

Characterizing site fidelity and habitat use of the eastern north Pacific gray whale
(*Eschrichtius robustus*) in Clayoquot Sound, British Columbia

by

Jacqueline Ann Clare
B.Sc., University of Victoria, 2011

A Thesis submitted in Partial Fulfillment
of the Requirements for the Degree of

MASTER OF SCIENCE

in the Department of Geography

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Supervisory Committee

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Abstract

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A small number of eastern north Pacific gray whales (*Eschrichtius robustus*), known as the Pacific Coastal Feeding Group (PCFG) forage during the summer months in the coastal waters between California and Alaska. Although several studies have analyzed the population structure of the PCFG, maternal learning and predator/prey dynamics have not been studied in detail. In this study I characterize fine scale habitat use and site fidelity of eastern north Pacific gray whales in one foraging site within the PCFG's foraging range. I approach this study by examining site fidelity to Clayoquot Sound in increasing detail at different time scales. Using the variability recorded in 17 field seasons of whale census surveys (1997-2013) as a proxy for fluctuations in prey, I suggest that the combination of physical properties of the study area and the life history characteristics of the primary prey species type enable Clayoquot Sound to persist as a foraging site through time. The analysis of photographic identification data collected between 1998-2013 indicates that Clayoquot Sound is one site within a larger foraging range, and that annual fluctuations in prey density are related to site fidelity and residency time. By identifying cow/calf pairs using photographic identification data collected between 1998-2013 I characterize internal recruitment via maternal learning within Clayoquot Sound. A calf's site fidelity is related to its mother's site fidelity, but its residency time is related to annual fluctuations in prey density. In contrast, a cow's residency time is not related to changes in prey, but increases in duration when accompanied by a calf. The interplay between fluctuations in prey productivity, and the age and gender of individuals, are the variables that most likely influence the distribution of PCFG whales intra- and inter-annually.

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Dedication

This thesis is dedicated to the gray whales of Clayoquot Sound, who allowed me to photograph and observe them. They taught me valuable lessons about life and myself, and inspired this work. If we treat them and their habitat with respect, we may be lucky enough that they will continue to return to Clayoquot Sound and inspire others.

Chapter 1 : Introduction

A population is a group of individuals that interbreed panmictically, for at least one breeding season, and whose members are part of a discrete breeding unit (Pielou 1979). Identifying populations of cetaceans is a complex task due to the cryptic nature of many species, the logistics of collecting data in the marine environment, and the challenge of selecting the appropriate spatial and temporal scale of study. Furthermore, population structuring can range from low-level segregation to subspeciation (Gaskin 1982), operating on a continuum with varying degrees of isolation making it difficult to determine the appropriate threshold to designate a group of whales as a separate population for management purposes.

The use of genetic markers is the most common technique for designating populations of cetacean species (*e.g.* Valenzuela *et al.* 2009, Mirimin *et al.* 2011, Amaral *et al.* 2012), with distinction measured by a significant difference in nuclear and mitochondrial DNA (mtDNA) (Mortiz *et al.* 1995). In recognition that populations are rarely discrete in nature, and relatively little was known about cetacean population structure below the species level (Gaskin 1982), the designation of a Management Unit (MU) was developed. MUs are defined as populations that are genetically distinct, but still have a limited dispersal with the larger population, and thus a significant difference in the frequency of nuclear alleles may not be present (Awise 2000). Instead, MUs may be differentiated using mtDNA, which is inherited only from the mother, and usually occurs when calves follow their mothers to specific foraging sites during their first year, and repeat the same migration for the duration of their lives (Katona & Beard 1990). The need to identify and protect these populations arises when they are demographically independent, which is defined as “a unit in which internal population dynamics are far more important for maintaining unit integrity than external dynamics” and corresponds with ecological time (Haig & Winker 2010, p.174). If resource managers do not recognize demographically independent populations because they are not distinguishable in terms of nuclear DNA (due to a low level of mixing that causes relative genetic homogeneity), but the amount of immigration is not sufficient to sustain that population during an anthropogenic disturbance, then that population may be at risk of extirpation

(Wade & Angliss 1997). Therefore, the MU designation is important for populations whose structure does not fall under the auspice of the traditional definition of a population. The challenge for resource managers is to successfully identify, and determine the level of isolation of these populations.

While the use of genetics offers a clear technique to measure population distinction, samples must be collected over an appropriate spatial and temporal scale otherwise the results may be inaccurate. However, there is no single appropriate scale at which to study ecological phenomena, and the interpretation of ecological systems vary depending on the spatial or temporal scale of study (Levin 1992). The spatial extent where samples are collected is critically important when the population in question is not separated by physical barriers and does not differ in morphology. The timing of sample collection is also crucial, especially in migratory species where individuals may show different patterns of site fidelity to breeding and feeding grounds when migrating long distances (Anderwald *et al.* 2011).

The subject of this study is the gray whale (*Eschrichtius robustus*), whose distribution and population structure has recently become a contentious issue. The gray whale is found in the north Pacific, and currently has two recognized populations in eastern and western coastal waters. Historically, a third population was thought to inhabit the north Atlantic, but was extirpated during the 18th century (Mead & Mitchell 1984). The western gray whale has not recovered since the cessation of whaling and thus is listed as critically endangered by the International Union for the Conservation of Nature (Reilly *et al.* 2008), with approximately 130 individuals left as of 2008 (Cooke *et al.* 2008). Although the exact distribution of the western gray whale is unclear, they are sighted annually foraging in the coastal waters of Sakhalin Island in eastern Russia during the summer (Swartz *et al.* 2006). During the winter months they migrate west and are sighted near Japan, Korea, and China (Swartz *et al.* 2006). However, recent tagging studies have recorded western gray whales migrating to the eastern north Pacific, which is thought of as eastern gray whale habitat (Weller *et al.* 2012, Weller *et al.* 2013).

In contrast to the western population, the eastern north Pacific gray whale has recovered from commercial whaling with approximately 19,000 individuals in the population (Laake *et al.* 2009). From a management perspective, the eastern north

Pacific gray whale is considered a conservation success. In the United States it was delisted under the Endangered Species Act (ESA) in 1994 because of its recovery since the moratorium of commercial whaling (Rugh *et al.* 1999). In Canada, the Committee on the Status of Endangered Wildlife (COSEWIC) designated the eastern north Pacific gray whale as a species of ‘special concern’ in 2004, which is defined as “a species that may become a threatened or an endangered species because of a combination of biological characteristics and identified threats” (COSEWIC 2004, p.vii).

The eastern north Pacific gray whale completes one of the longest migrations of any mammal, ranging from the arctic to Mexico (Pike 1962). It forages in the Bering and Chukchi seas in the summer months, and calves in sheltered lagoons in Baja California Sur during the winter months (Pike 1962). However, a small group of whales (~low hundreds; Calambokidis *et al.* 2010) known as the Pacific Coastal Feeding Group (PCFG; IWC 2010), does not complete the full migration, but instead forages in the coastal waters between northern California and southern Alaska (Gilmore 1960, Pike 1962, Calambokidis *et al.* 2002, Calambokidis *et al.* 2010). Unlike the rest of the eastern north Pacific population that primarily forage in arctic waters on benthic amphipods (*Ampelisca* spp.) (Bogoslovskaya *et al.* 1981, Nerini 1984), in southern foraging grounds PCFG whales forage on benthic, epi-benthic, and pelagic prey (Dunham & Duffus 2001, 2002). Foraging habits of PCFG whales have been most closely documented in the coastal waters of western Vancouver Island (Scordino *et al.* 2011), with epi-benthic mysids (family *Mysidae*) found to be the primary prey species (Dunham & Duffus 2001, 2002).

In several studies, scientists have attempted to understand the structure of the PCFG through the use of genetic analysis (Ramakrishnan & Taylor 2001, Ramakrishnan *et al.* 2001, Steeves *et al.* 2001, Frasier *et al.* 2011, Lang *et al.* 2011) but have reported different results (Calambokidis *et al.* 2010, Scordino *et al.* 2011). Ramakrishnan and Taylor conducted a baseline genetic study in 2001, where they tested whether it is appropriate to use mtDNA to differentiate PCFG whales from the rest of the eastern north Pacific population. They concluded that if the PCFG is an isolate and was founded by a single colonizing event in the last 100 years, after which there was no external recruitment, genetic differentiation would occur in 97.8 percent of trials (Ramakrishnan

& Taylor 2001). To follow up with this finding, Ramakrishnan *et al.* (2001) analyzed the haplotype diversity of 45 samples collected from British Columbia and Washington State, presumed to be PCFG whales but not verified with identification photographs, to test the hypothesis that the PCFG is a maternal genetic isolate established by a single founding event. They discovered that the number of haplotypes and haplotypic diversity were high in comparison to their simulated genetic samples, and reported a male biased sex ratio; both of which are inconsistent with the characteristics of a closed population. However, the authors only focused on the hypothesis that the PCFG was founded by a single and recent colonizing event, and did not evaluate the possibility of low levels of external recruitment, which would still require separate management of the PCFG (Ramakrishnan & Taylor 2001).

A variation of the Ramakrishnan *et al.* (2001) study was conducted by Steeves *et al.* (2001) who compared the haplotypic diversity of the PCFG to that of the rest of the eastern north Pacific population. They used biopsies from 16 gray whales in Clayoquot Sound and 41 biopsies opportunistically from whales migrating along the coast of North America and in the Bering Sea. The authors compared mtDNA and concluded that the whales from Clayoquot Sound did not significantly differ from the rest of the eastern north Pacific population, and did not find a gender bias in Clayoquot Sound whales (Steeves *et al.* 2001). However, the 41 whales were not verified as non-PCFG whales via photographic identification, and thus it is possible that individuals from this group may have included PCFG whales.

Building on the results of past genetic studies, two more PCFG studies were recently completed. Frasier *et al.* (2011) compared the mtDNA of 40 Clayoquot Sound whales to that of 105 whales representing the rest of the eastern north Pacific population. The 105 samples were not directly collected for this study, but were from the mitochondrial sequences reported in a study by LeDuc *et al.* in 2002. These samples included stranded whales along the coast of North America, and whales taken in subsistence hunts. The authors discovered a significant genetic difference between the two groups, and a slight female bias in the whales from Clayoquot Sound (Frasier *et al.* 2011). Based on these results, Frasier *et al.* (2011) assert that the PCFG should be considered a distinct management unit. However, this study was criticized because

Clayoquot Sound whales may not be representative of the whole PCFG, and because microsatellite evaluation was not conducted to determine if double sampling occurred (Wade *et al.* 2010, Scordino *et al.* 2011).

Although the methods used by Frasier *et al.* (2011) were criticized, the novel result renewed interest within the scientific community and prompted a study by Lang *et al.* in 2011. The authors tested if the results from Frasier *et al.* (2011) could still be achieved once the study's shortcomings were addressed. Lang *et al.* (2011) used samples from 99 PCFG whales and 103 whales representing the rest of the eastern north Pacific population, and they also eliminated duplicate samples by analyzing eight microsatellite markers. Two hypotheses were tested in their study. In the first hypothesis, the authors tested to see if population segregation occurs between the PCFG and rest of the eastern north Pacific population based on mtDNA and nuclear DNA. Samples collected north of the Aleutian Island chain were considered to be the rest of the eastern north Pacific population, and individuals sighted between northern California and southeastern Alaska were deemed to be part of the PCFG (Lang *et al.* 2011). With this hypothesis it was assumed that individuals utilize their respective feeding grounds in a uniform manner so that the sampling locations in each region did not matter (Lang *et al.* 2011). A low but statistically significant difference in mtDNA was found between the two groups (Lang *et al.* 2011). For the second hypothesis, the authors explored the possibility that there may be multiple feeding groups within the rest of the eastern north Pacific population. Lang *et al.* (2011) intended to biopsy whales from various sites within arctic foraging grounds, but the Chukotka region was the only site where enough samples were collected (n= 69). With this hypothesis, the authors also used more stringent sampling criteria to define PCFG whales. PCFG samples were only used if the whale was matched via photographic identification with high or medium confidence, and if it was sighted for two or more years within the PCFG foraging range to reduce the possibility of collecting samples from migrating whales (n= 71) (Lang *et al.* 2011). Although the authors were unable to determine if structuring occurs within arctic foraging grounds, they used the Chukotka data for comparison to the refined PCFG samples. A low but significant difference in mtDNA was found when the refined PCFG samples were compared to the samples from the Chukotka region, and to the rest of the

eastern north Pacific population. Lang *et al.* (2011) also found a female bias within the PCFG (1.5 females per male), and all groups (1.3-1.5 females per male). Based on these results, Lang *et al.* (2011) conclude that the PCFG is a demographically independent population.

The differences in the results of these studies illustrate the difficulties inherent in defining population structure in marine systems. The study by Lang *et al.* (2011) probably offers the most accurate portrayal of the level of isolation of the PCFG because the authors utilized recent genetic technology, had a large sample size, and described how the biological significance of genetic analysis is limited by sampling methods. However, Lang *et al.* (2011) could not determine if structuring is present within the rest of the eastern north Pacific population, and did not address the possibility of multiple foraging aggregations within the PCFG. If smaller undefined subdivisions are present in northern foraging grounds and/or in the PCFG, then samples should not be collected randomly in either region as haplotype diversity may differ between subgroups. Thus, a better understanding of fine spatial and temporal scale whale distributions will improve sampling design by determining the appropriate seasons and locations to collect samples.

Photographic identification of PCFG whales started in the 1970s, and demonstrated that some whales return regularly to forage on the west coast of Vancouver Island (Darling 1984). Beginning in 1998, a number of research groups collaborated to collect photographic identification data throughout the Pacific Northwest (*e.g.* Calambokidis *et al.* 2002, 2004, 2007, 2009, 2010) to document the movement of individuals intra- and inter-annually, and to estimate the size of the PCFG. In the most recent report, which includes 11 years of data (1998-2008) and spans from southern California to Kodiak, Alaska, the authors identified 876 unique whales (Calambokidis *et al.* 2010). Many of the sightings occurred in peripheral areas, such as Kodiak, Alaska, or were from early in the foraging season, and therefore only 51.9 percent of the whales were sighted more than once (Calambokidis *et al.* 2010). The authors identified 41 calves, with 54 percent resighted in at least one year, which may be indicative of internal recruitment (Calambokidis *et al.* 2010). The number of calves recorded was low and may have been biased by variability in data collection (Calambokidis *et al.* 2010). Using open and closed population models, and different geographic scales, Calambokidis *et al.*

(2010) estimate that the PCFG contains at most a few hundred individuals. The authors found that individuals fit into two groups: 1) whales that return frequently and make up most of the sightings, and 2) single visit whales that stop during the migration (Calambokidis *et al.* 2010). Whales that were seen more frequently had longer minimum residency times, and individuals with minimum residency times of 21 days or more were twice as likely to be sighted consecutively than whales with shorter minimum residency times (Calambokidis *et al.* 2004). Calambokidis *et al.* (2010) state that individuals that return frequently are most likely to be seen in multiple regions, with the highest interchange rate occurring between regions close in proximity (Calambokidis *et al.* 2004, Calambokidis *et al.* 2010). Despite the movement of individuals within the PCFG's foraging range, whales have some level of site fidelity to the different regions surveyed, as demonstrated by the difference in abundance estimates among the regions (Calambokidis *et al.* 2004).

The movement of whales among regions throughout the PCFG's foraging range is complex, with whales often moving in different directions at the same time of year (Calambokidis *et al.* 2002). Although the collaborative photographic identification studies provide valuable insight into coarse scale distributions of PCFG whales, there is a gap in knowledge about the variables causing different levels of site fidelity among regions. Maternal learning has been posited to be one mechanism structuring the PCFG and creating site fidelity (Calambokidis *et al.* 2010, Lang *et al.* 2011), but the intra-annual movements of whales within the Pacific Northwest suggest that differences in the distribution of prey may also drive their movement on multiple spatial and temporal scales (*e.g.* Fauchald 1999). In this study I will characterize fine scale habitat use and site fidelity of gray whales in Clayoquot Sound, British Columbia, which is one foraging site within the PCFG's foraging range. I carry out this analysis over a small spatial extent ($\sim 25 \text{ km}^2$) over a long time period (using data gathered over 17 years) so that I am able to analyze site fidelity to the area in detail and determine how it is affected by intra- and inter-annual changes in mysid abundance. While the results from this study will provide insight about how PCFG whales use one site within their foraging range, ideally they will be part of a larger collaborative study in the future.

In Chapter Two, I begin by examining why Clayoquot Sound persists as a foraging area for PCFG whales through time by examining the physical properties of sites where whales consistently forage. Using the variability recorded in 17 field seasons of whale census surveys (1997-2013) as a proxy for fluctuations in prey, I determine which sites within the study area are productive by the presence of foraging whales. In the first section of Chapter Two, I break the study area up into four sub-areas and nine time periods to examine how the distribution of foraging whales changes intra-annually. In the second section, I split the study area up into 60m² grid cells and analyze how the presence or absence of foraging whales changes in each grid cell over 17 years. By combining the results from both sections, I identify the sites where whales consistently forage and describe the site's characteristics such as water currents (Kopach 2004), benthic topographical complexity, and depth (Laskin *et al.* 2010) that may affect the quality of mysid habitat. I discuss how these factors, along with the life history characteristics of mysids (see Feyrer 2010, Burnham 2012), allow Clayoquot Sound to sustain foraging whales through time.

In Chapter Three, I assess the level of site fidelity of the whales in Clayoquot Sound, and I analyze how annual fluctuations in mysid density affects site fidelity and residency time. For this analysis I use photographic identification data collected bi-weekly between 1998-2000 and 2008-2013, and sporadically between 2001-2007. I also use photographic identification data taken opportunistically north of the study area in 2002, 2006-2010, and 2012 to estimate the exchange of individuals between Clayoquot Sound and another known foraging area. Based on the site fidelity index used in Mahaffy (2012), whales are classed as having either no site fidelity (sighted one year), a low/moderate level of site fidelity (2-8 years returned), or a high level of site fidelity (>9 years, 60 percent of years since 1998). If no site fidelity is observed, it is indicative of no, or weak, population structuring in Clayoquot Sound. A low/moderate mean level of site fidelity with low/moderate mean residency time, and moderate exchange of individuals between Clayoquot Sound and northern areas indicates that it is one foraging site within a larger foraging range, and part of a larger population such as the PGFG. A high level of site fidelity with residency times that approximately span the duration of the foraging season indicate that the whales of Clayoquot Sound form a closed sub-

population within the PCFG. If a low/moderate or high level of site fidelity is found, I will examine if annual fluctuations in mysid abundance affect site fidelity to Clayoquot Sound. Although prey productivity has been shown to affect the number of whales that are sighted per year in Clayoquot Sound (Dunham & Duffus 2001, Feyrer 2010), its affect on the type of whales that visit per year (single season whales versus returning whales) has not been studied. Defining the level of site fidelity to Clayoquot Sound lends insight to how PCFG whales use different foraging sites within their foraging range.

In Chapter Four, I characterize internal recruitment via maternal learning within Clayoquot Sound by focusing my analysis to cow/calf pairs and calculating each calf's site fidelity after its first summer. I identify cow/calf pairs using photographic identification data collected bi-weekly between 1998-2000 and 2008-2013, and sporadically between 2001-2007, as well as identification photographs from the opportunistic northern surveys. I describe differences in site fidelity among calves by analyzing their first year residency time, their mother's level of site fidelity, and the effect of annual fluctuations in mysid abundance. By examining internal recruitment at a fine spatial scale it facilitates a greater understanding of the process by which the PCFG was created and is maintained. Lastly, in Chapter five, I summarize the findings from the three previous chapters, discuss the implications of the results, and suggest directions for future work.

This study describes how PCFG whales use one site within their foraging range, and if part of a larger collaborative multi-scale study, can guide future genetic work and conservation efforts. A clearer understanding of the degree of the PCFG's genetic isolation, distribution, and population structure would enable resource managers to appropriately manage activities potentially impacting these whales such as an increase in coastal industrial development in important foraging areas (see Jayko *et al.* 1990, Moore & Clarke 2002, Fisheries and Oceans Canada 2010, D'Intino *et al.* 2013).

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Chapter 2 : Fine-Scale Distribution and Habitat Use of Gray Whales (*Eschrichtius robustus*) in Clayoquot Sound, B.C.

1. Introduction

Each year, the eastern north Pacific gray whale (*Eschrichtius robustus*) migrates from breeding grounds in Baja California Sur to the Bering and Chukchi Seas to forage on benthic ampeliscid amphipods (*Ampelisca* spp.) (Bogoslovskaya *et al.* 1981, Nerini 1984). However, a small number of whales (~low hundreds, Calambokidis *et al.* 2010) do not migrate to Arctic waters, but instead they forage in the coastal waters from Oregon to Alaska (Gilmore 1960, Pike 1962, Calambokidis *et al.* 2002, Calambokidis *et al.* 2010). This group is known as the Pacific Coastal Feeding Group (PCFG; IWC 2010) and Clayoquot Sound, British Columbia attracts a varying number of these whales each year due to the abundance of mysids (family *Mysidae*), which is their primary prey species in this area (Kim & Oliver 1989, Duffus 1996, Dunham & Duffus 2001, 2002, Stelle 2001, Feyrer & Duffus 2011, Feyrer & Duffus 2014).

In Clayoquot Sound, as in most ecosystems, the interplay between predator and prey shape top-down (predation) and bottom-up (resource limitation) forces. The number of foraging whales present in Clayoquot Sound differs yearly, and is essentially dictated by the whales themselves. High whale years are followed by at least one year where foraging activity is lower than average (Burnham 2012). This occurs because a high level of predation drives mysid populations to such low numbers that they require at least one year to recover beyond a threshold that attracts whales to the area (Burnham 2012). The years where the level of whale foraging is low represents a period of recovery, where mysids are able to reproduce with less predation. This interval of predator release enables a higher number of foraging whales to return the following year (Burnham 2012). Therefore, in Clayoquot Sound mysid recovery and persistence varies depending largely on predator effort, which is demonstrated with the strong correlation between the number of gray whales in Clayoquot Sound and the abundance and density of mysids (Olsen 2006, Feyrer 2010, Feyrer & Duffus 2014).

Although bottom-up forces such as average daily solar radiation and spring upwelling are not significantly correlated to annual gray whale foraging effort (Feyrer

2010), two components of mysid habitat, benthic topographical complexity and depth, have been shown to significantly predict whale habitat use (Laskin 2007). Benthic topographical complexity measures how frequently the slope of the seafloor changes, and is often associated with high species richness (Ardron 2002). Rocky reefs located in shallow water provide ideal mysid habitat because they are close enough to the shore to receive nutrients from the intertidal zone (Laskin *et al.* 2010), while providing refuge from strong currents and predators.

When foraging whales are directly compared to the distribution of their prey, they are one of the best measures of prey quality and distribution (Kenney *et al.* 1986, Murison & Gaskin 1989, Piatt & Methven 1992, Dunham & Duffus 2001, Croll *et al.* 2005). In this chapter, I will analyze the spatial and temporal patterns of gray whale foraging within the coastal waters of Flores Island, Clayoquot Sound (one site within the PCFG's foraging range) and characterize the interaction between top-down and bottom-up forces. This chapter is split into two broad sections differentiated by the temporal scales used to examine the distribution of foraging whales. In the first section, I will analyze how the distribution of foraging whales changes intra-annually. I will determine which sites within the study area contain high quality mysid habitat by tracking whale distributions within a foraging season, calculating benthic topographical complexity, and characterizing current velocity and flow direction. In the second section, I will analyze how foraging whales are distributed within the study area inter-annually, and determine how the presence or absence of foraging whales changes over 17 years. I will compare the frequency of foraging whales through time to benthic topographical complexity, and, by equating foraging persistence to mysid abundance, I will determine which sites contain mysids inter-annually. I will use the results from both sections to hypothesize which variables allow Clayoquot Sound to persist as a foraging site for PCFG whales.

2. Methods

2.1. Study Area

The study area is located in the southwest coastal waters of Flores Island, Clayoquot Sound, British Columbia (49°14'36"N, 126°6'10"W and 49°18'51"N, 126°14'30"W) and is approximately 25 km² (Figure 2.1). The study area contains a

variety of coastline and substrate types including sandy and rocky shorelines, small islands, and shallow reefs (Dunham & Duffus 2001), but is bordered by coastline and unproductive foraging areas (Pasztor 2008). Whale surveys are conducted along the 10 metre isobath to encounter the largest concentration of foraging whales and because mysid habitat in the study area is generally located near shore (less than one kilometre) above rocky substrate (Dunham & Duffus 2001, Laskin 2007, Feyrer & Duffus 2011).

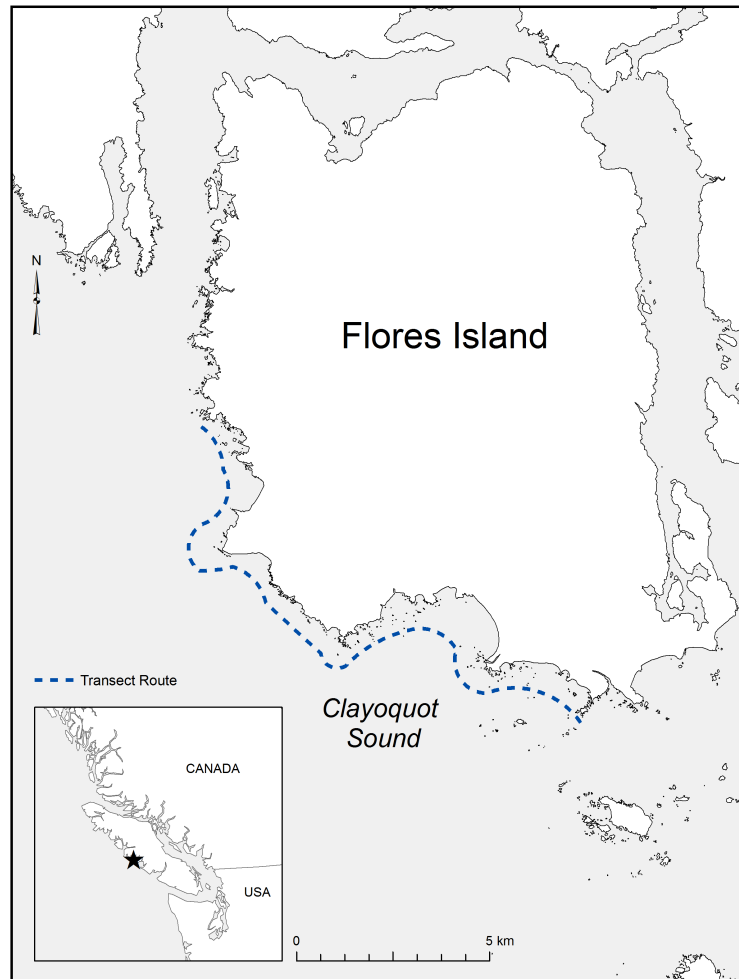


Figure 2.1. The study area is located in the coastal waters of Flores Island, Clayoquot Sound, British Columbia. The dotted line represents the location of the route driven during whale surveys.

2.2. Whale Data Collection

Whale foraging effort was recorded annually from 1997-2013 with biweekly (twice a week) boat-based surveys from May 24 to September 8, which corresponds with the gray whale summer foraging season. The boat followed a survey line situated over the 10 metre isobath, and travelled at 13 km/hr, faster than the average speed of a gray whale of which is typically between 7-9 km/hr (Urban-Ramirez *et al.* 2012) to minimize resightings. Unique pigmentation of individual whales was also used to prevent re-counting the same whale more than once per survey.

During each survey, a minimum of four observers searched 360 degrees for whale exhalations. Once a whale was sighted, it was approached and the observers determined if the whale was travelling or foraging based on area-restricted diving behaviour (Feyrer & Duffus 2014). The location and date of sighting of all foraging whales were recorded. Surveys were terminated if the Beaufort sea-state was greater than three, or if visibility was obstructed by fog. The data from these surveys are used to determine the mean number of whales per survey per year and provides a consistent measure of annual foraging effort based on the number of whales that the study area supports at one time.

2.3. Mysid Habitat Data

Benthic topographical complexity and depth data are from Laskin (2007) and are derived from bathymetric data. The bathymetric data were interpolated from multibeam sidescan sonar data to create a continuous raster surface (Laskin 2007). Benthic topographical complexity was extracted by calculating the number of changes in slope in the bathymetry using methods adapted from Ardron (2002), and has a resolution of 30 metres (Laskin 2007). The study area in Laskin (2007) was slightly smaller than the study area in used in this chapter, and thus the benthic topographical complexity and depth data do not span the most northerly and easterly extents of the study area (Figure 2.2 & 2.3).

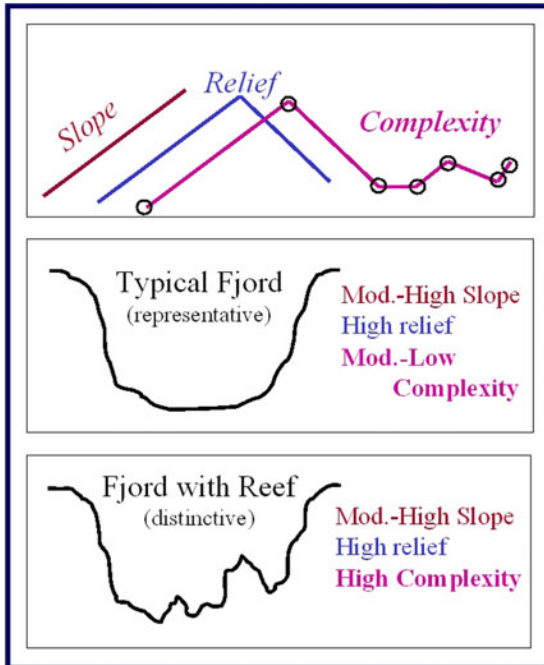


Figure 2.2. A graphic representation of the differences between slope, relief, and complexity. Slope measures steepness, relief refers to roughness, and complexity considers changes in slope (Ardron 2002).

