3 | 4.69 | 0.00 |
| 10 | 4.69 | 0.00 |
| 11 | 4.69 | 0.00 |
| 5 | 4.66 | 0.00 |
| 2 | 4.62 | 0.00 |
| 4 | 4.62 | 0.00 |
| 3 | 4.62 | 0.00 |
| 3 | 4.61 | 0.00 |
| 3 | 4.61 | 0.00 |
| 2 | 4.61 | 0.00 |
| 8 | 4.54 | 0.00 |
| 8 | 4.53 | 0.00 |
| 6 | 4.53 | 0.00 |
| 1 | 4.50 | 0.00 |

| Group Size | *Gi* Z Score | *Gi* P Value |
|---|---|---|
| 3 | 4.49 | 0.00 |
| 35 | 4.48 | 0.00 |
| 2 | 4.48 | 0.00 |
| 2 | 4.47 | 0.00 |
| 4 | 4.46 | 0.00 |
| 1 | 4.42 | 0.00 |
| 10 | 4.41 | 0.00 |
| 10 | 4.39 | 0.00 |
| 6 | 4.31 | 0.00 |
| 10 | 4.31 | 0.00 |
| 2 | 4.28 | 0.00 |
| 2 | 4.27 | 0.00 |
| 4 | 4.27 | 0.00 |
| 10 | 4.27 | 0.00 |
| 6 | 4.24 | 0.00 |
| 25 | 4.23 | 0.00 |
| 4 | 4.21 | 0.00 |
| 3 | 4.20 | 0.00 |
| 20 | 4.20 | 0.00 |
| 9 | 4.19 | 0.00 |
| 25 | 4.19 | 0.00 |
| 25 | 4.17 | 0.00 |
| 40 | 4.17 | 0.00 |
| 7 | 4.13 | 0.00 |
| 25 | 4.11 | 0.00 |
| 38 | 4.11 | 0.00 |
| 13 | 4.11 | 0.00 |
| 6 | 4.11 | 0.00 |
| 1 | 4.09 | 0.00 |
| 1 | 4.09 | 0.00 |
| 20 | 4.05 | 0.00 |
| 2 | 4.02 | 0.00 |
| 12 | 3.99 | 0.00 |
| 4 | 3.96 | 0.00 |
| 3 | 3.95 | 0.00 |
| 18 | 3.94 | 0.00 |
| 5 | 3.93 | 0.00 |
| 10 | 3.92 | 0.00 |
| 6 | 3.91 | 0.00 |
| 3 | 3.87 | 0.00 |
| 5 | 3.86 | 0.00 |
| 1 | 3.84 | 0.00 |
| 9 | 3.83 | 0.00 |
| 1 | 3.83 | 0.00 |
| 2 | 3.80 | 0.00 |
| 6 | 3.80 | 0.00 |

| Group Size | *Gi* Z Score | *Gi* P Value |
|---|---|---|
| 10 | 3.78 | 0.00 |
| 4 | 3.78 | 0.00 |
| 5 | 3.76 | 0.00 |
| 9 | 3.76 | 0.00 |
| 5 | 3.73 | 0.00 |
| 10 | 3.73 | 0.00 |
| 5 | 3.67 | 0.00 |
| 3 | 3.67 | 0.00 |
| 2 | 3.64 | 0.00 |
| 5 | 3.64 | 0.00 |
| 3 | 3.56 | 0.00 |
| 4 | 3.55 | 0.00 |
| 3 | 3.50 | 0.00 |
| 3 | 3.48 | 0.00 |
| 5 | 3.47 | 0.00 |
| 2 | 3.45 | 0.00 |
| 5 | 3.15 | 0.00 |
| 4 | 3.13 | 0.00 |
| 2 | 3.13 | 0.00 |
| 3 | 2.98 | 0.00 |
| 2 | 2.87 | 0.00 |
| 1 | 2.85 | 0.00 |
| 2 | 2.74 | 0.01 |
| 2 | 2.63 | 0.01 |
| 18 | 2.60 | 0.01 |
| 4 | 2.60 | 0.01 |
| 20 | 2.53 | 0.01 |

