RESTING METABOLISM, ENERGETICS, AND SEASONAL DISTRIBUTION OF PACIFIC WHITE-SIDED DOLPHINS

by

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Abstract

Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) are one of the most abundant cetaceans in British Columbia and throughout the North Pacific Ocean. However, little is known about their seasonal distributions and energy requirements. I analyzed sightings of dolphins attained opportunistically by volunteer observers and from scientific surveys—and found that Pacific white-sided dolphins have been seen with increased frequency along the BC coast over the past 54 years, and seasonally over the past 8 years. The sightings data showed a southward range shift from the 1950s to 2010, and a seasonal movement from offshore to nearshore waters concurrent with the timing of the herring spawn on the BC coast. I deduced whether seasonal movements reflect seasonal shifts in energy requirements by measuring resting metabolic rates and total energy intake for three captive white-sided dolphins twice per month for one year. Open-circuit gas respirometry revealed relatively high resting metabolic rates (~30 MJ day^{-1} or ~0.3 MJ $kg^{-1}day^{-1}$) suggesting that white-sided dolphins may need high-energy prey to fuel their energetic requirements. Average resting metabolic rates of the three dolphins were constant throughout the year despite an increase in food consumption in the fall (October to December). I used these average resting metabolic rates and other parameters associated with growth, activity and assimilation efficiency to inform a generalized bioenergetic model and estimate the food requirements of Pacific white-sided dolphins globally, regionally, and locally. My bioenergetic model predicted that wild dolphins require ~30 MJ day^{-1} for calves, ~60 MJ day^{-1} for juveniles, ~65 MJ day^{-1} for adults and pregnant females, and ~90 MJ day^{-1} for lactating females. These energy requirements are ~50% higher than observed for dolphins fed in captivity, and are generally higher than estimates for other similar sized small cetaceans inhabiting temperate waters. My model predicts that an average sized dolphin (78 kg) in the wild would consume ~10 kg of fish per day, or about 13% of its bodyweight. Pairing information about prey requirements and seasonal distributions of dolphins with fisheries data can be used to assess spatial overlap between dolphins and fisheries, and may assist in reducing entanglement, by-catch, and conflict over prey.

Preface

Various collaborators contributed data for analyses in this thesis. Stomach contents from by-caught and stranded dolphins, as well as Pacific white-sided dolphin sightings and survey tracklines from Cetacean Survey Cruises were provided by J.K.B. Ford at Fisheries and Oceans Canada. Sightings data collected opportunistically, as well as the model of observer effort were contributed by L.G. Barrett-Lennard and J.K.B. Ford at the BC Cetacean Sightings Network, through the Vancouver Aquarium and Fisheries Oceans Canada. I received statistical advice from R. Ahrens, B. Battaile, R. Joy, A. Thomas, and B. Young. Matthew Foster made the map shown as Figure 2.16 using NASA's Giovanni data.

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Chapter 1: Introduction

The Pacific white-sided dolphin (*Lagenorhynchus obliquidens*) is an abundant cetacean that inhabits the temperate North Pacific Ocean from California to the Bering Sea, and south to Taiwan (Stacey & Baird, 1991). They number ~1 million animals (95% CI ~200,000 - 4,000,000 Buckland *et al.*, 1993; 95% CI ~150,000 - 7,000,000 Miyashita, 1993) and exploit a large habitat that includes oceanic and nearshore waters. At least 25,000 of these ~1,000,000 dolphins in the North Pacific are thought to reside in the coastal waters of British Columbia (Williams & Thomas, 2007).

Sightings of Pacific white-sided dolphins by local mariners suggest that dolphins shifted their range in the mid-1980s to the nearshore waters on the north and central coasts of British Columbia (Heise, 1996). They also began to be regularly seen in the southern coastal waters of BC, including the Strait of Georgia which is considered one of the most heavily human-used marine ecosystems in Canada (DFO, 2012). Such decadal shifts in distributions may have increased the spatial overlap of dolphin and human uses.

Knowing where and when Pacific white-sided dolphins occur in British Columbia waters may help fisheries avoid catching and entangling dolphins, or other causes of conflict between anthropogenic activities and dolphin occurrences. Identifying the coastal areas and seasons when predator-prey spatial overlap occurs would also assist with managing a prey-base for dolphins and preventing competition between dolphins and fisheries over common prey resources.

Pacific white-sided dolphins are gregarious and forage in coordinated groups on high-energy fish species such as herring and salmon in British Columbia (Heise, 1997; Van Waerebeed & Wursig, 2002; Morton, 2000). These fish species are culturally and commercially important to people. White-sided dolphins are considered to be an acrobatic, high-energy species (Van Waerebeed & Wursig, 2002) that may have elevated energy needs and may exert ecosystem-level effects on prey. Marine mammals have often been cited as having heightened energy needs (Worthy, 2001; Benoit-Bird, 2004; Barlow *et al.*, 2008; Spitz *et al.*, 2010) that put them in conflict with fisheries (Trites *et al.*, 1997). However, the extent to which Pacific white-sided dolphins are detrimental to fisheries or to fish stocks, and currently, whether their nutritional needs are adequately met, are unknown.

1.1 Research

A quantitative investigation of the spatial distribution of Pacific white-sided dolphins in BC, both temporally and seasonally, is long overdue. Although anecdotal evidence indicates a shift in distribution to more southern waters since perhaps the 1950s, and a more recent shift into nearshore waters since the 1980s, no empirical evidence has been published to this end. Combining spatial distribution with food requirements of the dolphins would allow for estimates of biomass of fish consumed by dolphins in local areas, or near commercially or culturally important fish stocks.

Food requirements of cetaceans are difficult to quantify because they spend the majority of their time underwater where it is difficult to observe them. There are three common methods that researchers use to quantify food intake of cetaceans. Stomach content analysis of dead animals can provide information regarding which prey species are consumed. However, knowledge of the predator's feeding frequency and food passage rates is needed to determine ultimate food intake (Ohizumi & Miyazaki, 1998). Researchers have also estimated food requirements of wild dolphins and porpoises by determining the feeding rates of captive animals (Kastelein *et al.*, 1999; Kastelein *et al.*, 2000; Kastelein *et al.*, 2003b). However, food intake of captive and wild animals may differ from the food requirements of wild con-specifics due to different activity levels and different food availabilities.

A third method used to study cetacean food requirements is bioenergetic modeling. Bioenergetics is study of energy flow and energy transformation in living systems. Over the long-term, living systems will reach an energy balance where:

$$Consumption = feces + urine + respiration + production$$ [1]

Bioenergetics models have been used to estimate the food requirements of several species of cetaceans (e.g.,Kriete, 1995; Benoit-Bird, 2004; Williams *et al.*, 2004; Barlow *et al.*, 2008; Noren, 2010).

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[1] *respiration* includes maintenance and activity, and *production* includes growth, gestation and lactation

One of the major parameters used in bioenergetic models is a species-specific resting metabolic rate. Some research suggests the resting metabolic rates of marine mammals are elevated when compared with terrestrial species (Brodie, 1975; Snyder, 1983; Costa & Williams, 1999; Williams, 2001; Hunter, 2005). However, other researchers suggest that marine mammals and terrestrial mammals have similar maintenance metabolic rates (Gaskin, 1982; Lavigne, 1982; Worthy, 1987; Kasting *et al.*, 1989; Williams *et al.*, 1992).

1.2 Thesis Structure

My thesis contains 5 chapters beginning with this brief overview of my research objectives (Chapter 1). I then assess areas of high sightings density per unit of sightings effort of groups of Pacific white-sided dolphins on the coast of British Columbia (Chapter 2) using scientific surveys and opportunistic sightings by volunteers to identify dolphin hot-spots and seasonal and decadal changes in high-use areas. To determine the food requirements of Pacific white-sided dolphins and deduce whether or not seasonal changes in metabolism or food intake drive seasonal changes in distribution, I begin by measuring the resting metabolism of three dolphins for one year using open-circuit gas respirometry at the Vancouver Aquarium (Chapter 3). I use these measures of metabolism to construct a bioenergetic model that estimates the total food requirements of Pacific white-sided dolphins globally, regionally, and locally (Chapter 4). I then place the general conclusions from my analyses of spatial distribution and food requirements of white-sided dolphins in BC within a management framework. Data Chapters 2, 3 and 4 are written as manuscripts, and contain some necessary repetition of information.

Chapter 2: Seasonal and decadal shifts in the distribution of Pacific white-sided dolphins in coastal British Columbia

2.1 Summary

Pacific white-sided dolphins are thought to number ~1 million individuals in the North Pacific Ocean, and at least 25,000 in the British Columbia (BC) portion of their range. However, little is known about how white-sided dolphins are distributed over the oceanic and shelf regions of the North Pacific, and whether their distributions change seasonally. I used effort-adjusted sightings of Pacific white-sided dolphins in BC to identify seasonal hot-spots of dolphins from 2002 to 2010. I also used opportunistic sightings from the past 54 years to assess whether areas used by dolphins had changed with time. A kernel density analysis of high sighting densities of dolphins showed elevated use of the nearshore waters of the central BC coast in winter (January to March). The data also revealed a seasonal movement of dolphins from offshore waters (where sightings are highest during summer and spring) to nearshore waters in winter. This movement coincides with the spawning of Pacific herring (*Clupea pallasii*) on the BC coast, and may reflect a seasonal dietary preference of dolphins for herring. A non-effort-corrected analysis of opportunistically sighted dolphins showed that Pacific white-sided dolphins have been frequently sighted off southern Vancouver Island since the 1990s, and that their distribution has expanded southward in BC waters since the 1950s. This expansion may be related to the recovery of Pacific sardines (*Sardinops sagax*) in southern BC. Hot-spots of dolphin occurrences and data on seasonal movements can be used to assess spatial overlap with fisheries, and reduce entanglement, by-catch, or potential conflict over prey resources.

2.2 Introduction

At least 25,000 Pacific white-sided dolphins occur in the coastal waters of British Columbia (Williams & Thomas, 2007). This relatively small dolphin is likely the most abundant cetacean in BC waters, but is relatively poorly studied. Pacific white-sided dolphins are known to travel in large groups and forage cooperatively on salmon and herring in BC

(Heise, 1997; Morton, 2000), and are believed to have high daily food-requirements (Chapters 3 & 4). However, relatively little else is known about their ecology, habitat requirements or spatial distribution in BC waters.

Small cetaceans are inherently difficult and often cost-prohibitive to study in the wild. This is particularly true for determining where they go from day to day or from season to season. Systematic scientific surveys have been used with some success to identify habitat and patterns of use for some species of cetaceans (e.g., Barlow & Forney, 2007). However the surveys conducted to date in British Columbia have not always met the restrictive requirements of transect designs to quantitatively estimate habitat use or abundance (e.g., Ford *et al.*, 2010a). Opportunistic sightings collected by volunteer observers are another data source that can be used to assess animal distributions (e.g., Wing, 1943; Kerlinger *et al.*, 1984; Pandolfino & Seudkamp Wells, 2009), but may be limited by a lack of information about observer effort, and the difficulty of controlling the quality of incoming data (Evans & Hammond, 2004).

The spatial distribution of Pacific white-sided dolphins in British Columbia is unknown but can be assessed using two complementary datasets. The first dataset consists of 8 years of dedicated cetacean surveys conducted by Fisheries and Oceans Canada from 2002 to 2010 (DFO; http://www.pac.dfo-mpo.gc.ca/index-eng.htm), and the second dataset contains over 50 years of opportunistically reported dolphin sightings from observers across the British Columbia coast, although sightings prior to the 1990s were only sparsely collected (British Columbia Cetacean Sightings Network; BCCSN; http://wildwhales.org). I analyzed these two datasets separately to identify the coastal areas of British Columbia used by Pacific white-sided dolphins, and to assess whether their distributions change seasonally. I also used these data to assess whether temporal shifts have occurred over the past 5 decades in areas of importance to Pacific white-sided dolphins.

The goal of my study was to identify regionally important areas used by Pacific white-sided dolphins in British Columbia. I also aimed to assess temporal and seasonal changes in dolphin distributions, and to evaluate the merits of opportunistic data collected by volunteer observers relative to data from line transect surveys collected by trained scientists. My study shows how two complementary datasets can be used to answer important questions about the spatial distribution of under-studied species of cetacean. It also provides data on seasonal distributions of dolphins in British Columbia that may assist in reducing conflict with human use of the same areas.

2.3 Methods

Waters along the British Columbia coast (Fig. 2.1) were surveyed for Pacific white-sided dolphins by Fisheries and Oceans Canada (DFO) and by volunteers who reported opportunistic sightings of Pacific white-sided dolphins to the British Columbia Cetacean Sightings Network (BCCSN). I evaluated whether dolphins exhibited seasonal movements from offshore to nearshore waters. Offshore waters were defined as waters greater than 10 nautical miles from shore and encompassed the bulk of the BC coastline that resembles an open ocean environment. Nearshore waters were defined as waters within 10 nautical miles of shore and encompassed all the sheltered water ways in BC and areas where forage fish spawning events are likely. Survey methodologies are detailed below.

2.3.1 Scientific surveys for Pacific white-sided dolphins

Seasonal at-sea surveys were undertaken to detect cetaceans in BC waters from 2002–2010 (*winter*–January-March, *spring*–April-June, *summer*–July-September, and *fall*–October-December; see Ford *et al.*, 2010a). The surveys were conducted aboard Coast Guard research ships and other vessels ranging in length from 25.5–69.0 m, with observation platform heights from 7.0–12.8 m and cruising speeds from 7–12 knots (Ford *et al.*, 2010a). Two observers kept constant watch at bridge-height when conditions for "on-effort" observation status were met (i.e., Beaufort Sea State <5, visibility >1 nautical mile, ship speed > 5 knots). The observers stood at parallel sides of the ship on the observation platform, and scanned a 100° arc from 10° across the bow to 90° from the ship's heading in either port or starboard direction. Scans included all waters from alongside the ship to shore (narrow passages) or from alongside the ship to the apparent horizon. Observation scans alternated between naked-eye scans and binocular scans using Fujinon® 7×50 binoculars with a reticle.

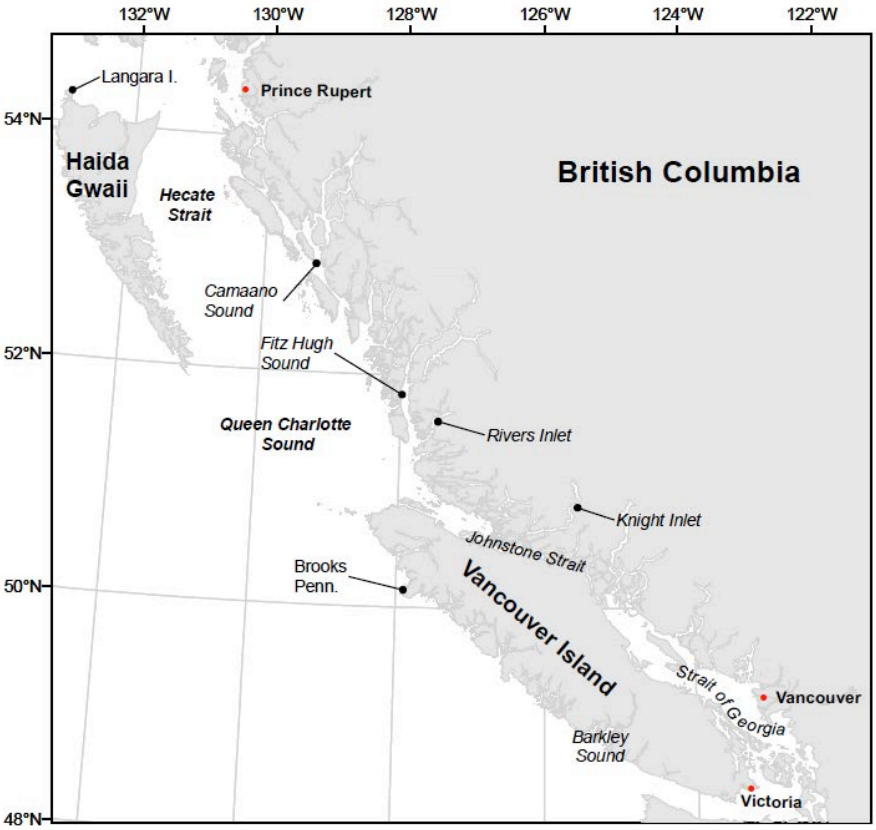

Figure 2.1 Coastal waters of British Columbia showing place names referred to in the text.

Survey methodology is described in detail by Ford *et al.* (2010a). In brief, observers sighting groups of Pacific white-sided dolphins immediately reported the distance (either as the proportion of a reticle measured from the horizon or from land, or in metres when cetaceans were within 500 m of the ship) and the bearing off the bow to the sighting (read from a pelorus). They often used a pair of "big-eyes" (Fujinon® 25×150 MTM heavy duty military binoculars with reticles) to count the number of individuals in the group. A group (constituting a sighting) of dolphins was defined as one cohesive unit of dolphins.

I plotted the ship tracks from GPS data and the locations of Pacific white-sided dolphin sightings following the methods of Lerczack and Hobbs (1998; see also Errata, 1998).

Survey Effort. I only used effort and sightings data collected when the ship and observers were deemed to be "on-effort". Ship track-lines covered on "on-effort" status and during each cruise were not always consistent from year to year or from season to season however surveys were conducted across multiple years and in all seasons (Ford *et al.*, 2010a). I divided the survey data into two subsets to deal with these inconsistencies and still meet my objectives to test for seasonal patterns of distribution in nearshore (within 10 nautical miles of shore) and offshore (greater than 10 nautical miles from shore) waters. One subset included all of the coastal areas that were surveyed in all seasons, and was composed of mostly nearshore waters. I used this data set to test whether sightings densities per unit effort in nearshore waters were significantly different between seasons. The second subset of data included both nearshore and offshore waters surveyed only in summers. I used this second data subset to test whether or not sightings densities per unit effort were significantly different between offshore and nearshore waters in summer.

The *Central Coast* of British Columbia was defined for this study as an area of ~8900 km^2 (~2600 nautical miles^2) that was surveyed multiple times (in part or in whole) in all four seasons and in multiple years from 2002–2010. Within this area, 5 surveys occurred during winter, 7 surveys occurred in spring, 11 surveys in summer, and 6 surveys in fall.