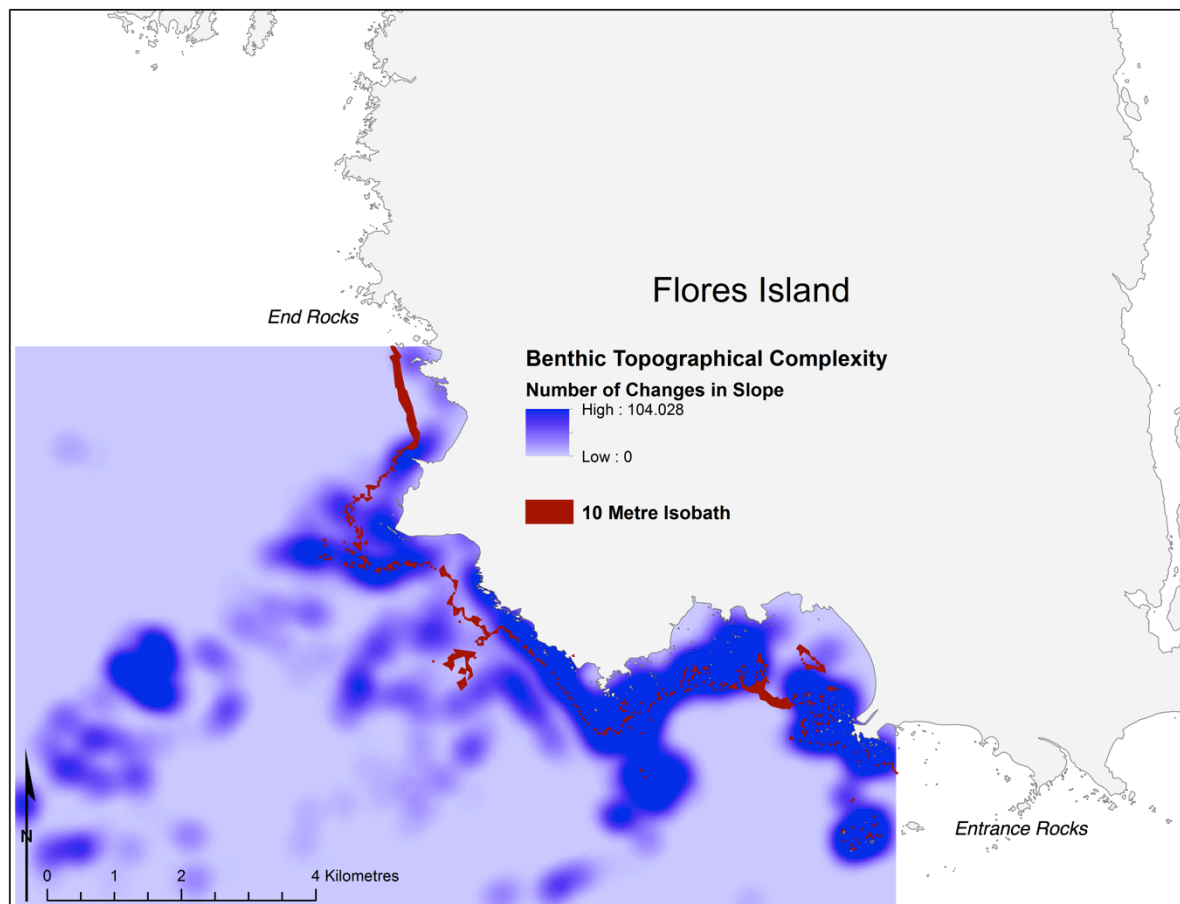


Figure 2.3. Benthic topographical complexity indicates areas with heterogeneous bathymetry and is represented by the blue surface. The values represent the number of changes in the slope of the seafloor. Areas that are approximately 10 metres in depth (>9 m to <11m) are found close to shore and are represented by red polygons.

3. Intra-Annual Habitat Use

3.1. Data Analysis

I will determine how differences in the distribution of foraging whales within each season reflect changes in the abundance and distribution of mysids, as given by annual mean number of whales per survey. To conduct this analysis, the study area is split into 4 sub-areas with the three major headlands (Red Rocks, Siwash Point, Rafael Point) acting as break points (Figure 2.4). The four sub-areas differ based on direction of exposure, bathymetry, and current flow direction and velocity (Kopach 2004, Patterson 2004). Sub-area 1 extends from Entrance Rocks to Red Rocks, and contains a shallow,

rocky, south-facing bay in between the two headlands. Sub-area 2 covers Cow Bay, which is the largest and most protected bay within the study area (Kopach 2004), and spans from Red Rocks to Siwash Point. Although Cow Bay contains a mixture of bathymetry types, the current direction constantly moves from east to west, with a convergence zone in the middle of the bay at the 10 metre isobath (Kopach 2004). Sub-area 3, between Siwash Point and Rafael Point, consists of exposed coastline, locally known as the Grassy Knoll, and a small embayment called Rafael Bay, both with a south westerly exposure. With separate water masses coming from Siwash Point and Rafael Bay, there is a convergence zone in the middle of the Grassy Knoll (Kopach 2004). Rafael Bay is more exposed than Cow Bay because of its south westerly exposure and it has higher current velocities due to water being funnelled into the bay from Rafael Point. Sub-area 4 has a western exposure and consists of a mixture of small bays and exposed coastline. It is the sub-area with the strongest flow velocities and highest amount of turbulence (Kopach 2004). Mean benthic topographical complexity values, measured by the number of changes in slope, are calculated for each sub-area using the Spatial Analyst toolset in ArcMap 10.0 (ESRI 2014).

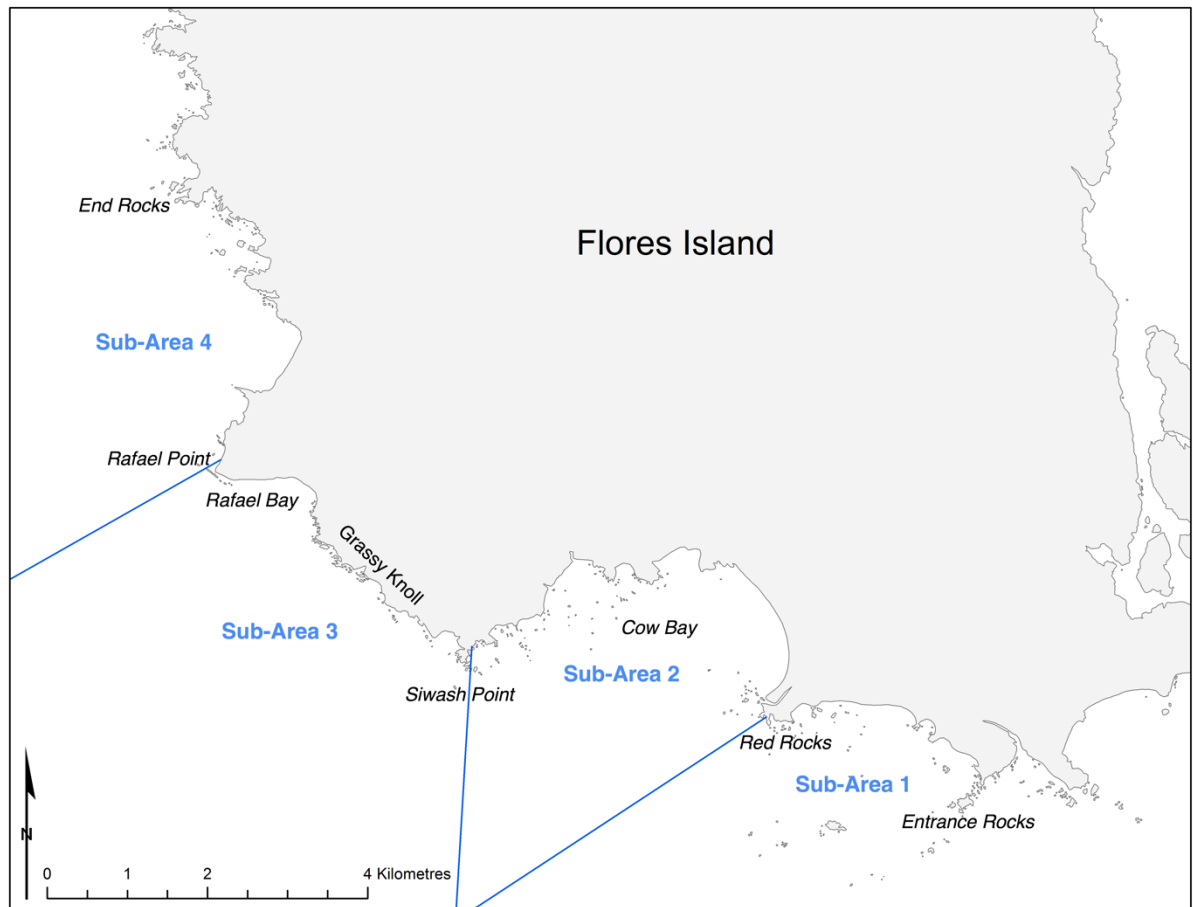


Figure 2.4. The study area is divided into 4 sub-areas with the headlands acting as break points. The rock features, locally known as Entrance Rocks and End Rocks, denote the southern and northern extents of the study area.

For each year, the location data from the whale surveys are aggregated into nine equal time periods starting May 24 and ending on September 8 (Table 2.1). Although whale surveys were collected regularly throughout the season, the number of surveys per time period may differ slightly depending on disruptions caused by bad weather. For each time period in each year, the number of foraging whales in each sub-area is calculated. These values are used to calculate the mean number of foraging whales per sub-area for each time period, and are used to determine the average distribution of whales in a season.

Table 2.1. The date ranges of each time period within an annual field season.

Period 1	May 24 - June 4
Period 2	June 5 - June 16
Period 3	June 17 - June 28
Period 4	June 29 - July 10
Period 5	July 11 - July 22
Period 6	July 23 - August 3
Period 7	August 4 - August 15
Period 8	August 16 - August 27
Period 9	August 28 - September 8

From 1997-2013, the number of whales in Clayoquot Sound fluctuates, with each year of higher than average foraging effort is generally followed by at least one year of lower than average forage effort and vice versa (Burnham 2012). To test if habitat use differs depending on whether mysid numbers are low after sustained predation or are in a period of recovery after predator release, each year is categorized as either being a ‘high mysid year’ or a ‘low mysid year’. Because mysid abundance data within the study area are only available for 2006-2008, the mean number of whales per survey is used instead to provide a consistent proxy for prey data throughout the duration of the study. To determine the threshold between high and low years, the mean number of whales per survey is calculated for each year and used to calculate the grand mean for all years (7.17 whales per survey) with a significant difference between the two classes ($\chi^2 = 170.468$, $p < 0.001$) (Table 2.2). For both high and low mysid years, the mean number of whales per sub-area per time period is calculated. A pair-wise comparison is made between the mean number of whales in each time period for the same sub-area during low and high mysid years using Spearman’s Rho to determine if the timing of foraging changes within the same sub-area when mysid abundance changes.

Table 2.2. The mean number of whales per survey is calculated and used as a threshold to distinguish high prey years from low years. Years where the mean number of whales per survey is greater than 7.17 whales, mysid abundance is considered to be relatively high and vice versa.

Year	Number of Surveys	Mean Number of Whales per Survey	Abundance (relative to grand mean)
1997	55	6.47	Low
1998	58	9.81	High
1999	30	3.50	Low
2000	31	3.59	Low
2001	43	2.37	Low
2002	43	10.56	High
2003	30	5.10	Low
2004	21	11.12	High
2005	26	2.23	Low
2006	31	7.21	High
2007	47	0.91	Low
2008	41	3.53	Low
2009	24	4.92	Low
2010	31	16.19	High
2011	36	11.36	High
2012	33	5.09	Low
2013	24	18.04	High

3.2. Results

On average for all years, sub-area 3 sustains the most foraging whales within the study area (9.26 whale mean), and sub-area 1, supports the smallest number of whales (4.05 whale mean). Although sub-area 2 sustains fewer whales than sub-area 3 (8.49 whale mean vs. 9.26 whale mean), it is used more consistently, as demonstrated by its relatively high minimum number of whales (4.62 whales). In contrast, the minimum number of whales in sub-area 3 is 1.38 whales. Sub-area 2 has the highest mean benthic topographical complexity (24.32 changes in slope), and sub-area 4 has the lowest value (6.43 changes in slope) (Table 2.3).

Table 2.3. The range and the mean number of whales per sub-area per season.

Sub-Area	Range	Mean Number of Whales	Mean Benthic Topographical Complexity (Mean Number of Changes in Slope)
1	1.31 - 7.81 whales	4.05	11.15
2	4.62 - 13.24 whales	8.49	24.32
3	1.29 - 18.44 whales	9.25	12.17
4	1.21 - 14.33 whales	6.78	6.43

On average, whales do not move randomly throughout the study area over a foraging season. Instead, they move from the southern end of the study area, to the northern end, and then return to the southern end. The majority of whales forage in sub-area 2 during periods 1-3, with sub-areas 1 and 3 becoming secondary foraging locales during period 3. In periods 4 and 5, sub-areas 2 and 3 contain the highest number of foraging whales, with sub-areas 1 and 4 used as secondary locations. In periods 6 and 7, sub-area 3 contains the highest number of whales, with sub-area 4 as the secondary location. In period 8, sub-areas 3 and 4 are the dominant foraging locations, with sub-area 2 as the secondary location. In period 9, sub-area 2 is once again the dominant foraging location with sub-areas 3 and 4 as the secondary locations. The data are presented in one graphic, instead of being plotted on multiple maps, so that all nine time periods can be compared concurrently (Figure 2.5).

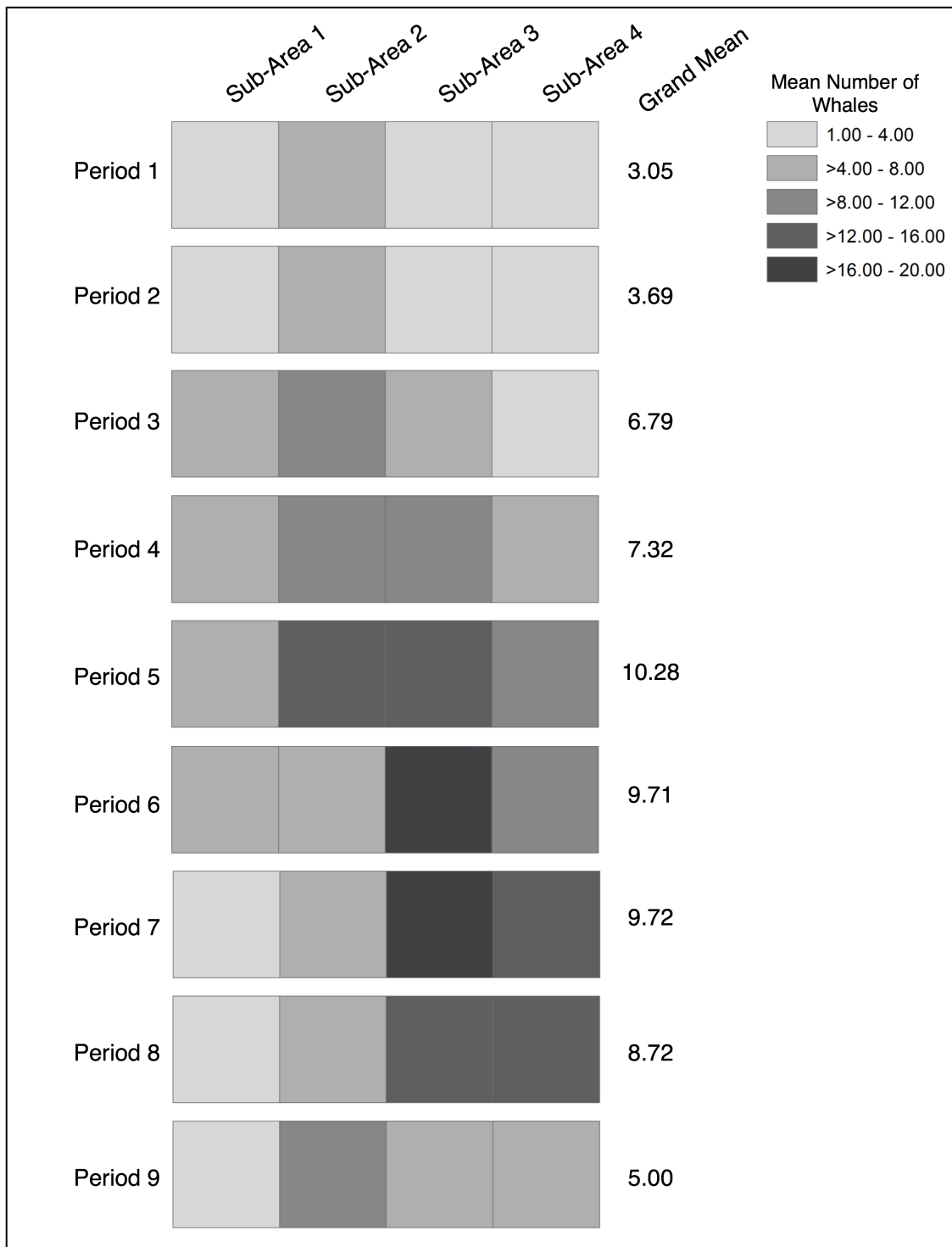


Figure 2.5. The distribution of foraging whales within the study area per time period. The values represent the mean number of whales per sub-area per time period.

Temporal patterning is evident when the arrival and departure of whales within each sub-area is examined. Sub-areas 1 and 2 have their foraging peaks at the beginning of the season during periods 3 and 5, experience a decline during periods 6-8, and receive a relative increase in whales during period 9. Sub-areas 3 and 4 peak towards the end of the season during periods 6-8, and undergo a steep decline during period 9 (Figure 2.6).

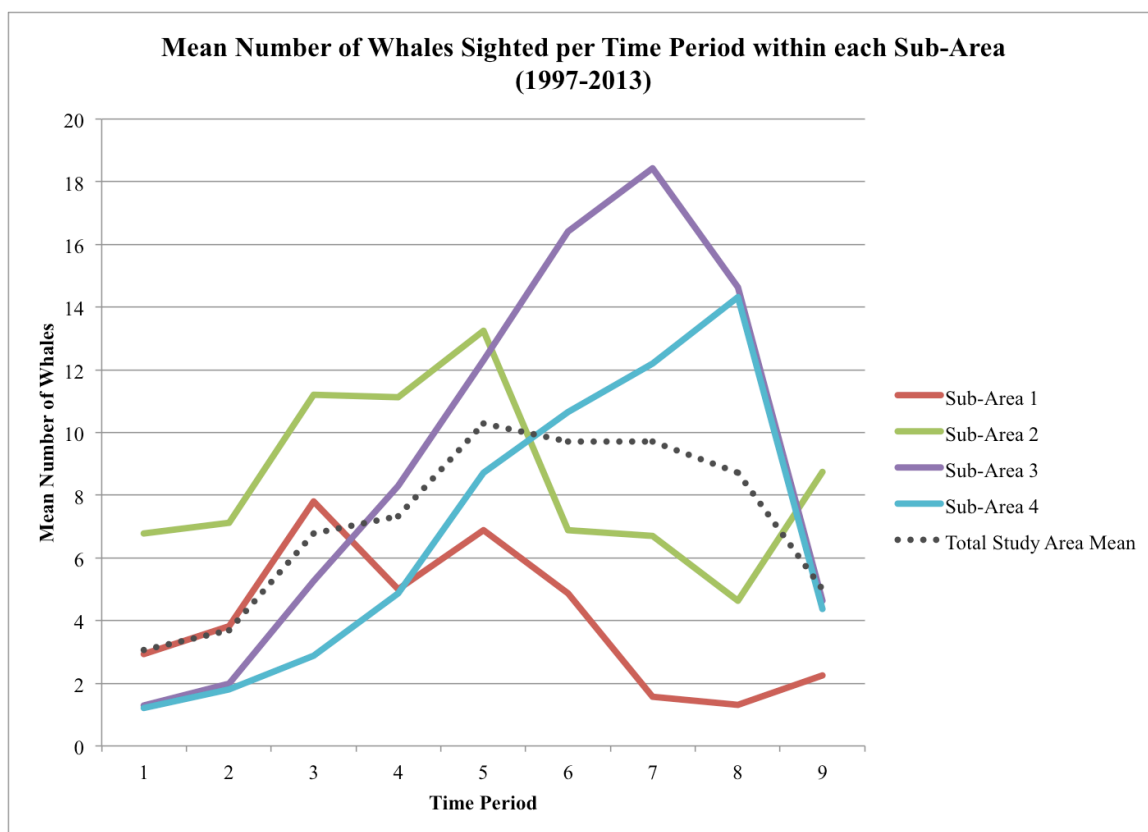


Figure 2.6. The mean number of whales per time period by sub-area (1997-2013).

Habitat use differs depending on the annual abundance of mysids. During low mysid years, on average, sub-area 2 sustains the most whales (6.11 whale mean), with the two largest peaks occurring during period 9 and period 5. Sub-area 3 supports 3.60 whales on average, and peaks during period 6. Sub-area 4 contains a similar mean number of whales (3.58 whales), but has two peaks occurring during periods 6 and 8. Sub-area 1 supports the fewest number of whales, with a mean of 2.19 whales, and its peak occurring during period 5 (Table 2.4 & Figure 2.7).

During high mysid years, sub-area 3 sustains the most foraging whales with a mean of 16.73 whales per year, peaking during period 7. Sub-area 2 supports the second largest quantity of foraging whales with a mean of 11.70 whales, peaking during period 3. Sub-area 4 sustains a mean of 11.24 whales, and peaks during period 7. Sub-area 1 has the lowest mean number of whales (6.46 whales), and peaks during period 3 (Table 2.4 & Figure 2.8).

Table 2.4. The range and the mean number of whales per sub-area during low and high mysid years.

Sub-Area	Range (High Mysid Years)	Range (Low Mysid Years)	Mean Number of Whales (High Mysid Years)	Mean Number of Whales (Low Mysid Years)
1	0.67 - 16.43 whales	0.88 - 4.50 whales	6.46	2.19
2	2.71 - 20.71 whales	2.75 - 10.60 whales	11.70	6.11
3	2.17 - 33.00 whales	0.63 - 7.11 whales	16.73	3.60
4	1.50 - 25.50 whales	1.00 - 8.86 whales	11.24	3.58

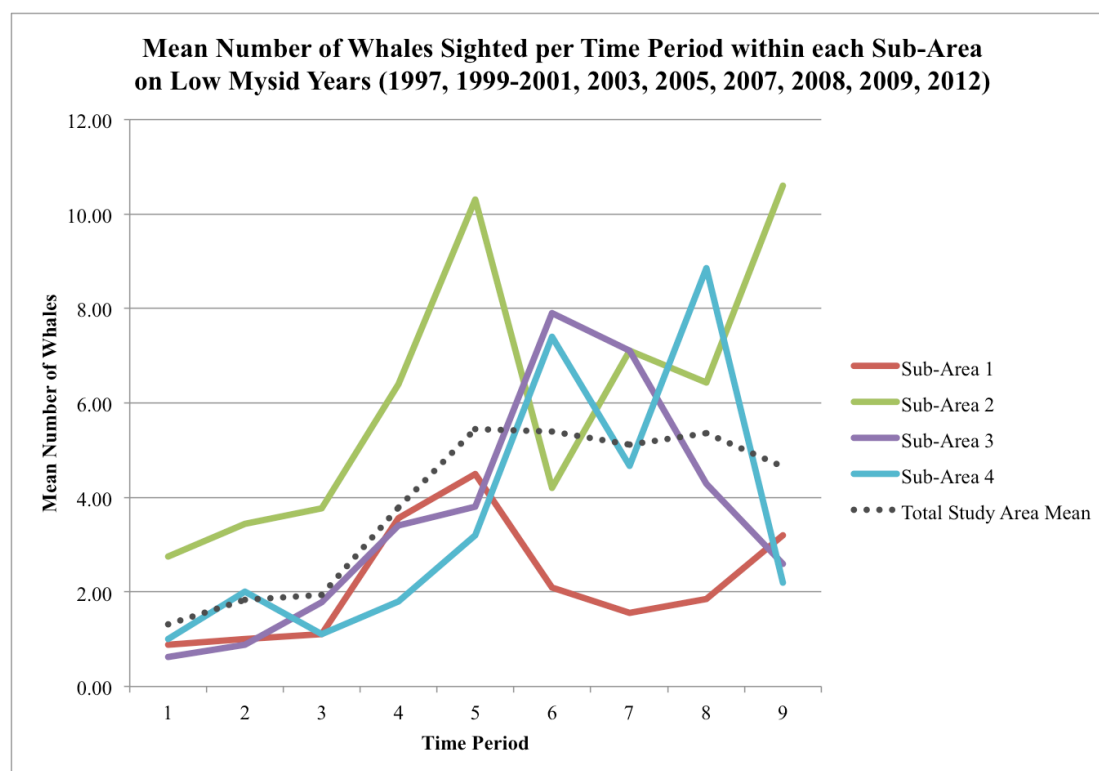


Figure 2.7. The mean number of whales per time period during low mysid years, aggregated by sub-area.

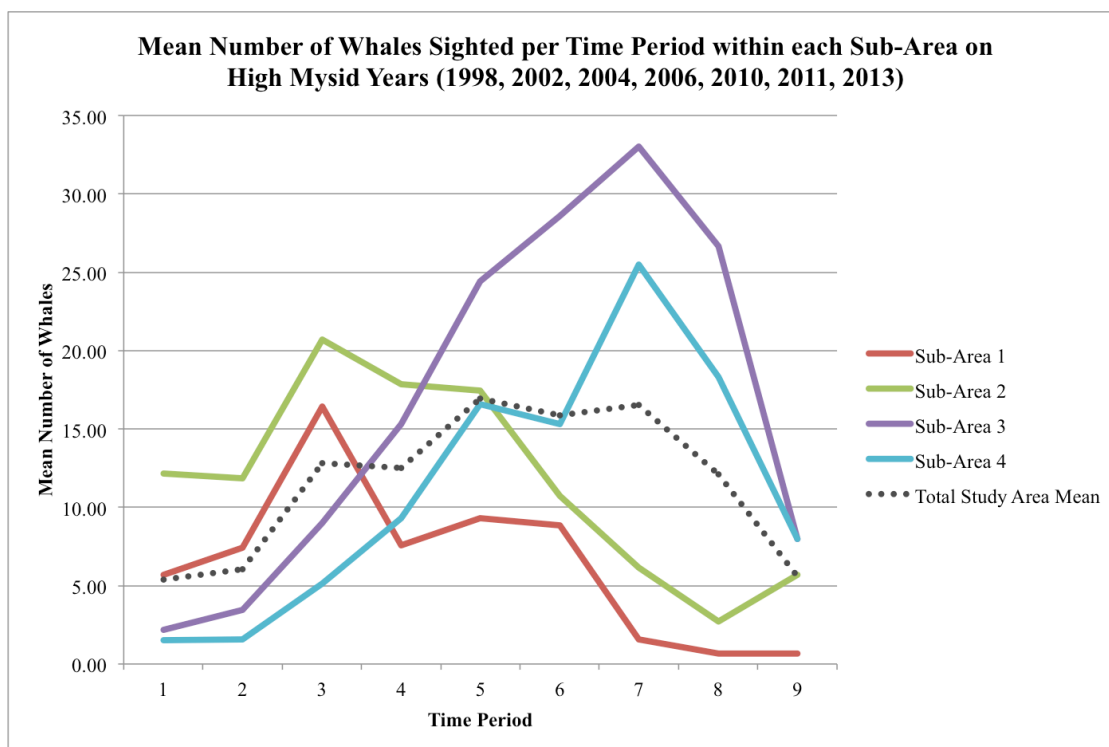


Figure 2.8. The mean number of whales per time period, during high mysid years, aggregated by sub-area.

When a pair-wise comparison is made between the mean number of whales in each time period for the same sub-area during low and high mysid years some differences are evident. The difference in mysid abundance affects the timing of foraging in sub-areas 1 and 2, but not in sub-areas 3 and 4 (Table 2.5).

Table 2.5. A comparison between the mean number of whales in each time period for the same sub-area during low and high mysid years. Timing of foraging differs between high and low mysid years in sub-areas 1 and 2.

	Sub-Area 1	Sub-Area 2	Sub-Area 3	Sub-Area 4
Spearman's Rho	$r_s = 0.134$ $p = 0.731$	$r_s = -0.417$ $p = 0.265$	$r_s = 0.967$ $p < 0.001$	$r_s = 0.833$ $p = 0.005$

3.3. Discussion

Whales are not distributed evenly throughout the study area with sub-area 3 containing the highest number of foraging whales within the study area (9.25 whale mean). Sub-area 2 contained a slightly lower number of whales (8.49 whale mean) but

had a higher minimum number of whales than sub-area 3 (4.62 whale mean vs. 1.38 whale mean). Sub-areas 4 and 1 consistently rank third and fourth in the number of foraging whales (6.78 whale mean vs. 4.05 whale mean respectively). When the whale data was split into high and low mysid years, the relative dominance of the sub-areas differed. During low mysid years, sub-area 2 contains the highest number of foraging whales, but during high mysid years, sub-area 2 and 3 switch ranks.

The difference in the number of foraging whales among the sub-areas may be related to the differences in habitat quality. Sub-area 2 has higher mean benthic topographical complexity than sub-area 3, meaning that mysids are better able to avoid predation by whales in sub-area 2 and thus are not predated beyond the period of recovery (Laskin *et al.* 2010). When the high and low years in each sub-area are correlated, the timing of the arrival and departure of foraging whales changes in sub-areas 1 and 2 ($r_s = 0.134$, $p = 0.731$ and $r_s = 0.417$, $p = 0.265$ respectively) but not in sub-areas 3 and 4 ($r_s = 0.967$, $p < 0.001$ and $r_s = 0.833$, $p = 0.005$ respectively). Usage by foraging whales in sub-areas 1 and 2 during high whale years coincides with the time periods when mysid abundance is low throughout the study area: during the beginning of the season when mysids are still maturing and swarm stabilization is occurring, and during the end of the season when sustained foraging pressure has reduced mysid swarms (Burnham 2012). This may be because benthic topographical complexity is the highest in sub-area 2 and thus it contains more mysids relative to the other sub-areas during time periods when mysid abundance is low. Mean benthic topographical complexity in sub-area 1 is similar to sub-area 3, and thus other variables such as lower current velocity may account for the presence of foraging whales in sub-area 1 during low mysid years. However, even during low mysid years, sub-area 2 is not dominant throughout the entire season with sub-areas 3 and 4 containing more foraging whales during periods 6-8. This is most likely due to a combination of swarm depletion following sustained predation in sub-area 2 and a concurrent increase in mysids in sub-areas 3 and 4.