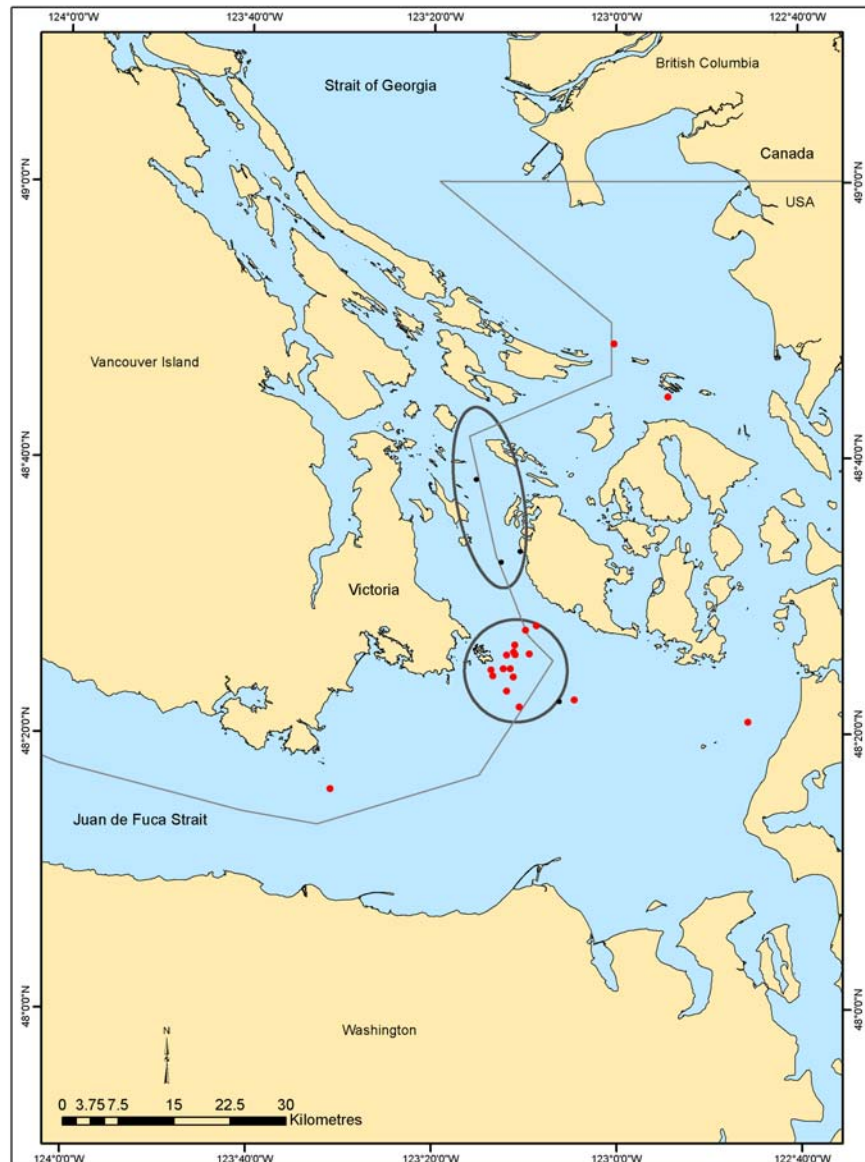**A17 Harbour and Dall's