I used ArcGIS version 9.3 (ESRI) to overlay each “on-effort” ship-survey track-line as it was recorded by GPS. I created a separate layer in the GIS for each season and included the track-lines from each cruise conducted in that specific season in all years. I used the *buffer* analyses tool to add a 3 nautical mile buffer around each track-line, and assumed a constant probability of detection within that buffer in all seasons. Restrictive criteria for “on-effort” status meant that sea states and visibility were relatively consistent between seasons while data were being collected. Once track-lines were buffered, I used the *merge* tool to combine all buffered track-lines into one polygon layer while maintaining a separate polygon for each buffered track-line. This allowed me to sum the number of overlapping buffers in each spatial area. I then overlaid a 5×5 km gridded cell layer and used the *clip* tool in ArcGIS to clip the grid to the coastline (Canadian vector shoreline basemap of British Columbia, Canadian Hydrographic Service, Department of Fisheries and Oceans). I performed a *spatial join* between the grid layer and the overlapping buffers layer, which allowed me to count the number of overlapping buffered track-lines in each grid cell. This count enabled me to quantify effort (defined as the number of times each grid cell was visited during “on-effort” survey status).

The *Extended Coast* study area was defined as an area of ~67,000 km^2 (19,500 nautical $miles^2$) that included both offshore and nearshore waters, and also encompassed much of the *Central Coast* study area. Parts of the *Extended Coast* of British Columbia were surveyed 15 times during summers between 2002 and 2010. I used the same methods that I employed for the *Central Coast* study area to determine survey effort for each grid cell in the *Extended Coast* study area.

Survey data – Sightings Density per Unit Effort (SDUE). Sightings density was determined by taking the number of groups of dolphins recorded within a grid cell (summed over all surveys in one season, or over all surveys in either nearshore or offshore grid cells), performing a *spatial join* to the grid cell to get a sightings *count* per grid cell, and dividing it by the area of the grid cell to determine the number of sightings per km^2 (= sightings density). I then divided the sightings density by the effort value (number of ship visits to grid cell while "on-effort") to obtain a single sightings density per unit effort (= SDUE) value for each polygon grid cell.

I calculated distance to shore and kernel densities using the *Hawth's toolbox* in ArcGIS to *convert polygons to points*. This gave me one point for each grid cell, which was placed in the center of the polygon, and had an associated sightings density per unit effort value. I used the Canadian vector shoreline basemap of British Columbia (Canadian Hydrographic Service, Department of Fisheries and Oceans) to determine distance to shore of each sightings density per unit effort point, and ran a *spatial join* between the sightings density per unit effort point layers and the BC coast layer. I classified all sightings density per unit effort points that occurred within 10 nautical miles of shore as "nearshore", and classified all sightings density per unit effort points that occurred over 10 nautical miles from shore as "offshore". I also used a *Kernel density* analyses tool from the *spatial analyst extension* in ArcGIS to visualize areas of dolphin sightings density per unit effort hot-spots on the coastline. I then exported my final GIS layer as a spreadsheet, and conducted data analyses using R (R Core Development Team, 2012).

Survey data – changes in group size. I used the non effort-corrected sightings data collected on the DFO surveys to assess whether the number of individuals in the groups of dolphins reported were significantly different between seasons (Central Coast), or between nearshore and offshore waters (Extended Coast). Observers counted and recorded the individuals in each group and as the "Best Count" in the DFO database. I performed a *spatial join* with the non effort-corrected sightings data and the BC Coastline layer to determine distance to shore of each sighting, and again classified all nearshore sightings as within 10 nautical miles of shore, and all offshore sightings are more than 10 nautical miles from shore. I exported the non effort-corrected data including the "Best Count" field from ArcGIS into a spreadsheet for data analyses in R (R Core Development Team, 2009).

Survey data analyses. To determine whether sightings density per unit effort was significantly different between seasons in the Central Coast (nearshore waters), I used a non-parametric Kruskal-Wallis test and a post-hoc pair-wise Wilcoxon rank-sum test with Bonferronni adjustments (R Core Development Team, 2009). However, I used a parametric Student's *t*-test to determine whether sightings density per unit effort differed significantly between nearshore and offshore waters in the Extended Coast study area (summers only; although my data were non-normal and could not be transformed to achieve normality due to over-dispersion—i.e., too many zeros). I used the t-test because the variances and magnitudes of skew between nearshore and offshore groups violated the assumptions of the Mann-Whitney-U and Wilcoxon Rank Sum non-parametric alternatives. Under such conditions (i.e., when two groups have different skews or variances), Whitlock and Schluter (2009) recommend using the t-test because the non-parametric tests are likely to find significant differences where none exist, and the t-test is robust to violations in the assumption of normality.

To determine whether group size was significantly different between seasons or between nearshore and offshore waters, I used a Kruskal-Wallis test (to compare mean group sizes by season) and Wilcoxon rank-sum tests (to compare mean group sizes in nearshore vs. offshore waters). Problems of over-dispersion did not apply and data met the assumptions of the non-parametric tests in this case because group size was determined from non-effort-corrected data.

2.3.2 Opportunistic sightings of Pacific white-sided dolphins

Sightings of cetacean and sea turtle occurrences in British Columbia waters have been collected since 2001 from volunteer observers by the BC Cetacean Sightings Network (BCCSN) — a collaboration between the Vancouver Aquarium and Fisheries and Oceans Canada (DFO). BCCSN staff also collected sightings extending back to 1956 from various sources, particularly ships logbooks, researchers notebooks, unsolicited reports from the public received by the Vancouver Aquarium, and reports solicited from a select group of mariners in the 1990's by John K.B. Ford, then a research scientist at the Vancouver Aquarium. Over 2,400 observers have reported the date, time, location, weather, species identification, group composition and animal behaviour information to the BCCSN (Smith *et al.*, 2006) since 2001. The database consists of over 50,000 reports of cetaceans and sea turtles, including over 4,000 sightings of Pacific white-sided dolphins from 1956–2010.

The BCCSN sightings data included self-reported confidence ratings from observers and confidence-level assignments from BCCSN staff, which rate how likely it was that the species was correctly identified. I omitted all sightings with confidence ratings of 'uncertain', 'possible', and 'probable' and only kept those sightings ranked as 'certain' by either the observer or the BCCSN. There were 3,079 records of Pacific white-sided dolphins with 'certain' identification sighted on the BC coast from 1956–2010. To avoid confounding factors between decadal and seasonal shifts in distribution, and to facilitate comparisons between the opportunistic BCCSN data and the DFO survey data, I limited 'certain' sightings to those reported from 2002–2010 for analyses of seasonal distributions. There were 2,253 groups of dolphins sighted between 2002 and 2010 that met these criteria.

Opportunistic sightings data effort. I relied on a model to estimate observer effort of BCCSN sightings (Smith *et al.*, 2006). This model was based on assumed or known distributions of 7 major observer groups, and covered a spatial area of about 600,000 km^2 (~170,000 nautical miles^2). The 7 major observer groups that contributed the bulk of the sightings data to the BCCSN were 1) large vessels (shipping traffic, BC Ferries, tug boat operators), 2) whale watchers, 3) population centers, 4) light-station keepers, 5) coastal parks, 6) coastal workers, and 7) frequent observers. The BCCSN constructed 7 different GIS layers to represent spatial distribution and effort of each observer type (Smith *et al.*, 2006).

Two models were constructed based on the division of observer distribution data into *summer* (May 1st to September 30th) and *winter* (October 1st to April 30th) layers (Smith *et al.*, 2006). A 5×5 km raster grid was used as a base layer for each of the 7 user-group layers. The BCCSN determined the distribution of the *large vessels* group using the Marine Communications and Traffic Services database which records ship locations and is mandatory for most vessels over 20 m long (Smith *et al.*, 2006). A cost-distance analysis in ArcGIS version 9.3 (ESRI) was used to model the spatial distribution of the *whale watcher, population center,* and *light-station* observer layers, assuming spatial distribution of these user groups was concentrated close to a home port and decreased with distance from the home port (Smith *et al.*, 2006). The spatial distribution of the *park users* and *coastal workers* layers were not modeled using decay functions, but rather were modeled using linear buffers along the coast. Observers belonging to the *frequent observers* layer were asked to map their own spatial distribution of effort (Smith *et al.*, 2006).

The effectiveness of each of the 7 major groups in reporting sightings to the BCCSN was assessed so that the model could be weighted to reflect the proportion of effort coming from each observer group layer (Smith *et al.*, 2012). Coefficients for effectiveness ratings were assigned by determining the proportion of total sightings made by each observer type (Smith *et al.*, 2006). Once spatial distribution and effectiveness coefficients were assigned to each layer, the 7 layers were summed in each raster cell of the 5×5 km grid cell layer, using the *raster calculator* function in ArcGIS. Values of effort in each grid cell were "normalized" by dividing each grid cell by the maximum effort recorded in any grid cell; Thus, each grid cell had a final effort value between 0 and 1 (Smith *et al.*, 2006). A final coefficient determined by the relative number of winter (23%) or summer (77%) sightings was used to weight each season (winter vs. summer), so that summer effort grid cells had a maximum value of 0.77 and winter grid cells had a maximum value of 0.23 (Smith *et al.*, 2006).

The effort model was constructed by Smith *et al.,* (2006), and I did not alter it, but did average the summer and winter effort model outputs to obtain an effort estimate for each of four seasons (*winter, spring, summer* and *fall*). For example, to determine effort in *spring* (April to June) I summed the effort values of each grid cell for 2 summer grid cells (May and June) and 1 winter grid cell (April) and then divided by three to have 1 *spring* grid cell value.

This method of averaging the model values in each grid cell allowed me to deal with the fact that I defined *spring* to include one month defined as *winter* by the BCCSN model and two months defined as *summer* by the BCCSN model. Sightings density per unit effort values were obtained following the same methodology used in the survey-based dataset from DFO.

Opportunistic data – changes in group size. I used observer-reported group-sizes of Pacific white-sided dolphins to test whether the numbers of individuals reported per group were significantly different between seasons, or between nearshore and offshore habitats. These data were spatially joined to the BC Coastline layer (to obtain a distance to shore) and then exported from ArcGIS as spreadsheets for analysis in *R*, using the same methods used for the survey-based dataset from DFO.

Opportunistic data analyses. I used parametric *t*-tests to compare the sightings density per unit effort between nearshore and offshore waters within each season, separately. I was unable to directly compare mean sightings density per unit effort between seasons because the effort model was "normalized" (in the case of the effort models, "normalized" means that each of values in each layer was divided my the maximum occurring value in each layer and in each season, so the results were a proportion of total effort within each season and were therefore not comparable between seasons). Opportunistic data were similar to survey data in that they were also over-dispersed and could not be normalized. Thus, I used the Students *t*-test rather than non-parametric tests in an effort to be conservative about finding significant differences following the logic described earlier and as described by Whitlock and Schluter (2009).

Decadal shifts in Distribution. I explored whether decadal shifts occurred in Pacific white-sided dolphin distribution by mapping non effort-adjusted sightings from opportunistic sightings reported by volunteer observers to the BC Cetacean Sightings Network (BCCSN) from 1956 to 2010. Data were segregated into ~5 year intervals and mapped over the same spatial extent to assess how sightings changed over time. All figures were produced in ArcView 9.3 using the BC Albers projection and NAD 1983 datum.

2.4 Results

2.4.1 Survey sightings all seasons: central coast of BC (nearshore waters)

Along the central coast, groups of Pacific white-sided dolphins were recorded 39 times in the 5 winter surveys, 9 times in the 7 spring surveys, 10 times in the 11 summer surveys, and 13 times in the 6 fall surveys. The greatest survey effort occurred in summer along the central coast and decreased in spring, fall, and winter, with the lowest survey effort occurring in winter (Fig. 2.2). Grid cells with the highest sightings density per unit effort values in the central coast occurred more frequently in winter than in other seasons (Fig. 2.3). Kernel-density analysis revealed hot-spots for dolphin sightings throughout the entire central coast in winter, and sparse hot-spots in other seasons (Fig. 2.4). Fitz Hugh Sound, Camano Sound, and the waters off Prince Rupert were the most pronounced hot-spots (Fig. 2.4).

The number of groups of dolphins sighted per unit effort (SDUE; number of groups of dolphins sighted per km^2 per visit to grid cell) on the central coast of BC in winter was significantly greater than sightings density per unit effort in all other seasons (Kruskal Wallis H_3=32.24, p<0.001; Fig. 4.5). Sightings density per unit effort was significantly higher in winter (p<0.002 in all pair-wise comparisons). Sightings density per unit effort was about 5 times greater in winter than in other seasons (0.0014 ± 0.0003 S.E. groups of dolphins sighted per unit effort in winter, and 0.0002 – 0.0003 in all other seasons, Fig. 2.5).

There was only weak statistical support for seasonal differences in group sizes of Pacific white-sided dolphins reported in the scientific survey data set (Kruskal Wallis H_3= 7.6, p=0.06). Group sizes in fall were 128 ± 59 (mean ± S.E.) individuals whereas group sizes approximated ~25 dolphins in all other seasons).

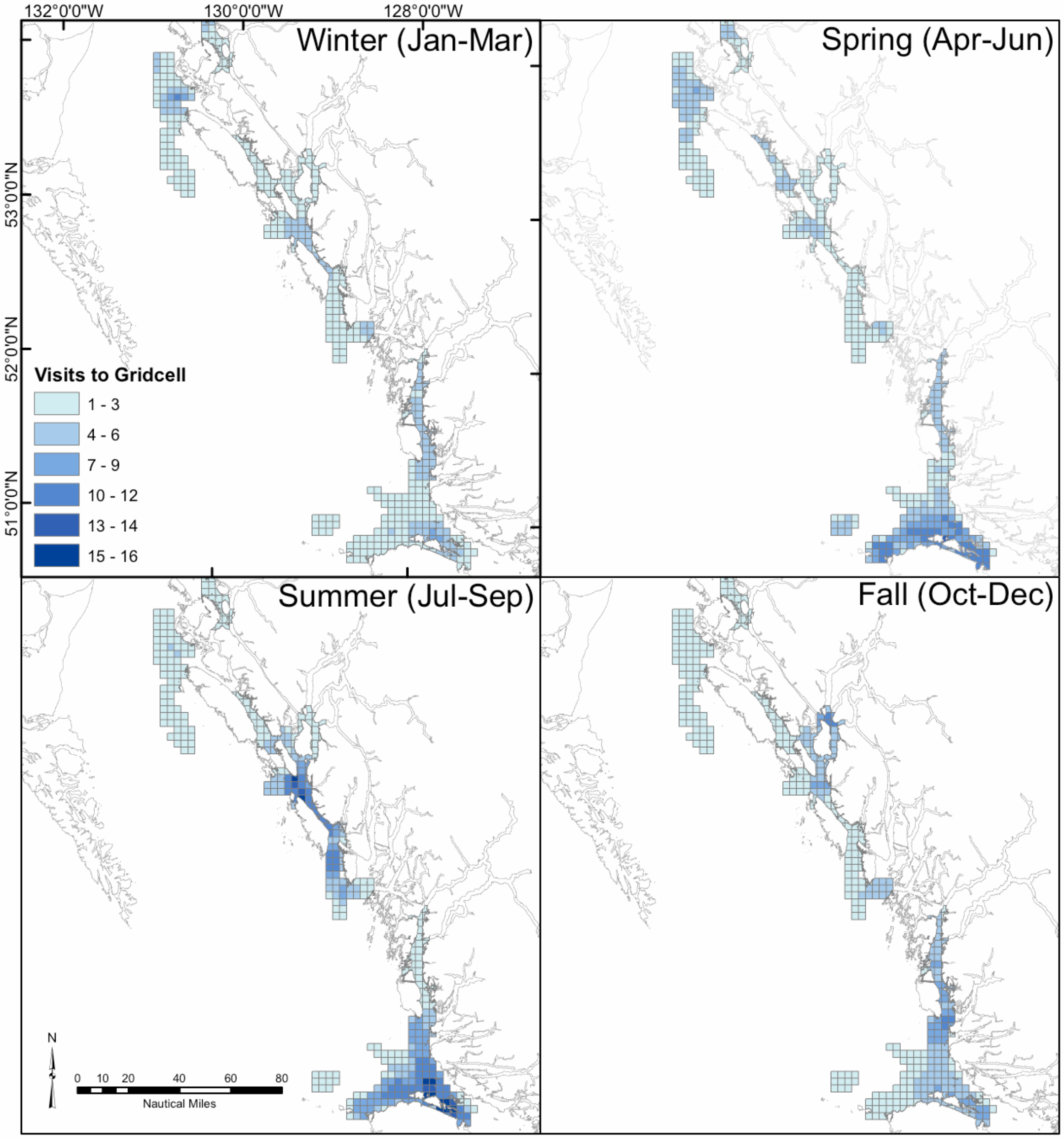

Figure 2.2 Seasonal numbers of visits (survey effort) by DFO research vessels conducting marine mammal surveys along the central coast of British Columbia from 2002-2010. Each gird cell is 25 km^2.