Along with offering protection from predation, areas with high benthic topographical complexity may also provide mysids with protection from hydrodynamic disturbances. In the study area, current velocity is primarily influenced by tidal fluctuations and prevailing winds (Kopach 2004). However, local bathymetry also alters

flow direction and velocity (Kopach 2004). It is energetically inefficient for mysids to swim at their maximum rate to maintain their position within strong currents (Kopach 2004), and thus flow velocities may influence the formation and distribution of mysid swarms. Although maximum swimming rates have not been measured for the mysid species in the study area, adult mysids (*Metamysidopsis elongata* spp.) off the coast of California can maintain their position in velocities up to 13 cm s^{-1} , while juvenile mysids need much calmer waters to remain in place (Clutter 1969). Sub-area 2 is the most protected bay in the study area, with mean current velocities measured at the 10 metre isobath averaging 11.2 cm s^{-1} (Kopach 2004). In sub-area 3, current velocities at the Grassy Knoll average 16.6 cm s^{-1} , and in Rafael Bay average 13.6 cm s^{-1} (Kopach 2004). In sub-area 4, current velocities were only measured at Rafael Point and average 18.7 cm s^{-1} (Kopach 2004). Given that sub-area 4 has a western exposure, the mean current velocities are most likely higher than in the other sub-areas. Current velocities were not measured in sub-area 1, but due to its southern exposure, velocities are probably low. Based on these values, it follows that mysids would expend less energy swarming in sub-area 2, in Rafael Bay (located in sub-area 3), and potentially in sub-area 1. However, differential transport of mysids by body size or age may influence the distribution of gray whales (Kopach 2004). The relatively calm waters and high benthic topographical complexity in sub-area 2 may facilitate greater juvenile mysid retention within the sub-area, thereby allowing for faster regeneration following predation. In the sub-areas with higher current velocities and lower benthic topographical complexity, juvenile mysids may be transported elsewhere, negatively impacting regeneration.

Although sub-area 2 has higher benthic topographical complexity and lower current velocity than sub-area 3, during high mysid years sub-area 3 contains more foraging whales. This may be related to differences in current origin and flow direction between sub-area 3 and sub-area 2. Currents can transport and aggregate zooplankton and nutrients (Franks 1992, Fr chet te *et al.* 1989, Guichard & Bourget 1998) influencing predator distribution (Beardsley *et al.* 1995, Chen *et al.* 1995, Kenney & Wishner 1995, Wishner *et al.* 1995). Specifically for mysids, current convergences have been related to nearshore mysid distributions in the coastal waters of California (Clutter 1967). Sub-area 3 has a convergence zone that is created by opposing water masses coming from Cow

Bay (sub-area 2) and from Rafael Bay (north part of sub-area 3) (Kopach 2004) and thus, mysid productivity in sub-area 2 may partially affect mysid abundance in sub-area 3. Essentially, sub-area 3 may have two inputs driving mysid abundance: *in situ* mysid generation and mysid advection from sub-area 2 and Rafael Bay. Following sustained predation, *in situ* mysid regeneration in sub-area 3 is probably slower than in sub-area 2 due to lower survivorship post-predation because of lower benthic topographical complexity. Therefore, sub-area 3 supports fewer foraging whales during low mysid years regardless of inputs from advection. After a period of predator release, local mysid generation in conjunction with continued advection from sub-area 2 may contribute to sub-area 3 surpassing sub-area 2 in mysid abundance, and thus sub-area 3 attracts more foraging whales during high mysid years. In contrast, sub-area 2 also contains a current convergence but it is generated by water flowing from the shore opposing an offshore current (Kopach 2004), and thus sub-area 2 primarily relies on local mysid generation. Intra-annual predator distribution primarily reflects differences in mysid productivity which is influenced by benthic topographical complexity, current velocity, and, potentially, advection.

4. Inter-Annual Habitat Use

4.1. Data Analysis

I will characterize fine spatial scale patterns of whale foraging behaviour by analyzing inter-annual temporal patterns of persistence and variability of locations of foraging whales. I will also examine how benthic topographic complexity is related to the distribution of foraging whales. This analysis builds on work by Nelson *et al.* (2009). For each year, whale locational data are smoothed into a continuous foraging surface using kernel density estimation in the Spatial Analyst toolset in ArcMap 10.0 (ESRI 2014). A grid cell size of 60 m² is selected for the foraging surface because it is the average size of a mysid swarm (Feyrer 2010). Based on the study by Nelson *et al.* (2009) a quartic kernel with a bandwidth of 230 metres is used. The 95th percentile is generated from the kernel density estimation surfaces for each year using the Isopleth tool in the Geospatial Modelling Environment (Beyer 2012), and is used as the threshold to identify the whales' foraging range (Nelson *et al.* 2009). The foraging range is then divided into

two categories: core and periphery. The core foraging area ($\sim 8 \text{ km}^2$) is determined by applying a 250 m buffer around the 10 metre bathymetric contour, and foraging locations outside of the core foraging area are considered the periphery ($\sim 22 \text{ km}^2$) (Nelson *et al.* 2009). The core foraging range approximately covers all near shore areas with high benthic topographical complexity and contains > 60 percent of whale sightings.

For each year, the cells where foraging whales are observed are assigned a value of 1, and all other cells are categorized as 0 (Nelson *et al.* 2009). The 17 years of data are then combined, and a binary Space Time String (STS) (Nelson *et al.* 2009) is created for each grid cell in both the core and peripheral foraging areas (Figure 2.9). The STS's are 17 digits in length and consist of 1s and 0s. The first digit in the STS denotes the foraging state in 1997, and the last digit signifies the foraging state in 2013. For example, a cell with a string '01100010100110101' denotes that whales foraged in 1998, 1999, 2003, 2005, 2008, 2009, 2011, and 2013.

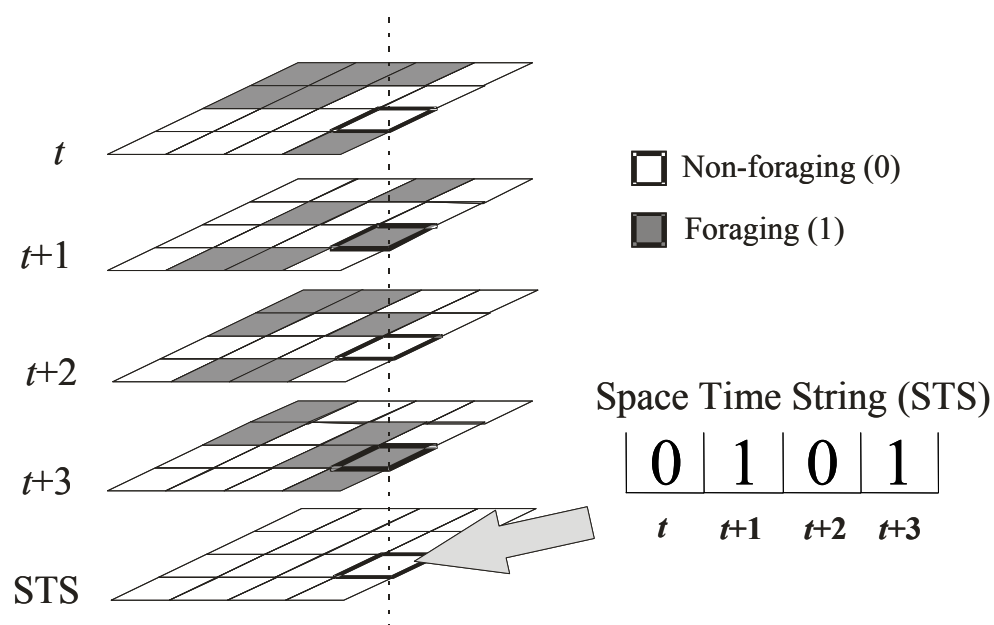


Figure 2.9. The process of generating the STSs by concatenating foraging presence (1) or absence (0) for each cell through time (Nelson *et al.* 2009).

The properties of the STSs provide a mechanism for quantifying predator/prey dynamics over many time periods (Nelson *et al.* 2009). STSs that contain a high number of foraging years (1s) denote areas where whales forage and mysids probably persist

inter-annually. STSs that change foraging state frequently represent areas where mysids are able to regenerate after a period of recovery, and STSs that contain a high number of non-foraging years (0s) denote cells where mysid recovery never occurs, or takes a relatively long time to occur (Figure 2.10). For each cell, the number of foraging years (the number of 1s per STS) and the number of inter-annual changes in foraging state (variability) is summed, and the maximum number of consecutive foraging years and non-foraging years are calculated. From these values, the mean number of foraging years, non-foraging years, maximum number of consecutive foraging years and non-foraging years, and the number of changes of foraging state are calculated for the total foraging range, the core foraging area, and the peripheral foraging area.

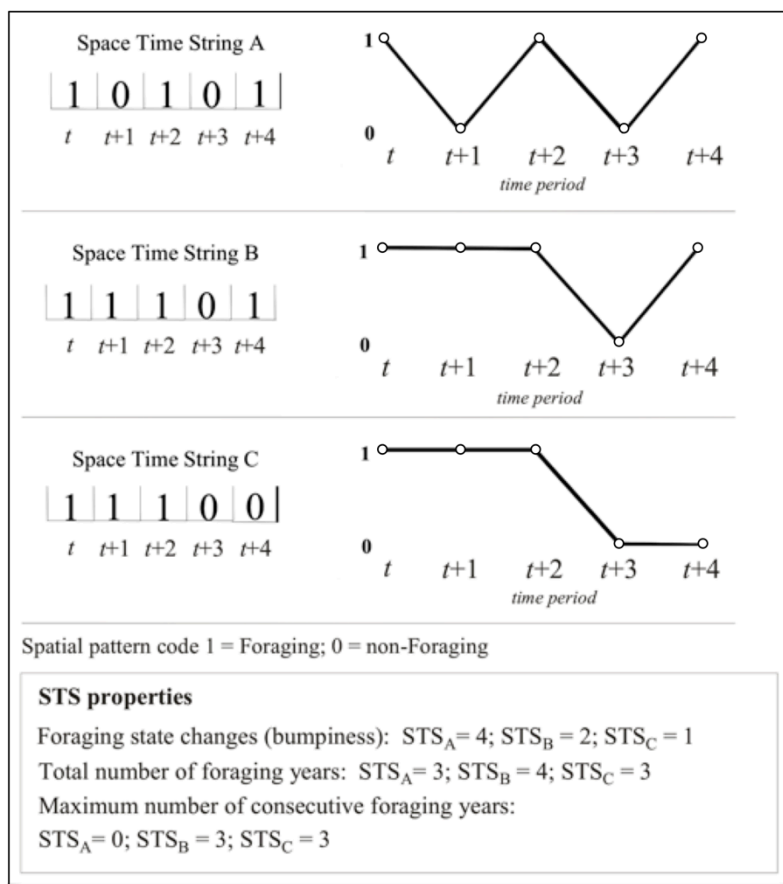


Figure 2.10. Properties of the STSs (Nelson *et al.* 2009).

To determine if the annual distribution of whales in the study area is related to annual foraging effort, the number of cells (out of a possible 8354 cells) that contain

foraging whales in each year is calculated. Years where a high number of cells contain 1s indicates that foraging was distributed throughout the study area, and/or a relatively high number whales were present within the study area. Years where a small number of cells contain 1s indicates that foraging was more clustered and/or a relatively fewer number of whales were present within the study area. Spearman's Rho is used to determine if there is a relationship between the annual number of cells that contained foraging whales and the mean annual number of whales per survey. A high Spearman's Rho value suggests that when foraging is distributed throughout the study area, a high number of whales are present and vice versa. A low Spearman's Rho value indicates that years when foraging is distributed throughout the study area, the mean annual number of whales is low, and thus the number of whales within the study area does not necessarily influence the distribution (dispersed vs. clustered) of foraging whales.

To determine if the differences in foraging effort within the core and peripheral foraging areas are related to mysid habitat quality, benthic topographical complexity is compared to the number of foraging years and the number of changes of foraging state. Mean benthic topographical complexity is calculated in the core and peripheral foraging areas. To determine if benthic topographical complexity is higher in cells where mysids persist inter-annually, cells are aggregated according to the number of foraging years (range= 1-17 foraging years), and mean benthic complexity values are calculated for each group of cells using the Spatial Analyst toolset in ArcMap 10.0 (ESRI 2014).

4.2. Results

Out of 8354 cells there are 1848 unique STSs. The most common STS (010000000000000000) occurred in 537 cells, with the majority of these cells located within the peripheral foraging range. Nine cells have foraging whales observed in all 17 years, and are located within the core foraging area. The number of foraging years and the number of changes in foraging state vary between the core and peripheral foraging areas (Figures 2.11 & 2.12). The core foraging area has the highest mean number of foraging years, maximum consecutive foraging years, and changes in foraging state (Table 2.6). However, two discrete sections of the core foraging range mostly contain

empty cells. The peripheral foraging area has the highest mean number of non-consecutive foraging years.

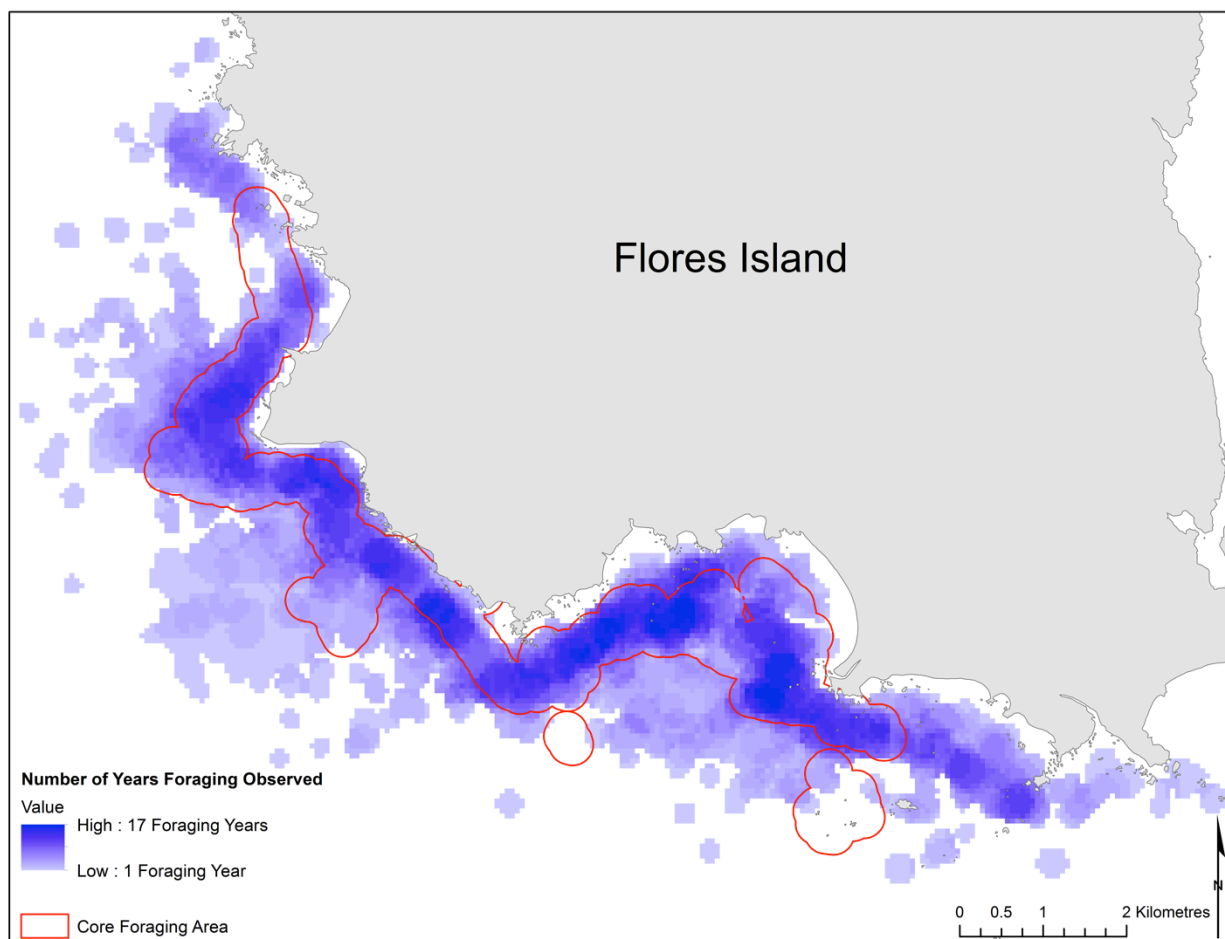


Figure 2.11. The number of foraging years as calculated from the STSs.

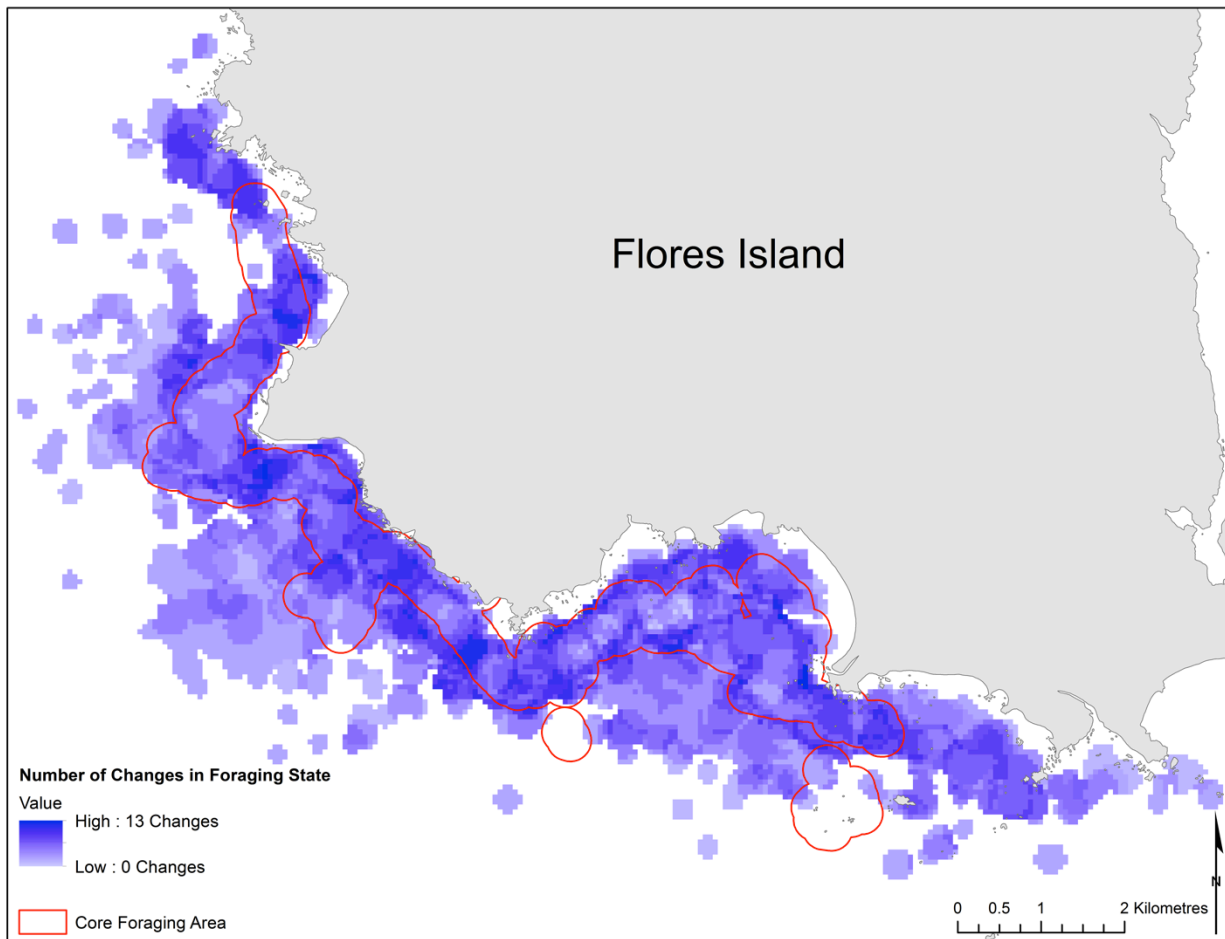


Figure 2.12. The number of changes in foraging state as calculated from the STS.

Table 2.6. The properties of the STSs for the core foraging area, the peripheral foraging area, and the total foraging range.

	Core Foraging Area	Peripheral Foraging Area	Total Foraging Range
Mean Number of Foraging Years (1s)	9	3	6
Mean Number of Non-Foraging Years (0s)	8	14	11
Mean Maximum Number of Consecutive Foraging Years	4	2	3
Mean Maximum Number of Consecutive Non-Foraging Years	5	10	8
Mean Number of Changes in Foraging State	6	4	5

The year with the highest number of cells containing foraging whales is 1998 (5183 cells out of 8354 cells), and the year with the lowest number of cells containing foraging whales is 2007 (1202 cells out of 8354 cells). The annual number of cells that contain foraging whales is correlated to annual foraging effort with a significant positive correlation between the two variables ($r_s = 0.762$ $p < 0.001$) demonstrating that when foraging is distributed throughout the study area, generally a high number of whales are present and vice versa (Figure 2.13).

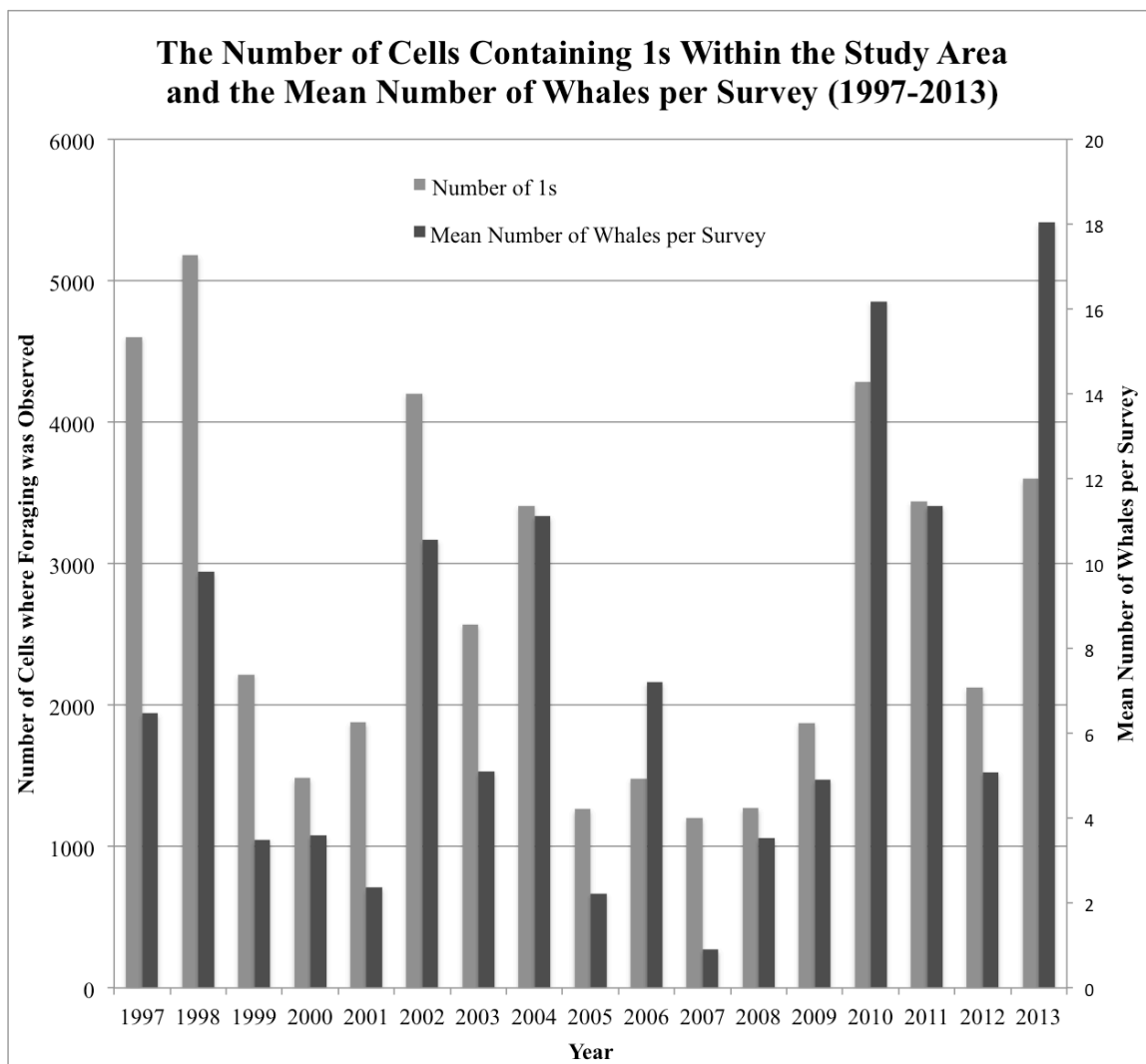


Figure 2.13. The number of cells containing 1s (out of a possible 8354 cells) and the mean number of whales per survey.

Mean benthic topographical complexity values varied between the core, peripheral, and total foraging area. The core foraging area has the highest value of benthic topographical complexity with a mean of 34.51 changes in slope per cell, whereas the peripheral foraging area had, on average, 9.97 changes in slope per cell. There is a strong significant positive correlation ($r_s = 0.998$, $p < 0.001$) between mean benthic topographical complexity and the number of foraging years in each cell (Figure 2.14).

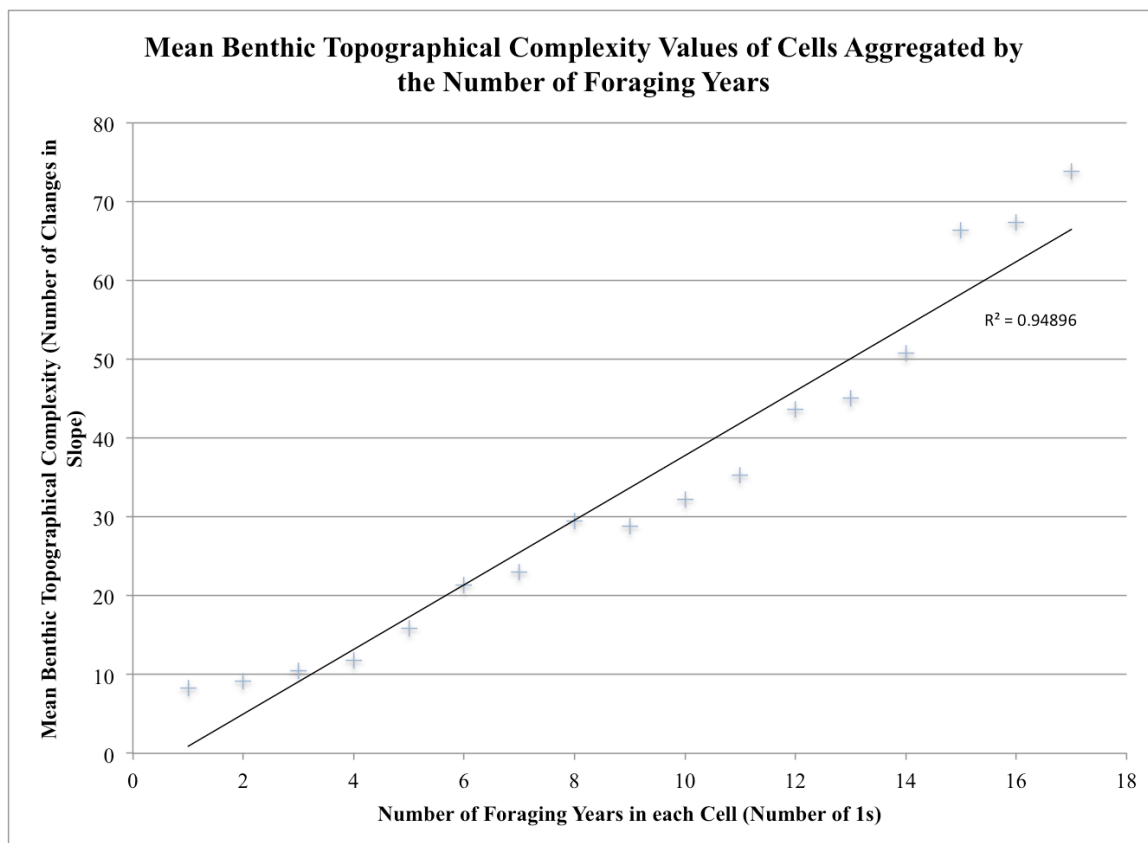


Figure 2.14. The number of foraging years in each cell is correlated to mean benthic topographical complexity.