Porpoise Calf Sightings.**
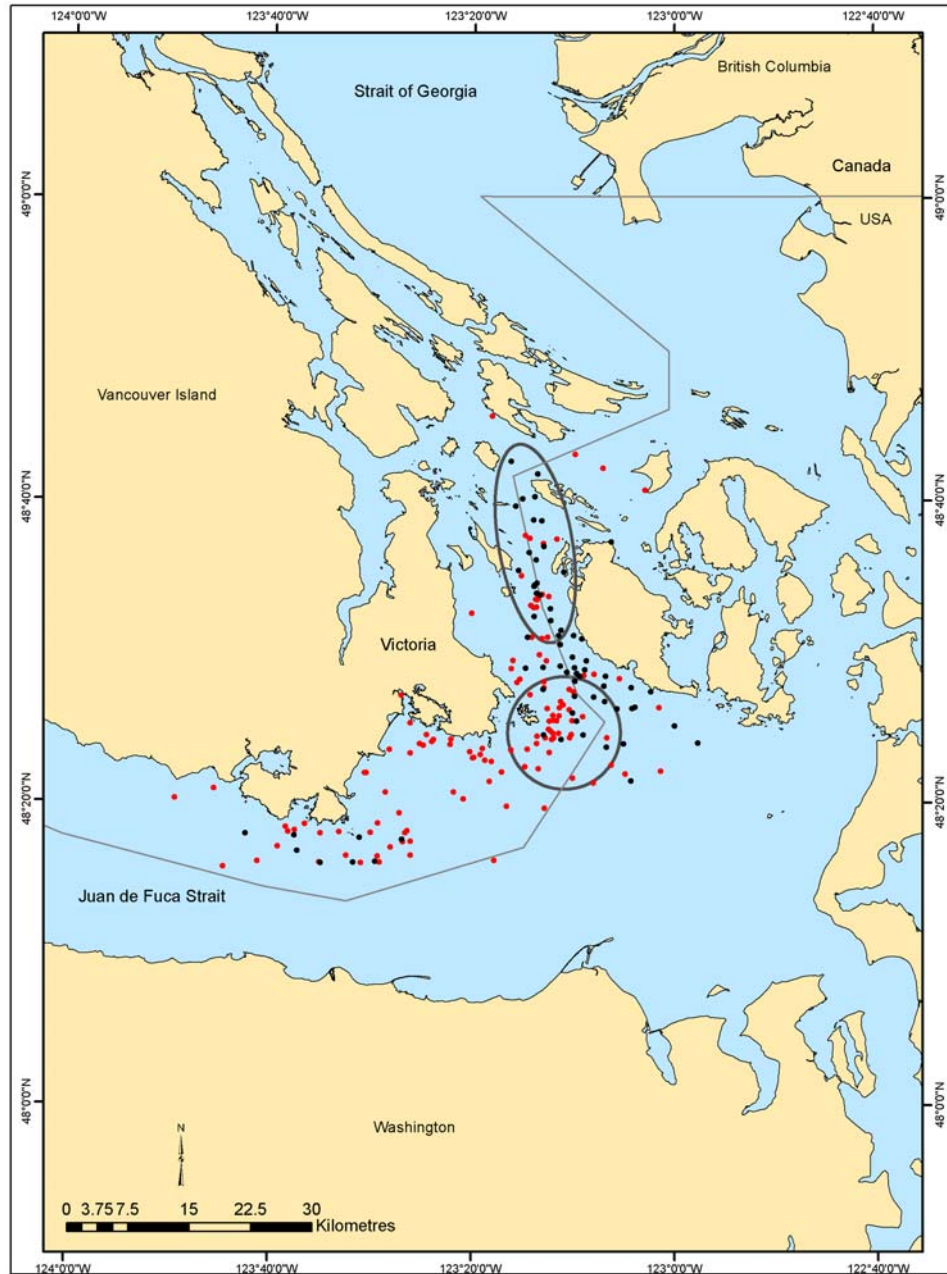