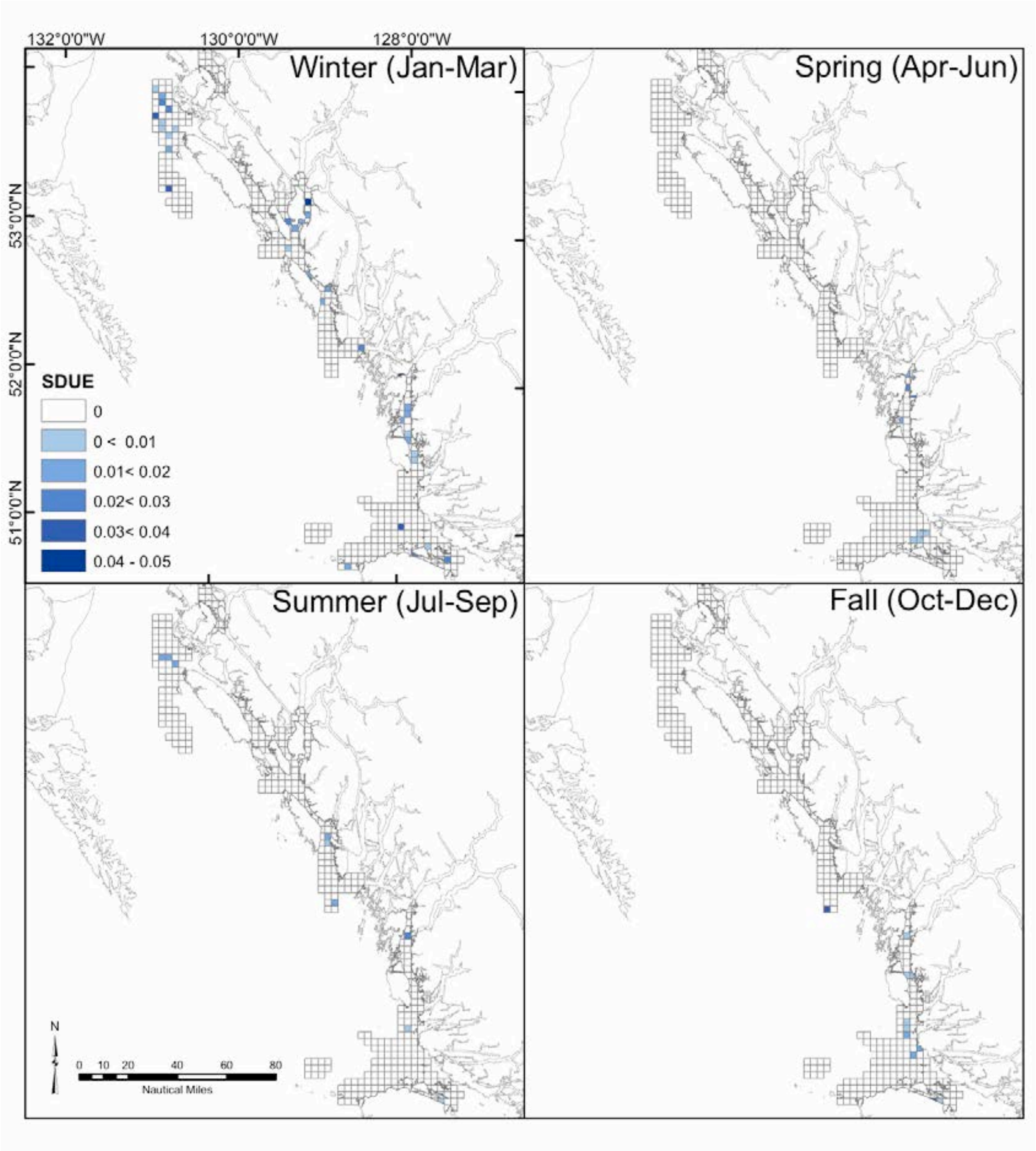

Figure 2.3 **Seasonal numbers of groups of Pacific white-sided dolphins (densities per unit effort within each 25 km^2 grid cell) during DFO marine mammal survey cruises along the central coast of British Columbia from 2002-2010.**

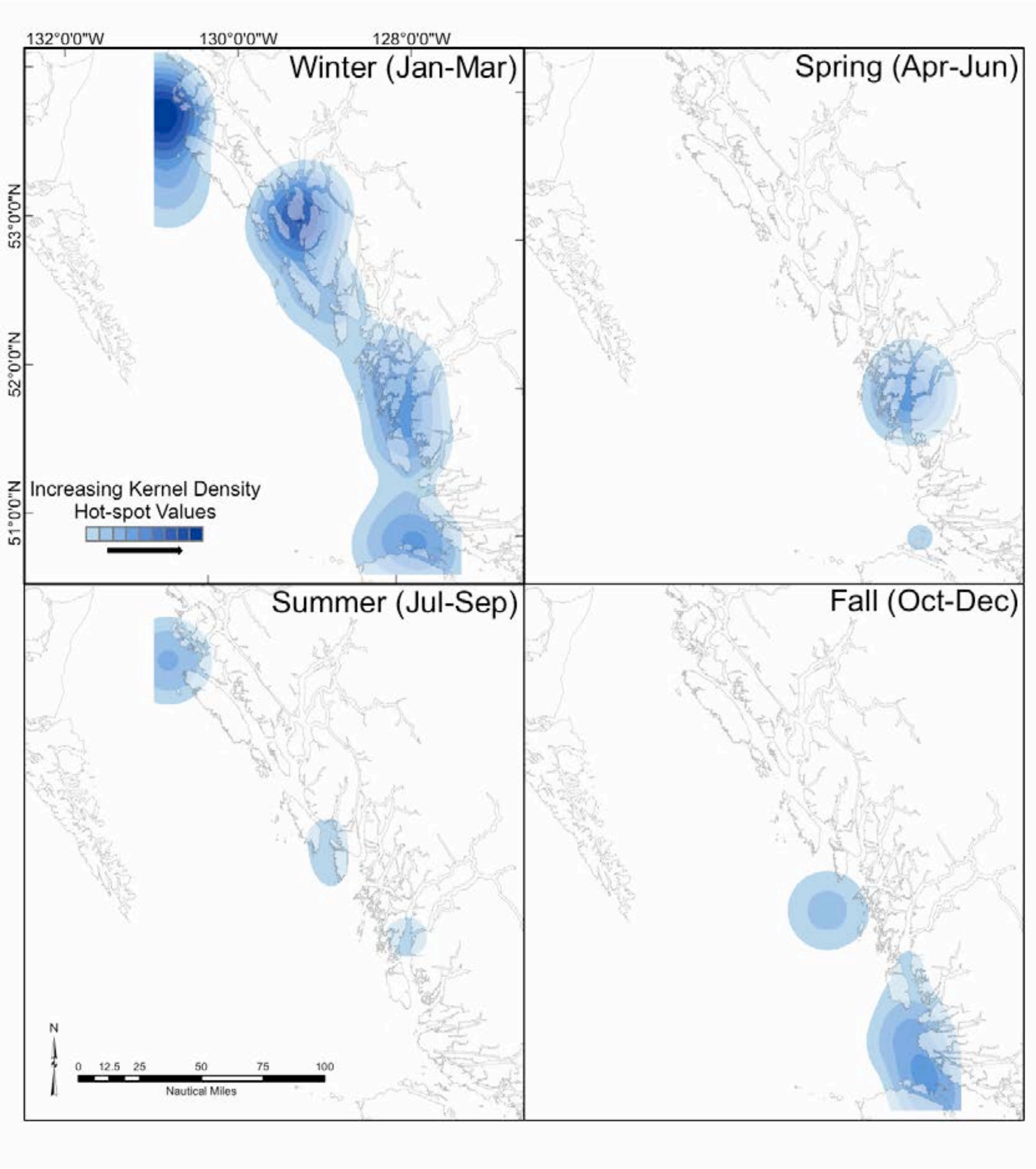

Figure 2.4 Seasonal hot-spots of sightings of Pacific white-sided dolphin groups obtained from Kernel Density analyses of survey data collected by DFO along the central coast of British Columbia from 2002-2010.

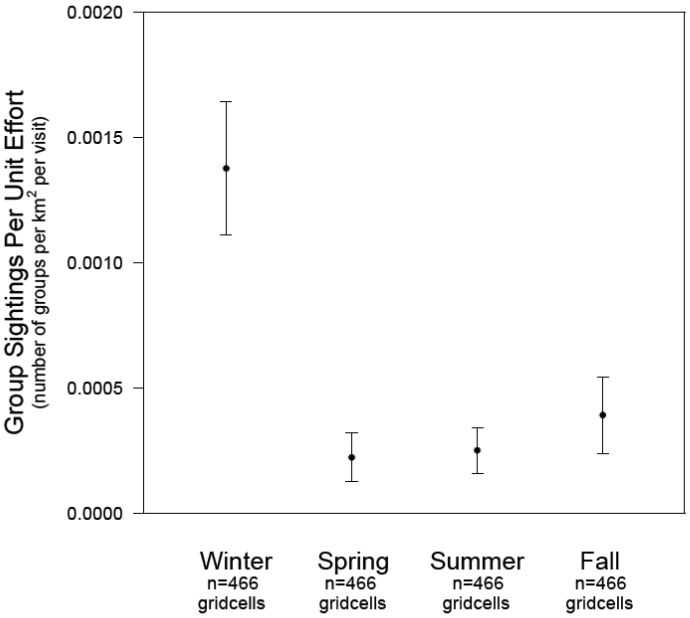

Figure 2.5 Mean numbers of groups of Pacific white-sided dolphin groups sighted by season (winter, spring, summer, fall) per unit effort in the inside passage of British Columbia from 2002-2010. Number of dolphins per unit effort were significantly greater in winter than in all other seasons. Survey data were collected by DFO. Filled circles indicate mean number of groups sited and bars show standard errors of the means.

2.4.2 Survey sightings summer: BC coast (nearshore and offshore waters)

Groups of dolphins were sighted 42 times in nearshore waters and 60 times in offshore waters during the 15 summer surveys conducted on the extended coast (July-September, 2002–2010). Summer survey effort occurred in both nearshore and offshore waters, and was greatest in the nearshore waters surrounding the southern coast of Haida Gwaii (Fig. 2.6). Sightings density per unit effort was highest off the west coast of Vancouver Island (Fig. 2.7) and kernel density hot-spot analyses revealed the offshore waters off Barkley Sound and Queen Charlotte Sound had the highest sightings density per unit effort in summer (Fig. 2.8).

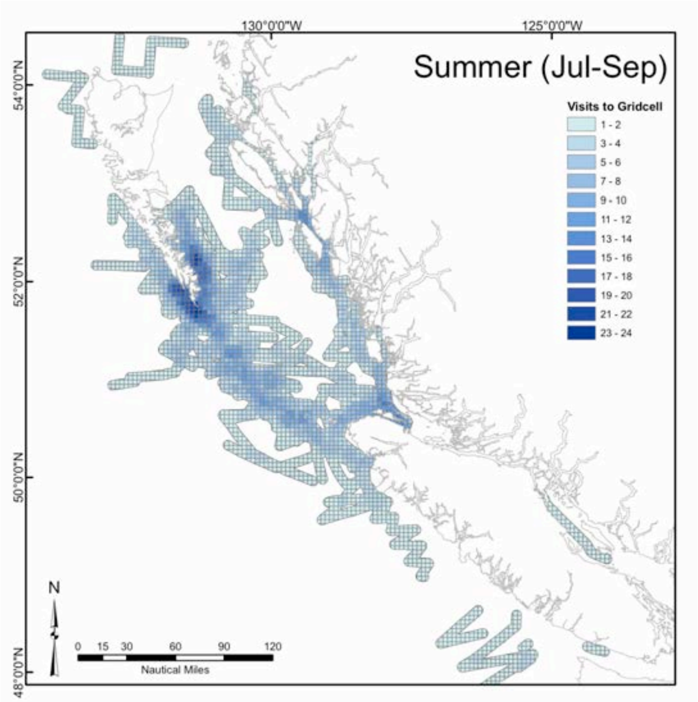

Figure 2.6 **Distribution of summer survey effort for marine mammals (number of visits per 25 km^2 grid cell) conducted by DFO along the coast of British Columbia from 2002-2010.**

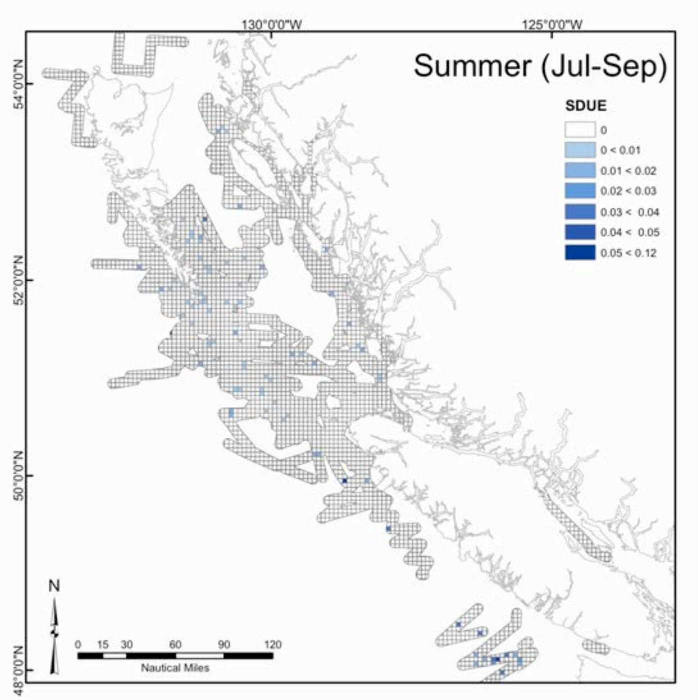

Figure 2.7 **Numbers of groups of Pacific white-sided dolphins sighted per unit effort (densities per unit effort per 25 km^2 grid cell) during DFO summer marine mammal cruises from 2002-2010 along the coast of British Columbia.**

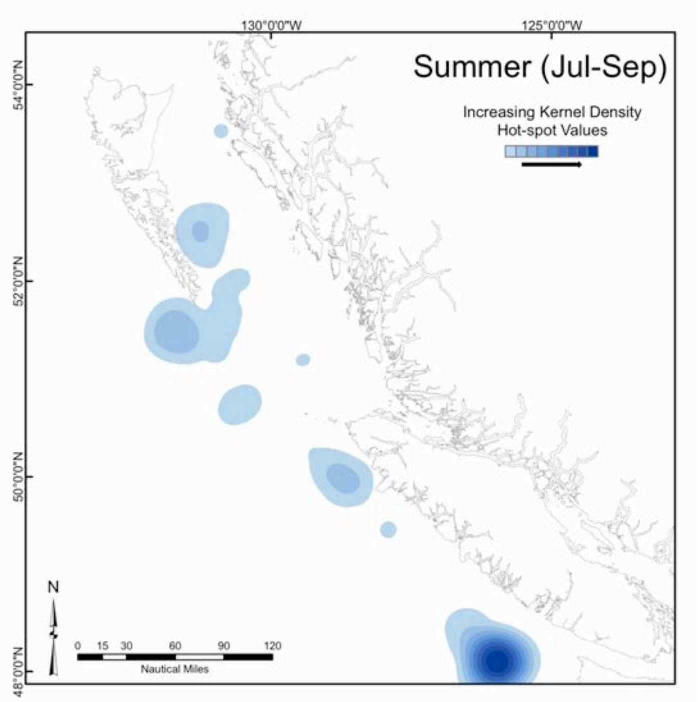

Figure 2.8 Hot-spots of Pacific white-sided dolphin distributions obtained from Kernel Density analyses of survey data collected by DFO in summers between 2002-2010.

Summer sightings density per unit effort of Pacific white-sided dolphins differed significantly between offshore and nearshore waters in summer ($t_{2361}=-3.76$, $p<0.001$; Fig. 2.9). The sightings density per unit effort was about 4 times greater in offshore waters than in nearshore waters (i.e., 0.0057 ± 0.00011 S.E. sightings density per unit effort in offshore waters versus 0.0014 ± 0.000031 in nearshore waters). Group sizes of dolphins did not differ significantly between nearshore or offshore waters ($W=777$, $p=0.07$).

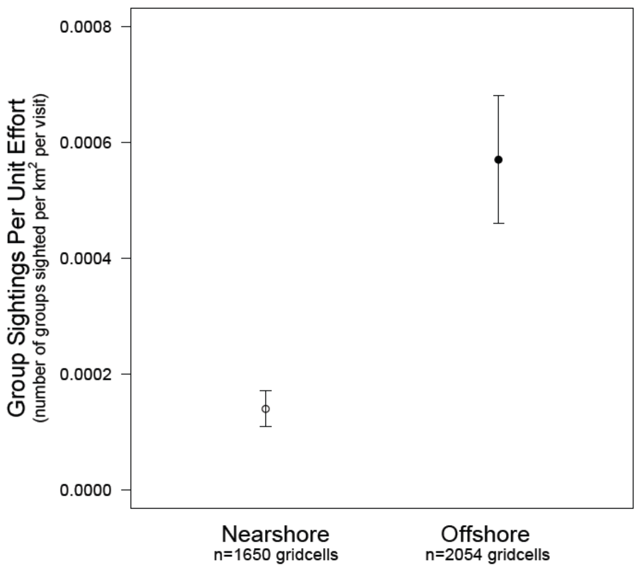

Figure 2.9 Mean number of groups of Pacific white-sided dolphins sighted per unit effort on the coast of British Columbia in summers from 2002-2010 from data collected by DFO. Numbers of groups per unit effort were significantly different between nearshore and offshore waters. Filled circles indicate mean number of groups sited and bars indicate standard error of the mean.

2.4.3 Opportunistic sightings in all seasons: nearshore and offshore waters

Dolphin sightings were reported 266 times in *winter* (January to March), 640 times in *spring* (April to June), 957 times in *summer* (July to September) and 293 times in *fall* (October to December) from 2002 to 2010. Modeled survey effort indicated that the greatest effort occurred in summer along the entire BC coast and decreased in spring, fall, and winter (Fig. 2.10). Effort was greater in offshore areas during spring and summer than it was in winter or fall (Fig. 2.10). Areas of highest effort in all seasons included the southeastern coast of Vancouver Island (Strait of Georgia), the southwestern coast of Vancouver Island (off Barkley Sound), the north coast of Vancouver Island (Johnstone Strait), the north coast of BC (off Prince Rupert) and the northern tip of Haida Gwaii (Langara Island) (Fig. 2.10).

Grid cells with the highest sightings density per unit effort occurred throughout the central coast in winter, in the open ocean off Queen Charlotte Sound in spring and summer, and off Prince Rupert and the west coast of Vancouver Island in fall (Fig. 2.11). Kernel-density analysis revealed hot-spots for dolphin sightings in both nearshore and offshore waters off Calvert Island, Fitz Hugh Sound, Rivers Inlet, and in Knight Inlet in winter (Fig. 2.12). Hot-spots for dolphin sightings occurred in Queen Charlotte Sound and the southern Hecate Strait during spring and summer; and were highest in the northern Hecate Strait and the waters off the west coast of Vancouver Island near Brook's Peninsula during the fall (Fig. 2.12).