4.3. Discussion

In general, there are three main categories of STSs: STSs with a high number of 1s, STSs with a high number of 0s, and STSs with a high number of changes in foraging state. The cells with STSs that contain a high number of 1s (≥ 9 years with foraging whales) are located within the core foraging area. In these cells, whales return regularly and thus mysids must be recovering annually or bi-annually after predation, which is demonstrated by a high number of foraging years, and a high maximum number of consecutive foraging years. The cells with STSs that contain a high number of 0s are located in the peripheral foraging area, with whales returning to forage an average of 3 out of 17 years. These cells reflect areas where mysid recovery occurs infrequently and/or where mysids are subject to advection. The cells that have STSs with a high number of changes in foraging state are mostly within the core foraging area, but are located on its perimeter. The presence of whales in these cells are most likely related to

overall annual prey density (Nelson *et al.* 2009) with foraging occurring in these cells when mysids are abundant throughout the study area. Cells that have a high number of changes in inter-annual foraging are situated on the perimeter of core foraging area, close to cells where mysids are consistently present. Their close proximity may be a result of mysids repopulating adjacent areas via population expansion after a period of recovery. This is reflected in the difference in distribution of foraging whales between years when mysid abundance is high and when mysid abundance is low. The significant positive relationship between the annual number of cells that contain '1s' and annual foraging effort, demonstrates that years when the number of foraging whales is high, mysid abundance must also be high, and foraging whales tend to spread throughout the study area (Figure 2.13). Thus a relatively high number of cells, including some cells with a high number of changes in foraging state, will have an annual value of 1. Years where annual foraging effort is low, foraging tends to be more clustered and thus in relatively fewer cells will have an annual value of 1.

The inter-annual presence or absence of whales in a cell most likely reflects habitat quality from a prey perspective. While mysid recovery and persistence varies depending on predator effort and site location, it is likely related to depth and benthic topographical complexity (Laskin 2007). The core foraging area, where 60 percent of the foraging whale sightings occur, is centred on the 10 metre isobath and has a higher mean value of benthic topographical complexity than the peripheral foraging area. The link between benthic topographical complexity and mysid persistence is further demonstrated by the strong significant positive correlation between mean benthic topographical complexity and the number of foraging years in each cell. In cells where the topography is complex, mysids are better able to avoid predation by gray whales, and thus are not predated beyond the point of recovery (Laskin *et al.* 2010). However, there are two discrete sections of the core foraging area, which have high mean benthic topographical complexity, where no foraging whales were sighted. The main physical difference between the two unused core sections and the rest of the core foraging area is their distance from shore. Although they have high benthic topographical complexity, perhaps these unused areas have higher current velocities due to their offshore location, which may hinder mysid retention. Cells located near the 10 metre isobath, that also have high

benthic topographical complexity, may provide ideal mysid habitat because they are close enough to the shore to receive nutrients from the intertidal zone (Laskin *et al.* 2010), while providing refuge for mysids from mechanical disturbances such as strong currents and tidal fluctuations.

5. Synthesis

The intra- and inter-annual habitat use analyses both examine the distribution of whales within the study area, which is a response to mysid abundance and distribution (Feyrer & Duffus 2014). The intra-annual analysis examined how changes in the abundance and distribution of mysids translate to fine scale temporal changes in the abundance and distribution of whales within the study area. The inter-annual analysis characterized fine scale spatial patterns of foraging behaviour, mediated by the presence or absence of mysids, within the study area by tracking changes in whale distributions between seasons. The main difference between the two analyses is the scale at which they were conducted. The intra-annual habitat analysis employed a coarser spatial scale (4 sub-areas approximately 7 km² each) but a finer temporal scale of 2-week periods. The inter-annual habitat analysis used a finer spatial scale (8354 cells with an area of 60 m²) but had a coarser temporal scale of 1-year periods.

When the distribution of foraging whales are analyzed within a foraging season, spatial and temporal patterns are evident, and are related to mysid productivity. From a spatial perspective, the study area is used differently depending on whether mysid abundance was relatively low or high throughout the study area. In a season following heavy predation, sub-area 2 contains the highest number of foraging whales when mysids are in a period of recovery and their abundance is relatively low throughout the study area. In a season after a period of predator release, sub-area 3 contains the highest number of foraging whales when mysid abundance is relatively high throughout the study area. Analysis of the fine scale temporal pattern yielded similar results. Sub-area 2 contains the highest number of foraging whales during the periods within a season when mysid abundance is low, such as at the beginning and end of the season. Sub-area 3 contains the highest number of foraging whales when mysid abundance peaks intra-annually. These results depict sub-area 2 as the nucleus of the study area that sustains

foraging whales even when mysid abundance is low elsewhere. Sub-area 2 has a higher mean benthic topographical complexity and lower current velocity than sub-area 3, suggesting that these variables may be an important part of mysid recovery and persistence.

The relationship between benthic topographical complexity and mysid persistence is also demonstrated with the inter-annual analysis. The cells that contain a high number of foraging years also have high mean values of benthic topographic complexity and are located in Cow Bay, which is within sub-area 2. The difference in how the study area was aggregated with the inter-annual analysis (core vs. periphery instead of sub-areas) demonstrated that, although there are differences in the number of foraging whales between sub-area 2 and sub-area 3, there is also a strong association with the 10 metre isobath. The combination of these results provides evidence that low current velocity, shallow depth, and high benthic topographical complexity are important components of mysid habitat and facilitate mysid recovery post-predation.

While gray whales preferentially target mysids in Clayoquot Sound (Kim & Oliver 1989, Duffus 1996, Dunham & Duffus 2001, 2002, Feyrer & Duffus 2011, Feyrer & Duffus 2014), whales will opportunistically forage on crab larvae (*Pachycheles* and *Petrolisthes* spp.) and ampeliscid amphipods, which may also influence some of their movements within the study area. Crab larvae are located approximately 1 km offshore of Rafael Point in sub-areas 3 and 4, and amphipod habitat is located in sub-area 2 in sandy substrate that covers approximately 10 km² of the bottom of Cow Bay (Dunham & Duffus 2001). Whales have been observed foraging on crab larvae when they are sufficiently concentrated, but these foraging events only last an average of 2 to 3 days (Dunham & Duffus 2001). Whales have been observed foraging on amphipods in late August (periods 8-9), when mysid abundance has decreased, and amphipod body size has increased (Dunham & Duffus 2001). In the intra-annual analysis, the presence of amphipods in Cow Bay may partially account for the increase of foraging whales in sub-area 2 during period 9. The episodic presence of crab larvae off Rafael Point may increase the number of whales in sub-areas 3 and 4 during August (see Dunham & Duffus 2001). In the inter-annual analysis, alternate prey types may account for the presence of whales in some of the cells in the peripheral foraging area. Although other

prey species types may influence the movements of foraging whales for short durations of time in Clayoquot Sound, mysids are a more prevalent and consistent prey source (Dunham & Duffus 2001), and therefore primarily drive the distribution of whales (Feyrer & Duffus 2014).

Since foraging whales have used the study area for at least 17 years, it appears that the combination of physical features and primary prey type within the study area allow the coastal waters of Flores Island to persist as a foraging site for PCFG whales. In comparison, Ahous Bay, which is a former foraging site within Clayoquot Sound, was used extensively between 1988-1992, but is now only occasionally visited by foraging whales (Duffus 1996, Pers. Comm, Pers. Obs. 2010-2013). Ahous Bay differs from the study area in terms of substrate and primary prey species, with gray whales foraging on ampeliscid amphipods. Amphipods are sediment-dwelling invertebrates that are associated with sandy substrate in waters 0-25 metres in depth (Dunham & Duffus 2001). Since gray whales feed on amphipods by creating large pits in the benthos (Ray & Schevill 1974, Nerini & Oliver 1983, Nerini 1984, Swartz & Jones 1987), the sandy substrate does not provide any refuge from predation. Furthermore, the life history characteristics of ampeliscid amphipods, such as long generation times and slow growth rates, translate into slow recovery times after sustained predation by gray whales (Coyle *et al.* 2007). Ampeliscid amphipod juveniles do not disperse from their natal locations, and thus they congregate in dense patches making them vulnerable to large, highly mobile predators such as gray whales (Coyle *et al.* 2007). In contrast, the resilience of mysids in the study area is related to shorter generation times (Mauchline 1980), and to their habitat providing refuge from predation due to its high complexity. Instead of declining through time, mysid populations can recover following a release from predation. The dynamic equilibrium between top-down and bottom-up forces forms interdependent oscillations in predator-prey populations as reflected through the highs and lows in annual foraging effort (Burnham 2012).

It is the ability of different sites, such as the study area, to provide consistent prey resources through time that attract and support PCFG whales. The PCFG has a low but significant difference in mitochondrial DNA (mtDNA) in comparison to the rest of the eastern north Pacific population, but it may also differ in terms of ecology. While the

PCFG's foraging grounds are primarily coastal and located further south than the rest of the eastern population, it is unclear whether the prey species type differs between the two groups as well. Described as highly flexible feeders (Calambokidis 2013), PCFG whales have been observed feeding on benthic, epi-benthic, and pelagic prey (*e.g.* Dunham & Duffus 2001) which contrast with the general pattern of benthic foraging on amphipods in arctic feeding grounds (Nerini 1984, Moore *et al.* 2007). Perhaps the PCFG's foraging range is composed of different foraging sites containing a variety of prey types that are operating in offset cycles of boom-and-bust, with one site's season of predator release as another site's season of heavy predation. For example, Calambokidis *et al.* (2009) state that the decline in sightings of the coast of southern Vancouver Island during 2007 was due to whales moving to the coastal waters of Washington and Oregon. Whales could be moving between different foraging sites, inter- and intra-annually, similar to how whales moved between the different sub-areas described in this chapter. Thus, at a large scale, the collection of these sites may provide a consistent source of prey, even though at a small scale they may differ in prey productivity between years.

6. Conclusion

Both top-down and bottom-up forces play important roles in the distribution of foraging whales on various spatial and temporal scales. Predation reduces mysid abundance, whereas habitat characteristics such as benthic topographical complexity, depth, and current flows mediate the rate of mysid recovery. The demise and recovery of mysids is demonstrated intra-annually by foraging whales utilizing different areas within the study area at different times. Inter-annually, the STSs act as a signal for mysid recovery and foraging persistence. Although 17 years of data suggest that a dynamic equilibrium is occurring in the study area between predator and prey, factors such as climate change or other anthropogenic disturbances may alter the balance within the study area or elsewhere along the migratory route. Future work should focus on identifying the sites where PCFG whales frequent, and the types of prey that are being consumed. Greater ecological understanding of the PCFG would enable more informed conservation decisions, and thus better protect the genetic diversity of the entire eastern north Pacific population.

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Chapter 3 : The Relationship Between Site Fidelity and Prey Productivity of Gray Whales (*Eschrichtius robustus*) in Clayoquot Sound, B.C.

1. Introduction

Site fidelity is defined as the return or reutilization by an individual of a previously occupied location (Switzer 1993, Giuggioli & Bartumeus 2012) and is a well documented trait in mammals (e.g. Primates, Jolly 1972; Cervidae, Houston 1974; Rodentia, Krebs *et al.* 1976; Cetacea, Baker *et al.* 1990), and in bird species (e.g. Austin 1949, 1951) (Greenwood 1980). Among different species, factors such as an individual's age (Austin 1949, Greenwood & Harvey 1982, Newton & Marquiss 1982, Baker *et al.* 1995, Harkonen & Harding 2001, Cameron *et al.* 2007), knowledge of alternate areas (Beletsky & Orians 1987, Part & Gustafsson 1989, Bensch & Hasselquist 1991), and breeding behaviour (Schmidt 2007) may influence site fidelity. Differing levels of site fidelity have been recorded in odontocetes (e.g. Simoes-Lopes & Fabian 1999, Aschettino *et al.* 2011, Mahaffy 2012, Alves *et al.* 2013) and in mysticetes (e.g. Clapham *et al.* 1993, Best 2000, Calambokidis *et al.* 2001, Valenzuela *et al.* 2009), but the factors that influence fidelity to breeding or foraging habitats vary depending on the species.

For migratory baleen whales, breeding generally occurs in warm waters at lower latitudes during the winter, whereas foraging occurs at higher latitudes during the summer (Evans & Stirling 2001, Stevick *et al.* 2002). Site fidelity can occur to both breeding and feeding grounds, but the degree of fidelity can differ between the two locations (Wedekin *et al.* 2010). For the eastern north Pacific gray whale (*Eschrichtius robustus*) site fidelity has yet to be defined, but it appears that individuals display locational preferences in breeding grounds (Jones 1990, Goerlitz *et al.* 2003) and foraging areas (Calambokidis *et al.* 2002, Calambokidis *et al.* 2010, Lang *et al.* 2011), but fidelity at the two locations may not be related (e.g. Baker *et al.* 2013). Eastern north Pacific gray whales overwinter in Baja California, Mexico, concentrating in three major calving lagoons: Laguna San Ignacio, Laguna Ojo de Liebre (Scammon's Lagoon), and Bahia Magdalena (Alter *et al.* 2009). Genetic research demonstrated that there is a small but significant difference between whales utilizing specific breeding lagoons and whales

overwintering outside of the lagoons (Goerlitz *et al.* 2003). A more recent study found that there is a small but significant departure from panmixia between whales sampled in Laguna San Ignacio and whales sampled in Bahia Magdalena (Alter *et al.* 2009). These data suggest that the eastern north Pacific gray whale exhibits some level of philopatry to their natal lagoons (Goerlitz *et al.* 2003), which is reflected by the genetic differentiation between individuals using different lagoons.

Genetic differentiation has also been recorded between different foraging areas for the eastern north Pacific gray whale (Frasier *et al.* 2011, Lang *et al.* 2011). While the majority migrate from Mexico to forage in the Chukchi and Bering Seas (Pike 1962), a smaller group of whales (~low hundreds, Calambokidis *et al.* 2010) known as the Pacific Coastal Feeding Group (PCFG; IWC 2010), forage between northern California and southern Alaska (Gilmore 1960, Pike 1962, Calambokidis *et al.* 2002, Calambokidis *et al.* 2010).

Recent research has focused on calculating the abundance of the PCFG (Calambokidis *et al.* 2010) and the level of genetic distinction between the PCFG and the rest of the eastern north Pacific population (Lang *et al.* 2011). This is partly due to the recent interest in the resumption of whaling by the Makah Tribe in Washington, which is in an area that is used by both PCFG and migrating whales (see Scordino *et al.* 2011). In general, the amount of protection afforded to a population of whales is based on its abundance (Kareiva *et al.* 2006), and level of external recruitment (*e.g.* NMFS 2005). However, calculating abundance accurately is a challenging task that is subject to error (see Laake *et al.* 2009), and the results from genetic analysis may be biased by sampling design, location, and season (see Wade *et al.* 2010).

Genetic analysis is an important technique used to quantify large-scale population dynamics of the eastern north Pacific gray whale, but it has not yet been able to discern if population structure is present on a fine scale. If smaller undefined subdivisions are present within the PCFG (Frasier *et al.* 2011), then geneticists should not collect samples randomly throughout the PCFG's foraging range as haplotype diversity may differ between subgroups, leading to erroneous results when the PCFG is compared to the main population. In addition to increasing the accuracy of genetic analysis, understanding the

fine-scale dynamics of PCFG whales is also necessary for conservation given that small populations tend to be more vulnerable to disturbance (Soulé 1987).

One way to construct a biologically meaningful genetic study is to establish if site fidelity to foraging sites exists within the PCFG's range, determine the rate of exchange between sites, and then to use those results to direct a sampling program. Measuring the level of site fidelity within the PCFG's home range can also help identify important productive foraging sites, which may not be easily recognizable without characterizing the intensity of space use (Barraquand & Benhamou 2008). Thus, if site fidelity is detected it can provide support for creating new marine protected areas and for greater efficiency in existing ones (Mason & Lowe 2010). The resumption of aboriginal whaling is one perceived threat to PCFG whales, but habitat protection may become paramount as threats such as an increase in industrial coastal development impact key habitat (see Jayko *et al.* 1990, Moore & Clarke 2002, Fisheries and Oceans Canada 2010, D'Intino *et al.* 2013).

I address the current knowledge gap in gray whale population structure by characterizing the fine scale population dynamics at one site within the PCFG's foraging range. More specifically, I assess the level of site fidelity of the whales in Clayoquot Sound through the analysis of photographic identification data. If site fidelity is present in Clayoquot Sound, I will analyze the group of whales that return to Clayoquot separately from whales that are only sighted once to determine if patterning is present in the number of years, and the specific years, that they return. Although other scenarios are possible I am testing three hypotheses:

1. Gray whales randomly forage in Clayoquot Sound and no site fidelity is observed. This hypothesis would be supported by no, or very low numbers of, returning whales per year (high annual number of single visit whales), and is indicative of no, or weak, population structuring in Clayoquot Sound.
2. Low/moderate site fidelity is present in Clayoquot Sound. This hypothesis would be supported by higher than random whale returns, low/moderate residency time, and regular exchange of individuals between Clayoquot Sound and adjacent areas. Acceptance of this hypothesis would indicate that Clayoquot Sound is one

foraging site within a larger foraging range, and part of a larger population such as the PGFG.

3. High site fidelity is present in Clayoquot Sound. This hypothesis would be supported by repeated sightings of the majority of individuals throughout the duration of the study and residency times that approximate the length of the foraging season. This hypothesis is indicative of a closed subpopulation of whales within the PCFG

If the second or third hypothesis is supported, I will examine if annual fluctuations in prey productivity affect site fidelity to Clayoquot Sound. While prey productivity has been shown to affect the number of whales that are sighted per year in Clayoquot Sound (Dunham & Duffus 2001, Feyrer 2010), its influence on the type of whales that visit per year (single season whales versus returning whales) has not been studied. Although mysid habitat is found in various locations within Clayoquot Sound (Dunham & Duffus 2001, Olsen 2006, Pastor 2008, Burnham 2012), the level of mysid density and biomass fluctuates intra- and inter-annually (Olsen 2006, Feyrer & Duffus 2014). Years when there is a high abundance of whales, mysid population and density is high, and years where the number of foraging whales is low, mysid population and density is also low (Feyrer & Duffus 2014). I will determine if annual fluctuations of mysid density influence the annual mean level of site fidelity of whales in Clayoquot Sound by investigating two hypotheses:

4. Annual fluctuations of mysid density are not related to annual whale returns in Clayoquot Sound. This hypothesis will be accepted if there is no correlation between prey density (represented by foraging effort) and mean return count, as well as prey density (represented by foraging effort) and mean residency time.
5. Annual fluctuations of mysid density are related to the mean level of site fidelity of whales that visit Clayoquot Sound per year (single season whales versus returning whales). This hypothesis would be supported by differences in the mean level of site fidelity and mean residency time that correspond with fluctuations in mysid density.

In this chapter, there are two objectives: to quantify the level of site fidelity of the whales in Clayoquot Sound, and to analyze how prey productivity is related to whale returns.

2. Methods

2.1. Study Area

The study area is located on the southwest coast of Flores Island, Clayoquot Sound, British Columbia (49°14'36"N, 126°6'10"W and 49°18'51"N, 126°14'30"W) and is approximately 25 km² (Figure 3.1). The study area contains a variety of coastline and substrate types including sandy and rocky shorelines, small islands, and shallow reefs (Dunham & Duffus 2001), but is bordered by coastline and unproductive foraging areas (Pasztor 2008, Feyrer 2010). Mysid habitat in the study area is located near shore (less than one kilometre) and on rocky substrate (Dunham & Duffus 2001, Laskin *et al.* 2010, Feyrer 2011). Research took place from May 24 to September 8, which corresponds with the gray whale summer foraging season.

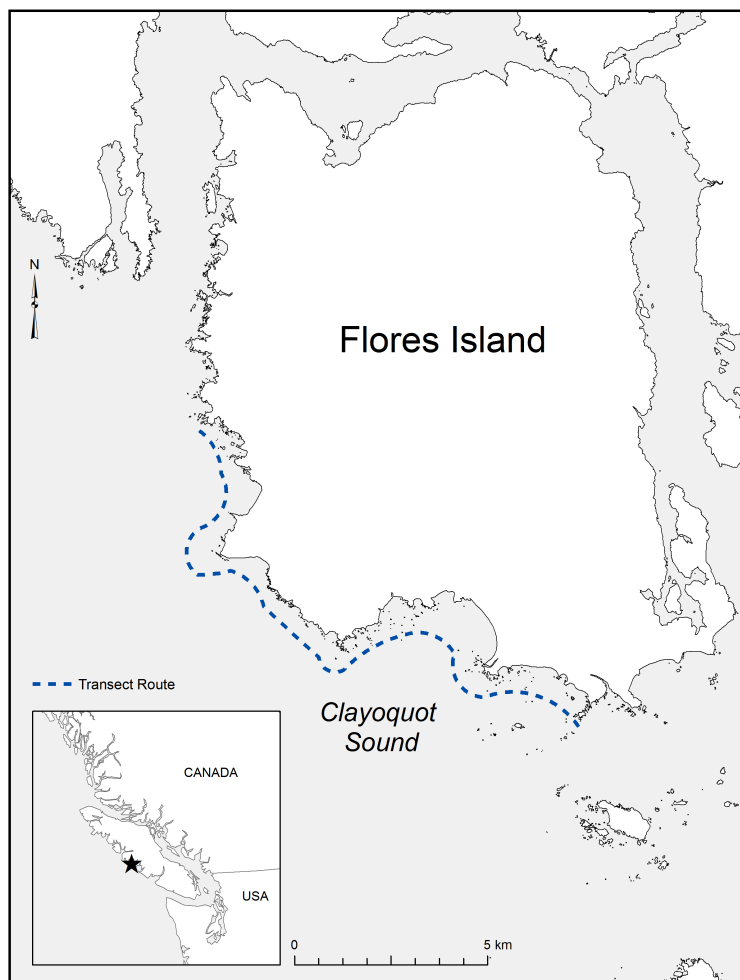


Figure 3.1. The study area is located in the coastal waters of Flores Island, Clayoquot Sound, British Columbia. The dotted line represents the location of the route used in whale surveys.

2.2. Data Collection

Whale foraging effort was recorded annually from 1997-2013 with biweekly boat based surveys from May 24 to September 8. Fair weather conditions were required for these surveys, and they were terminated if visibility was impeded by fog, or if the Beaufort sea-state was greater than three. The vessel followed a survey line that approximately follows the 10 metre isobath. To minimize double counting individuals, the boat traveled at 13 km/hr, since the average speed of a gray whale is typically between 7-9 km/hr (Urban-Ramirez *et al.* 2012). A minimum of four observers searched 360 degrees for whale ventilations. Once a whale was sighted it was approached, and the

observers determined if the whale was travelling or foraging based on area-restricted diving behaviour (Feyrer & Duffus 2014). The date of sighting and its location were recorded. Identification photographs were taken of each individual between 1998-2000 and 2008-2013 based on the methods described in Calambokidis *et al.* (2010). No identification photographs were taken in 2001, and from 2002-2007 photographs were only taken during some of the surveys (Table 3.1). During 2003 and 2005, the corresponding dates for identification photographs were not recorded aside from the year.

The photographic identification data is used to calculate the annual number of whales that visit Clayoquot Sound each year and annual residency time. The foraging whale locational data that was recorded during all surveys all years is used to provide a consistent measure of annual foraging effort based on the mean number of whales per survey per year. Prey data was not consistently measured during the duration of this study, but Feyrer and Duffus (2014) measured mysid density and whale foraging effort in Clayoquot Sound from 2006-2008 and found a significant positive correlation between the two variables. Dunham and Duffus (2001) and Olsen (2006) also describe the close relationship between mysid density and the number of foraging whales per year in Clayoquot Sound in their respective studies. Therefore, in this chapter, annual foraging effort is used as a proxy for mysid density each year.

Table 3.1. Surveys occurred biweekly from May 24-September 8. Identification photographs were taken during the surveys between 1998-2000 and 2008-2013, and sporadically between 2001-2007. Opportunistic identification photographs that were taken outside of these dates (but within 30 days) are included in this analysis (May 1-May 24, and September 9-September 15). The asterisks denote years where photographs were not taken during every survey (2001-2007).

Year	Number of Surveys	Number of Surveys where photo id occurred	Date Range	Mean Number of Whales per Survey	Annual Number of Whales
1997*	55	0	June 29-Sept 4	6.47	n/a*
1998	58	58	June 6-Aug 26	9.81	51
1999	30	30	June 3-Aug 26	3.50	37
2000	17	17	June 6-Aug 12	3.59	40
2001*	46	0	May 25-Sept 8	2.37	n/a*
2002*	43	3	May 24-Sept 5	10.56	41 *
2003*	30	n/a	May 27-Sept 7	5.10	62*
2004*	25	15	May 24-Sept 12	11.12	27*
2005*	26	n/a	May 31- Sept 7	2.23	6*
2006*	33	4	May 19-Aug 25	7.21	23*
2007*	53	8	May 26-Sept 8	0.95	7*
2008	17	17	May 24-Sept 4	3.53	29
2009	24	24	May 27-Aug 9	4.92	48
2010	33	33	May 26-Sept 9	16.19	58
2011	36	36	May 25-Sept 6	11.36	56
2012	33	33	May 25-Sept 2	5.09	47
2013	24	24	May 25-Sept 1	18.04	95

Photographic identification is used to “capture” each new whale per year, and then used to “recapture” the returning individual in subsequent years. When possible, left side, right side, and fluke photographs are taken of each individual (see Calambokidis *et al.* 2010). Optimal identification photographs capture each individual at a 90-degree angle facing the sun or in diffuse lighting. Ideally, photographs are taken when the whale is diving, rather than in the middle of a ventilation sequence, to maximize body and fluke

exposure. An image is taken when the dorsal hump is in the middle of the frame to provide a consistent reference when comparing individuals (Figure 3.2).



a) Example of an identification photograph of the right side of a gray whale.



b) Example of an identification photograph of the left side of a gray whale.

Figure 3.2. An example of right (a) and left (b) identification photographs. For the purpose of consistency between images, the photograph is taken at a 90-degree angle, when the whale is diving, and when the dorsal hump is in the middle of the frame. Distinctive pigmentation is used to identify each individual.

Each whale is identified by the pattern of markings on their left and right flanks, as well as by their distinctive knuckle profiles and dorsal humps (Lien & Katona 1990, Calambokidis *et al.* 2010). Because scars can vary between years (old ones fade, while new ones accumulate) matches are made using permanent pigmentation, which is a reliable method of identifying gray whales (Darling 1984). Photographs were matched manually by a minimum of two experienced analysts using a catalogue that was compiled with photographs taken by past researchers from 1998 to 2010, and photographs I took from 2011 to 2013. Photographs taken before 2011 were reanalyzed and matched to ensure accuracy. If a new whale could not be matched it was given a unique number and added to the master catalogue. If the photograph was poor quality, or if only a left side was photographed, then it was added to the temporary catalogue to prevent internal duplication (n= 62 temporary entries). If higher quality images, or right side

photographs, were obtained for whales in the temporary catalogue then they were moved into the master catalogue. The date of each sighting was recorded and used to estimate the length of residency within each year, excluding 2001-2007.

Opportunistic surveys were also conducted north of the study area in 2002, 2006-2010, and 2012. The same protocols used during the Clayoquot Sound surveys were followed, although timing and effort differed between years (Table 3.2). Identification photographs were taken during these surveys and stored separately from Clayoquot Sound catalogue. The length of the northern surveys varied. They all started at Sharp Point, with the shortest surveys terminating at Estevan Point, and the longest surveys ending at Catala Island (Figure 3.3). The distance of the survey line between Sharp Point and Catala Island is approximately 90 km. The data from these surveys is used to estimate the exchange of individuals between Clayoquot Sound and an adjacent foraging site.

Table 3.2. The number and the date range of northern surveys per year. For each year, the number of whales that was sighted in the northern surveys, in both areas, and the total number are listed.

Year	Number of Surveys	Date Range	Number of Whales Sighted North Only	Number of Whales Sighted in Clayoquot Sound and North	Total Number of Whales Sighted
2002	4	July 3-Sept 3	41	14	55
2006	4	May 28-June 6	11	4	15
2007	1	August 7	0	1	1
2008	1	May 25	1	0	1
2009	1	June 6	0	1	1
2010	1	June 23	3	4	7
2012	1	July 4	8	4	12

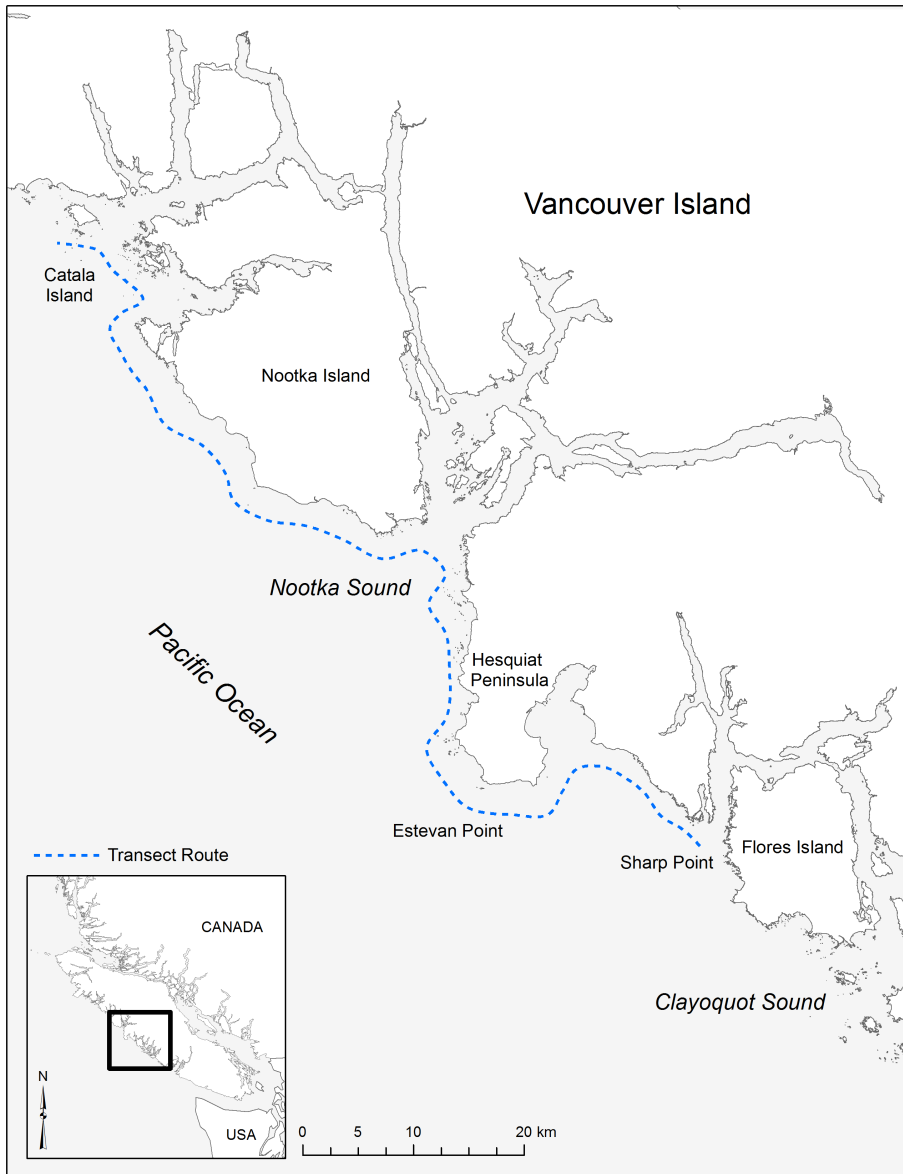


Figure 3.3. The northern surveys start at Sharp Point on Vancouver Island and, at their maximum extent, end at Catala Island.