**Figure A17.1 Harbour and Dall's porpoise calf sightings from Study Area B (1995–1996, 1998–2008) with hot spots circled in grey. Harbour porpoise are represented in red and Dall's porpoise are represented in black.**

**A18 Harbour and Dall's Porpoise High-Density Sightings.**
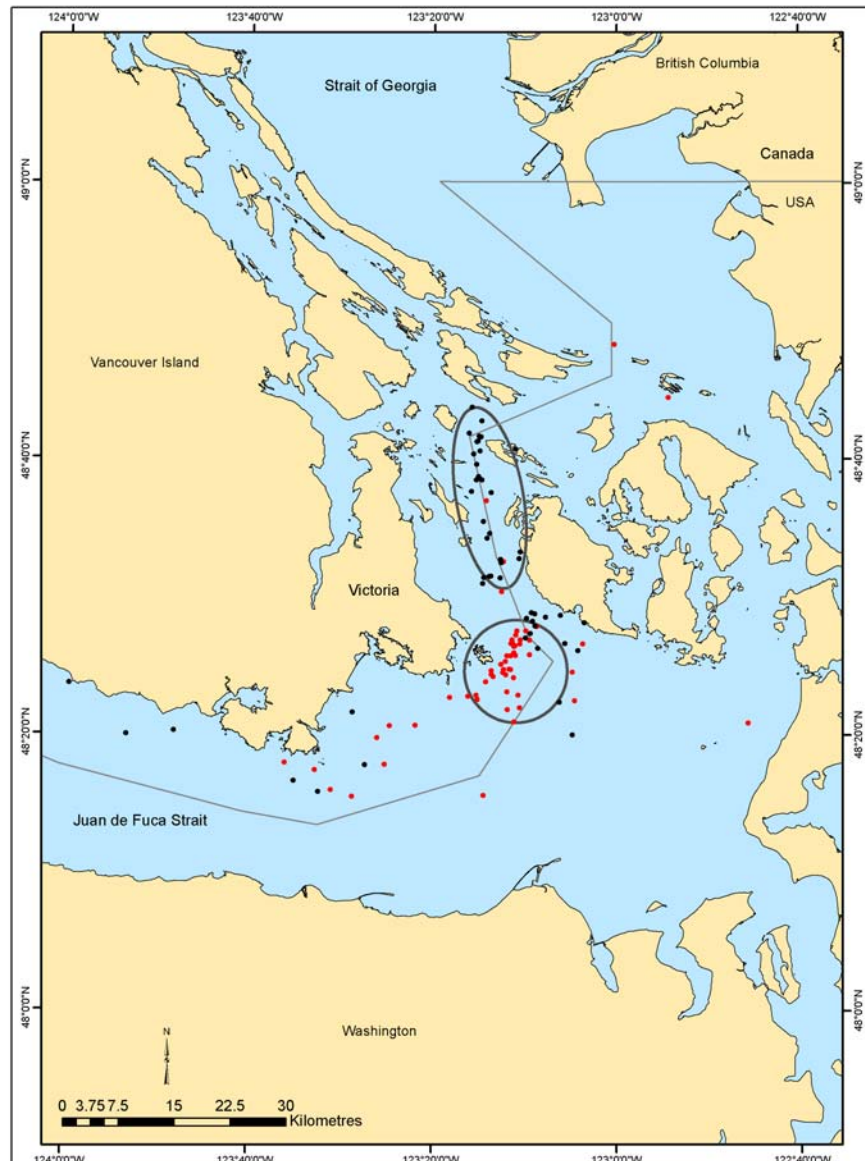


**Figure A18.1 Harbour and Dall's porpoise high-density sightings *(n≥15)* from Study Area B (1995–1996, 1998–2008) with hot spots circled in grey. Harbour porpoise are represented in red and Dall's porpoise are represented in black.**

**Figure A18.2 Harbour and Dall's porpoise high-density sightings (n≥50) from Study Area B (1995–1996, 1998–2008) with hot spots circled in grey. Harbour porpoise are represented in red and Dall's porpoise are represented in black.**

**A19 Standardised Coefficients for Integrative Model.**

**Table A19. 1 Standardised coefficients for physical and biological integrative model.**

| Variable | Full Model | Number of Groups Index Removed | Index of Conspecifics Removed | Both Social Indices Removed |
|---|---|---|---|---|
| Ebb Current | 0.0199 | 0.0345 | 0.1267 | 0.1146 |
| April-October | 0.0079 | 0.0268 | -0.3099 | -0.3271 |
| Full and New Moon | 0.0555 | 0.0412 | 0.3259 | 0.3399 |
| Index of Conspecifics | 0.9754 | 0.9717 | — | — |
| Number of Groups Index | 0.0499 | — | -0.0424 | — |