Sightings density per unit effort was significantly higher in nearshore waters than in offshore waters during winter (t_{9536}=1.93, p=0.05; Fig. 2.13a). However, during spring, sightings density per unit effort was reversed and was greater in offshore waters than in nearshore waters (t_{7501}=-2.31, p=0.03; Fig. 2.13b). Sightings density per unit effort was also greater during summer in offshore waters than in nearshore waters (t_{7708}=-3.15, p=0.01; Fig. 2.13c) and did not differ significantly between the two areas in fall (t_{7379}=-0.667, p=0.51; Fig. 2.13d).

Mean group sizes reported in the opportunistic data set differed significantly between nearshore and offshore waters (W=184367, p=0.01; 58 ± 2.6 individuals per group in nearshore waters, and 73 ± 7.9 individuals in offshore waters). Group sizes reported in the BCCSN data also differed between seasons (*winter, spring, summer,* and *fall*; H_3 =18.06, p<0.001), and were larger in the fall compared with the spring (W=92603, p<.001) and summer (W=137661, p<.001). Statistical significance was not detected for differences in group sizes between sightings reported in fall and winter (Fig. 2.14).

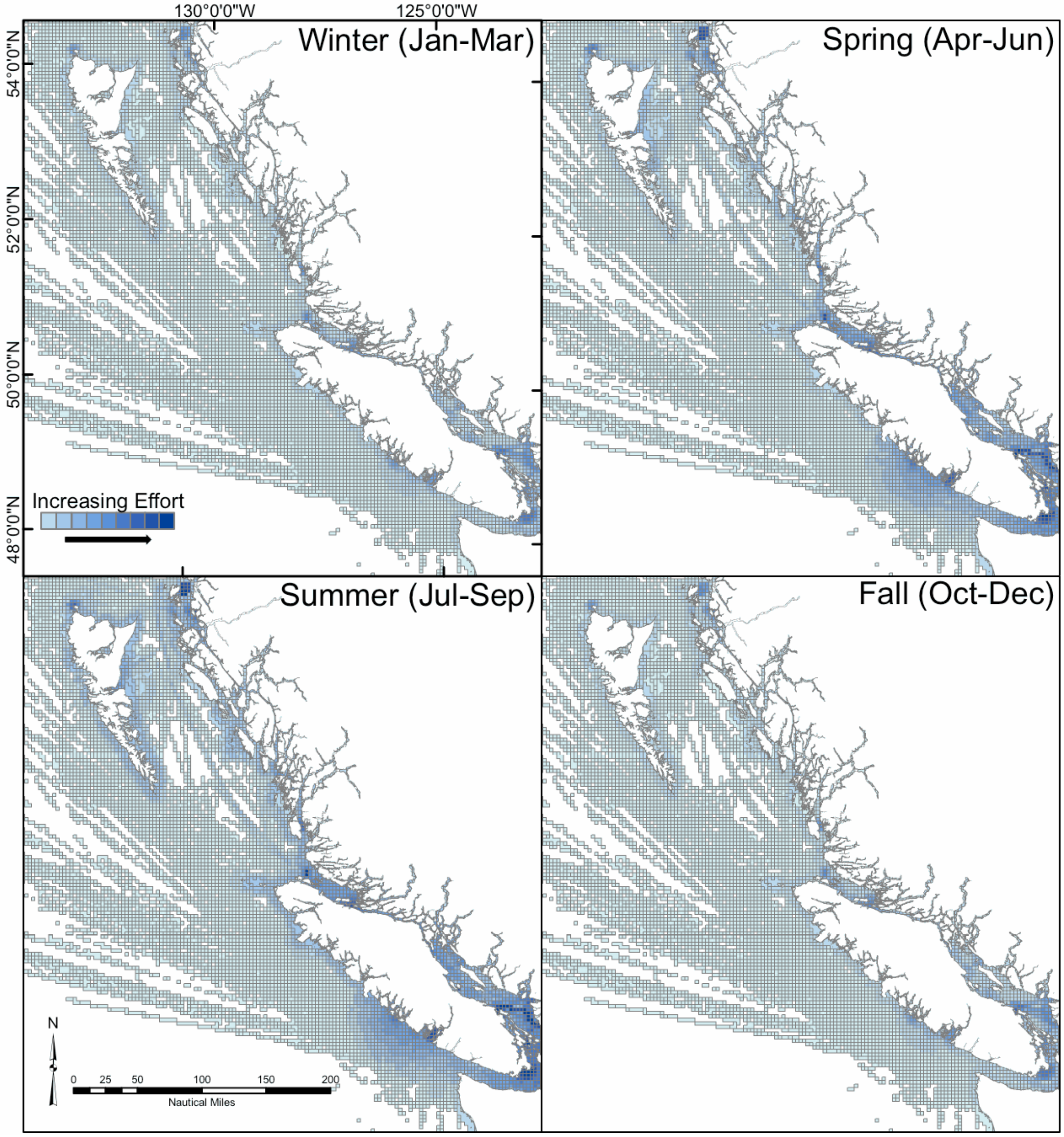

Figure 2.10 Distribution of opportunistic effort by season as modeled by the BC Cetacean Sightings Network across the coast of British Columbia (2002-2010).

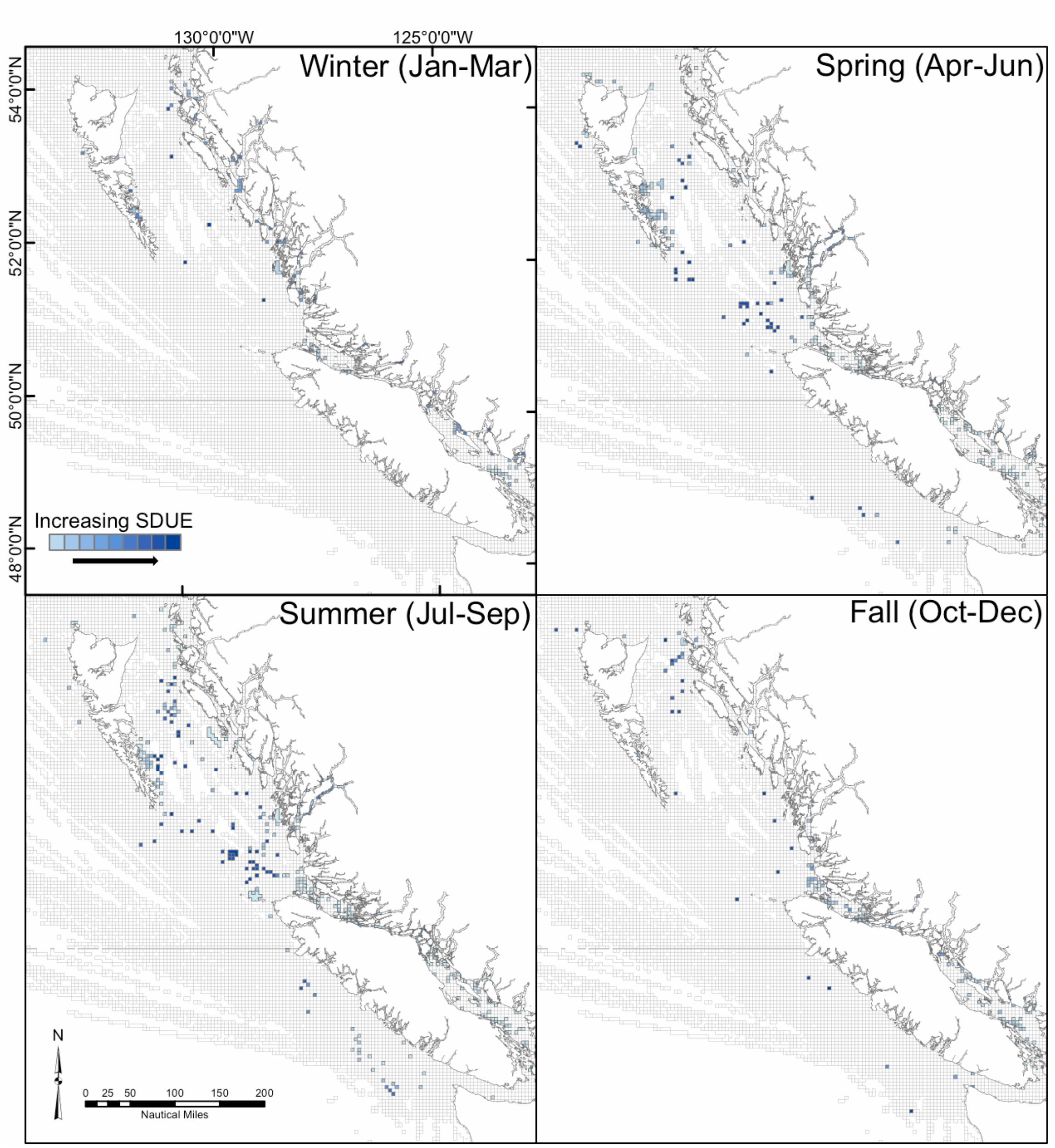

Figure 2.11 Seasonal sightings densities of Pacific white-sided dolphins per unit effort (SDUE) based on model predictions of effort and sightings reports. SDUE refers to the number of groups sighted in each 25 km^2 grid cell per proportion of effort (Figure 2.10) within each season (winter, spring, summer, and fall). Sightings were made on opportunistically and collected by the BC Cetacean Sightings Network (2002-2010).

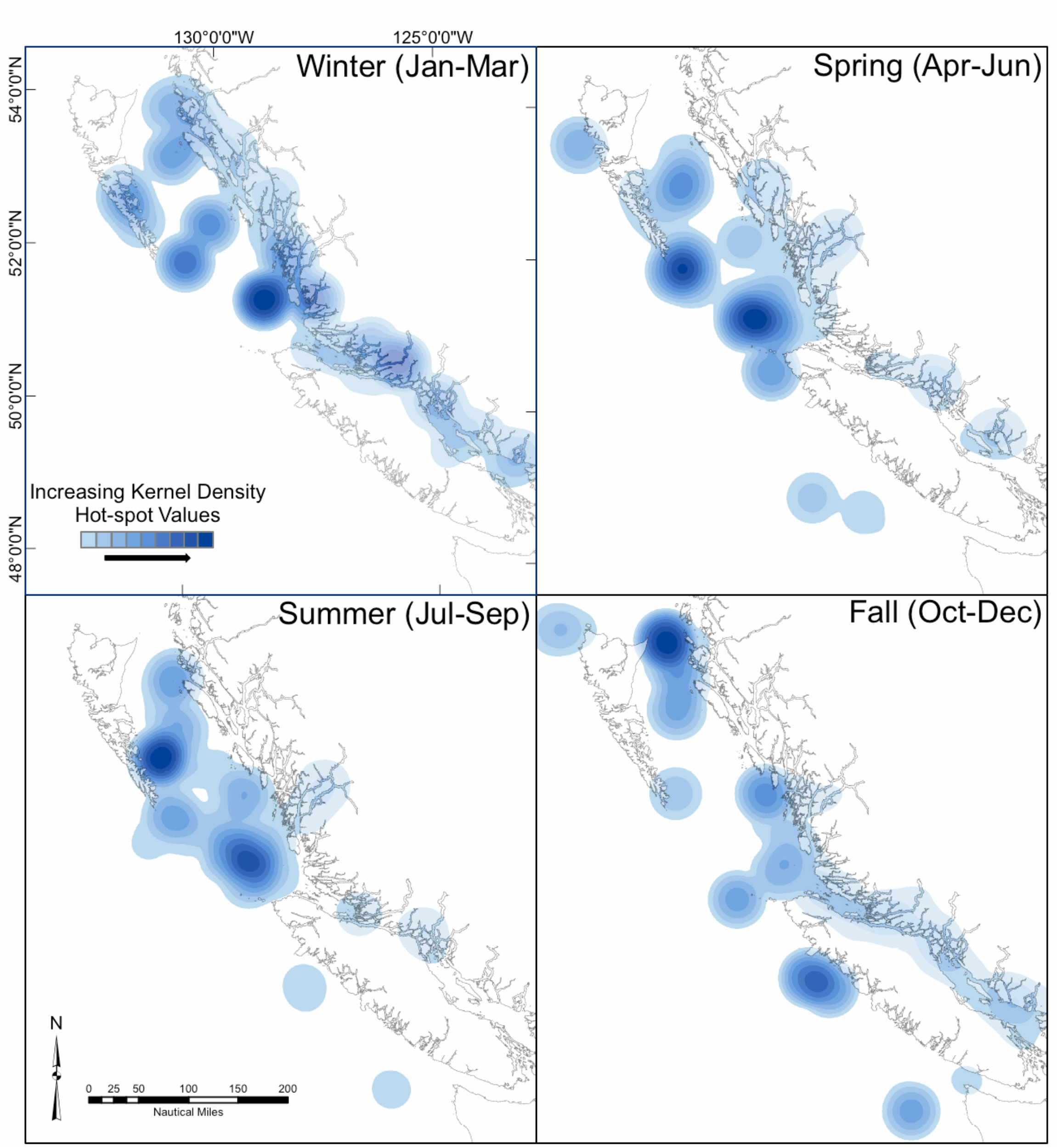

Figure 2.12 Seasonal hot-spots of Pacific white-sided dolphin distributions obtained from Kernel Density analyses of opportunistic sightings compiled by the BC Cetacean Sightings Network (2002-2010).

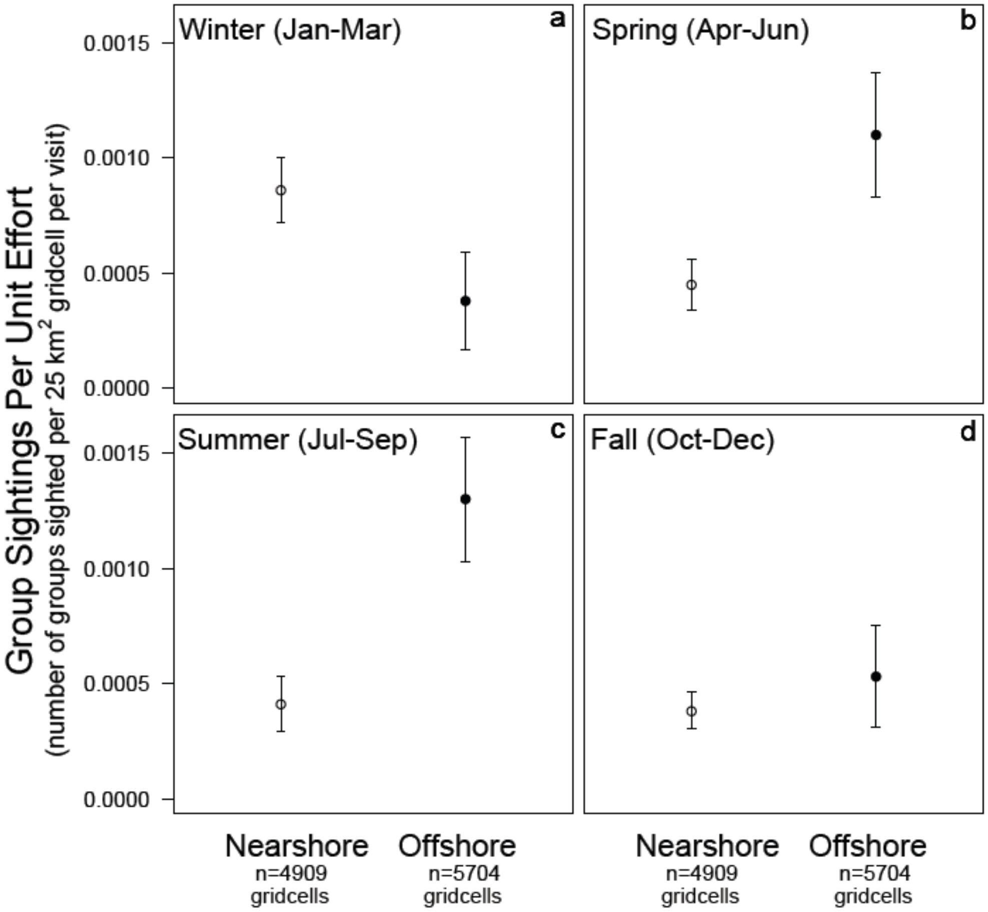

Figure 2.13 Seasonal mean numbers of groups of Pacific white-sided dolphins sighted opportunistically in the nearshore and offshore waters of British Columbia. Mean numbers of groups of dolphins in nearshore vs. offshore waters were significantly different from each other in all seasons except fall. Data are from the BC Cetacean Sightings Network (2002-2010). Bars indicate standard error of the mean.

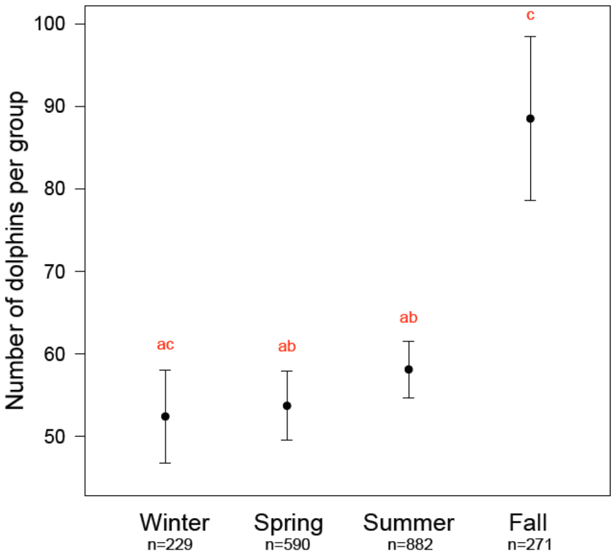

Figure 2.14 Number of individual Pacific white-sided dolphins sighted per group sightings reported opportunistically through the BC Cetacean Sightings Network (2002-2010). Bars indicate standard error of the mean. Letters a-c represent statistically significant differences between each season.

2.4.4 Decadal shifts in dolphin distribution

Decadal changes occurred in the distribution of dolphins. Only two groups of dolphins were sighted south of the northern tip of Vancouver Island between 1956 and 1989, and none were sighted on the east coast of Vancouver Island south of Johnstone Strait. However, sightings began to increase in these areas starting in the early 1990s when 12 groups were sighted on the south west coast of Vancouver Island and 2 were sighted in the Strait of Georgia (southeast coast of Vancouver Island). By the late 1990s, sightings began increasing in the Strait of Georgia and along the southwest coast of Vancouver Island, such that dolphins were sighted frequently in the Strait of Georgia by the early 2000s. Sightings have been common in the Strait of Georgia and the southwest coast of Vancouver Island from 2005-2010 (Fig. 2.15).