2.3. Data Analysis

2.3.1. Assessing the Level of Site Fidelity and Duration of Residency Time

A discovery curve is used to calculate the trend of the number of whales added to the master catalogue (known as the catalogue from herein) based on photographic identification data from 1998 to 2013. Positive linear growth indicates that the whales recorded in Clayoquot Sound are part of a larger population, and a curve that decelerates through time indicates that the cumulative number of sightings in Clayoquot Sound is

representative of the total number of individuals in the population (*e.g.* Aschettino 2010, Alves *et al.* 2013, Mahaffy 2012, Fearnbach 2012)

Each whale's level of site fidelity to Clayoquot Sound is measured by calculating its return count, which is the number of years that the individual returned since 1998. Based on the site fidelity index used in Mahaffy (2012), whales that were sighted a minimum of nine out of 15 years (60 percent of years since 1998) are classed as exhibiting a high level of site fidelity to Clayoquot Sound. Individuals that were sighted in more than one year but in less than nine years are defined as having low/moderate site fidelity. Whales that are only sighted during one year are termed "single visit whales" and have no site fidelity to Clayoquot Sound. For each year, the number of whales in each site fidelity class is calculated. For example, if an individual has a return count of four years (returned four years between 1998-2013) then it is grouped in the low/moderate site fidelity class for each one of those years. This data is then used to calculate the mean annual return count of the whales sighted for each year, and the number of whales in each class of the site fidelity index in an average year.

Site fidelity describes how often a whale returns to an area, but it does not capture the duration of the visit. Measuring residency time provides greater insight on habitat use. One technique used to evaluate residency, termed permanence, describes the time span that an individual is recorded within a foraging season (Ballance 1990). Sighting dates were only consistently recorded between 1998-2000 and 2008-2013, and thus residency time is only calculated for whales sighted during this period ($n=208$). Residency time is calculated per whale per year. Each whale's return count is compared to its mean residency time to test if there is a relationship between the two variables. I expect a positive correlation between an individual's residency time and return count because I expect that whales with a higher level of site fidelity to Clayoquot Sound will stay longer each year on average than whales with little or no site fidelity to the area. The data in this correlation, as with all correlations in this chapter, are tested for normality using the Shapiro-Wilk test, and if are normally distributed they are compared using Pearson's R (r), otherwise they are compared using Spearman's Rho (r_s). Variables are only considered to be correlated if the correlation coefficient is greater than the

critical value of Pearson's R or Spearman's Rho at the 0.05 alpha level and respective degrees of freedom (df).

The data from the northern surveys is used to estimate the exchange of individuals between Clayoquot Sound and another known foraging area, in an attempt to measure the level of site fidelity of the individuals that forage in multiple sites. The mean return count is calculated for whales that were sighted in both Clayoquot Sound and during northern surveys. The number of years each whale was sighted during northern surveys is compared to the number of years that it was seen in Clayoquot Sound to determine the likelihood of a whale being photographed in both locations during the same year.

Separating single visit whales from returning whales allows closer examination of site fidelity among returning whales. Returning whales are clustered according to each individual's time series, which is based on the combination of the number of years an individual returns, as well as the specific years it returns. For each year, every whale is assigned a 1 or 0 denoting whether it was sighted or not, resulting in 117 time series. For example, the time series 0110001010010010 represents a whale that was sighted in 1999, 2000, 2004, 2006, 2009, and 2012. Prior to clustering the data, each time series was fitted to an Autoregressive (AR) model for feature extraction and dimensionality reduction. In the AR model, the method used to estimate the parameters is conditional maximum likelihood (CMLE) using ordinary least squares (OLS), with a lag of one year. The parameters are transformed to ensure stationarity using the transformation presented by Jones (1980). Next, the fitted parameters for each time series were clustered using a k-means approach. The optimal number of clusters was found using the Silhouette coefficient (see Rousseeuw 1987) where a higher score indicates more meaningful clusters. Lastly, for every whale in each cluster, residency time was calculated and then the mean residency time for each cluster was compared using an Analysis of Variance (ANOVA).

2.3.2. Testing the Relationship Between Prey Productivity, Site Fidelity and Residency Time

Annual foraging effort and the annual number of whales are compared to mean annual return count (excluding 2001, 2005 and 2007 due to insufficient data) to determine if prey productivity is related to which whales (the number of whales with low

site fidelity versus the number of whales with high site fidelity) forage in Clayoquot Sound per year. I predict that years where annual foraging effort and the annual number of whales are high the mean annual return count will be low, because the years when mysid density is high more single visit whales and non-PCFG whales will forage in the study area.

The number of single visit whales is calculated for each year where sufficient data are available (1998-2000 and 2008-2013). The number of single visit whales per year is compared to annual foraging effort to determine if annual changes in mysid density are related to the annual number of single visit whales. I expect a significant positive relationship between these variables because high prey productivity attracts a high annual number of whales, and thus more non-PCFG and opportunistic single visit whales will be attracted to the study area.

The number of single visit whales is calculated for two-week intervals during the foraging season (May 16-30, June 1-15, June 16-30, July 1-15, July 16-31, August 1-15, August 16-31, September 1-15) to capture how fine scale temporal changes in prey productivity influence the number of single visit whales. For each year, the date where the highest number of whales was recorded is calculated from the foraging surveys to measure intra-annual fluctuations in mysid density. The mean number of whales sighted per survey during each two-week interval is also calculated and compared to the number of single visit whales sighted during the same time period. I anticipate that there is a significant positive relationship between the number of single visit whales per two-week interval, and the mean number of whales recorded per survey during the same interval.

Annual foraging effort and the annual number of whales are compared to mean annual residency time to determine if prey productivity is related to length of stay. This analysis is conducted on the nine years where residency data are available (1998-2000 and 2008-2013). I expect a positive relationship between annual foraging effort and mean annual residency time. I also expect a positive relationship between the annual number of whales and mean annual residency time. I predict that higher mysid density influences whales to stay longer in Clayoquot Sound to forage.

2.3.3. Data Analysis Summary

Calculations and hypotheses are summarized for section 2.3.1 (Table 3.3) and for section 2.3.2 (Table 3.4).

Table 3.3. Summary of calculations and hypotheses for section 2.3.1.

Assessing the Level of Site Fidelity and Duration of Residency Time	
1. Discovery curve	The equation of the discovery curve is calculated. Positive linear growth indicates that the whales recorded in Clayoquot Sound are part of a larger population, and a curve that decelerates through time indicates that the cumulative number of sightings in Clayoquot Sound is representative of the total number of individuals in the population.
2. Mean return count of whales in catalogue & mean annual return count	The mean return count of all whales in the catalogue and the mean return count of the whales sighted during each year are calculated.
3. Number of whales per site fidelity index class	The mean number of whales per site fidelity index class (<i>i.e.</i> single visit, low/moderate site fidelity, and high site fidelity) is calculated.
4. Northern survey data	The mean return count of whales that are sighted in Clayoquot Sound and during the northern surveys is calculated.
5. Residency time	Residency time is calculated per whale per year and is used to calculate mean residency time.
6. Spearman's Rho: comparison between (a) mean return count and (b) mean residency time	I expect a positive relationship between (a) and (b).
7. Returning whale cluster analysis and mean residency time ANOVA	I expect a high Silhouette coefficient, which indicates strong clustering. I expect a significant difference in mean residency time between the clusters.

Table 3.4. Summary of calculations and hypotheses for section 2.3.2.

Testing the Relationship Between Prey Productivity, Site Fidelity and Residency Time	
8. Pearson's R: comparison between (a) mean annual return count and (b) annual foraging effort & (a) mean annual return count and (c) annual number of whales	I expect a negative relationship between (a) and (b) & (a) and (c).
9. Spearman's Rho: comparison between (a) the number of single visit whales per year and (b) annual foraging effort	I expect a positive relationship between (a) and (b).
10. Pearson's R: comparison between (a) number of single visit whales during each two-week interval and (b) mean number of whales per survey during each two-week interval	I expect a positive relationship between (a) and (b).
11. Spearman's Rho: comparison between (a) mean annual residency time and (b) annual foraging effort & (a) mean annual residency time and (c) annual number of whales	I expect a positive relationship between (a) and (b) & (a) and (c).

3. Results

3.1. Assessing the Level of Site Fidelity and the Duration of Residency Time

The equation of the discovery curve for the cumulative number of individuals added to the catalogue is $y = 0.93x + 63.6$ which closely approximates positive linear growth ($r^2 = 0.795$, $p < 0.001$) (Figure 3.4).

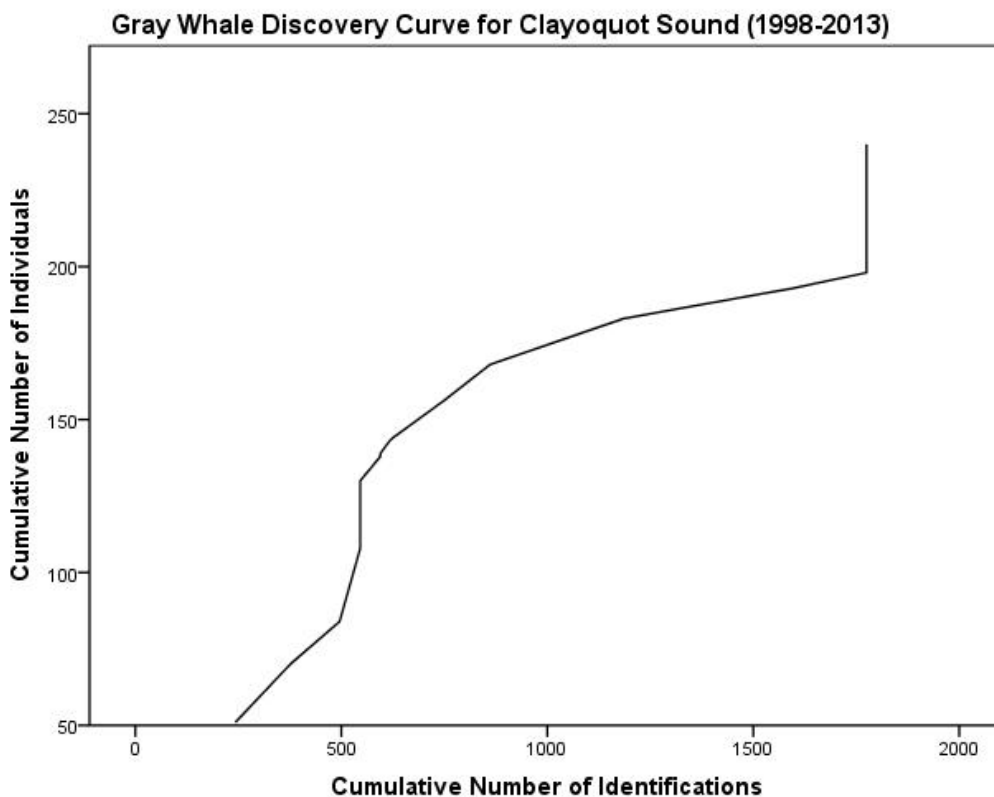


Figure 3.4. Rate of discovery of new individuals with the cumulative number of individuals recorded versus the cumulative number of identifications made (maximum of one identification per day). The growth rate is positive and linear ($r^2 = 0.795$, $p < 0.001$, $n = 16$).

There are 240 unique whales in the catalogue and 62 in the temporary catalogue. The majority of individuals (125 whales) were sighted only once since 1998 (single visit whales) and 115 whales were sighted a minimum of two years (returning whales) (Table 3.5). The maximum number of years a whale was sighted is 11 years ($n = 2$). The mean return count of the whales from the catalogue is 2.61 years. However, the utility of this value is limited because although single visit whales form over half the catalogue, they make up only a small proportion of the whales sighted in Clayoquot Sound per year (mean of 8 single visit whales), because their numbers accumulate over the years. A more accurate portrayal of the level of site fidelity to Clayoquot Sound is obtained with the mean annual return count, which is based on the return counts of the individuals sighted in each year. Mean annual return counts ranged from 3.47 to 6.23 years, with a grand mean of 5.01 years (Table 3.6). During an average year, 42 whales are sighted in Clayoquot Sound with 8 single visit whales, 27 whales with a low/moderate level of site

fidelity, and 7 whales with a high level of site fidelity (Table 3.7). Thus, on average, the group of individuals that forage in Clayoquot Sound each year have a low/moderate level of site fidelity.

Table 3.5. Summary of the return counts for whales in the master catalogue from 1998-2013. The majority of the individuals are single visitors (n= 123), whereas 115 individuals have a return count of two years or higher.

Return Count (number of years returned since 1998)	Number of Whales
1	123*
2	34
3	25
4	17
5	10
6	7
7	8
8	5
9	7
10	2
11	2

***includes six calves sighted in 2013**

Table 3.6. The number of whales aggregated using the site fidelity index. The annual number of whales ranges from 6-95 individuals, with a mean of 42 individuals. The annual mean return count ranges from 3.47-6.23 years, with a grand mean of 5.01 years.

Year	Number of Whales Sighted per Year			Total Number of Whales	Mean Return Count
	No Site Fidelity (Single visit whales)	Low/Moderate Site Fidelity (2-8 year return count)	High Site Fidelity (9-11 year return count)		
1998	11	30	10	51	4.75
1999	10	20	7	37	4.30
2000	6	26	8	40	5.08
2002	7	25	9	41	4.83
2003	8	47	7	62	4.26
2004	4	19	4	27	5.00
2005	0	6	0	6	5.50
2006	1	16	5	22	6.23
2007	0	5	2	7	6.14
2008	9	14	6	29	4.69
2009	8	31	9	48	5.50
2010	10	37	11	58	5.03
2011	4	42	10	56	5.23
2012	3	37	7	47	5.19
2013	42	44	9	95	3.47
Grand Mean				42	5.01

Table 3.7. The number of whales in the catalogue and the mean number of whales per year aggregated using the site fidelity index. Based on these results, the majority of whales that visit Clayoquot Sound during an average year have a low/moderate level of site fidelity, even though the majority of the whales in the catalogue are single visit whales.

Level of Site Fidelity	Number of Whales in the Master Catalogue	Mean Number of Whales per Year
None (Return count= 1 year)	123*	8
Low/Moderate (Return count= 2-8 years)	106	27
High (Return Count= 9-11 years)	11	7

*includes six calves sighted in 2013

The mean residency time for whales in Clayoquot Sound is 23 days per year (the foraging season spans approximately 115 days per year). Mean annual residency time ranges from 1 to 113 days per season. There is a significant positive correlation between a whale's return count and its mean residency time ($r_s = 0.419$, $p < 0.001$, $n = 166$; excludes new whales sighted in 2013).

During the northern surveys 79 individuals were sighted. Out of the 79 individuals, 54 were also sighted in Clayoquot Sound (22.5 percent of the whales in the catalogue) (Table 3.8). The mean return count (number of years sighted in Clayoquot Sound) of the 54 whales is 4.19 years. The individuals that were sighted for a minimum of two years north of Clayoquot Sound have a mean return count of 5.14 years (Table 3.9).

Table 3.8. The number of whales per return count (number of years an individual was sighted in Clayoquot Sound) that were sighted north and in the study area from 1998-2013.

Return Count	Number of Whales (Individuals Sighted in Clayoquot Sound and in Northern Surveys)
1	9
2	12
3	12
4	9
5	4
6	4
7	4
8	2
9	6
10	1
11	1

Table 3.9. Summary of the individuals that have been sighted in more than one year during northern surveys.

Whale ID Number	Number of Years Sighted North	Number of Years Sighted in Clayoquot Sound (Return Count)	Number of Sightings in Both Locations Within the Same Year
157	2	2	0
182	2	2	1
018	2	4	0
060	2	6	0
024	2	7	2
034	2	7	2
071	2	8	0
038	2	9	2
016	3	4	0
047	3	4	1
026	3	9	1

Returning whales were analyzed separately from single visit whales, and were clustered based on the combination of the number of years each individual returns, as well as the specific years they return. The k-means approach yielded 35 clusters with a Silhouette coefficient score of 0.7947 (Figure 3.5). A high Silhouette coefficient generally indicates that the algorithm has found a strong clustering structure (Rousseeuw 1987). Only the clusters that had a membership greater than two are plotted with 12 clusters that include 50 whales (Table 3.10). Mean residency time does not significantly differ between clusters ($F(11, 38) = 0.889, p = 0.558$).

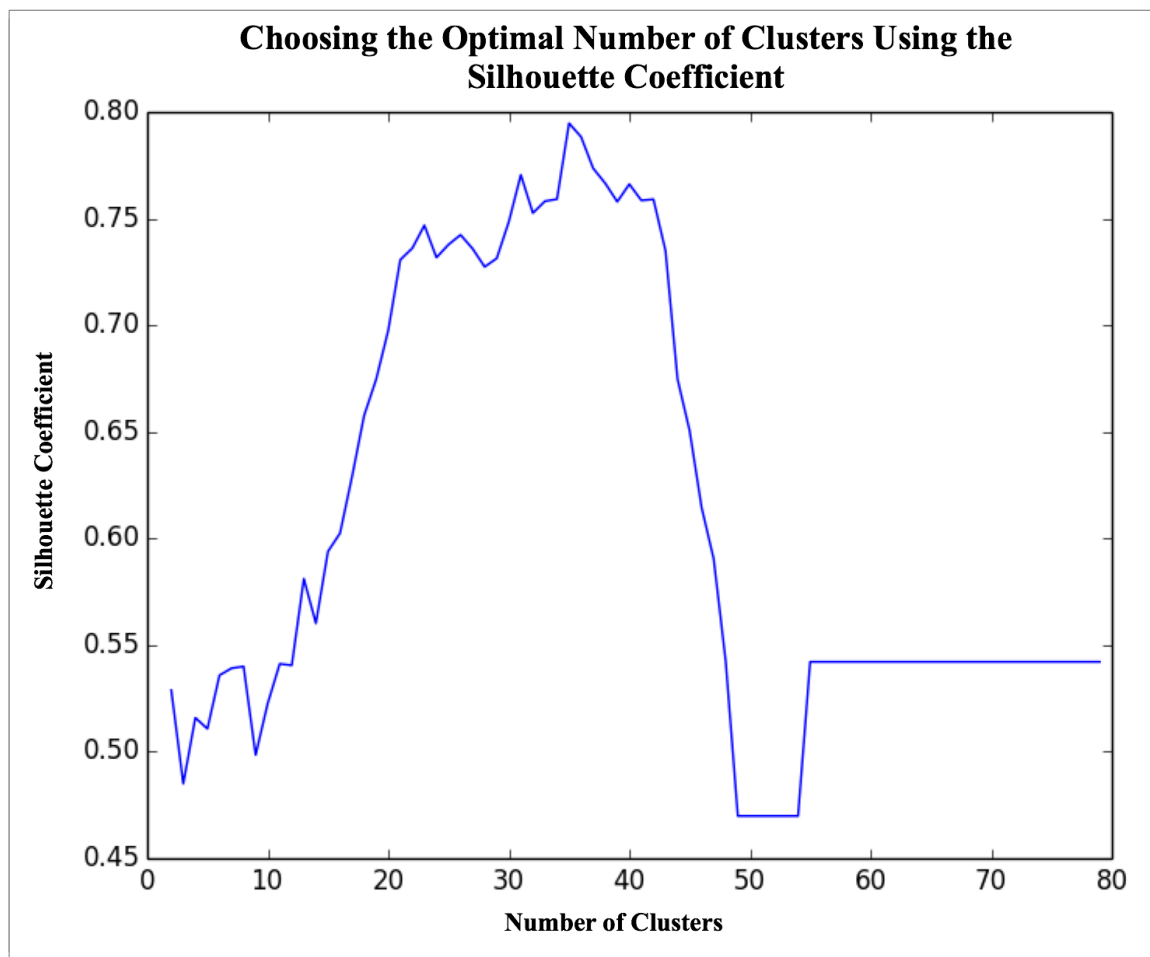


Figure 3.5. The number of clusters is calculated using an iterative approach that yielded a maximum Silhouette coefficient value of 0.7947 with 35 clusters.

Generally, there are two types of clusters: one type (Clusters 1, 3, 4, 6, 7, 8, 10, 11, and 12) contains individuals with lower levels of site fidelity and sporadic returns, and the other type (Clusters 2, 5, and 9) contains individuals with higher levels of site fidelity and consecutive returns during the same years.

Cluster 2 contains seven individuals, of which two are calves born in 2002 and 2005 (087 and 141 respectively). The return count of the whales in this cluster ranges from 6-8 years. The majority of the returns occurred from 2008 onwards, with intermittent returns between 2002-2008. Three individuals were sighted for 6 consecutive years (2008-2013), and three other individuals were sighted for 5 consecutive years (2009-2013). Annual foraging effort varied greatly between 2008-2013 (3.35-

18.04 whales per survey), indicating that mysid density probably also fluctuated considerably when the individuals from this cluster were present.

Cluster 5 contains five individuals including one calf born in 2009 (146). In this cluster, all whales returned consecutively between 2008-2013 with no sightings in the first 10 years of the study. This cluster has the largest variation in site fidelity, with return counts of these individuals ranging from 3-6 years.

Cluster 9 consists of three individuals all with a high level of site fidelity to Clayoquot Sound. These whales returned most years, regardless of mysid density.

With the other type of clusters (Clusters 1, 3, 4, 6, 7, 8, 10, 11, and 12), returns are intermittent and dispersed from 1998-2013, with no apparent relationship with high mysid density. Many of the whales in these clusters were also sighted during the northern surveys, indicating that some individuals may have used northern foraging sites during years when they were not sighted in Clayoquot Sound.

The cluster analysis demonstrates that patterning is present among groups of returning whales. For whales with a high level of site fidelity to Clayoquot Sound, annual mysid density does not appear to be the main variable influencing which years they return.

Table 3.10. The AR model plot matrix. Presence of a whale is denoted by a black or grey shaded box. The difference in the intensity of the shading (black versus grey) differentiates the clusters.

	Whale Number	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013
Cluster 1	016	■		■								■	■				
	032	■	■											■		■	
	012	■	■				■						■				
Cluster 2	159									■			■	■	■	■	■
	087					■						■	■	■	■	■	■
	105						■	■					■	■	■	■	■
	128									■		■	■	■	■	■	■
	135									■		■	■	■	■	■	■
	141					■	■	■	■					■	■	■	■
	089								■				■	■	■	■	■
Cluster 3	051					■								■		■	
	108						■			■				■			
	119									■		■			■		
	176							■					■			■	
	005	■						■							■		■
	050		■					■		■							
Cluster 4	039	■		■									■	■		■	
	060	■					■						■		■	■	■
	075			■								■	■		■	■	
Cluster 5	158														■	■	■
	140												■	■	■	■	■
	146												■	■	■	■	■
	129											■	■	■	■	■	■
	149														■	■	■

	Whale Number	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013
Cluster 6	095						■								■	■	
	113						■								■	■	
	143												■	■		■	
	157						■							■	■		
	058						■								■	■	
Cluster 7	144													■	■		■
	147													■	■		■
	052		■	■													■
Cluster 8	008	■					■										■
	017	■		■											■		
	077	■					■			■							
	007	■		■		■											
Cluster 9	019	■		■		■	■							■	■	■	■
	059	■	■			■	■						■	■	■	■	■
	003	■	■	■							■	■	■	■	■		■
Cluster 10	103					■	■	■									
	139													■	■	■	
	183											■	■	■			
	083					■	■	■									
Cluster 11	121					■				■				■			■
	132							■				■		■			■
	067			■			■								■		■
Cluster 12	053		■			■											■
	107						■								■		■
	167										■			■			■
	049		■											■			■

3.2. Testing the Relationship Between Prey Productivity, Site Fidelity and Residency Time

There is no correlation between the mean annual return count and annual foraging effort ($r = -0.317$, $p = 0.291$, $n = 13$), but there is significant negative correlation between the mean annual return count and the annual number of whales ($r = -0.667$, $p = 0.013$, $n = 13$). The negative correlation between the mean annual return count and the annual number of whales indicates that during years when mysid density is low, the whales that forage in Clayoquot Sound have a higher level of site fidelity than whales that forage during high mysid density years (Figure 3.6).

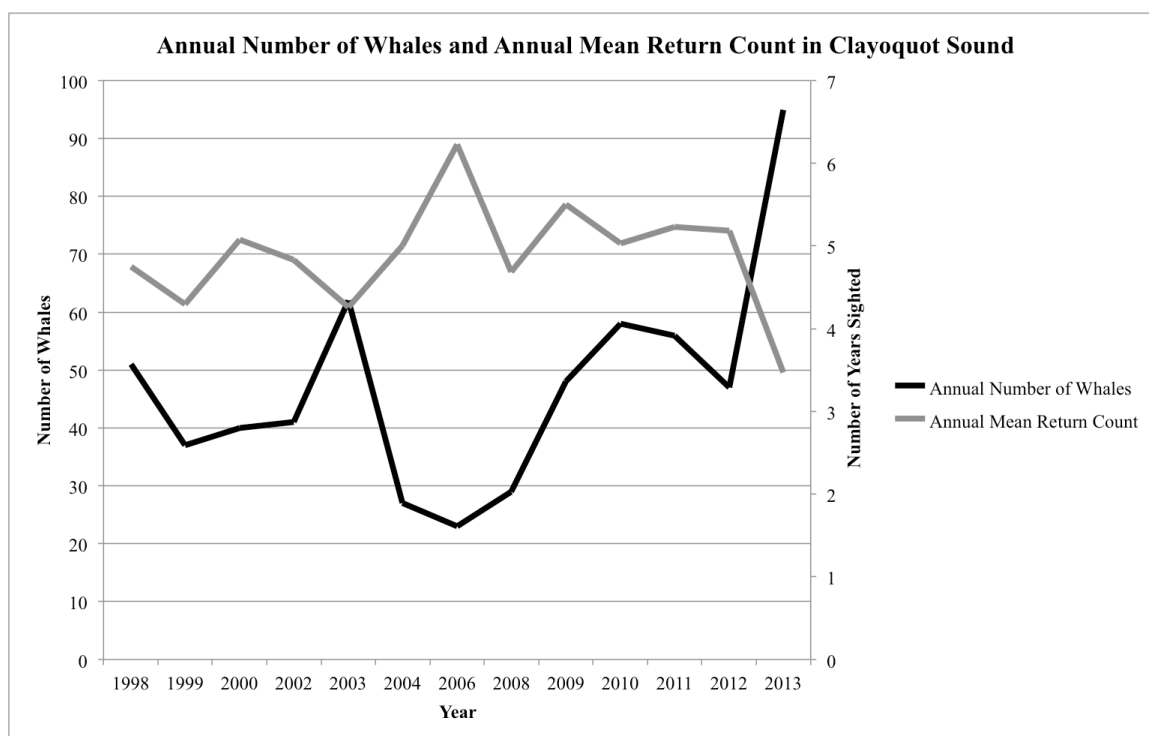


Figure 3.6. A comparison between the annual mean return count and the annual number of whales over time. Data are not available for 2001, 2005, or 2007.

The annual number of single visit whales is compared to annual foraging effort to determine if annual changes in mysid density are related to the number of single visit whales per year. There is no correlation between the annual number of single visit whales and annual foraging effort ($r_s = 0.290$, $p = 0.449$, $n = 9$). To determine if within-season changes in prey productivity is related to the number of single visit whales, the

foraging season is aggregated in to two-week intervals (May 16-30, June 1-15, June 16-30, July 1-15, July 16-31, August 1-15, August 16-31, September 1-15) and the number of single visit whales is calculated for each interval. The two-week interval that has the highest number of single visit whales is August 1-August 15, with a total of 44 single visit whales sighted in 1998-2000 and 2008-2013 (Figure 3.7). The two-week intervals at the beginning and end of the foraging season have the lowest number of single visit whales. For six out of nine years, the peak date (the date when the highest number of whales was sighted per year) occurred between August 1-August 15 (1998,1999, 2008, 2009, 2011, 2013) (Table 3.11). The relationship between the number of single visit whales per two-week interval, and the mean number of whales per survey for each two-week interval, is positive and significant ($r= 0.916$, $p= 0.001$, $n= 9$) (Figure 3.8). These results demonstrate that on an intra-annual basis the timing of the peak number of single visit whales coincides with the timing of the peak in mysid density as given by annual foraging effort (Figure 3.8). This indicates that single visit whales are opportunistic foragers that use Clayoquot Sound during periods when mysid density is high.