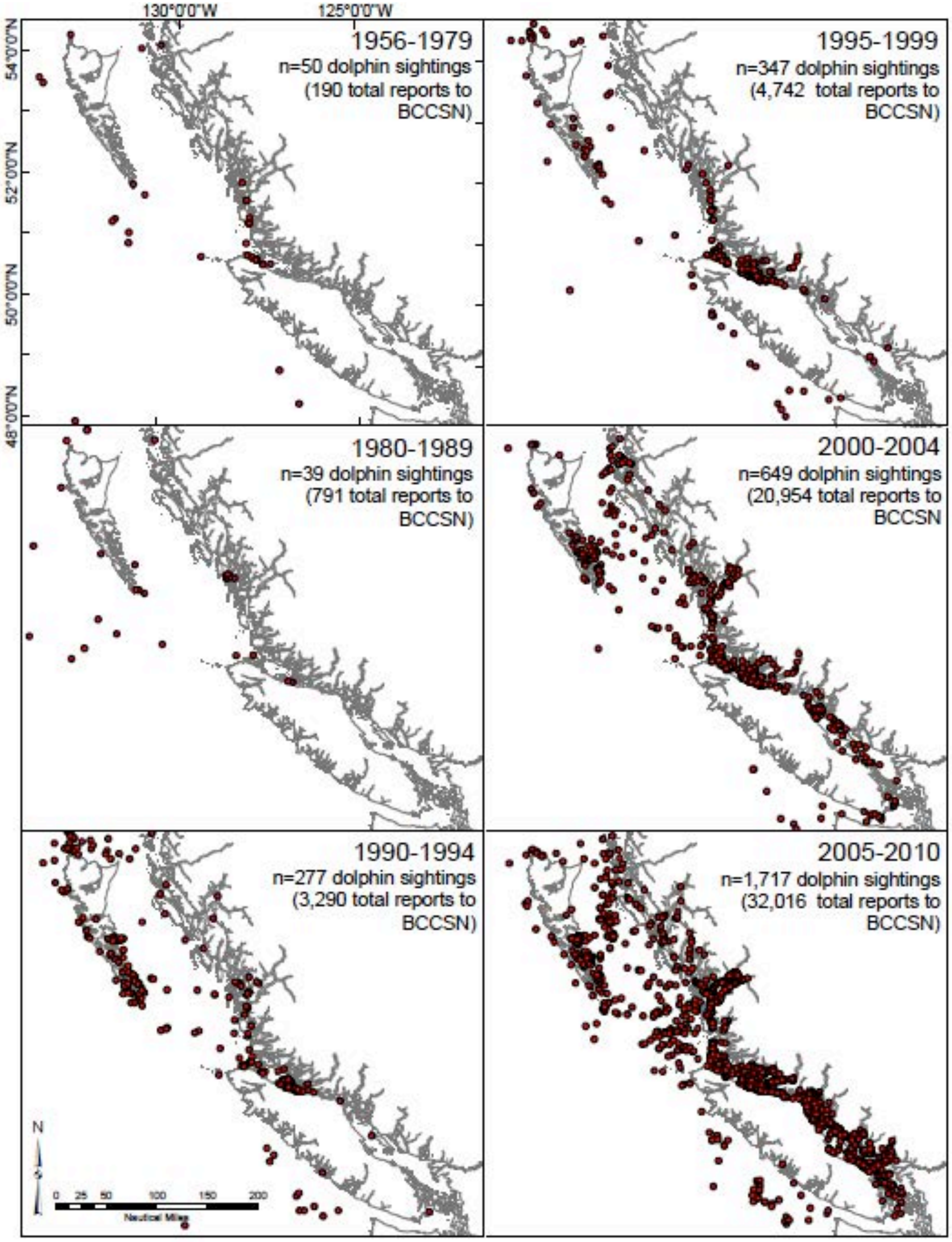

Figure 2.15 Sightings of Pacific white-sided dolphins in British Columbia from 1956 to 2010. Sightings data are from the BC Cetacean Sightings Network. Sightings are opportunistic and not corrected for effort. Numbers of dolphin sightings are presented in relation to total number of reports received by the sightings network in each time period. The figure is meant to show the south-ward range expansion and not the increase in total sightings which is a reflection of increased observer effort.

2.5 Discussion

In the mid to late 1900s, Pacific white-sided dolphins were thought to be an open-ocean species and were infrequently seen in the nearshore waters of British Columbia until the 1980s, although evidence from First Nation midden sites suggests that dolphins occurred in nearshore waters historically (see McMillan *et al.,* 2008; Heise, 1996). The reason for the temporary absence of white-sided dolphins in nearshore waters is unknown, however, they now regularly occur in the nearshore waters. Data from the line-transect surveys and opportunistic sightings further suggest that the nearshore central coast of BC is an especially important area for dolphins in winter, and that the range of Pacific white-sided dolphins has expanded since the 1950s to more southern waters of BC than previously indicated. This range expansion may have increased the spatial overlap between dolphin habitat and areas of high human-use.

Dolphins have been regularly sighted since the late 1990s in the Strait of Georgia—one of the areas of greatest human-use in Canada—with high levels of recreational boat traffic, commercial shipping lanes, and recreational and commercial fisheries (DFO, 2012). Knowing where and when Pacific white-sided dolphins occur in British Columbia waters may assist fisheries managers in avoiding entanglement or by-catch of dolphins, or other causes of conflict between human uses and dolphin occurrences. Such information about habitat-use of small cetaceans has been applied in the North Pacific (Ferrero *et al.*, 2002) and off the coast of California (Forney *et al.*, 1994). Knowing the coastal areas and seasons when predator-prey spatial overlap occurs may also ensure an adequate prey-base for dolphins if fisheries management includes predator requirements of dolphins into catch quotas for fishers. Further, my results may contribute to determining areas of important or perhaps critical habitat for Pacific white-sided dolphins.

2.5.1 Study limitations

Despite the methods used to estimate effort for the opportunistically collected dolphin sightings being plausible representations of true effort, I was unable to precisely quantify observer effort for the opportunistic dataset. The effort model constructed by Smith *et al.* (2006) for the opportunistic sightings lacked sufficient data to compare total sightings density per unit effort values between seasons. The spatial extent covered by the DFO survey data varied between some years and seasons, and the lack randomized or replicated survey tracks with equidistant spacing made common spatial analyses techniques inappropriate for my research (Ford *et al.*, 2010a). Despite these drawbacks, the extensive research into the modeled observer effort for opportunistic sightings, and the repeated visits to the same grid cells in the surveyed sightings allowed a novel evaluation of spatial use of the BC coast by dolphins to be made.

Combining the two datasets proved to be a useful way to identify areas used by Pacific white-sided dolphins in British Columbia. Using the volunteer observer data provided additional insights that would have been unobtainable from line-transect surveys alone. Such data provides baseline information useful for managers assessing spatial overlap between predator and prey populations and human use. In addition, my study should inform management of areas of local conservation importance for Pacific white-sided dolphins in BC.

2.5.2 Seasonal changes in group sizes

The opportunistically collected data indicates that group sizes of Pacific white-sided dolphins increased in fall, but the biological significance of this is unclear and although a trend towards larger group sizes in fall occurred in the survey data it was statistically insignificant ($p=0.06$). One possible explanation for an increase in numbers of dolphins sighted per group in fall is the addition of new calves (which are typically born in late August). Calf numbers may directly increase group-size, or the presence of calves may result in groups of dolphins with calves coming together to reduce risks of predation by killer whales or sharks. Changes in group size could also reflect a change in foraging strategies due to seasonal changes in diet or foraging strategies that are associated with larger pod sizes.

2.5.3 Seasonal movements of Pacific white-sided dolphins

Both the line transects and opportunistically collected data sets revealed that sightings density per unit effort of Pacific white-sided dolphins was highest in nearshore waters in winter, and highest in offshore waters in summer. These data suggest an offshore to nearshore movement rather than a northward or southward movement of Pacific white-sided dolphins in BC.

The elevated sightings of dolphins in nearshore waters from January to March were concurrent with the presence of large aggregations of herring in sheltered waters near spawning-sites on the outer coast of BC (Haegele & Schweigert, 1985). Dolphins may move into nearshore waters to exploit seasonally dense aggregations of herring. Herring have been noted as the most common species (by % occurrence) in their diet (Heise, 1997). The elevated metabolic rates (Chapter 3) and high energy requirements of dolphins (Chapter 4) may make it advantageous or even necessary for Pacific white-sided dolphins to consume high-energy prey, such as Pacific herring.

Although the seasonal movements of dolphins between offshore and nearshore waters may be prey-driven, such movements could also act to reduce encounters with predators. Since the early 1990s, at least two stranding events of tens of Pacific white-sided dolphins have occurred in Higgins Pass — a convoluted waterway along the Central Coast of British Columbia (J.K.B. Ford, *pers. comm.*). Nearshore waters may make Pacific white-sided dolphins more susceptible to predation, and could cause dolphins to move offshore if predator numbers seasonally increase in nearshore waters. Effort-corrected sightings of transient killer whales in the nearshore waters of southeast Alaska were elevated in summer (Dahlheim *et al.*, 2009; Dahlheim & White, 2010). In British Columbia, occurrence of transient killer whales peaks in late summer and early fall — likely in response to harbour seal weaning (J.K.B. Ford, *pers. comm.*)

Thermal constraints could also motivate a shore-ward migration in winter. Moving to warmer waters could reduce the metabolic cost of thermoregulation and minimize the energetic costs associated with sloughing off skin (and diatoms; Durban, 2012). Such a phenomenon has been proposed to explain the rapid, long-distance migrations of Antarctic killer whales from polar waters to near-equatorial waters (Durban, 2012). Pacific white-sided dolphins have often been sighted in winter in the nearshore waters of British Columbia with conspicuous diatom coverings (L.G. Barrett-Lennard, *pers. comm.*).

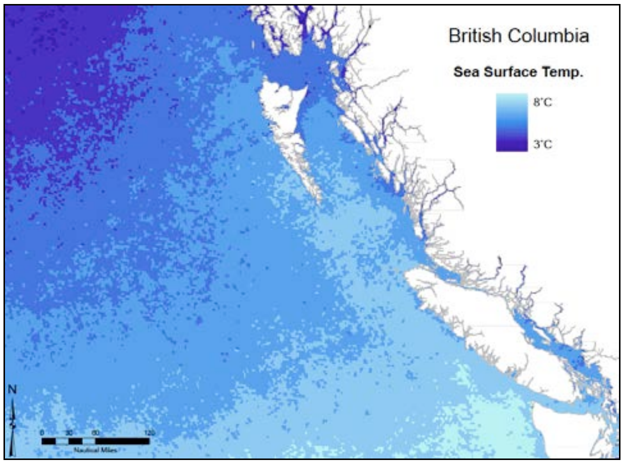

Figure 2.16 Average sea surface temperature measured in February from 2002 to 2010 inclusive: image created by Matthew Foster using data collected by MODIS mission scientists and produced with the Giovanni online data system developed and maintained by the NASA GES DISC (Acker & Leptoukh, 2007).

At a large scale, sea surface temperatures collected by MODIS mission scientists and produced with the Giovanni online data system developed and maintained by the NASA GES DISC (Acker & Leptoukh, 2007) indicate that the sea surface temperatures (SST) in the far offshore waters of BC are cooler than waters nearer to shore (~5°C difference in SST; Fig. 2.16).

2.5.4 Decadal southward shifts in dolphin distributions in British Columbia

Pacific white-sided dolphins have colonized or possibly re-colonized the waters of southern Vancouver Island since the 1950s. Their bones have been found in First Nation middens along the BC coast, for example in Haida Gwaii (Szpak *et al.*, 2009) and on Valdes Island, in the Strait of Georgia (Matson & McIay, 1996; cited in Heise, 1996). Sightings have steadily increased around southern Vancouver Island (early 1990s to 2010) and reports of Pacific white-sided dolphins in the Strait of Georgia are now common year-round.

It is unclear why sightings of dolphins around southern Vancouver Island have increased over the last two to three decades. One hypothesis is that the return of sardines to southwestern Vancouver Island provides another high-energy prey-pulse that dolphins can exploit. Sardines migrate from California to waters off the southwest coast of Vancouver Island in spring, and reside through summer and early fall to feed (Schweigert *et al.*, 2010). Sardines were absent from BC waters in the early 1940s and re-appeared in 1992 (DFO, 2008; Schweigert *et al.*, 2010). Steady increases in sardine catch-rates off the west coast of Vancouver Island through the 1990s and 2000s (DFO, 2008) correspond with increasing sightings of dolphins in that area. Sardines are now found in the Strait of Georgia, Queen Charlotte Sound, and the Hecate Strait, as well as in some inlets up the BC coast and west coast of Vancouver Island in winter (Schweigert *et al.*, 2010). Both seasonal and temporal shifts in dolphin distribution may be linked to prey, or to other ecological constraints of Pacific white-sided dolphins. Such shifts in distribution could have important ecological implications.

2.5.5 Implications

My research provides baseline information of the spatial ecology of a relatively understudied yet abundant species. Spatial information about fisheries can be combined with seasonal dolphin hot-spots to mitigate incidents of by-catch and entanglement. My results can also be used to determine the extent of overlap between dolphins and prey which, if combined with daily prey requirements of Pacific white-sided dolphins (Chapter 3), and local or seasonal diet information, can be used to provide estimates of daily biomass consumption in specific areas along the BC coastline. Such information would be important for managing commercial fisheries catch-rates to sustain prey for Pacific white-sided dolphins.

Deducing the determinants of cetacean distribution is a challenging task. My research shows decadal and seasonal changes in areas used by dolphins, which could reflect a change in the distribution and abundance of prey, or could reflect behavioral changes to reduce predation or physiological constraints. My research also shows that habitat used during one decade may not be the habitat used in a future decade. Identifying important, or even critical, habitat for Pacific white-sided dolphins will require further research into what drives the hot-spots I identified.

Chapter 3: Seasonal resting metabolic rates and food intake of captive Pacific white-sided dolphins

3.1 Summary

Pacific white-sided dolphins consume species of prey that change seasonally in numbers, distribution and energy density. However, it is not known how the energetic requirements of Pacific white-sided dolphins may change with season. I recorded daily energy intake of three adult Pacific white-sided dolphins over 12 consecutive months, and measured their corresponding resting metabolic rates twice per month using gas respirometry. Mean mass-specific (± S.E.) resting metabolic rates were 0.29 ± 0.005 MJ $kg^{-1}day^{-1}$ (~30 MJ day^{-1}). Resting metabolic rates were comparable with those of other small cetaceans, and accounted for ~70% of the dolphins' total energy intake. Linear mixed effects models showed that pool temperature, air temperature, total food intake, body mass, and season did not influence the measured metabolic rates. Despite seasonally constant resting metabolic rates, total food intake varied seasonally and was highest during the fall (October to December). Resting metabolic rate, body mass, and pool and air temperatures did not influence food intake according to the models. However, small fluctuations in bodyweight appeared to occur in relation to food intake at the individual-level. Seasonal variation in total food intake of captive dolphins may be indicative of seasonally varied energy requirements in the wild.

3.2 Introduction

Concerns about dolphin conservation and the effect dolphins have on marine ecosystems typically revolve around the amounts and types of food that dolphins need to consume to support healthy populations (e.g., Ford *et al.*, 2010b) or the extent to which they compete with fisheries for commercially important species (e.g., Trites *et al.*, 1997; Lockyer, 2007). Bioenergetic models that predict the amounts of food required by cetaceans have been used to inform management to this end (Kriete, 1995; Benoit-Bird, 2004; Williams *et al.*, 2004; Barlow *et al.*, 2008; Noren, 2010). However, none of the existing models have considered that energy needs of dolphins and other small cetaceans might change with season and that food requirements might therefore not be constant throughout the year.

Seasonal changes in feeding rates have been documented in small cetaceans housed in aquaria. For example, the food intake of a captive dusky dolphin (*Lagenorhynchus obscurus*) varied seasonally and was generally above average in fall and winter, and below average in spring and summer (Kastelein *et al.*, 2000). Similarly, seasonal increases have been documented in the food intake of bottlenose dolphins (*Tursiops truncatus*) when pool temperatures were low (Cheal & Gales, 1992). Seasonal decreases in food consumption of captive Amazon river dolphins (*Inia geoffrensis*) were noted in the mating season (Kastelein *et al.*, 1999), and variation in killer whale intake (*Orcinus orca*) was also proposed to be related to changes in behaviour (Kastelein *et al.*, 2003a). All of these studies suggest there is some degree of seasonality in the food intake of captive cetaceans. Whether or not this trend is similarly expressed in wild con-specifics is unknown.

Food intake may also vary in response to seasonal changes in resting metabolism, which, as a basic physiological function, has been suggested to more likely be similar between wild and captive animals. Monitoring seasonal changes in resting metabolism and food intake of cetaceans in captivity should therefore contribute to understanding whether seasonality in energy needs is an innate process that should be considered when assessing the food requirements of wild cetaceans. However, there are no published studies of seasonal resting metabolic rates for small cetaceans.

I tested whether resting metabolic rates and food requirements vary seasonally in small cetaceans, using the Pacific white-sided dolphin as a model species. Pacific white-sided dolphins are one of the most abundant and gregarious cetaceans in the North Pacific Ocean, and potentially play a large ecological role as an apex predator. They inhabit both open ocean and nearshore environments, and therefore may experience acute changes in prey availability that could drive seasonal changes in food intake and energetic requirements. Physiological adaptations to seasonally changing prey requirements may be innate and could therefore be expressed in the resting metabolism of captive animals.

I used three Pacific white-sided dolphins housed at the Vancouver Aquarium to test whether food ingestion and resting metabolic rates varied seasonally over a one-year period, and whether changes in resting metabolism and total food intake were related. I compared these measurements of resting metabolic rates with those of terrestrial and marine mammals.