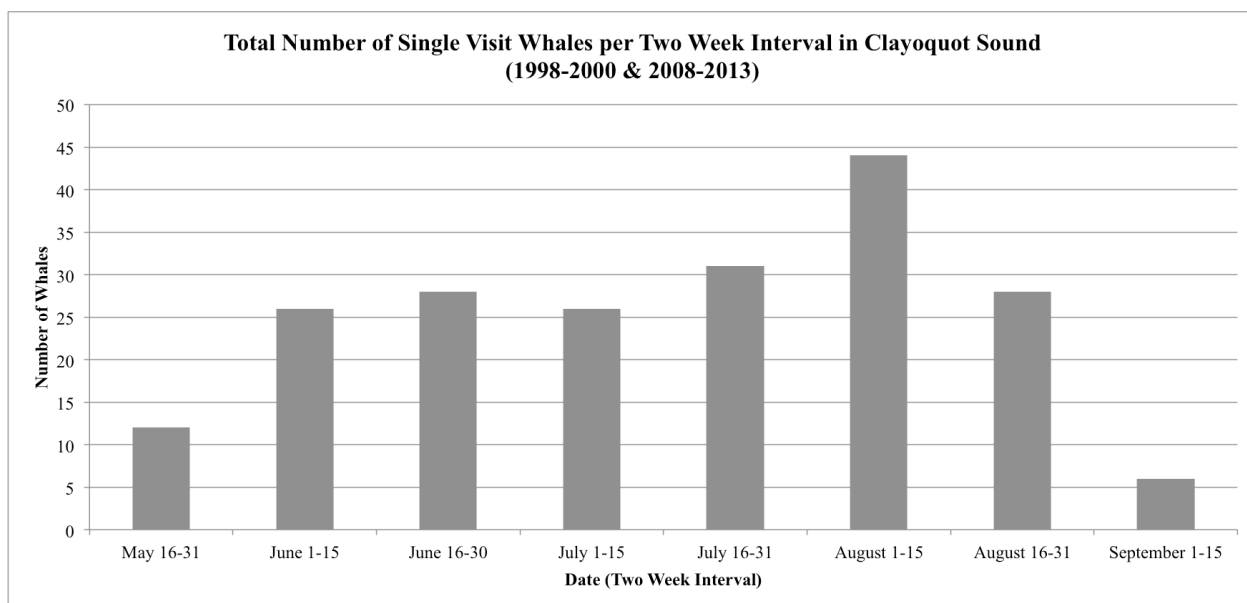


Figure 3.7. The total number of single visit whales per two-week interval for 1998-2000 and 2008-2013.

Table 3.11. The survey date when the highest number of whales was sighted. The majority of peak dates occurred between August 1-August 15 (n= 6).

Year	Peak Date	Number of Whales
1998	August 10	25
1999	July 3 & August 4	7
2000	July 18	10
2008	August 2	12
2009	August 5	13
2010	August 26	28
2011	August 7	22
2012	June 6	14
2013	August 5	38

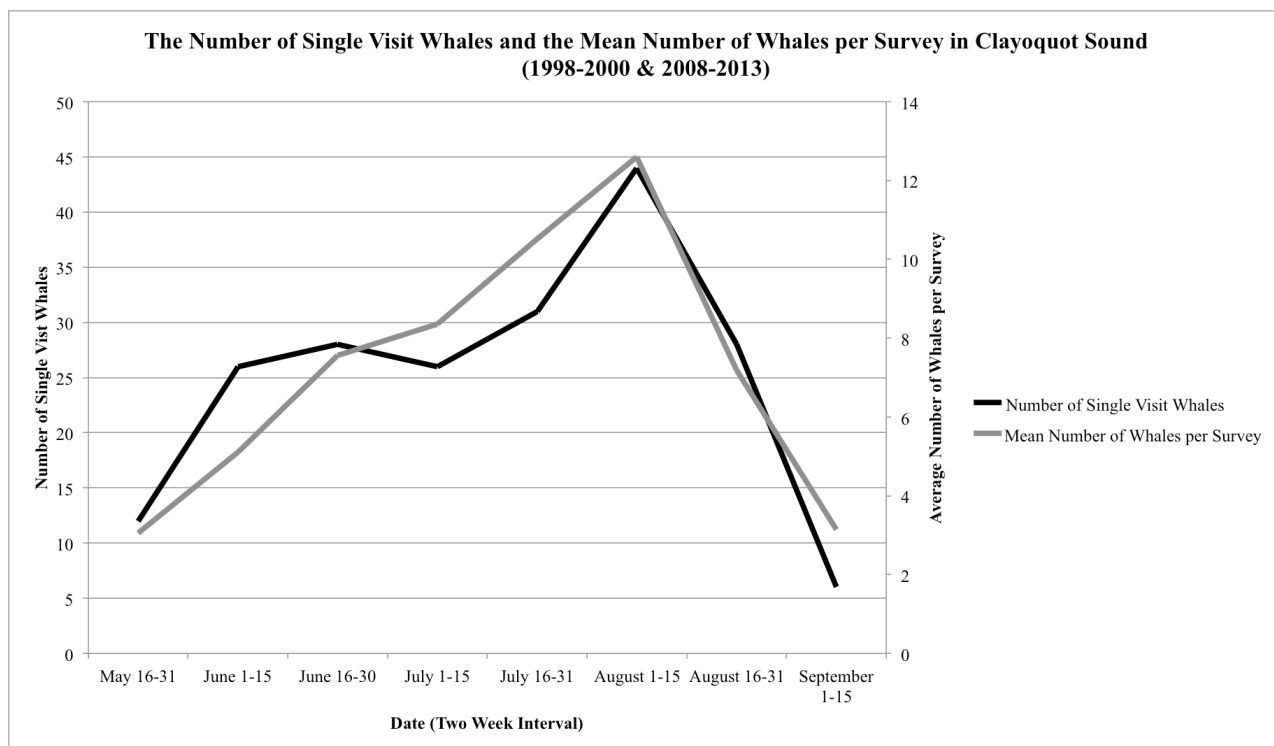


Figure 3.8. The number of single visit whales in comparison to the mean number of whales per survey for each two-week interval.

To determine if annual mysid density is related to the amount of time foraging whales spend in the study area each year, mean annual residency time is compared to annual foraging effort and the annual number of whales. There is a strong significant

positive correlation between mean annual residency time and annual foraging effort ($r_s=0.933$, $p<0.001$, $n=9$). The correlation between mean annual residency time and the annual number of whales is also positive and significant ($r_s=0.850$, $p=0.004$, $n=9$). These results suggest that mean annual residency time is related to mysid density (Figure 3.9).

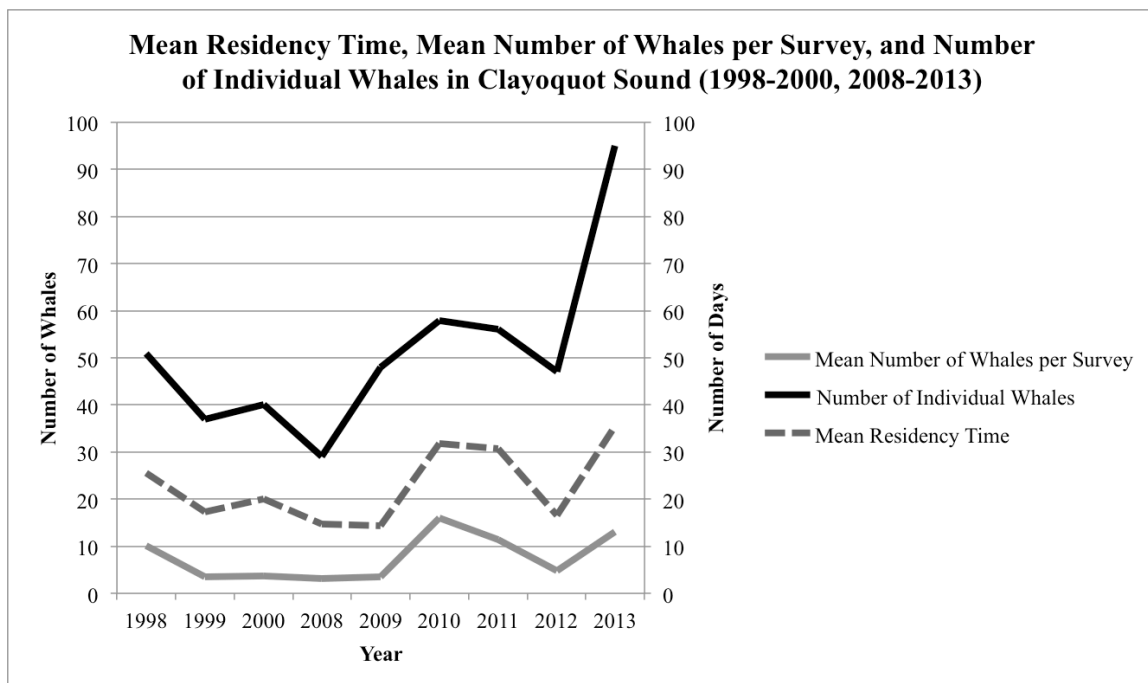


Figure 3.9. Comparison of annual mean residency time (number of days), annual mean number of whales per survey, and the annual number of whales for 1998-2000 and 2008-2013.

3.3. Results Summary

Results are summarized for section 3.1 (Table 3.12) and for section 3.2 (Table 3.13).

Table 3.12. Summary of results for section 3.1.

Assessing the Level of Site Fidelity and Duration of Residency Time	
1. Discovery curve	The equation of the discovery curve for the cumulative number of individuals added to the catalogue is $y = 0.93x + 63.6$ which closely approximates positive linear growth ($r^2 = 0.795$, $p < 0.001$).
2. Mean return count of whales in catalogue & Mean annual return count	The mean return count of whales from the catalogue is 2.61 years, and the mean annual return count is 5.01 years, which is a low/moderate level of site fidelity.
3. Number of whales per site fidelity index class	In an average year, 42 whales are sighted in Clayoquot Sound (based on the mean number of whales per year), with 8 single visit whales, 27 whales with a low/moderate level of site fidelity, and 7 whales with a high level of site fidelity. Thus, on average, the group of individuals that forage in Clayoquot Sound each year have a low/moderate level of site fidelity.
4. Northern survey data	A comparison between Clayoquot Sound whale survey data and northern whale survey data revealed that 54 individuals have been sighted in both locations (22.5 percent of whales from the catalogue).
5. Residency time	Mean residency time is 23 days per year.
6. Spearman's Rho: comparison between (a) mean return count and (b) mean residency time	An individual's (a) mean return count is significantly positively correlated to its (b) mean residency time ($r_s = 0.419$, $p < 0.001$, $n = 166$; excludes new whales sighted in 2013).
7. Returning whale cluster analysis and residency time ANOVA	When returning whales are analyzed separately from single visit whales, and clustered based on their time series, the k-means approach produced 35 clusters with a Silhouette coefficient score of 0.7947. Within clusters 2, 5 and 9, whales generally returned during the same years and for the same number of years. In clusters 1, 3, 4, 6, 7, 8, 10, 11, and 12 mean return counts were lower, and years that individuals returned were more sporadic. Mean residency time does not significantly differ between the clusters.

Table 3.13. Summary of results for section 3.2.

Testing the Relationship Between Prey Productivity, Site Fidelity and Residency Time	
8. Pearson's R: comparison between (a) mean annual return count and (b) annual foraging effort & (a) mean annual return count and (c) annual number of whales	There is no correlation between the (a) mean annual return count and (b) annual foraging effort. However, there is a significant negative correlation between (a) mean annual return count and the (c) annual number of whales, indicating that during productive prey years, a greater number of single visit whales, and whales with a low level of site fidelity to Clayoquot Sound, will be present than during poor prey years.
9. Spearman's Rho: comparison between (a) the annual number of single visit whales per year and (b) annual foraging effort	There is no correlation between (a) the annual number of single visit whales and (b) annual foraging effort.
10. Pearson's R: comparison between (a) number of single visit whales during each two-week interval and (b) mean number of whales per survey during each two-week interval	Within season changes of prey productivity are analyzed by calculating the number of single visit whales for two-week intervals. There is a significant positive relationship between (a) the number of single visit whales per two-week interval and (b) the mean number of whales per survey for each two-week interval. Intra-annually, the timing of the peak number of single visit whales corresponds with the peak of mysid density, indicating that single visit whales tend to be opportunistic feeders that forage in Clayoquot Sound when mysid density is high.
11. Spearman's Rho: comparison between (a) mean annual residency time and (b) annual foraging effort & (a) mean annual residency time and (c) annual number of whales	(a) Mean annual residency time is significantly positively correlated to (b) annual foraging effort. (a) Mean annual residency time is significantly positively correlated to (c) the annual number of whales, demonstrating that residency time is related to mysid density on an intra- and inter-annual basis.

4. Discussion

4.1. The Level of Site Fidelity and Duration of Residency Time

Positive linear growth of the discovery curve indicates that the whales of Clayoquot Sound are part of a larger population and that the number of individuals identified is not a representative of the total number of whales in the population (*e.g.* Aschettino 2010, Fearnbach 2012). The mean annual return count ranged from 3.47 to 6.23 years, with a mean of 5.01 years. Similarly, when the mean number of whales for each class of site fidelity was calculated, the majority of whales (27 out of 42) have a low/moderate level of site fidelity. On average, whales stay for 23 days per year (approximately 21 percent of the foraging season), with residency ranging from 1 to 113 days. A whale's mean residency time is positively correlated to its mean return count, indicating that an individual's level of site fidelity influences how long it stays in Clayoquot Sound. Thus, individual differences in site fidelity may account for differences in residency time among whales during the same year.

The northern surveys found that almost one quarter of the whales sighted in Clayoquot Sound were also sighted outside the study area. Furthermore, the individuals that were recorded in both locations were sighted, on average, for 4.19 years in Clayoquot Sound, which indicates regular movement into and out of the study area. Whales that were sighted for a minimum of two years north of the study area have a mean return count of 5.14 years in Clayoquot Sound, demonstrating that whales with a fairly high level of fidelity to Clayoquot Sound utilize other foraging areas as well. However, a travelling gray whale can reach the farthest extent of the northern survey (Catala Island) within a day, and thus the high flux of individuals between the two locales is not surprising. This study needs to be repeated on a larger spatial scale to better understand the movements of PCFG whales.

Separate analysis of returning whales allowed the examination of site fidelity to be narrowed down to the group of whales that regularly use Clayoquot Sound. The cluster analysis reveals that individuals with a high level of site fidelity return to Clayoquot Sound regardless of mysid density. For example, in Clusters 2, 5, and 9 individuals returned up to six years consecutively, during which time mysid density

fluctuated, suggesting that these individuals may not base their settlement on last year's foraging success (e.g. Krebs 1971). Cluster 5 contains individuals that were only sighted from 2008 onward. Although the absence of these whales prior to 2008 may be a result of sporadic photographic identification data collection, it may also reflect recent recruitment. These individuals could be external recruits, opportunistic foragers, or they could also be juvenile whales born more recently but not recorded in Clayoquot Sound. The presence of one calf in Cluster 5 and two calves in Cluster 2 suggests that individuals with a high level of site fidelity to Clayoquot Sound may be internal recruits, but more data and further analysis is required for confirmation. In the other clusters, the years when individuals returned tended to be isolated. However, 24 of the 50 whales included in this analysis were sighted at least once during the northern surveys, indicating that these whales may return to the general region each year, but not specifically Clayoquot Sound. Photographic identification data is needed from other foraging sites within the PCFG's foraging range to determine where these individuals are foraging during years when they are not sighted in Clayoquot Sound.

The ANOVA of mean residency time between clusters yielded insignificant results, which is unexpected given the positive correlation between an individual's return count and mean residency time. However, individuals were clustered using the overall shape of their time series, not just the number of years that they were sighted. Additional data such as age, gender, and whether an individual is an internal or external recruit, should be integrated into the AR model in future research to increase the ecological and biological meaning of the results.

Based on the low/moderate level of site fidelity, and the high flux of whales between Clayoquot Sound and northern foraging areas, I will accept the second hypothesis proposed in this chapter. In this hypothesis, Clayoquot Sound is one foraging site within a larger foraging range. These results also indicate that the whales of Clayoquot Sound do not form a closed population, but are probably part of larger population such as the PCFG.

4.2. The Relationship Between Prey Productivity, Site Fidelity and Residency Time

There is no relationship between mean annual return count and annual foraging effort. However, there is a negative correlation between mean annual return count and the number of whales per year. The difference between the results of the two correlations is unexpected because the variation in annual foraging effort is very similar to the variation in the annual number of whales, but the insignificant correlation may be due to the small sample size. The negative relationship between mean annual return count and the number of whales per year suggests that mysid density may be one factor that affects an individual's level of site fidelity. This indicates that the number of whales fluctuates inter-annually in Clayoquot Sound primarily due to changes in abundance of single visit whales per year. Fewer single visit whales forage in Clayoquot Sound during years when mysid density is low, and their absence causes the mean return count to increase. Whales that have a higher level of fidelity to Clayoquot Sound return to forage in years when mysid density is lower, and this implies that prey productivity affects whales differently depending on their level of site fidelity. Single visit whales tend to be more opportunistic than whales with high site fidelity, and may site switch depending on the level of prey productivity in Clayoquot Sound and in other locales.

There is no correlation between the number of single visit whales per year and annual foraging effort, which may be due to the small sample size. However, when the number of single visit whales is examined at a finer temporal scale there is a significant relationship between the abundance of prey and the number of single visit whales. When each season was aggregated into two-week intervals, there was an uneven distribution of single visit whales, with the highest number present in Clayoquot Sound during the first two weeks of August. This trend suggests that their presence is influenced by a pulsed variable such as prey. In the months of March and April, the decrease in low-pressure weather systems and increase in sunlight increases phytoplankton productivity (Willette *et al.* 1999, Harris *et al.* 2009), which provides energy for mysids. In late May, mysid populations are still growing and forming stable swarms following the spring bloom (Burnham 2012). It takes juvenile mysids approximately 60 days to become sexually mature (Mauchline 1980, Wittmann 1984, Stelle 2001, Mulkins *et al.* 2002), which roughly coincides with the peak of whale foraging activity in the beginning of August.

The two-week interval from August 1-15 was the period that contained the most peak dates (highest number of whales per survey). As expected, there was a strong significant positive relationship between the number of single visit whales and the mean number of whales per survey when each year was aggregated into two-week intervals. This result indicates that single visit whales are opportunistic foragers that use Clayoquot Sound during periods when mysid density is high.

Mysid density is also related to residency time, with a strong positive relationship between mean annual residency time and the number of whales per year. Years when mysid density is high, on average, whales will stay in Clayoquot Sound longer in comparison to years with low prey productivity. The same relationship was seen between mean annual residency time the mean annual number of whales per survey.

Based on the negative relationship between mysid density and mean return count, and the positive relationship between mysid density and residency time, I will accept my fifth hypothesis: inter- and intra-annual changes in mysid density are related to the average level of site fidelity of individuals visiting Clayoquot Sound each year and their mean annual residency time.

4.3. Synthesis

The results from this chapter do not support the results from Frasier *et al.* (2011), whose study was also centred in Clayoquot Sound, but are in line with the results presented in a collaborative photographic identification study for the entire PCFG range by Calambokidis *et al.* (2010). Frasier *et al.* (2011) contend that the whales of Clayoquot Sound form a distinct population, whereas Calambokidis *et al.* (2010) state that although individuals return frequently to certain areas within the Pacific Northwest they do not form closed populations. Calambokidis *et al.*'s (2010) findings are supported here by the low/moderate level of site fidelity exhibited by the majority of whales foraging in Clayoquot Sound, and the regular exchange of individuals between the study area and northern sites. Calambokidis *et al.* (2010) describes single visit whales as stragglers from the northern migration. However, single visitors are challenging to characterise because it is difficult to differentiate PCFG whales that are moving between different foraging

areas, from delayed migrating whales, or from individuals that are truly new recruits to the PCFG (*e.g.* Barendse *et al.* 2013).

The dynamics of whales that exhibit low/moderate site fidelity are also problematic to characterize, but arguably the most important to understand. The majority of whales that visit Clayoquot Sound are from this group, and thus their movements between foraging sites would provide insight into whether sub-structuring is present within the PCFG, and the appropriate spatial scale to effectively manage human activities in their home range. Calambokidis *et al.* (2010) state that while there is extensive exchange of individuals among regions within the PCFG's foraging range, whales do not move randomly among areas. Instead, the rate of interchange between areas is dependent on the proximity of the regions (Calambokidis *et al.* 2010). For example, movement between southern Vancouver Island and western Vancouver Island occurs more frequently than the exchange between northern British Columbia and California (Calambokidis *et al.* 2010).

The group of whales that exhibit a low/moderate level of site fidelity has the longest temporal range in comparison to the other two groups, with return counts spanning 2-8 years. It is possible that many whales from this class should be included in the third class (high site fidelity) given that the class boundaries are arbitrary, and the relatively small size of the study area. For example, the results from the northern surveys and cluster analysis demonstrate that during some years, whales that exhibit a low/moderate level of site fidelity to Clayoquot Sound may only be sighted in adjacent areas, and not in the study area. These whales may have a high level of site fidelity to western Vancouver Island, but not to Clayoquot Sound. Thus, the classification of the majority of whales as having a low/moderate level of site fidelity to Clayoquot Sound should only be interpreted in the context of this study.

There is not one accepted definition of high or low site fidelity given that the number of sightings of an individual is dependent on the duration of the study, the frequency of surveys, the size of the study area, and the life history of the species of interest. In comparison to the results from this study, Clapham *et al.* (1993) describe humpback whales (*Megaptera novaeangliae*) in the southern Gulf of Maine as having high annual return rates and residency times. Clapham *et al.* (1993) collected data daily

from 1979-1988, and recorded 518 unique whales of which the majority were resighted up to 9 years (the duration of their study) with a mean residency time of 88 days (44% of the foraging season, in comparison to the mean residency time in this study which is 21% of the season). The study by Barendse *et al.* (2013) on humpback whales off the west coast of South Africa is an example of a foraging area with individuals that have lower site fidelity than recorded in this study. The authors recorded 289 individuals from 1983-2008, with 68 individuals resighted at least once, and a mean residency time of 31.4 days (8.6% of the year). However, the authors state that the low annual returns and residency time should be interpreted in the context of the area's dual function as a migratory route and seasonal foraging area since the majority of non-resighted individuals were observed during the migratory season (Barendse *et al.* 2013). Thus the temporal scale used in the study by Barendse *et al.* (2013) may have biased the authors' interpretation of the results.

The challenge when attempting to characterize the PCFG is that the results are dependent on the scale of observation. Our interpretation of ecological systems vary depending on the spatial or temporal scale of study, and there is no single appropriate scale at which to study ecological phenomena (Levin 1992). While the study by Lang *et al.* (2011) provided a sound description of the level of genetic isolation of the PCFG from the rest of the eastern north Pacific population, it did not address the possibility of sub-structuring within the PCFG or the rest of the eastern north Pacific population. The study by Calambokidis *et al.* (2010) provided insight into the movements of individuals between foraging areas, but it did not discuss the potential mechanisms causing differing levels of site fidelity between individuals. While this study has a relatively long temporal range that allowed for more opportunity to capture and recapture individuals, it has a limited spatial extent. However, the small study area permitted frequent whale surveys, and a fine scale view of site fidelity of one area within the PCFG's range.

Even if movement patterns of PCFG whales are defined, the challenge lies in determining what the biological significance is of the different foraging areas. The results presented in this chapter, and in the study by Calambokidis *et al.* (2010), suggest that core groups of PCFG whales return to specific areas between Alaska to California. This finding begs the question of whether the PCFG is homogenous and/or if specific foraging sites within the PCFG's range are more productive in terms of prey, and thus

sustain more foraging whales than others. If the PCFG is deemed to be demographically independent from the rest of the eastern north Pacific population, an effective conservation strategy is to protect important foraging and breeding locations (Ingram & Rogan 2002, Bailey & Thompson 2009). A clearer understanding of the ecological interactions between whales and their prey is required to find out why individuals have site fidelity to specific foraging areas between California and southern Alaska.

While previous studies have analyzed the relationship between fluctuations in prey and the abundance of gray whales in Clayoquot Sound (*i.e.* Dunham & Duffus 2001, Olsen 2006, Burnham 2012, Feyrer & Duffus 2014), until now, no one has investigated how changes in prey productivity affect site fidelity. There is a positive relationship between the number of whales and mysid density (Feyrer & Duffus 2014), but the results from this chapter suggest that prey productivity may affect individuals differently depending on their level of site fidelity. Whales with higher levels of site fidelity will return to Clayoquot Sound in relatively unproductive years, whereas whales with little or no site fidelity to Clayoquot Sound will forage elsewhere. However, for all whales, a minimum prey threshold exists where individuals will leave the study area once the number of mysid patches (Olsen 2006), or mysid swarm density (Feyrer & Duffus 2014), becomes too low to be profitable (Dunham & Duffus 2001). The positive correlation between annual foraging effort and mean annual residency time indicates that during poor prey years, whales stay for a relatively short period of time in Clayoquot Sound in comparison to productive years. Thus, loyal whales will visit the study area, search for prey, and then leave after the energy expended in searching for prey becomes too high. In comparison, single visit whales will spend less time searching for prey in Clayoquot Sound, or will not stop in the study area.

These differences in foraging tactics between single visit whales and returning whales brings to light an interesting link between site fidelity and optimal foraging theory, which states that individuals will employ foraging tactics that maximize their net energy intake per unit time (see MacArthur & Pianka 1966, Charnov 1976). Given that single visitors and returning whales differ in how they optimize time spent in different areas, if higher quality foraging areas are available but returning whales remain in lower quality sites, then site fidelity may be a suboptimal form of behaviour (Switzer 1993).

However, when an individual fails to move to a higher quality territory (see Krebs 1971, Best 1977, Bernard & LaPointe 1984) it may be due to the energy associated with movement if the quality of alternate habitats is unpredictable (Switzer 1993), despite the relatively low cost of locomotion (Williams 1999). Due to the patchy distribution of mysid swarms (Feyrer 2010), some individuals may be reluctant to leave a foraging site in which they have had previous success, and thus they exhibit a higher level of site fidelity to Clayoquot Sound.

There are different variables that influence the distribution of gray whales in Clayoquot Sound, and at a broader scale, between California and Alaska. One of the biggest challenges in this chapter is differentiating the ecological signal from the noise, a task that is complicated by the biases inherent with choosing an appropriate sampling regime and the scale of study. Yet, amid these challenges, scientists should continue studying the gray whale, given that their habitat spans international boundaries, a factor which may become problematic as anthropogenic activities increase in the marine environment. Despite recent genetic work demonstrating a significant difference between the PCFG and the rest of the eastern population (*e.g.* Lang *et al.* 2011), the fine scale distributions and mechanisms causing the observed population structure are still undefined. Understanding these variables may change our perspective about the social dynamics of gray whales, and will help increase the efficiency of conservation efforts.

5. Conclusion

In this chapter I assessed the level of site fidelity of the whales foraging in Clayoquot Sound and analyzed whether mysid density is related to site fidelity and residency time. My results demonstrate that, on average, the whales sighted in Clayoquot Sound have a low/moderate level of site fidelity and residency time, which indicates that they are probably part of a larger population such as the PGFG, or a smaller subpopulation within it. These findings also imply that Clayoquot Sound is one foraging site within a larger foraging range such as western Vancouver Island, but given the relatively high return counts of several individuals, in addition to the results from the study by Calambokidis *et al.* (2010), PCFG whales do not move randomly between California and Alaska. The majority of research pertaining to whale conservation is

focused on population estimates rather than ecology (Kareiva *et al.* 2006). Yet, the link between mysid density and site fidelity discussed in this chapter demonstrate the importance of incorporating ecological data into resource management. Protecting important foraging areas, identified by the distribution of whales within the PCFG's foraging range through time, may be an effective conservation strategy. When testing the level of genetic differentiation between the PCFG and the rest of the eastern population, sampling distribution should be based on the results of collaborative photographic identification work to help detect if sub-structuring is present within the PCFG. Defining population structure is a complicated task that requires a collaborative multi-scale approach and the incorporation of ecological data. While I analyzed the relationship between prey productivity and site fidelity, it is not unreasonable to expect that there are a number of other variables at play, which presents many opportunities for interesting future research.

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Chapter 4 : Gray Whale (*Eschrichtius robustus*) Internal Recruitment via Maternal Learning in Clayoquot Sound, B.C.

1. Introduction

When mother and offspring have similar but complex behaviour it indicates vertical cultural transmission via social learning (Rendell & Whitehead 2001). The transfer of specific migratory routes, foraging tactics, and other behaviours is prevalent in social odontocetes such as beluga whales (*Delphinapterus leucas*) (e.g. O’Corry-Crowe *et al.* 1997, Colbeck *et al.* 2013) and killer whales (*Orcinus orca*) (e.g. Yurk *et al.* 2002). Mysticetes are typically less gregarious than odontocetes, but maternally directed cultural transfer has also been proposed as the mechanism enabling some populations from different species to return to specific feeding grounds (e.g. Clapham *et al.* 2008, Valenzuela *et al.* 2009, Carroll *et al.* 2013). For example, humpback calves (*Megaptera novaeangline*) follow their mothers on their first migration from calving grounds to foraging sites, and subsequently repeat the same migration for the duration of their lives (Katona & Beard 1990). The differentiation of mtDNA haplotypes between migratory routes provides evidence for maternal learning (Baker *et al.* 1990), and given that individuals from different foraging grounds utilize the same breeding grounds, genetic inheritance of migratory behaviour is unlikely (Clapham & Mayo 1987).

With the eastern north Pacific gray whale (*Eschrichtius robustus*), a similar pattern in foraging segregation is present. An estimated 200 individuals (Calambokidis *et al.* 2010), known as the Pacific Coastal Feeding Group (PCFG; IWC 2010), demonstrate site fidelity to the coastal waters between northern California and south-eastern Alaska. The PCFG have a low but significant difference in mtDNA in comparison to whales foraging in the Bering and Chukchi Seas, but not a significant difference in nuclear DNA (Lang *et al.* 2011). This indicates that mating is random with respect to feeding grounds (Lang *et al.* 2011, D’Intino *et al.* 2013), and thus the differentiation of mtDNA is caused by calves following their mothers to southern feeding grounds during their first foraging season and returning in subsequent years (Calambokidis *et al.* 2010, Lang *et al.* 2011, Scordino *et al.* 2011).