3.3 Methods

3.3.1 Study animals

I obtained data from three adult Pacific white-sided dolphins housed at the Vancouver Aquarium (British Columbia, Canada) since 2001 (a male M001 – *Spinnaker*) and 2005 (two females, F001 – *Hana* and F002 – *Helen*). These three dolphins were by-caught in fishing nets near Japan in three separate incidents in the 1990s and early 2000s, and were believed to be in their late teens (F001) and early 20s (M001 and F002) at the time of my study (January to December 2011). The dolphins were maintained in three interconnected outdoor pools (2460.5 m^3, 1135.6 m^3, and 189.3 m^3) with filtered sea water pumped from the Burrard Inlet, and were exposed to ambient environmental conditions. Pool temperatures ranged from ~10-15°C over the 12 month study period.

The dolphins were fed approximately 8-9 kg of food daily, in a mixture of about 40% herring, 40% capelin, 10% salmon and 10% squid supplemented with vitamins (MAKE). Energy density of the prey was extrapolated from proximate composition analysis. Food intake was dictated by animal trainers and feeding rates were based on animal motivation to perform requested behaviours. Motivation was kept constant throughout the year, and I assumed motivation was related to hunger.

3.3.2 Data collection

I used open-circuit gas respirometry to measure the oxygen consumption of each dolphin while it rested in a vertical and near-stationary position under a floating respirometry dome. The dome measured 1.4m×1.1m×0.7m ($l \times w \times h$, volume = 1078 L) and had a small feeding tube (designed to preclude air loss) mounted on the top (Fig. 3.1). A hose was run from the respirometry dome to a mass flow pump on the dock. Data were collected twice per month for each dolphin between 0800 and 0900 hrs.

Figure 3.1 Experimental set up showing dolphin F001 stationed under the respiratory dome. The vacuum hose runs from the dome to the pump (far right to far left of photo) and ex-current air is sub-sampled in the Sable system (black boxes) where gas concentrations are determined.

Ambient air was drawn through the respiratory dome at a rate of 350 L min^{-1} to prevent build-up of carbon dioxide and stagnant air from accumulating in the corners of the dome. Ex-current airstream was continuously sub-sampled and gas concentrations were determined in a desiccated sub-sample of expired air using either a Sable System FC-1B oxygen analyzer and a CA-1B carbon dioxide analyzer coupled to a MODEL mass flow generator, or a FoxBox integrated gas analyses unit (Sable Systems, Las Vegas, NV, USA). Gas analyzers were periodically calibrated against gases of known concentrations as per manufacturer recommendations. Electronic drift during trials was accounted for using ambient air to baseline gas concentrations at the start and end of each trial. A Sable data acquisition system was used to calculate the average gas concentrations over each one-second interval (Sable Systems, Salt Lake City, Utah). Respiration rate, pool temperature and air temperature were recorded during trials.

The dolphins were fasted overnight (>15 hrs) prior to data collection. Fasted dolphins were weighed on a slide-out scale (± 0.10 kg) within 24 hrs of each trial. During trials dolphins were fed small pieces of herring, capelin and squid to maintain their position under the dome. Energetic costs associated with digestion were considered to be negligible over the short duration of the trials (e.g., Williams *et al.*, 1993) and based on observation that the measured heat increment of feeding in bottlenose dolphins begins to affect resting metabolic rate measurements ~25 minutes after feeding and peaks about an hour after ingestion (Yeates & Houser, 2008). The dolphins were non-reproductive and presumed to be within their thermal neutral zone for the 12-month study period because the temperature range experienced by dolphins at the Vancouver Aquarium (~5°C) is far less than temperature ranges experienced by dolphins in the wild (~15°C).

The dolphins were trained to maintain a vertical position while in the dome (Fig. 3.1) based on pre-trial tests that revealed the dolphins used more frequent fluke strokes and pectoral fin movements to maintain horizontal than vertical position. The dolphins were near-stationary and held their heads above the surface of the water. On occasion, a dolphin would submerge and follow a drifting piece of fish. We aborted the trial if the dolphin breathed outside the dome, or was submerged deeper than 2 m for more than 5 seconds. The dolphins were acclimatized to the equipment and experimental procedures over a 10-month period prior to data collection to ensure they were calm during data collection. During this time, the dolphins were trained to perform resting metabolic rate trials using standard operant conditioning procedures. All training and experimental protocol was conducted voluntarily by the dolphins, and with approval of the Vancouver Aquarium Animal Care Committee, and UBC Animal Care permit A10-0015.

3.3.3 Data analyses

Rates of oxygen consumption were calculated for the last 5.5 minutes of each 10 minute trial, which was when gas concentrations (O_2 and CO_2) in the respiratory dome were level and animals were considered to have met resting condition (typically occurred 3 to 3.5 minutes after the start of the trial; see oxygen consumption trace, Appendix A). Resting metabolic rate (RMR) was calculated as the 2-minute minimum oxygen consumption within the last 5.5 minutes of the trial. Although the exact conversion between rate of oxygen consumption and energy used depends on the specific energy source the animal uses, the variation is small in mammals (Blaxter, 1989). I therefore converted oxygen consumption (L day^{-1}) to energy requirements (MJ day^{-1}), using the assumption that 1 L of oxygen was equivalent to 20.1 kJ (e.g., Rosen & Renouf, 1998).

I used linear mixed-effects models to determine whether total or mass-specific (per kg) RMR varied with an individual's mass, total energy (food) intake, air temperature, or pool temperature. I used the same models to test whether RMR varied seasonally, where seasons were defined as *winter* (Jan-Mar), *spring* (Apr-Jun), *summer* (Jul-Sep), and *fall* (Oct-Dec). Linear mixed-effects models were built in R version 2.14.1 (R Core Development Team, 2009) with the package *nlme* (Pinheiro *et al.*, 2009) using the maximum likelihood method. Season was input as a fixed effect, and mass, total food intake, air temperature and pool temperature were input as random effects. I used a nested model design, whereby air temperature and pool temperature were nested in season, and where food intake and mass were nested in animal ID. Animal ID was incorporated into all the models as a random (aka repeated measures) effect. I varied the number of fixed and random effects in each model to determine which were important in predicting resting metabolic rate. I used Akaike Information Criterion (AIC) model selection to determine the model that best-fit the data (lowest AIC score). I repeated this process for absolute and mass-specific food intake; however I used metabolic rate as a random effect instead of using food intake as a random effect. I used a post-hoc general linear hypotheses and multiple comparison test (glht) using the *Tukey* method to test for significant differences in food intake or resting metabolic rate in different seasons (multcomp package in R; Hothorn 2012).

3.4 Results

3.4.1 Individual-level energetics

A general trend was seen whereby food intake was inversely related to body mass in individuals (Fig 3.2a-c; Fig. 3.3a & b); however mass was not a significant parameter in the linear mixed effects models I used to predict total food consumption or resting metabolic rates (see next section). No clear seasonal trends in body mass were seen in all animals, although the females showed decreases in mass from winter to summer and increases in mass in fall (Fig.3.2a & b, Fig. 3.3a) and the male showed a sharp decrease in mass in summer followed by an increase in mass in fall (Fig. 3.2c & Fig. 3.3a).

A probable training effect was seen while measuring RMR in one of the dolphins (F001). Her metabolic rate was equivalent to about 135% of total food intake at the start of the study in winter, and steadily decreased to about 94% of total food intake in the fall (Fig. 3.3b & c). Her mean (± S.E.) metabolic rate at the start of the study in winter was 49.48 ± 1.39 MJ day^{-1} (0.39 ± 0.02 MJ kg^{-1} day^{-1}) and metabolic rates decreased over the following 12 months until the study ended in the fall (41.54 ± 1.39 MJ day^{-1}; 0.33 ± 0.01 MJ kg^{-1} day^{-1}; Fig. 3.3c). Due to the both the training effect and the overall high level of observed metabolic rate relative to food intake, I did not believe that results from F001 approached a metabolic rate that could be classified as 'resting'. Thus, I did not test whether F001's metabolic rate changed with season and omitted F001 from further results regarding the 'resting' measurements.

The mean resting metabolic rates of the two remaining dolphins averaged 32.15 ± 0.50 MJ day^{-1} (0.29 ± 0.01 MJ kg^{-1} day^{-1}; Fig. 3.3c). The mean resting rate of the female (F002) was 31.24 ± 0.67 MJ day^{-1} or 0.28 ± 0.01 MJ kg^{-1} day^{-1}, which was equivalent to 62% of her total daily food intake (Fig. 3.3 b & c). The mean resting rate of the male (M001) was 33.25 ± 0.70 MJ day^{-1} or 0.30 ± 0.01 MJ kg^{-1} day^{-1} and accounted for 84% of his total daily food intake (Fig. 3.3 b & c).

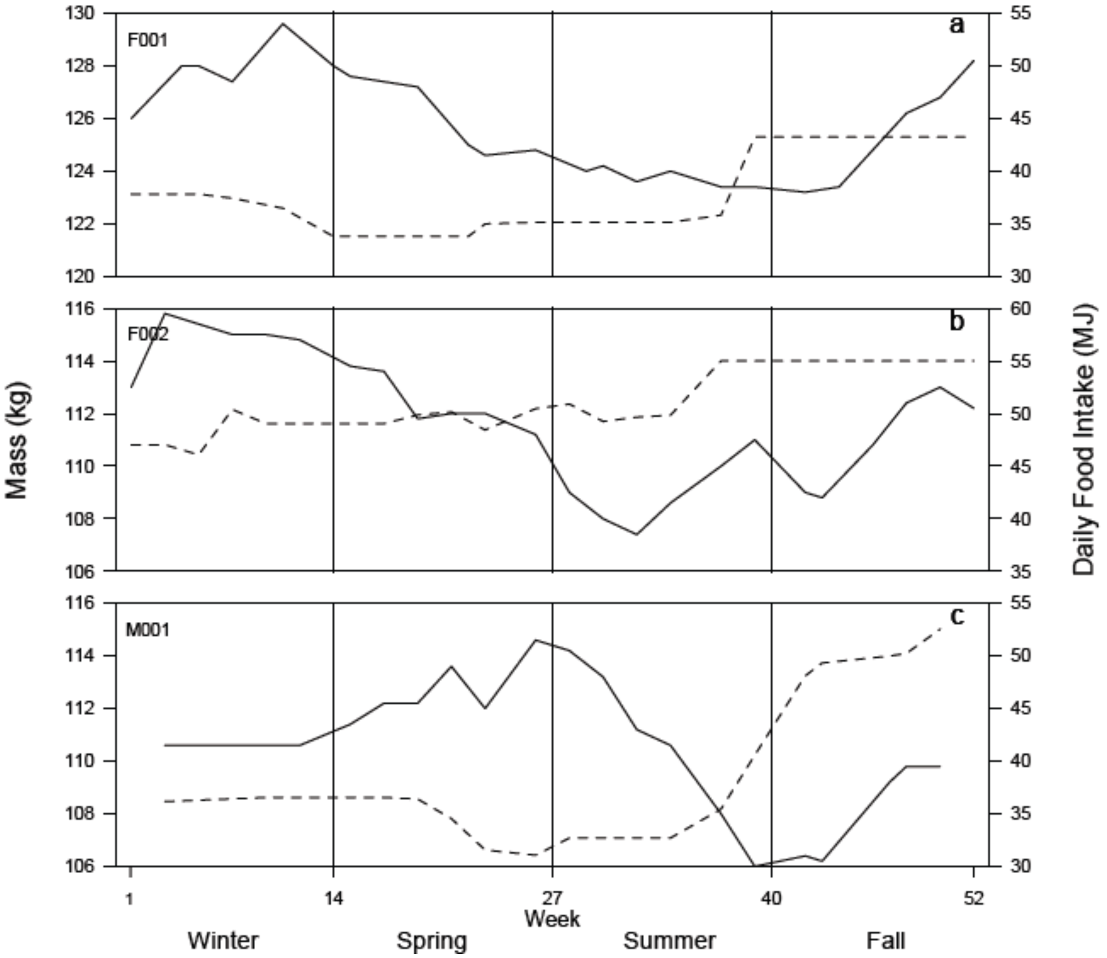

Figure 3.2 Weekly mass measurements of three dolphins F001 (a), F002 (b) and M001 (c) from the 1st to the 52nd week of 2011 (solid line) and weekly average daily food intake of three dolphins in 2011 (dashed line). Vertical lines delineate seasons (*winter, spring, summer* and *fall*). Note the y-axes scales for each animal have different intercepts, but have a 10 kg range (mass) and a 25 MJ range (food intake) for each individual.

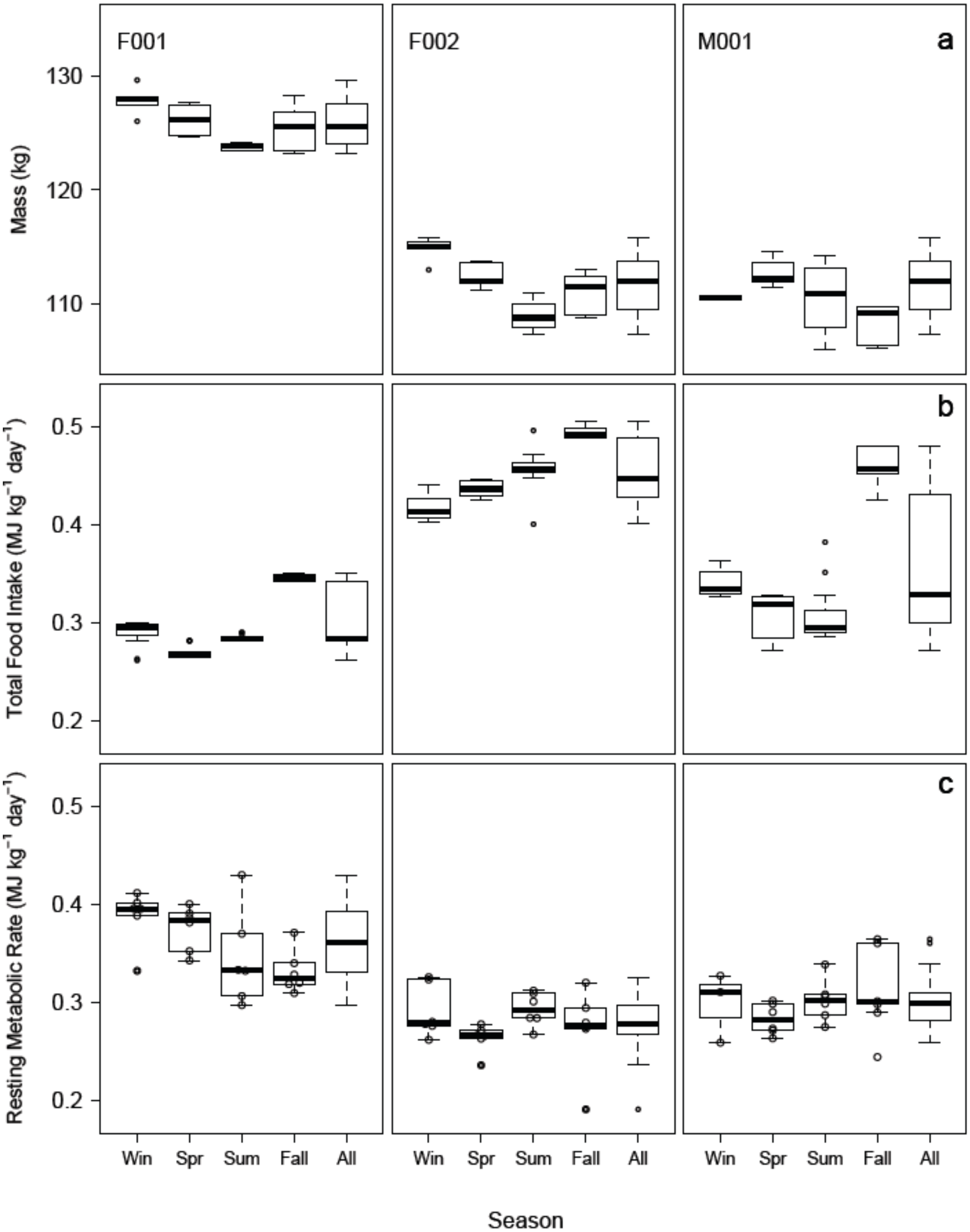

Figure 3.3 **Study results showing individual animals and a comparison of seasonal mean mass, seasonal mean total food intake and seasonal mean resting metabolic rates: a) mass in kg, b) mass-specific food intake in MJ kg^{-1} day^{-1}, and c) mass-specific resting metabolic rate in MJ kg^{-1}day^{-1}**

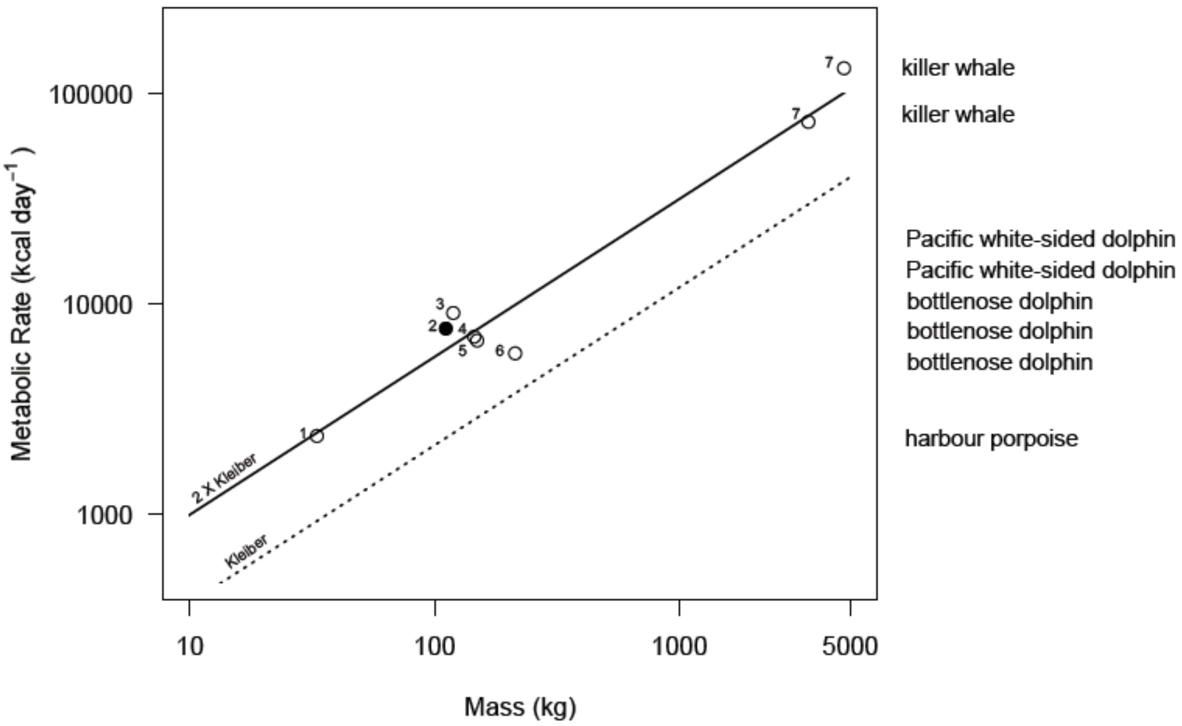

Figure 3.4 Resting metabolic rates of dolphins and porpoises as predicted by body mass. The dotted line represents Kleiber's mouse to elephant curve (Kleiber, 1975) and the solid line represents 2 times Kleiber's predictions which is where small cetaceans typically fall (Costa & Williams, 1999). Species names along the right margin correspond with circles at the same coordinates. The filled circle (2) are data from M001 and F002 (this study), and open circles indicate data from previously published research: (1) Karandeeva et al. (1973) (3) Ohizumi et al. (2009), (4) Williams et al. (1993), (5) Williams et al. (2001), (6) Karandeeva et al. (1973), and (7) Kriete (1995). Some of these data were previously summarized in Costa and Williams (1999) and Hunter (2005).