The low level of mtDNA differentiation and the high mtDNA haplotype diversity within the PCFG is indicative of a population that is structured primarily by maternal learning but where low-level external recruitment also occurs (Lang *et al.* 2011). The proportion of internal versus external recruitment is important to quantify because if recruitment is mostly internal, then the PCFG represents a demographically independent management unit with potential conservation significance (Lang *et al.* 2011, Scordino *et al.* 2011). When structuring exists in a population, different groups require separate management consideration because disturbances may disproportionately affect the smaller group instead of being absorbed evenly throughout the population (Clapham *et al.* 2008). For example, loss of cultural memory is proposed to have caused the lack of recovery of humpback and blue whales (*Balaenoptera musculus*) at South Georgia, where the memory of that specific habitat was extirpated along with the whales (Clapham *et al.* 2008). Industrial developments, such as the proposed increase of fossil fuel pipelines on the coast of British Columbia could impact PCFG matrilineal lines disproportionately under the assumption of a single eastern north Pacific population (D'Intino *et al.* 2013) through ship strikes, toxic spills, and noise pollution (*e.g.* Jayko *et al.* 1990, Moore & Clarke 2002). If whales with site fidelity to southern feeding grounds are removed, and external recruitment into the PCFG is negligible, then knowledge of southern feeding grounds may be lost and localised extirpation may occur (D'Intino *et al.* 2013).

The amount of external recruitment into the PCFG is challenging to calculate. One estimate by Calambokidis *et al.* (2010), found that on average 22.7 new whales were sighted in the PCFG per year, and from those new whales, 10.1 whales on average were seen in subsequent years. Although these whales may represent individuals that are external recruits they could also be whales that were not recorded as calves, given that many areas between southern Alaska and northern California are remote and data collection is minimal. Furthermore, it is challenging to differentiate PCFG whales from opportunistic migrating whales travelling to northern feeding grounds because their migration route travels past southern feeding areas (Calambokidis *et al.* 2010). Even if the annual number of external recruits into the PCFG is known, the relationship between the rate of immigration and demographic independence is not clearly understood (Waples & Gaggiotti 2006). External recruits may not be equivalent to internal recruits in terms

of behaviour and life history, and thus measuring the rate of immigration may not be a reliable indication of demographic independence (Waples & Gaggiotti 2006).

Given that the rate of external recruitment is not necessarily a useful gauge of demographic independence, I will analyze fine scale internal recruitment of PCFG whales by characterizing maternal learning within Clayoquot Sound (one site within the PCFG's range). I will identify cow/calf pairs, track the number of years each calf returns to Clayoquot Sound, and describe differences in site fidelity among calves by analyzing their first year residency time, their mother's level of site fidelity, and the effect of annual fluctuations in prey. I will compare the site fidelity and residency time of calves and cows to the unclassified whales of Clayoquot Sound to determine if ontogenetic changes affect usage of Clayoquot Sound.

2. Methods

2.1. Study Area

The study area is situated in the south-western coastal waters of Flores Island, Clayoquot Sound, British Columbia (49°14'36"N, 126°6'10"W and 49°18'51"N, 126°14'30"W) and is approximately 25km² (Figure 4.1). The topography of the study area includes sandy and rocky shorelines, small islands, and shallow reefs (Dunham & Duffus 2001), and is surrounded by land and unproductive foraging areas (Pasztor 2008, Feyrer 2010). The primary prey for gray whales in Clayoquot Sound is epi-benthic mysid shrimp (family *Mysidae*) (Kim & Oliver 1989, Duffus 1996, Dunham & Duffus 2001, 2002, Stelle 2001, Feyrer & Duffus 2011) which are located near shore in shallow waters (~10 metres) above rocky substrate (Dunham & Duffus 2001, Laskin *et al.* 2010, Feyrer & Duffus 2011). Research took place from May 24 to September 8, which corresponds with the gray whale summer foraging season.

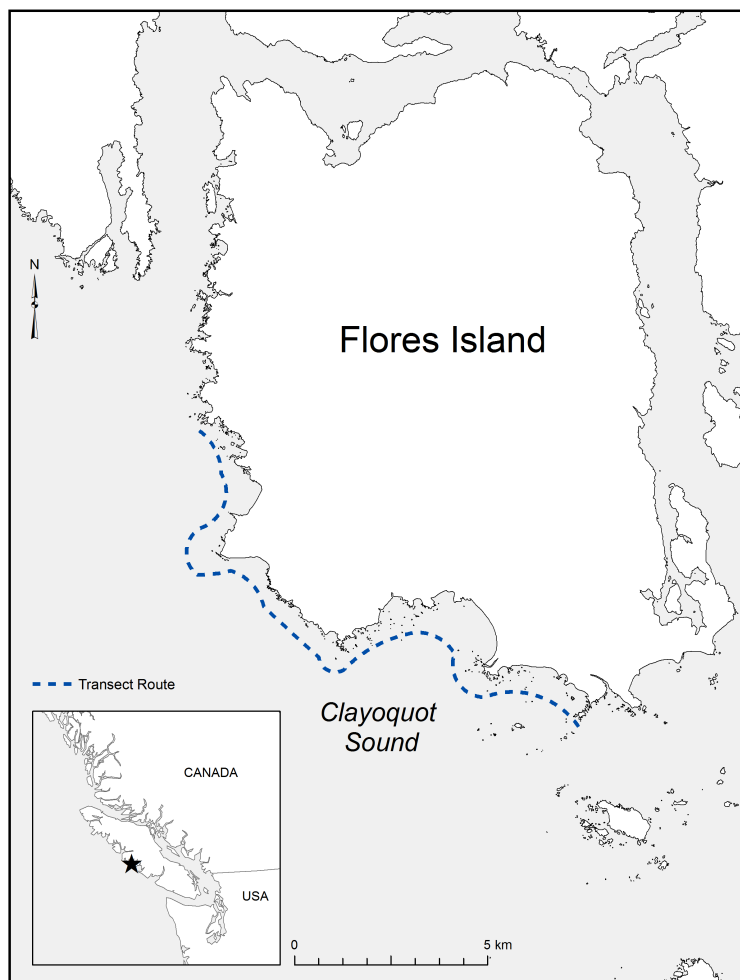


Figure 4.1. The study area is located in the coastal waters of Flores Island, Clayoquot Sound, British Columbia. The dotted line represents the location of the route driven during whale surveys.

2.2. Data Collection and Definitions

2.2.1. Whale Surveys

Whale foraging effort was recorded annually with biweekly boat based surveys from May 24 to September 8 since between 1997-2013. Surveys were conducted in fair weather to maximize sightings, and were terminated if the Beaufort sea-state was greater than three, or if visibility was obscured by fog. The boat followed a survey line that follows the 10 metre isobath to encounter the largest concentration of foraging whales. To avoid double counting individuals, the vessel travelled at 13 km/hr, which is faster

than the average speed of a gray whale at 7-9km/hr (Urban-Ramirez *et al.* 2012). A minimum of four observers searched 360 degrees for whale ventilations, and once a whale was sighted it was approached, and the observers determined if it was travelling or foraging based on area-restricted diving behaviour (Feyrer & Duffus 2014). The location and date of sighting of all foraging whales were recorded. Identification photographs were taken of each foraging whales between 1998-2000 and 2008-2013 based on the methods described in Calambokidis *et al.* (2010). No identification photographs were taken in 2001, and from 2002-2007, photographing effort was sporadic and only occurred during some surveys (Table 4.1). The identification photographs taken in 2003 and 2005 have no dates associated with them other than the year.

Table 4.1. Surveys occurred biweekly from May 24-September 8. Identification photographs were taken during the surveys between 1998-2000 and 2008-2013, and sporadically between 2001-2007. Opportunistic identification photographs that were taken outside of these dates (but within 30 days) were included in this analysis (May 1-May 24, and September 9-September 15). The asterisks denote years where photographs were not taken during every survey (2001-2007).

Year	Number of Surveys	Number of Surveys where photo id occurred	Date Range	Mean Number of Whales per Survey	Annual Number of Whales
1997*	55	0	June 29-Sept 4	6.47	n/a*
1998	58	58	June 6-Aug 26	9.81	51
1999	30	30	June 3-Aug 26	3.50	37
2000	17	17	June 6-Aug 12	3.59	40
2001*	46	0	May 25-Sept 8	2.37	n/a*
2002*	43	3	May 24-Sept 5	10.56	41 *
2003*	30	n/a	May 27-Sept 7	5.10	62*
2004*	25	15	May 24-Sept 12	11.12	27*
2005*	26	n/a	May 31- Sept 7	2.23	6*
2006*	33	4	May 19-Aug 25	7.21	23*
2007*	53	8	May 26-Sept 8	0.91	7*
2008	17	17	May 24-Sept 4	3.53	29
2009	24	24	May 27-Aug 9	4.92	48
2010	33	33	May 26-Sept 9	16.19	58
2011	36	36	May 25-Sept 6	11.36	56
2012	33	33	May 25-Sept 2	5.09	47
2013	24	24	May 25-Sept 1	18.04	95

Photographic identification is a method used to “capture” each new whale sighted in Clayoquot Sound per year, and then used to “recapture” the individual upon its return. Whenever possible photographs of the left and right side of the body, as well as the flukes, were taken (see Calambokidis *et al.* 2010). To remain consistent between images, photographs were taken at a 90-degree angle, while the whale is diving, and when its

dorsal hump is in the middle of the frame (Figure 4.2). If the photograph was poor quality, or if right side images were unavailable, then the whale was added to the temporary catalogue and not included in data analysis to prevent internal duplication. If higher quality images, or right side photographs, were later taken for individuals in the temporary catalogue, then they were moved into the master catalogue.



a) Example of an identification photograph of the right side of a gray whale.



b) Example of an identification photograph of the left side of a gray whale.

Figure 4.2. An example of right (a) and left (b) identification photographs. For the purpose of consistency between images, the photograph is taken at a 90-degree angle, when the whale is diving, and when the dorsal hump is in the middle of the frame. Distinctive pigmentation is used to identify each individual.

Each whale is identified by the unique pigmentation and by their distinctive knuckle profiles and dorsal humps (Lien & Katona 1990, Calambokidis *et al.* 2010). Photographs were matched by two experienced analysts using a catalogue containing images taken by past researchers from 1998 to 2010, and photographs I took from 2011 to 2013. I re-matched all photographs taken prior to 2011 to ensure accuracy. When a whale could not be matched to the master or temporary catalogue it was assigned a unique number and added to master catalogue. The date of each sighting within each year was also recorded and used to calculate the annual residency time of each individual.

Along with the whale surveys in Clayoquot Sound, opportunistic surveys were also conducted north of the study area in 2002, 2006-2009, 2010, and 2012. The same survey procedures were followed but the timing and effort differed between years (Table 4.2). Identification photographs were taken during these surveys and stored separately from Clayoquot Sound catalogue. The length of the northern surveys varied depending on weather conditions, but all surveys began at Sharp Point, the shortest surveys ended at Estevan Point, and the longest surveys terminated at Catala Island (Figure 4.3). The distance of the survey line between Sharp Point and Catala Island is approximately 90 km.

Table 4.2. The number and the date range of northern surveys per year. For each year, the number of whales that was sighted in the northern surveys, in both areas, and the total number are listed.

Year	Number of Surveys	Date Range	Number of Whales Sighted North Only	Number of Whales Sighted in Clayoquot Sound and North	Total Number of Whales Sighted
2002	4	July 3-Sept 3	41	14	55
2006	4	May 28-June 6	11	4	15
2007	1	August 7	0	1	1
2008	1	May 25	1	0	1
2009	1	June 6	0	1	1
2010	1	June 23	3	4	7
2012	1	July 4	8	4	12

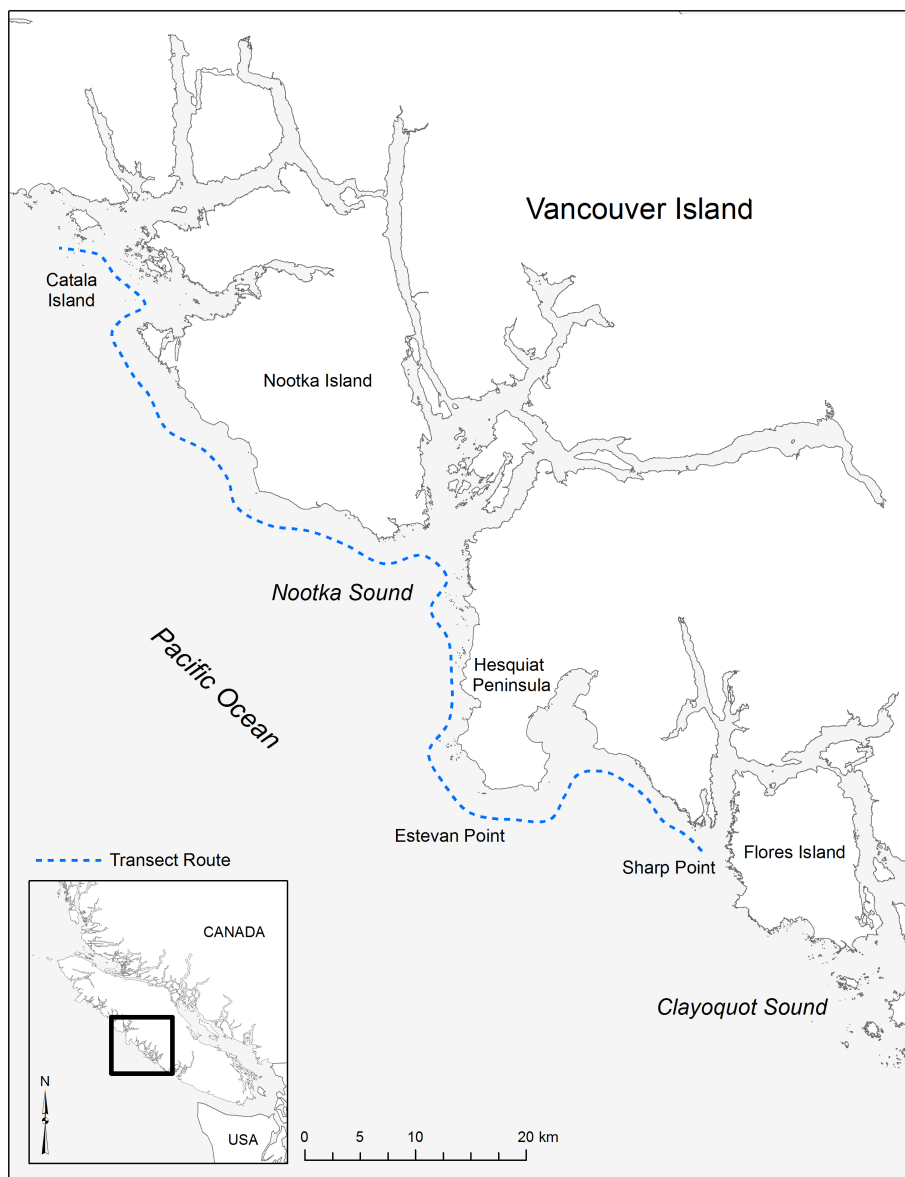


Figure 4.3. The northern surveys start at Sharp Point on Vancouver Island and, at their maximum extent, end at Catala Island.

2.2.2. Whale Data

Calves are identified by their small body size and their close proximity to an adult-sized animal (Perryman & Lynn 2002, Barendse *et al.* 2013, Sumich *et al.* 2013). In this chapter, the term “calf” is still used after an individual’s first foraging season, and hence this group contains the data for all known internal recruits in Clayoquot Sound until they reach sexual maturity at a maximum age of 11 years (Rice & Wolman 1971). With capture-recapture surveys beginning in 1998, any calf born before 2002 would be

considered an adult as of 2009. However, there were only two calves that were first sighted prior to 2002, and neither was sighted since their first foraging season. A distinction is made when I analyze first year calves (calves accompanied their mothers during their first foraging season) separately from returning calves (whales that have returned to the study area any year after their first foraging season).

Cows are distinguished by their relatively large body size and their association with a calf. If a cow returns to Clayoquot Sound solo, it is still included with the “cow” group although a distinction is made between years when a cow is solo and when accompanied by a calf.

2.2.3. Prey Data

The annual number of whales in Clayoquot Sound differs and is dependent on the amount of foraging pressure from the previous year, with high whale years usually followed by at least one year where the number of foraging whales is lower than average (Burnham 2012). In this top-down driven system, mysid abundance varies depending on annual foraging effort which is demonstrated with the significant positive correlation between annual mysid swarm density and the number of foraging whales in Clayoquot Sound (Feyrer & Duffus 2014). To test if site fidelity and residency time of cows and calves are related to annual fluctuations in prey, each year is categorized as either being a ‘high mysid year’ or a ‘low mysid year’ (Table 4.3). Because mysid abundance data within the study area are only available from 2006-2008, the mean number of whales per survey is used instead to provide a proxy for prey data throughout the duration of the study. To determine the threshold between high and low years, the mean number of whales per survey is calculated for each year and used to calculate the grand mean for all years (7.17 whales per survey) with a significant difference between the two classes ($\chi^2 = 170.468$, $p < 0.001$).

Table 4.3. The mean number of whales per survey is calculated and used as a threshold to distinguish high prey years from low years. Years where the mean number of whales per survey is greater than 7.17 whales, mysid abundance is considered to be relatively high and vice versa.

Year	Number of Surveys	Mean Number of Whales per Survey	Abundance (relative to grand mean)
1997	55	6.47	Low
1998	58	9.81	High
1999	30	3.50	Low
2000	31	3.59	Low
2001	43	2.37	Low
2002	43	10.56	High
2003	30	5.10	Low
2004	21	11.12	High
2005	26	2.23	Low
2006	31	7.21	High
2007	47	0.91	Low
2008	41	3.53	Low
2009	24	4.92	Low
2010	31	16.19	High
2011	36	11.36	High
2012	33	5.09	Low
2013	24	18.04	High

2.3. Data Analysis

2.3.1. Assessing the Level of Site Fidelity and Duration of Residency Time

Return count, which describes the number of years that a whale is sighted, is calculated for each cow and calf, and is used as a measure of site fidelity. Based on the site fidelity index described in Mahaffy (2012), whales that were sighted a minimum of nine out of 15 years (60 percent of years since 1998) are classed as exhibiting a high level of site fidelity. Individuals that were sighted more than one year but less than nine years are defined as having low/moderate site fidelity, and whales that are only sighted during one year are considered to have no site fidelity to Clayoquot Sound.

The calf's return counts are standardised based on the number of years since its first summer so that the return counts of calves that were born in the later portion of the study are not underestimated. For example, if a calf was first sighted in 2008 and has a return count of 4 years, its standardized return count is 67 percent (4 years sighted/6 potential sighting years). Using Spearman's Rho, each calf's standardised return count is compared to its mother's return count. I expect a positive correlation between the two variables because it would indicate that site fidelity might be a learned quality passed down via matrilineal learning.

Residency time measures the duration of an individual's visit to Clayoquot Sound per year (Balance 1990), and provides a finer scale view of habitat use than return count (or standardized return count for calves). Residency time is calculated annually for calves and cows that were sighted during the years 1998-2000 and 2008-2013. For each individual, mean residency time is compared to return count (or standardized return count for calves) using Spearman's Rho. I expect a positive correlation between the two variables because individuals that return more frequently most likely stay longer.

The location where a calf spends its first summer, along with the duration of residency at that location, is dictated by the cow until the calf is weaned, and may affect its subsequent level of site fidelity to that area (*e.g.* Katona & Beard 1990). Residency time of each cow/calf pair varies, and while the cause of these differences are unclear, I hypothesize that cow/calf pair residency time is influenced by the cow's level of site fidelity to Clayoquot Sound. The residency time of each cow/calf pair is calculated, and Spearman's Rho is used to test if there is relationship between a cow's return count and the number of days a cow/calf pair remains in Clayoquot Sound during the calf's first summer. An unpaired samples t-test is used to discover if first year residency time significantly differs between single visit and returning calves. A significant result indicates that the duration of first year residency may affect a calf's site fidelity to Clayoquot Sound

To test for differences in site fidelity and residency time among cows, three different t-tests are executed. An unpaired samples t-test is used to compare cows that have been sighted with multiple calves, to cows that have only been sighted with one calf. Another unpaired samples t-test is used to compare the residency time of cows that

were exclusively sighted when accompanied by a calf, to the residency time of cows that return to Clayoquot Sound as mothers or solo. A paired samples t-test is used to evaluate if annual residency times differs between years when a cow is accompanied by a calf and years when a calf returns solo.

The data from the northern surveys is used to characterize the exchange of individuals between Clayoquot Sound and another known foraging area. The number of cow/calf pairs that were sighted during northern surveys is calculated, and the number of individuals that utilize both Clayoquot Sound and northern foraging grounds is determined.

2.3.2. Testing the Relationship Between Prey Productivity, Site Fidelity and Residency Time

Mysid density is represented by annual foraging effort. The date of the first sighting of cow/calf pairs each year is calculated and compared to the arrival of the peak number of whales to help determine if cow/calf pairs arrive and forage in Clayoquot Sound with the majority of whales when mysid density is highest. If the arrival of cow/calf pairs corresponds with the peak in mysid density then it suggests that the presence of cow/calf pairs is largely influenced by changes in mysid density, whereas arrival prior to the peak suggests Clayoquot Sound may offer other benefits such as shelter from predators or lower competition when feeding. To test if there is a relationship between the level of mysid density during a calf's first foraging season and its subsequent site fidelity, the annual number of whales present in each calf's first year is correlated to its standardized return count using Spearman's Rho.

For calves and cows, the mean number of whales per survey is compared to annual residency time using Spearman's Rho to test if yearly variations in mysid density are related to the duration of residency of both groups. To follow, mean residency time is calculated for high and low mysid years, and an unpaired samples t-test is used to evaluate if there is a significant difference in residency time between the two.

2.3.3. Comparison Between Calves, Cows, and the Unclassified Whales of Clayoquot Sound

The Clayoquot Sound catalogue contains 190 unique individuals that are of unknown gender and age. These whales are most likely a mixture of external recruits, opportunistic single season visitors, and internal recruits born prior to 1998 (including post-breeding adults). Although the 190 whales may contain some unrecorded cows and calves, this study provides an opportunity to determine if “known” internal recruits differ in site fidelity and residency time from other whales foraging in Clayoquot Sound. The mean return count and mean residency time of cows and calves are compared to those of the unclassified whales within the Clayoquot Sound catalogue. A comparison is also made between the correlation coefficients among calves, cows, and the unclassified whales to examine how variations in prey are related to site fidelity and residency time for each of the groups.

3. Results

3.1. Assessing the Level of Site Fidelity and Residency Time

3.1.1. Cow/Calf Pairs

There is a significant positive correlation between a cow’s return count and her calf’s standardised return count (excluding calves from 2013) ($r_s = 0.839$, $p < 0.001$, $n = 18$), which suggests that site fidelity may be a learned quality transferred from mother to offspring (Figure 4.4). There is also a positive significant correlation between a cow’s return count and the number of days a cow/calf pair remains in Clayoquot Sound during the calf’s first summer ($r_s = 0.435$, $p = 0.048$, $n = 21$), indicating that the duration of a calf’s first year residency is related to its mother’s site fidelity.

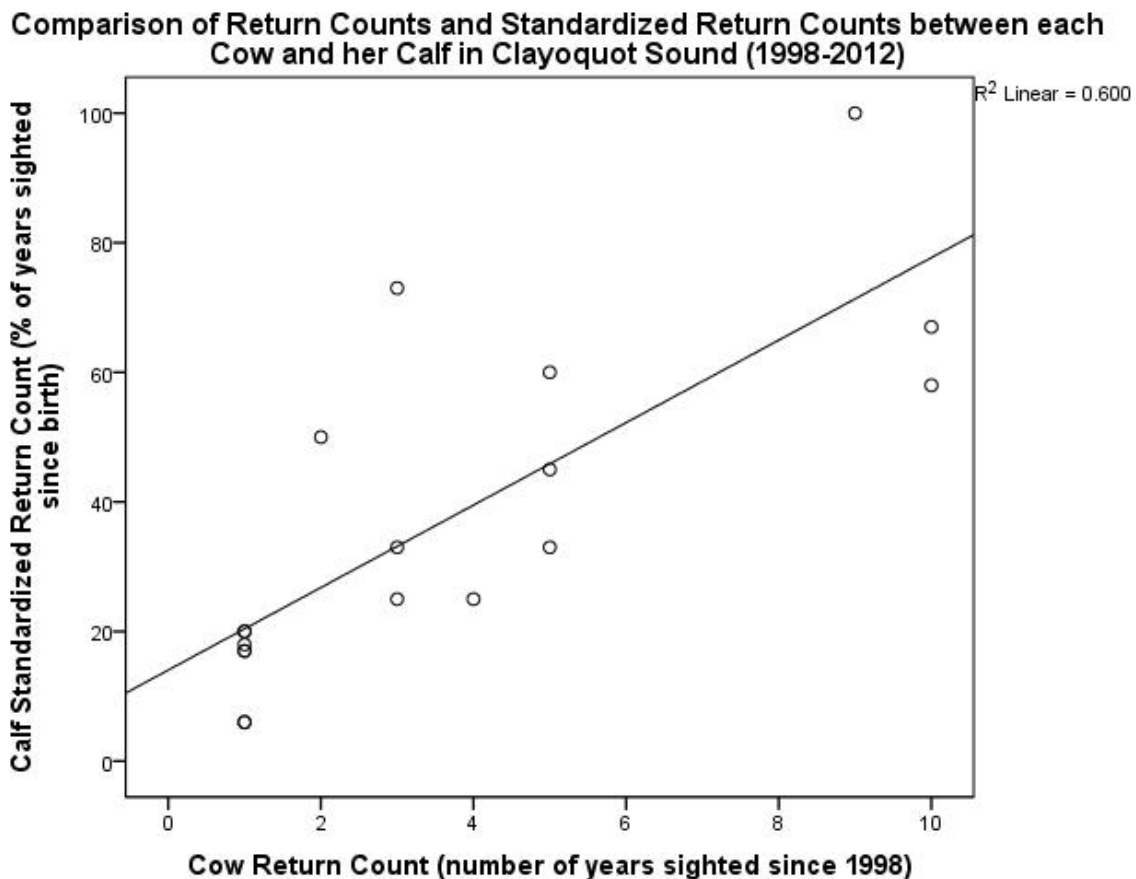


Figure 4.4. There is a positive correlation between each cow's return count and her calf's standardized return count.

3.1.2. Calves

There are 30 calves that were sighted in Clayoquot Sound since 1998, with a mean of 2.44 calves per year (excluding data from 2001-2007) (Table 4.4). Calves comprise 12.5 percent of the individuals in the catalogue of 240 whales. The number of returning calves is high, with 41 percent resighted at least one year after their first foraging season (Table 4.5). The mean return count is 2.54 years, and the mean standardized return count is 38.75 percent (excluding calves sighted in 2013).

Table 4.4. The number of calves sighted per year in Clayoquot Sound. No identification photographs were taken in 2001, and photographing effort was variable between 2002-2007, and therefore the annual number of calves recorded during those years may not be accurate.

Year	Number of Calves
1998	2
1999	0
2000	0
2001	n/a*
2002	3*
2003	4*
2004	0*
2005	1*
2006	0*
2007	0*
2008	2
2009	5
2010	2
2011	3
2012	2
2013	6

Table 4.5. The number of calves aggregated by return count in Clayoquot Sound.

Return Count	Number of Calves
1	18 (includes 6 calves from 2013)
2	5
3	0
4	2
5	2
6	1
7	1
8	1

Residency time is high, with calves staying a mean of 44 days per year (excludes first year residency time). Each calf's standardized return count is significantly positively correlated to its mean residency time ($r_s = 0.669$, $p < 0.001$, $n = 24$) (2013 calves

were not included), suggesting that calves with a higher level of site fidelity on average stay longer each season than calves with a lower level of site fidelity to Clayoquot Sound.

The mean first year residency time of single visit calves is 12 days, $n=12$, while the mean first year residency time of calves that return to Clayoquot Sound is 41 days, $n=4$. There is not a significant difference between first year residency time of single visit and returning calves ($t(3.80) = -1.541$, $p=0.201$), but this result was probably influenced by the small sample size resulting from the lack of first year residency data recorded between 2001-2007. While some calves were born between 2008-2013, the opportunity for those individuals to return was lower, and thus returning calf residency data is sparse during that period.

During the northern surveys, three first year calves were sighted that were not subsequently recorded in Clayoquot Sound, and one first year calf was sighted which was re-sighted in Clayoquot Sound during the same year. There was one calf recorded during its fourth summer, which was first sighted in, and previously returned to, Clayoquot Sound.

3.1.3. Cows

There are 20 known cows that were sighted in Clayoquot Sound since 1998, which is 8.3 percent of the individuals in the catalogue of 240 whales. The mean return count is 3.76 years. The mean return count of cows that visit Clayoquot Sound exclusively when accompanied by a calf is lower (1.13 years, $n=13$) than cows that return to Clayoquot Sound as mothers or during solo years (5.58 years, $n=7$) (Table 4.6).

Table 4.6. The number of cows aggregated by return count in Clayoquot Sound.

Return Count	Number of Cows
1	7
2	2
3	3
4	1
5	2
6	1
7	0
8	1
9	2
10	1

Residency time is fairly high, with cows foraging in Clayoquot Sound for a mean of 21 days. Each cow's return count is correlated to its mean residency time ($r_s = 0.490$, $p = 0.033$, $n = 19$). Residency time differs among cows, with a significant difference between cows that visit Clayoquot Sound exclusively when accompanied by a calf (13 days), and cows that return to Clayoquot Sound as mothers or solo (35 days) ($t(15) = 2.318$, $p = 0.035$). There is also a difference in residency time among years, with a significant difference in mean annual residency time when cows are accompanied by a calf (35 days) versus when they are solo (20 days) ($t(8) = 2.528$, $p = 0.035$).