3.4.2 Resting metabolic rates

The average metabolic rates for the two dolphins that met the criteria for 'resting', were about 3 times Kleiber's predictions for adult terrestrial mammals (3.19 ± .051 times Kleiber), and were slightly elevated from predictions for marine mammals (Costa & Williams, 1999) and measurements of other small cetaceans (Fig. 3.4). Pacific white-sided dolphins measured in this study and by Ohizumi *et al.*, (2009) had the highest metabolic rate of all the small cetaceans thought to meet Kleiber's criteria and thus shown in Fig. 3.4, with the exception of one male killer whale (Kriete 1995).

The AIC values indicated that the linear mixed effects model that best described the absolute resting metabolic rates of the two dolphins was the null model that accounted for repeated measures only, and did not include the effects of season, pool or air temperatures, total food intake, or body mass (AIC=241.76, log likelihood=-117.88; Table 3.1 & Fig. 3.5a). The same was true for the model that best described the mass-specific (per kg) metabolic rates of the two dolphins (AIC = -180.83, log likelihood = 93.41; Table 3.1 & Fig. 3.5b).

3.4.3 Total food intake

Mean (± S.E.) average daily energy intake was 42.23 ± 0.60 MJ day^{-1} (0.37 ± 0.01 MJ kg^{-1} day^{-1}; Fig. 3.5c & d). The model that best fit the total food intake data included only the fixed effect of season and only the random effect of dolphin (AIC=338.16, log likelihood=-162.08; Table 2.2; Fig. 3.5c). Models that included nested effects of pool temperature, air temperature, individual mass, and resting metabolism did not improve the model fit (Table 3.2). The model that best-fit the mass-specific (per kg) food intake data also accounted for season, but was not influenced by any other parameters (AIC=-303.04, log likelihood=158.52; Table 3.2; Fig. 3.5d). Post-hoc glht results revealed that total food intake was significantly highest in fall (October – December; mean 49.56 ± 3.61 MJ day^{-1}; p<.001) and relatively constant during the other seasons (Fig. 3.5c). Mass-specific (per kg) food intake was also significantly highest in fall (October – December; mean 0.43 ± 0.04 MJ kg^{-1}day^{-1}; p<0.01) and relatively constant in all other seasons (Fig. 3.5d).

Table 3.1 Linear mixed-effects model results used to determine the best model to describe the resting metabolic rate data. AIC=Akaike's Information Criterion.

Model	df	AIC	ΔAIC	logLik
Total Resting Metabolic Rate				
Null (only accounts for random effect of Animal ID)	3	241.76	0.00	-117.88
Mass (nested in Animal ID)	4	242.43	0.67	-117.22
Total food intake (nested in Animal ID)	4	243.76	2.00	-117.88
Mass (nested in Animal ID) and total food intake (nested in Animal ID)	5	244.44	2.68	-117.22
Season and mass (nested in Animal ID)	5	244.98	3.22	-115.49
Total food intake (nested in Animal ID) and Season	7	245.71	3.95	-115.86
Season	7	245.71	3.95	-115.85
Season with nested air temperature	8	246.51	4.75	-115.25
Season and mass (nested in Animal ID) and total food intake (nested in Animal ID)	8	246.98	5.22	-115.49
Season with nested pool temperature	8	247.25	5.49	-115.62
Season with nested pool and air temperature	9	249.76	8.00	-117.88
Mass-specific (per kg) Resting Metabolic Rate				
Null (only accounts for random effect of Animal ID)	3	-180.83	0.00	93.41
Mass (nested in Animal ID)	4	-179.80	1.03	93.90
Total food intake (nested in Animal ID)	4	-178.83	2.00	93.41
Season and mass (nested in Animal ID)	7	-178.17	2.66	96.08
Total food intake (nested in Animal ID) and Season	7	-177.93	2.90	95.96
Season	7	-177.92	2.91	96.96
Mass (nested in Animal ID) and total food intake (nested in Animal ID)	5	-177.80	3.03	93.90
Season with nested air temperature	8	-177.70	3.13	96.84
Season and mass (nested in Animal ID) and total food intake (nested in Animal ID)	8	-176.17	4.66	96.08
Season with nested pool temperature	8	-175.93	4.90	95.96
Season with nested pool and air temperature	9	-173.93	6.90	95.96

Table 3.2 Linear mixed-effects model results used to determine the best model to describe the food intake data. AIC=Akaike's Information Criterion.

Model	df	AIC	ΔAIC	logLik
Total food intake				
Season	7	338.16	0.00	-162.08
Season with nested pool temperature	8	339.71	1.55	-161.86
Season with nested air temperature	8	340.16	2.00	-162.08
Season with nested pool and air temperatures	9	341.71	3.55	-161.86
Season and mass (nested in Animal ID)	7	366.17	28.01	-176.08
Resting metabolism (Nested in Animal ID) and Season	7	367.44	29.28	-176.70
Season and mass (nested in Animal ID) and resting metabolism (nested in Animal ID)	8	368.17	30.01	-176.08
Mass (nested in Animal ID)	4	430.85	92.69	-211.42
Mass (nested in Animal ID) and resting metabolism (nested in Animal ID)	5	432.84	94.68	-211.42
Null (only accounts for random effect of Animal ID)	3	436.41	98.25	-215.20
Resting metabolism (nested in Animal ID)	4	438.41	100.25	-215.20
Mass-specific (per kg) food intake				
Season	7	-303.04	0.00	158.52
Season with nested pool temperature	8	-302.88	0.16	159.44
Season with nested air temperature	8	-301.04	2.00	158.52
Season with nested pool and air temperatures	9	-300.88	2.16	159.44
Season and mass (nested in Animal ID)	7	-268.12	34.92	141.06
Resting metabolism (Nested in Animal ID) and Season	7	-266.61	36.43	140.31
Season and mass (nested in Animal ID) and resting metabolism (nested in Animal ID)	8	-266.12	36.92	141.06
Mass (nested in Animal ID)	4	-212.36	90.68	110.18
Mass (nested in Animal ID) and resting metabolism (nested in Animal ID)	5	-210.36	92.68	110.18
Null (only accounts for random effect of Animal ID)	3	-203.92	99.12	104.96
Resting metabolism (nested in Animal ID)	4	-201.92	101.12	104.96

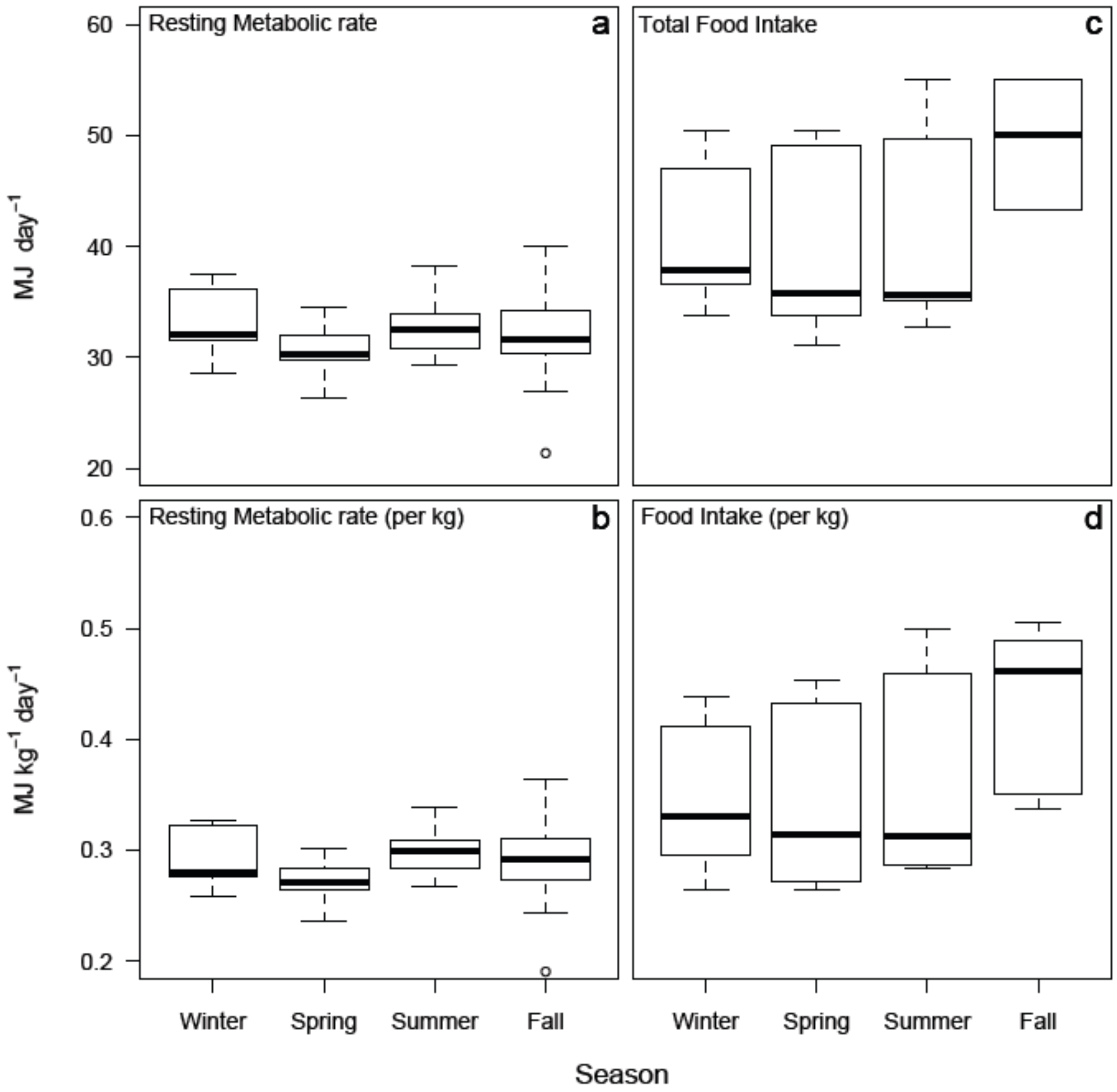

Figure 3.5 **The effect of season on a) resting metabolic rate, b) mass-specific (per kg) resting metabolic rate, c) total food intake and d) mass-specific (per kg) food intake. Food intake measurements are presented for all three Pacific white-sided dolphins while resting metabolic rate measurements are presented for only the 2 Pacific white-sided dolphins that were judged to meet testing criteria. Food intake was significantly greater in fall (October to December) than in other seasons.**

3.5 Discussion

Measurements of resting metabolism provide a standard physiological comparison, but must be undertaken under specific conditions, which are often not adequately evaluated. I set out to measure the metabolic rates of three individual Pacific white-sided dolphins, but had to omit data from one individual that had an elevated metabolic rate, exhibited an apparent training effect, and displayed subtle behaviour deemed to be slightly nervous or perhaps excited. For example, she occasionally moved up and down in the dome (submerging her head) and often watched the trainers with unusually widely opened eyes. It was surprising to see a training effect after 10 months spent conditioning animals to the study. This dolphin had a metabolic rate while at rest which was at times about 140% higher than could be met by her total food consumption. Whether or not wild cetaceans elicit similar nervous or excited responses and thereby increase their energetic requirements in response to anthropogenic interactions is unknown. However, the effect of subtle changes in behavioural state on metabolism should always be considered when measuring resting metabolic rates of cetaceans, particularly for studies conducted over a shorter term.

Vocalization is another factor that can increase metabolic rate (Holt *et al.*, 2011). Dolphin M001 chirped while in the dome, and was known to spontaneously chirp while engaged in low-energy activities (B. Sheehan, Vancouver Aquarium Curator, *pers. comm.*). However, none of the oxygen consumption data from M001 resembled data seen by Holt *et al.* (2011) when her animals were asked to vocalize, and I therefore suspect there is a metabolic difference between spontaneous chirping and requested vocalizations (possibly due to excitement or brain engagement/activity differences in spontaneous vs. requested behaviours), and that my reported resting metabolic rates are accurate measures for M001 and F002.

The average resting metabolic rates measured for the remaining two Pacific white-sided dolphins approximated resting metabolic rates measured for several other cetaceans although they were higher than some species. The resting metabolic rates of the two Pacific white-sided dolphins (M001 and F002) were constant throughout the year despite their increased food intake in the fall. Similarly, changes in food intake did not influence measured resting metabolic rates.

The extent to which my results are representative of dolphins in the wild is uncertain given that the behaviours and activities of dolphins in aquaria do not necessarily mimic those of wild dolphins. I am also uncertain whether the occasional heating of the water in the dolphin habitat at the Vancouver Aquarium influenced my results, and I recognize that my conclusions are limited by the small number of animals studied. Despite such shortcomings, the data collected from the three individuals represent the most comprehensive energetics study conducted to date with Pacific white-sided dolphins, and the only cetacean energetics study that has spanned multiple seasons and examined both resting metabolic rates and total calories ingested. As such, it provides a starting point upon which further energetic studies of small cetaceans can build.

3.5.1 Resting metabolic rates

There has been disagreement among scientists regarding how many calories marine mammals require to meet maintenance requirements. Some research suggests the resting metabolic rates of marine mammals are elevated when compared with terrestrial species (Brodie, 1975; Snyder, 1983; Costa & Williams, 1999; Williams, 2001; Hunter, 2005). Other researchers suggest marine mammals have similar maintenance metabolic rates as their terrestrial counterparts (Gaskin, 1982; Lavigne, 1982; Worthy, 1987; Kasting *et al.*, 1989; Williams *et al.*, 1992). Since cetaceans don't always "rest" the same way terrestrial animals do, these comparisons are difficult. For example, even when dolphins sleep they swim and maintain movement whereas many terrestrial mammals do not, and cetaceans stationing under a metabolic chamber are required to maintain some posture to keep their blowhole at the surface.

Metabolic rates of the two Pacific white-sided dolphins that met the criteria for 'resting' were high but within the expected range of values predicted by Costa and Williams (1999), and were elevated from basal metabolic rate measurements of terrestrial mammals. Whether or not the elevated metabolic rates are due to adaptations for life in a marine environment or due to a carnivorous diet, as suggested by Williams (2001), was not tested in this study.

When compared with other small cetaceans, Pacific white-sided dolphins had somewhat similar resting metabolic rates, however they were elevated from those of the majority of small cetaceans. This high metabolic rate may be associated with Pacific white-sided dolphins having unusually large thyroids (relative to their body sizes), which is indicative of a high metabolic rate in other mammals (Ridgeway & Patton, 1971). Pacific white-sided dolphins are known to exhibit sudden bursts of high activity (for example in predator avoidance and in acrobatic displays) which supports the idea of their having a metabolism that can support physiological readiness for high energetic output (fast muscles).

Resting metabolic rates accounted for about 70% of total energy intake. These results were not unprecedented — resting metabolic rates of other Pacific white-sided dolphins accounted for ~60-80% of total metabolizable energy intake at an aquarium in Japan (Ohizumi *et al.*, 2009). A behavioural explanation for the high proportion of total energy intake allotted to resting metabolic rate may have to do with activity levels of the dolphins. Activity budgets previously constructed for these same three dolphins at the Vancouver Aquarium in June and July of 2010 indicated that F002 (RMR ~60% total intake) spent about 35% of her time resting, and about 60% of time in low-energy, stereotypical behaviours (Javdan, 2010). The male, M001 (RMR ~80% total intake) spent 78% of his time resting, about 10% of his time engaged in surface activities (vocalizing at the surface, breaching, tail slapping, bubble blowing) and ~5% of his time engaging in social and sexual activities (Javdan, 2010). Between January 30th and February 4th 2012, I conducted three 24-hr ethograms using scan-sample techniques to record each individual's activity state (low, medium or high) every 15 minutes. I also concluded that the dolphins spend the majority of their time (~80%) at rest or engaged in low-energy activities (Appendix B). These results confirm that the activity levels of all individuals were generally low, and explain the relatively high proportion of total energy intake that was accounted for by resting metabolic rates.

Resting metabolic rates for Pacific white-sided dolphins were seasonally constant. In the absence of other seasonal measurements of resting metabolic rates of other cetaceans, it is unclear if this is typical of cetaceans. Research with other marine mammals has sometimes shown seasonal changes in resting metabolic rates. Resting metabolic rates may for example be depressed in times of low food availability (Rosen & Renouf, 1998; Fuglei & Oritsland, 1999; Rosen & Trites, 2002), or may change seasonally with physiological or morphological changes such as molting (Donohue *et al.*, 2000), or as an adaptation to temperature changes (Williams *et al.*, 2001; Yeates & Houser, 2008).

Pacific white-sided dolphins are not known to undergo a seasonal molt or major changes in body condition, and presumably live in water temperatures that are within their thermal neutral zone (Ferrero *et al.*, 2002). The limited research on the ecology of Pacific white-sided dolphins supports my finding that their high metabolic rates remain relatively constant throughout the year.