Seven individuals have had two calves since 1998, with a mean of 4.43 years between calves (range of 2-8 years). The mean return count of cows with multiple calves is 4.71 years, which does not significantly differ from the return count of cows that have only been sighted with one calf (3.50 years) in Clayoquot Sound ($t(15.029) = -0.866$, $p = 0.400$). The residency time of cows with multiple calves (17.14 days) does not significantly differ from the residency time of cows that have only been sighted with one calf (22 days) ($t(16.906) = 0.753$, $p = 0.462$).

During the northern surveys, seven cows were recorded that have also been sighted in Clayoquot Sound for at least one year. Out of the seven cows, five were sighted north during non-calf years only, one was sighted with a calf in both locations during the same year, and one was sighted north with a calf in one year and solo in Clayoquot Sound during different years. One cow/calf pair was exclusively sighted during the northern surveys.

3.2. Testing the Relationship Between Prey Productivity, Site Fidelity and Residency Time

3.2.1. Cow/Calf Pairs

The mean first sighting date of cow/calf pairs is June 19 (May 24 to August 4), which is over a month earlier than the arrival of the peak number of whales in Clayoquot Sound (average date range = August 1 to August 15) (Table 4.7). This difference in timing indicates that cows are bringing their calves to Clayoquot Sound prior to the peak in mysid production.

Table 4.7. The number of first sightings of cow/calf pairs per month compared to the mean number of whales per survey from 1998-2013 (excluding data from 2001-2007).

Date	Number of First Sightings of Cow/Calf Pairs	Mean Number of Whales per Survey
May	2	1.59
June	17	6.33
July	3	9.44
August	2	9.89

3.2.2. Calves

There is no correlation between annual foraging effort during a calf's first foraging season and its subsequent standardized return count ($r_s=0.175$, $p=0.413$, $n=24$), indicating that the amount of mysid density during a calf's first foraging season is not related to its level of site fidelity to Clayoquot Sound.

There is a significant positive correlation between a returning calf's annual residency time and annual foraging effort ($r_s=0.654$, $p<0.000$, $n=31$) (excludes first year residency time). Years when annual foraging effort was high (1998, 2010, 2011, 2013) returning calves had significantly different residency times than during years when annual foraging effort was low (1999, 2000, 2008, 2009, 2012) ($t(28.980)=-5.492$, $p<0.000$) (61 day mean versus 11 day mean, excludes first year residency time). These results suggest that annual fluctuations in mysid density are related to how long returning calves stay in Clayoquot Sound each year.

3.2.3. Cows

There is no correlation between a cow's annual residency time and annual foraging effort ($r_s=0.096$, $p=0.518$, $n=48$). The residency time of cows does not significantly differ ($t(46.643)=1.164$, $p=0.250$) between years with high annual foraging effort (1998, 2010, 2011, 2013) and years with a low annual foraging effort (1999, 2000, 2008, 2009, 2012) (26 day mean versus 18 day mean). These results indicate that annual fluctuations of prey are not related to the duration of residency for cows in Clayoquot Sound.

3.3. Comparison between Calves, Cows, and the Unclassified Whales of Clayoquot Sound

The mean return count of calves (2.54 years) is very similar to the mean return count of the unclassified whales from the catalogue (2.55 years, n= 190, excludes cows and calves). The mean return count of cows is 3.76 years which is defined as a low/moderate level of site fidelity, but is higher than the mean return count of unclassified whales (2.55 years) (Table 4.8).

There is a significant positive correlation between return count and residency time for calves, cows, and the unclassified whales from the catalogue. There is a significant positive correlation between a calf's annual residency time and annual foraging effort, and between annual residency time and annual foraging effort of the unclassified whales. There is no correlation between a cow's annual residency time and annual foraging effort (Table 4.8).

The mean residency time of calves (43 days) is higher than that of the unclassified whales (22 days), and cows (21 days). Calves have the greatest difference in residency time between high and low whale years (mean 50 day difference), whereas cows had no significant difference (mean 8 day difference). The unclassified whales from the catalogue had an 11 day difference in residency time between high and low whale years (Table 4.8).

Table 4.8. A comparison of site fidelity and residency time among calves, cows, and the unclassified whales in the catalogue.

	Calves	Cows	Unclassified Whales
Mean Return Count	2.54 years (38.75% Standardized Return Count)	3.76 years	2.55 years
Level of Site Fidelity	Low/Moderate	Low/Moderate	Low/Moderate
Mean Residency Time	43 days	21 days	22 days
Return Count vs. Residency Time	Significant Positive Correlation	Significant Positive Correlation	Significant Positive Correlation
Annual Residency Time vs. Annual Number of Whales	Significant Positive Correlation	No Correlation	Significant Positive Correlation
Mean Residency Time during “High” whale years	61 days	26 days	29 days
Mean Residency Time during “Low” whale years	11 days	18 days	18 days
Difference in Mean Residency Time between “High” and “Low” whale years	Significant Difference	No Significant Difference	Significant Difference

4. Discussion

The results from this chapter suggest that maternal learning is how whales are internally recruited into the PCFG. Even though this chapter only focused on one site within the PCFG’s range, a high number of calves were recorded. Since 1998 (with minimal data collection from 2001 to 2007), 30 calves (12.5 percent of the catalogue) have been sighted in Clayoquot Sound, which is a mean of 2.44 calves per year. In comparison, shore-based surveys of all migrating gray whales (not just the PCFG) from 2001 to 2009 yielded variable annual calf abundances ranging from 256 to 1528 individuals, with a mean of 737 calves per year (Perryman *et al.* 2010). Until now, the only PCFG calf estimate is from Calambokidis *et al.* (2010) who recorded 41 calves out of a total of 876 unique individuals (4.6 percent of their catalogue) from 1998 to 2008. Unfortunately, the study from Calambokidis *et al.* (2010) cannot be directly compared to this chapter because their study area was much larger (spanned from California to southern Alaska), and their number of calves was underestimated due to data collection inconsistencies between collaborators. However, the percentage of calves that were

resighted is independent of the number of calves recorded, and Calambokidis *et al.* (2010) reported that 54 percent of the calves in their study were resighted in at least one year, which is fairly similar to the percentage of returning calves reported in this chapter (50 percent). The higher resighting percentage reported by Calambokidis *et al.* (2010) is most likely related to the larger area surveyed in their study, which provided more opportunities for recording returning individuals. In this chapter, several cows and calves were recorded during the northern surveys that were also sighted in Clayoquot Sound, indicating that Clayoquot Sound is one foraging site within a larger foraging range. Thus, calves may have fidelity to a larger area, such as western Vancouver Island, and return to an adjacent site instead of Clayoquot Sound, and would be considered to be single visitors.

While almost half of all calves sighted in Clayoquot Sound return for at least one year, site fidelity differs between individuals and appears to be influenced by their mother's site fidelity and the duration of residency during their first summer. There was no correlation between the mean number of whales per survey during a calf's first summer and its subsequent standardized return count, suggesting that a calf's site fidelity is not primarily dictated by prey resources. Instead, a calf's standardized return count is positively correlated with its mother's return count, indicating that site fidelity is a trait that is transferred between mother and offspring. There is also a significant positive correlation between a cow's level of site fidelity and the duration of her calf's first year residency time. These results suggest that the duration of a calf's first year residency, which is governed by its mother, is how knowledge about specific foraging sites is communicated between cows and calves. The importance of the duration of first year residency is also demonstrated with the large difference between single visit and returning calves: 12 days versus 41 days respectively. Although the difference in first year residency is not statistically significant due to the low sample size, it is similar to the result reported by Weinrich (1998) for humpback whales. Similar to gray whales, humpback calves follow their mothers to specific foraging locations, and calves that spend greater than 10 days at a site are more likely to return to that site than cow/calf pairs that had residency times less than 10 days (Weinrich 1998). Due to sparse data I cannot calculate a threshold of first year residency time that can predict whether a calf

will return to Clayoquot Sound, but the large difference in residency time between single visit and returning calves suggests that the duration of first year residency plays a strong role in a site fidelity.

Among the cows, individual differences in site fidelity and residency time are present and may account for the differences in their calf's first year residency time. A cow's residency time is correlated to its level of site fidelity, and further relationships between residency time and site fidelity are evident once the group is split based on usage. Generally, there are two groups of cows that use Clayoquot Sound: one group (a) that only returns when accompanied by a calf, and the other group (b) that returns when accompanied by a calf and when solo. Residency time and site fidelity are lower for cows that only use Clayoquot Sound when accompanied by a calf (a) in comparison to cows that return regardless (b). Interestingly, the mean residency times of the two groups of cows are very similar to the mean first year residency times of single and returning calves: cows that only return to Clayoquot Sound with a calf (a) stay for a mean of 13 days, whereas cows that return with a calf and when solo (b) have a mean residency time of 35 days. Success of a whale foraging in a patchy environment may be partially dependent on the exposure to variety of feeding locations as a calf, with any one area containing a sufficient amount of prey at any given time (Weinrich 1998). If Clayoquot Sound is one location within a larger foraging range, then cows with high site fidelity to adjacent sites may forage in Clayoquot Sound if prey availability is relatively low at their primary foraging location and relatively high in Clayoquot Sound.

Within the group (b) of cows that returns to Clayoquot Sound with or without a calf, residency time also differs, with a significantly higher duration of residency time when a cow is accompanied by a calf versus when it is solo. The presence of a calf increases a cow's residency time, with cows being the only demographic whose annual residency time is not correlated with annual foraging effort. Because of the need to replenish blubber reserves after the northbound migration, the location of most foraging gray whales is closely associated with the presence of high levels of prey (Dunham & Duffus 2001, Feyrer & Duffus 2014). However, despite a cow's high nutritional demands of lactation (Lockyer 1981) and a growing calf's caloric requirements, many cow/calf pairs will forage in Clayoquot Sound during low mysid years.

The mean first sighting date of cow/calf pairs is roughly 41 days earlier than the arrival of the peak number of whales each summer. Cows will bring their calves to Clayoquot Sound early in the season instead of maximizing energy intake by foraging in other locations prior to peak of mysid density in Clayoquot Sound. Cows may select foraging locations that offer other benefits such as reduced feeding competition and protection from killer whale (*Orcinus orca*) predation on calves. There is an annual average of 100 killer whales that assemble around Unimak Island, Alaska (a main access point for gray whales entering the Bering Sea) in May and June, with an approximate consumption estimate of 100 calves and 20 juvenile gray whales (Matkin & Durban 2013). While killer whales also forage in various locations along the west coast of Vancouver Island, their concentrations are lower, and the varied topography in Clayoquot Sound offers calves protection from attacks. If a calf is able to make it to shallow water during an attack, it cannot be held underwater and drowned, nor can it be attacked from below (Matkin & Durban 2013). Clayoquot Sound makes a good nursery given that it has areas that contain mysid habitat (which is essential for lactating cows needing to intake energy) in very close proximity to shallow water, ideal for hiding and protecting calves when killer whales are in the region. However, mysid density differs between years (Feyrer & Duffus 2014), with low prey resources during years following sustained foraging pressure (Feyrer & Duffus 2011). Thus, each year, cows must weigh the benefit of residing in sheltered waters versus the cost of foraging in Clayoquot Sound when mysid density is low. In comparison to non-parenting whales that do not benefit from sheltered waters (since adults are rarely preyed upon) cows may tolerate lower mysid densities, which is reflected in the lack of relationship between annual residency time and annual mysid density.

In contrast to cows, the residency time of returning calves is tightly coupled with fluctuations in annual mysid density. If a calf returns to Clayoquot Sound, the duration of its stay is highly variable (with a mean difference of 50 days between high and low mysid years) and strongly influenced by mysid density, suggesting that they are opportunistic foragers. Despite the strong relationship between prey and residency time, a returning calf's residency time is also linked to its level of site fidelity, with a significant positive correlation between a calf's standardized return count and its mean

residency time. Thus, while annual mysid density (as given by the mean number of whales per survey) is the primary factor that is related to the duration of a returning calf's residency time, its level of site fidelity, which is related to its mother's site fidelity, also plays an important role. The influence of mysid density on residency time may change as female calves reach sexual maturity, with a transition from prey dominated residency patterns characteristic of calves, to residency patterns primarily governed by the presence of offspring. Although not recorded in this study, once female calves reach sexual maturity, presumably they will bring their offspring to the region that they visited during their first summer (as demonstrated by the significant difference in mtDNA between the PCFG and the rest of the eastern population, *e.g.* Lang *et al.* 2011) and their residency time will be less governed by prey. Unfortunately, because the gender of the calves is unknown, and because this study does not extend beyond the juvenile stage of these calves, it is unclear if the aforementioned patterns of site fidelity and residency time are specific to certain age and sex classes. For example, it is unclear whether adult males have the same level of site fidelity and patterns of residency time as breeding females, or if they tend to retain the opportunistic foraging tactics observed with the returning calves. Past genetic research of the PCFG has yielded a variety of results in regard to gender, with Ramakrishnan *et al.* (2001) finding a male biased sex ratio and Frasier *et al.* (2011) and Lang *et al.* (2011) finding a female bias. Knowing the gender ratio of the whales that forage in Clayoquot Sound, and for a larger spatial range such as western Vancouver Island, would help determine the function of the PCFG and sites such as Clayoquot Sound. Of particular interest would be a comparison of the gender ratio during high and low mysid years to determine if spatial use is, at least in part, sex dependent. Furthermore, a longer-term study is needed to confirm if the high variability in residency time of the returning calves is a function of age, or if it is typical behaviour of individuals that are not raising offspring. Given that juvenile marine mammals tend to require more energy relative to their body mass than mature marine mammals (Innes *et al.* 1987), and that juvenile mammals generally have higher energy requirements than similar-sized adults (Brody 1945, Wieser 1984), once a calf reaches sexual maturity it may have more flexibility in foraging tactics. Adult whales may be able reach satiation at lower mysid densities than juvenile whales, and bigger bodied adults may compete better with other

individuals during years when mysid density is low, resulting in a smaller variation in residency time between high and low mysid years. Thus, patterns in residency time may differ between juvenile and adult whales and may also differ by gender and reproductive status (*e.g.* Valsecchi *et al.* 2010).

When cows and returning calves are compared to the unclassified whales in the catalogue, differences were evident between the three groups. Returning calves and cows were the most dissimilar, with the unclassified whales situated between the two groups. The mean residency time of the unclassified whales was very similar to that of the cows, but like the calves, they had a significant difference in residency between high and low mysid years. Interestingly, there are a number of whales in the unclassified group that are considered to have a high level of site fidelity, or are at the upper end of the low/moderate group, that are not known to be cows. These individuals are sighted in Clayoquot Sound during low mysid years, which indicates that loyalty to Clayoquot Sound is not specific to cows. Thus, while Clayoquot Sound functions as a nursery for many cow/calf pairs, other adult whales also use the site regularly.

While this study has focused on fine scale internal recruitment patterns, the results from this chapter should also be situated in the context of broader temporal and spatial scales. The presence of a group of whales with site fidelity to Clayoquot Sound offers an opportunity to analyze the origin of site fidelity to southern feeding grounds, and more generally, the conception of the PCFG. Given that foraging sites such as Clayoquot Sound offer appreciable shelter from killer whales for cow/calf pairs, it is curious that only some cows decide to reside in southern feeding grounds while others continue to the Bering and Chukchi Seas. The origin of the PCFG is unknown but was probably based on a combination of factors such as an increase in sea ice during the Pleistocene glacial maxima and the subsequent usage of southern feeding grounds (Lang *et al.* 2011, Pyenson & Lindberg 2011). Gray whales may have survived glacial episodes by employing diverse foraging techniques that allowed them to switch from suction feeding on benthic prey in the arctic, to filter feeding in southern feeding grounds similar to PCFG whales (Pyenson & Lindberg 2011). However, these filter feeding gray whales were probably the most vulnerable to commercial whaling because of their proximity to coastal human settlements, their preference for sheltered embayments, and because of

their long residency time (Pyenson & Lindberg 2011). During post-whaling population growth, the PCFG may have arisen from a foraging specialization that was maintained by a small number of surviving individuals and passed down via maternal learning to their calves. If this hypothesis of the conception of the PCFG is correct, cows with site fidelity to southern foraging locations such as Clayoquot Sound are passing down knowledge to their offspring that has been maintained by specific matrilineal lines since the last epoch. The results from this chapter indicate that maternal learning, and more generally internal recruitment into the PCFG, is an important and complex process that facilitates the transfer, and maintenance, of knowledge through time. The PCFG should be managed as a demographically independent unit to protect the individuals passing this knowledge to their offspring.

5. Conclusion

In this chapter I characterized internal recruitment, and more specifically, maternal learning at a fine scale in Clayoquot Sound. I discovered some calves never return to the study site whereas other calves return almost every year since their birth. My analysis demonstrated that a calf's level of site fidelity is not related to the level of prey present during its first summer, but instead is related to its mother's level of site fidelity and the duration of its first year residency time. The large variation of site fidelity observed among the calves is related to the large variation in site fidelity among the cows. Cows that only used Clayoquot Sound when accompanied by a calf had a lower level of site fidelity than the cows that visited Clayoquot Sound regardless of whether they were nursing a calf. Clayoquot Sound offers shelter from killer whale attacks on calves while still providing prey resources for lactating cows.

I examined how annual variability in mysid density (as given by the mean number of whales per survey) is related to the residency time of cows and calves, and found that calves had a large difference in residency time between high and low mysid years. The annual residency time of cows is not related to changes in the mean number of whales per survey, but is related to the presence of a calf. I hypothesized that as juvenile whales reach sexual maturity their residency patterns will become more similar to those of the cows because their caloric requirements will decrease relative to their mass, and they will be better able to compete with bigger bodied adults. Future research should focus on how gender and age affects residency time and site fidelity.

The results of this chapter demonstrate that internal recruitment is a complex process that requires further analysis. Any new research focusing on the PCFG should study internal recruitment patterns at a fine scale in other locations, and be collaborative to better quantify the exchange of individuals within the PCFG. This knowledge would allow the scientific community to better define what is meant when a whale is classified as an internal or external recruit, and to understand the relative importance of both in creating population structure.

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Chapter 5 : Conclusion

The objective of this study is to characterize fine scale habitat use and site fidelity of eastern north Pacific gray whales (*Eschrichtius robustus*) in one foraging site within the Pacific Coastal Feeding Group's (PCFG) foraging range. I approach this study by examining site fidelity to Clayoquot Sound in increasing detail at different time scales. The impetus for this study is the gap in knowledge about the variables that drive the changing distribution of whales within the PCFG's foraging range (e.g. Calambokidis *et al.* 2010). Although various genetic studies (e.g. Ramakrishnan *et al.* 2001, Steeves *et al.* 2001, Frasier *et al.* 2011, Lang *et al.* 2011) and collaborative photographic identification studies (e.g. Calambokidis *et al.* 2002, 2004, 2007, 2009, 2010) have been carried out, the variables that potentially structure the PCFG, such as maternal learning and predator/prey dynamics, have not been studied in detail. Due to the low but significant difference in mtDNA between the PCFG and the rest of the eastern north Pacific population, Lang *et al.* (2011) suggest that maternal learning may be creating intergenerational site fidelity to the PCFG's foraging range. However, changes in the distribution of prey within the PCFG's foraging range likely drive the movement of whales on multiple spatial and temporal scales (e.g. Fauchald 1999) and thus may also influence site fidelity. I examine these variables in this thesis.

In Chapter Two, I analyze why Clayoquot Sound endures as a foraging area for PCFG whales through time by identifying the properties of sites where whales forage intra- and inter-annually. Using the variability recorded in 17 field seasons of whale census surveys (1997-2013) as a proxy for fluctuations in prey, I determine which sites within the study area are productive by the presence of foraging whales. In the first section of Chapter Two I track the distribution of foraging whales intra-annually in four different sub-areas within the study area at a fine temporal scale of nine 2-week periods. The distribution of foraging whales changes through space depending on whether mysid abundance (given by the mean number of whales per survey) is relatively low or high throughout the study area. In a season following heavy predation when mysid abundance is relatively low, sub-area 2 (Cow Bay) contains the highest number of foraging whales. After a period of predator release when mysid abundance is relatively high, the majority

of foraging whales are located in sub-area 3 (Siwash Point to Rafael Point). Analysis of the fine scale temporal distribution of foraging whales produces similar results. Sub-area 2 contains the highest number of whales in the time periods when mysid abundance is relatively low during the beginning and end of the season. Sub-area 3 contains the majority of foraging whales mid to late season when mysid abundance peaks intra-annually. Based on the results of the intra-annual spatial and temporal analysis, Cow Bay is the core of the study area that sustains foraging whales when mysid abundance is low elsewhere. In comparison to the other sub-areas, Cow Bay has the highest benthic topographical complexity and lowest current velocity, suggesting that these properties influence mysid recovery and persistence.

In the second section of Chapter Two, I examine the inter-annual distribution of foraging whales over a finer spatial scale (60 m² cells) but a coarser temporal scale of 1-year periods for 17 years. The cells where foraging whales were observed the most frequently are located in Cow Bay, but foraging persistence is also strongly associated with the 10 metre isobath. Similar to the intra-annual analysis, the presence of foraging whales through time is related to high benthic topographical complexity, with a strong positive correlation between cells that contain a high number of foraging years and high mean benthic topographical complexity. The combination of the results from the intra- and inter-annual analysis suggests that high benthic topographical complexity, low current velocity, and shallow depth are important constituents of mysid habitat and facilitate mysid recovery after predation. The sustained pressure from foraging whales and the recovery of mysids create interdependent oscillations in predator-prey abundance forming the dynamic equilibrium (Burnham 2012), which has occurred in the study area for the past 17 years.

Although mysid productivity has been shown to affect the number and distribution of whales in Clayoquot Sound (Dunham & Duffus 2001, Olsen 2006, Feyrer 2010, Burnham 2012, Feyer & Duffus 2014), its influence on site fidelity has not been studied. In Chapter Three, I begin by assessing the level of site fidelity of the whales in Clayoquot Sound, and then analyze how annual fluctuations in mysid density (given by the mean annual number of whales per survey) are related to site fidelity and residency time. For this analysis I use photographic identification data collected twice a week

between 1998-2000 and 2008-2013, and sporadically between 2001-2007. I also use photographic identification data taken opportunistically north of the study area in 2002, 2006-2010, and 2012 to estimate the exchange of individuals between Clayoquot Sound and another foraging area. I found, on average, a low/moderate level of site fidelity and that whales also regularly feed in northern foraging areas. These results indicate that the study area is one site within a larger foraging range, and the whales of Clayoquot Sound are part of a larger population such as the PCFG.

Using the mean number of whales as a proxy for mysid density, I test how mysid density is related to site fidelity and residency time. I found a negative relationship between the annual number of whales and mean annual return count, indicating that during high mysid years, a greater number of single visit whales, and whales with a low level of site fidelity to Clayoquot Sound, are present than during poor prey years. I examine the affect of intra-annual changes in mysid density by calculating the mean number of whales per survey for two-week intervals. There is a significant positive relationship between the number of single visit whales and the mean number of whales per survey for each two-week interval, indicating that single-visit whales tend to be opportunistic feeders that visit Clayoquot Sound when mysid density is high. Mysid density, represented by the mean number of whales per survey, is also related to residency time with a strong positive correlation between the two variables. Based on these results I accept the hypothesis that mysid density is related to the mean level of site fidelity and residency time of whales foraging in Clayoquot Sound annually.

In Chapter Four, I characterize internal recruitment via maternal learning within Clayoquot Sound. I identify cow/calf pairs using photographic identification data collected bi-weekly between 1998-2000 and 2008-2013, sporadically between 2001-2007, and from opportunistic northern surveys. I found a positive correlation between a cow's site fidelity and the number of days the pair remains in the study area. There is also a positive correlation between a cow's site fidelity and her calf's site fidelity. These results indicate that site fidelity may be transferred from mother to offspring, and that the duration of a calf's first year residency time is related to its mother's site fidelity. Site fidelity varies between calves with some individuals never returning to the study site, whereas others return almost every year since their birth.

The level of mysid density (given by the mean annual number of whales per survey) during a calf's first summer is not related to a calf's site fidelity to the study area, but instead is related to the large variation in site fidelity among the cows. Cows that only use the study area when accompanied by a calf have a lower average level of site fidelity than cows that forage in the study area with or without a calf. Within the group of cows that returns to Clayoquot Sound regardless of maternal status, residency time also differs, with a significantly higher duration of residency time when a cow is accompanied a calf. The presence of a calf is the only variable that appears to affect a cow's residency time, with cows being the only demographic whose annual residency time is not correlated to annual mysid density (represented by the mean annual number of whales per survey). Instead, cows may be selecting the study area because it offers other benefits for their offspring such as reduced feeding competition and protection against killer whale (*Orcinus orca*) predation. In contrast to cows, calves have a large difference in annual residency time between high and low mysid years. I hypothesize that as female juvenile whales reach maturity, their residency patterns will be governed less by fluctuations in prey, and more by the presence of offspring. Because the gender of the calves is unknown, it is unclear whether patterns of site fidelity and residency time are specific to certain age and sex classes. Future research should focus on whether adult males and post-breeding females have similar residency times as juvenile whales. The results from this chapter demonstrate that internal recruitment is a complex process that maintains spatial knowledge through time.

Understanding the variables that affect the level of site fidelity of PCFG whales to different foraging areas is of value because they are ecologically, culturally, and economically important. In Clayoquot Sound, gray whales have a strong top-down effect on the community structure of prey species (Feyrer 2010, Burnham 2010, Feyrer & Duffus 2011), have a foraging association with marbled murrelets (*Brachyramphus marmoratus*) (Muirhead 2010), and other undocumented ecological relationships. The presence of foraging whales in Clayoquot Sound is also vitally important to the local tourism industry, and is part of the cultural identity of the local First Nation (Duffus *et al.* 2013). Thus, effective management and the conservation of PCFG whales are important to the local ecosystem and people in areas they occupy. Although the absence of

differentiation in nuclear DNA between the PCFG and the rest of the eastern north Pacific population indicates some mixing, the significant difference in mtDNA suggests that the PCFG is demographically independent (Lang *et al.* 2011). Managing two populations as one when dispersal between them is low could result in depleting one of the populations (Taylor 1997). Evidence from whaling data suggest that sub-populations of baleen whales existed that were depleted by commercial whaling and failed to recover (Clapham *et al.* 2008). Proposed threats to eastern north Pacific gray whales include entanglement in fishing gear (Baird *et al.* 2002), and disturbances to breeding, feeding and migratory areas (see Rugh *et al.* 1999, Moore & Clarke 2002, Fisheries and Oceans Canada 2010). Although governments are able to manage the frequency of anthropogenic disturbances, the effectiveness of conservation efforts may be increased if important foraging and breeding locations are protected (Ingram & Rogan 2002, Bailey & Thompson 2009).

The conclusions drawn from this study should be interpreted in the context and limitations of this research. The aggregation and classification of spatial and temporal data may have introduced statistical bias (*e.g.* the modifiable areal unit problem; Jelinski & Wu 1996), but allowed data to be analyzed at a finer resolution. Direct measurements of mysid density may have increased the accuracy of the statistical tests used to assess the relationship between site fidelity and prey productivity, but even with the addition of mysid data, the inherent noise in ecological data and the confounding linkages to other foraging areas would still be problematic (Feyrer 2010). Photographic identification has been shown to be a reliable method of identifying gray whales (Darling 1984, Calambokidis *et al.* 2010), and any errors associated with matching individuals were minimized by the reanalysis of all matches made prior to 2011, and through redundancy of experienced matchers for all photographs between 2011-2013. The 62 whales in the temporary catalogue that were not included in this analysis may represent unique individuals, and thus the total number of individuals sighted in Clayoquot Sound since 1997 ($n=240$) may be underestimated. Site fidelity may have also been underestimated due to the lower photographic identification data collection effort between 2001-2007, but these potential underestimations most likely did not significantly impact my overall assessment of site fidelity to Clayoquot Sound. The size of the study area is also a

limitation because it restricted analysis of coarse scale PCFG whale distributions, but its relatively small size permitted frequent and detailed analysis of habitat use, site fidelity, and internal recruitment. However, gender and age data for a higher number of individuals would have allowed a more concrete analysis of the relationship between ontogenesis and site fidelity, and should be the subject of future work.

In this study I set out to characterize fine scale habitat use and site fidelity of gray whales in Clayoquot Sound to gain a better understanding of the influence that maternal learning and fluctuations of prey have on site fidelity. The results from this study indicate that while Clayoquot Sound is part of a larger foraging range, some individuals have a high level of site fidelity to the area specifically. The large difference in residency time between juvenile whales and cows, during high and low mysid years, indicate that age, gender, and reproductive status may affect site fidelity. Cows may tolerate lower prey densities in sites that offer protection for their calves, and thus their intra-annual movements among foraging areas may differ to those of adult males, non-breeding females, and juvenile whales. The movements of non-parenting whales are most likely governed by the distribution of prey as indicated by the positive relationship between residency time and annual foraging effort. When mysid productivity is high in Clayoquot Sound, a higher number of single visit whales, and individuals with a low return count, are observed. These individuals may be juveniles, males, and females without calves that move throughout the PCFG's foraging range selecting areas with high prey productivity relative to other sites. Sites such as Clayoquot Sound, that persist as foraging areas amid cycles of predator disturbance and prey recovery, are most likely part of a network of foraging areas where spatio-temporal fluctuations in prey density affect the movements of whales intra- and inter-annually. It is the interplay between fluctuations in prey productivity, and the age and gender of individuals, that most likely influence the distribution of PCFG whales intra- and inter-annually. Based on these results, it is clear that further analysis is needed to gain a better understanding of the relative strength of these variables. Future work should be collaborative and include variables such as ecological data, age, and gender to better understand the population structure of the PCFG. Specifically, the relative importance of internal and external recruitment should be studied to determine if PCFG cows are exclusively internal recruits. If externally

recruited whales bring their calves to the PCFG's foraging range, and these calves return to the region as adults with their own calves, then, from a management perspective, any losses of PCFG whales may be offset by immigration into the group (Lang *et al.* 2011). However, if the majority of cows are internally recruited then the PCFG should be managed separately from the rest of the eastern north Pacific population. Collaborative long-term photographic identification studies and genetic research are needed to better understand the roles of internal and external recruitment.

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