3.5.2 Seasonal changes in total food intake

Total energy (food) consumption increased in fall for all three dolphins (October-December), with the greatest increase occurring for the male. Contrary to predictions, the increased food intake in fall was not matched by a change in resting metabolic rate.

Food intake among mammals is known to be influenced by a variety of factors, such as changes in resting metabolism (Rosen & Trites, 2002), ambient temperature (Cheal & Gales, 1992; Kastelein *et al.*, 2000), diet (Knott, 1998), body condition (Lager *et al.*, 1994), food availability (Aleksiuk, 1970; Moen, 1978; Knott, 1998), and behaviour and activity (Rosen & Renouf, 1998; Kastelein *et al.*, 1999). Of these factors, changes in diet, resting metabolism, and pool temperature did not predict the food consumption of my study animals. The linear mixed-effects models were constructed to infer population trends from limited data in a small sample using a repeated measures framework. As such, the models identify overall trends in the data. Changes in mass occurred with different timing and to different extents in each study animal thus no over-arching trends were noted in the models. However, at an individual-level, changes in body mass appeared to be related to changes in food intake, and therefore changes in mass, as well as the remaining factors (behaviour and food availability) are discussed as potential mechanisms to explain the seasonal changes observed in total food consumption.

The male dolphin lost about 10 kg over the summer. During this period of weight loss, his food intake was not significantly different than it was in winter or spring, therefore it is likely that he used more energy in some other aspect of his energy budget during the summer, which resulted in an energy deficit and subsequent mass-loss. Changes in behaviour could affect energy used. Pacific white-sided dolphins are known to have seasonally distinct reproductive cycles, with the majority of successful mating occurring in August (Robeck *et al.*, 2009). It is thus possible that mating behaviour in summer increased the energy used by M001, and that hormonal changes associated with the mating season may have prevented an increase in appetite to match increased energy output due to sexual behaviour (testrosterone levels in male Pacific white-sided dolphins peak in July (Robeck *et al.*, 2009). This may have led to a compensation in food intake in fall. Both female dolphins lost weight in spring and early summer, but maintained a stable or increasing weight in late-summer before showing weight increases in fall. Again, spring weight-loss was likely due to changes in energy used, since food consumption remained constant until fall, and may have been related to mating behaviours and associated hormonal changes. The females may also be triggered to put on weight in late summer and early fall as an adaption to fuel a potential pregnancy; Pacific white-sided dolphin conceptions peak from August to October (Robeck *et al.*, 2009).

Alternatively, changes in mass and food intake may have been related to innate adaptations to seasonal aggregations of high-energy prey in the wild. Seasonal changes in body mass of polar or subpolar mammals are often the result of changes in lipid stores as a result of changes in food availability, for example during times of low food availability or high energy demands, a mammal may catabolize its fat stores (Lager *et al.*, 1994). It is therefore possible that in spring and summer a lack of food availability in the wild causes Pacific white-sided dolphins to lose mass, and that in times of high food availability dolphins store excess energy as lipid. Prey availability was not changing seasonally at the Vancouver Aquarium, so this adaptation to prey-pulses would have to be innate if it where to explain the changes in food intake in these three study animals.

On the coast of British Columbia (where these dolphins now reside) a prey-pulse of high-energy salmonids and herring (both common in the diet) occurs in fall (Heise, 1997; Morton, 2000; Chapter 3). However, in waters near Japan (where these dolphins were captured), Pacific white-sided dolphins primarily consume sardines (Miyazaki *et al.*, 1991) and anchovy (Kitamura *et al.*, 2008). The energetic densities of these fish are typically highest in spring and summer in Japan (Shirai *et al.*, 2002; Ikeda, 1987), when the dolphins were losing weight at the Aquarium in BC. One possibility to explain the weight-loss is that the energetic density of the prey consumed by the dolphins at the Aquarium remained constant in spring and summer, and dolphins did not increase the biomass they were consuming sufficiently to prevent weight-loss.

The difficulty in ascertaining the extent and cause of the changes in food intake are partly due to the small sample size in this study. Seasonal changes in food consumption were smaller for the females and much larger for the male. Further data collection spanning years and sexes of dolphins, and across other aquaria, could determine whether seasonal trends in food consumption are sex-specific, are related to body mass, or occur in Pacific white-sided dolphins at the population-level.

3.5.3 Ecological implications and conclusions

Resting metabolic rates of Pacific white-sided dolphins were generally high, although comparable to other cetaceans. Recent literature indicates that high metabolic rates may be driven by a high mitochondrial density in muscle tissue—an adaption to fuel the pursuit of high-energy prey (Spitz *et al.*, in review). Although the mitochondrial density of Pacific white-sided dolphin muscles has not yet been assessed, their activities in the wild indicate that they would have fast muscles, as they are commonly cited as one of the most acrobatic and active cetaceans. If dolphins require a lot of energy to fuel and maintain fast-muscles and high-cost activities, I would expect them to preferentially consume a high-energy diet.

The diets of Pacific white-sided dolphins vary geographically across the Pacific Ocean but are generally composed of high-calorie, lipid-rich forage fish (Stroud *et al.*, 1981; Walker *et al.*, 1986; Miyazaki *et al.*, 1991; Walker & Jones, 1993; Black, 1994; Heise, 1997; Morton, 2000; Kitamura *et al.*, 2008). Other species of cetaceans—common dolphins, harbour porpoise, and resident killer whales—selectively pursue high-energy prey, likely to fuel high caloric requirements (Spitz *et al.*, 2010; Spitz *et al.*, in review; Ford *et al.*, 2010b). Pacific white-sided dolphins with potentially high costs of living may also rely on high-energy prey. The potential for an energetic reliance on high-energy prey makes Pacific white-sided dolphins more susceptible to competition from fishers than previously thought and has implications for fisheries management.

Chapter 4: A bioenergetic model to assess the food requirements of Pacific white-sided dolphins

4.1 Summary

Pacific white-sided dolphins are a gregarious species distributed across the temperate Pacific Ocean. They have the potential to impact prey populations and to be impacted by changes in prey abundance. To determine required prey biomass, I estimated the food requirements of individual Pacific white-sided dolphins using a generalized bioenergetic model that accounted for different age classes and reproductive stages (calf, juvenile, adult, pregnant and lactating). Monte Carlo simulations incorporating variability in model parameters (body mass, growth rate, costs of gestation and lactation, metabolic rate, cost of transport, and assimilation efficiencies) were used to predict caloric requirements. Mean (± S.D.) total energy requirements were 32.5 ± 4.5 MJ day^{-1} for calves, 60.6 ± 3.3 MJ day^{-1} for juveniles, 65.0 ± 1.7 MJ day^{-1} for adults, 66.0 ± 1.7 MJ day^{-1} for pregnant females, and 89.60 ± 15.21 MJ day^{-1} for lactating females. Sensitivity analysis revealed that these estimates of food requirements were most sensitive to uncertainty in metabolic rates and energetic costs of activity. Estimated mass-specific (per kilogram) energy requirements were elevated in calves (1.25 ± 0.16 MJ kg^{-1} day^{-1}), juveniles (0.82 ± 0.05 MJ kg^{-1} day^{-1}) and lactating females (0.92 ± 0.16 MJ kg^{-1} day^{-1}) when compared with non-reproductive adults and pregnant females (~0.67 ± 0.02 MJ kg^{-1} day^{-1}). Based on a diet of primarily high-energy fish species, an average sized dolphin (78 kg) would consume approximately 10 kg of fish per day, or about 13% of its bodyweight.

4.2 Introduction

The Pacific white-sided dolphin is an abundant cetacean that inhabits the temperate North Pacific Ocean from California to the Bering Sea, and south to Taiwan (Stacey & Baird, 1991). They number ~1 million animals (95% CI ~200,000 - 4,000,000 Buckland *et al.*, 1993; 95% CI ~150,000 - 7,000,000 Miyashita, 1993) and exploit a large habitat including both oceanic and nearshore waters. Pacific white-sided dolphins are gregarious and forage in coordinated groups (Heise, 1997; Van Waerebeed & Wursig, 2002), and are considered to be an acrobatic and high-energy species (Van Waerebeed & Wursig, 2002). As such, they may have elevated energy needs and may exert ecosystem-level effects on prey.

Pacific white-sided dolphins primarily consume high-energy fish, including anchovy, sardine, herring, salmon, hake and squid that are commercially or culturally valuable (Stroud *et al.*, 1981; Walker *et al.*, 1986; Miyazaki *et al.*, 1991; Walker & Jones, 1993; Black, 1994; Heise, 1997; Morton, 2000; Kitamura *et al.*, 2008). Marine mammals have often been cited as having heightened energy needs (Worthy, 2001; Benoit-Bird, 2004; Barlow *et al.*, 2008; Spitz *et al.*, 2010) that put them in conflict with fisheries (Trites *et al.*, 1997). However, the extent to which Pacific white-sided dolphins are detrimental to fisheries or to fish stocks, or whether their nutritional needs are adequately met is unknown.

Concerns about the conservation of Pacific white-sided dolphins, as well as the potential for this species to deplete fish stocks or compete with commercial fisheries, can be addressed in part with an estimate of the prey requirements of the dolphins. It is difficult to address the prey requirements of cetaceans since most foraging and prey consumption occurs beneath the sea surface. One method used to study the food requirements of fish, birds, and mammals is bioenergetic modeling (Laurence, 1977; Edwards, 1992; Bunce, 2001; Winship *et al.*, 2002). Bioenergetic modeling has also frequently been used to estimate the food needs of cetaceans (Kenney *et al.*, 1986; Benoit-Bird, 2004; Lockyer, 2007; Barlow *et al.*, 2008; Noren, 2010). However, a bioenergetic model has never been constructed for Pacific white-sided dolphins.

I constructed a generalized bioenergetic model to predict the food requirements of individual dolphins in various reproductive stages. My model provides the first estimates of wild Pacific white-sided dolphin food consumption, and provides direction for future research by identifying which bioenergetic parameters have the greatest influence over total energy needs. Estimates of food requirements may assist local fisheries management and provide a global perspective on the nutritional and conservation needs of white-sided dolphins in the North Pacific.

4.3 Methods

I used a bioenergetic model based on body mass, production, metabolic rate, activity, heat increment of feeding, and digestive efficiency to predict the food requirements of wild Pacific white-sided dolphins. Requirements were determined for calf, juvenile, adult, pregnant, and lactating dolphins. Model parameters were tested for sensitivity to provide direction for future research.

4.3.1 Individual energy requirements

Life-history stages were classified as calves, juveniles, and adults. Animals aged newborn to 1 year old were considered calves, based on research indicating that Pacific white-sided dolphin calves are weaned at about one year old (Ferrero & Walker, 1996; Heise, 1997b). Animals greater than 1 and less than 8 years old were classified juvenile, based on the age of sexual maturity which is thought to occur at about 8 years (Heise, 1997b). All animals 8 years and older were considered sexually mature adults (males, non-pregnant females, pregnant females, lactating females).

Food requirements were calculated for each age category. Food requirements for adult males and adult, non-reproductive females were not predicted separately because length-at-age estimates for male and female Pacific white-sided dolphins do not differ significantly (Heise, 1997b). Food requirements for pregnant or lactating females were predicted by adding the daily energetic costs of these pregnancy or lactation to the requirements of resting adults.

Gross energy requirements (*GER*) were estimated for each age class of dolphin using the equation

$$GER = \frac{\left(P + E_m + A\right)}{\left(1 - E_{hif}\right)\left(E_{f+u}\right)} \qquad \textit{Eqn. 1}$$

where P is production (growth), E_m is maintenance (resting metabolism and thermoregulation), A is activity, E_{hif} is the heat increment of feeding as a proportion of *GER*, and E_{f+u} is the fecal and urinary digestive efficiency as a proportion of *GER* (see Winship *et al.* 2002; Iverson *et al.* 2010).

Production (P). Lengths of Pacific white-sided dolphins of various age classes were estimated from a von Bertalanffy growth model fit to body length data taken from Heise (1997b). Confidence intervals (95% CI) were generated by bootstrapping these data 1000 times, and then selecting the 25th and 975th bootstrapped replicates to approximate the CI (R Core Development Team, 2009; Whitlock & Schluter, 2009) (Fig. 4.1a). I applied this same method to the mass-at-length data contained in Heise (1997b) (Fig. 4.1b), and then combined the two growth models in the bioenergetic model framework to determine mass-at-age.

The two growth models were combined by inputting one of the randomly selected bootstrapped von Bertalanffy length curves (between the 25th and 975th percentiles of the length-at-age relationship) into a randomly selected curve from the bootstrapped mass-at-length curves. Combining these two curves produced a mass-at-age curve that incorporated variability from both length and mass estimates. I repeated this 1000 times to estimate a range of mass-at-age curves and a 95% CI. I determined yearly changes in mass from each mass-at-age curve, and divided the difference by 365 to determine daily changes in mass ($\triangle M$). No seasonal patterns in growth were assumed to occur because seasonal patterns in growth have not been observed in Pacific white-sided dolphins.

I estimated the daily energetic cost of changes in mass by multiplying the daily change in mass by total body proportions of blubber and lean body mass, the energetic densities of lipid and protein, and the efficiency of production of lipid and protein. I divided the body into two categories: lean body mass and fat mass, where lean body mass included protein, water, and bone (Iverson *et al.*, 2010). Unfortunately, the proportion of the body composed of blubber or lean body mass were not available for Pacific white-sided dolphins, so these proportions were taken from another small temperate cetacean, the harbour porpoise (*Phocoena phocoena*).

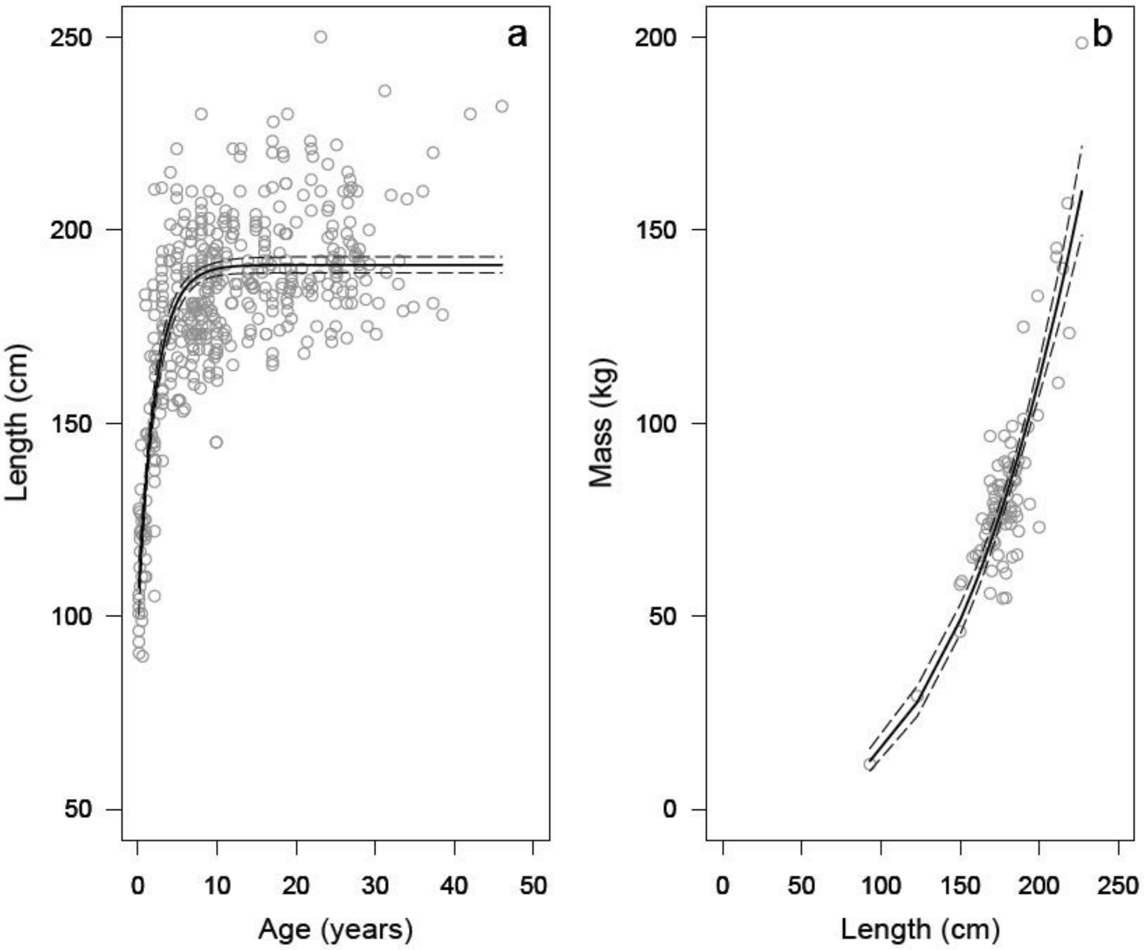

Figure 4.1 The relationships between (a) length and age, and between (b) mass and length of Pacific white-sided dolphins; data from Heise (1997b). Solid lines represent mean growth curves and dashed lines represent the 95% confidence interval of the growth models.

Mean (± S.D.) proportions of blubber (P_{blu}) in the bodies of harbour porpoise were 37.45% (± 6.13) for calves, 29.62% (± 2.04) for sexually immature males, 26.49% (± 2.46) for mature males, 25.81% (± 2.75) for pregnant non-lactating females, and 23.54% (± 3.97) for lactating females (McLellan *et al.*, 2002). I assumed that these proportions of blubber were consistent between Pacific white-sided dolphins and harbour porpoise, and between males and resting females. Thus I used these normally distributed values in my model. I also assumed the proportion of lipid (P_{lip}) in the blubber of Pacific white-sided dolphins was normally distributed with mean (± S.D.) of 81.5 ± 7.8%, based on data collected from 5 Pacific white-sided dolphins (G.A.J. Worthy, Physiological Ecology and Bioenergetics Lab, University of Central Florida, *pers. comm*). I further assumed that lean body mass was 73% water (P_w) based on early work that showed this proportion to be constant across mammalian taxa (Pace & Rathburn, 1945). Standardized energy densities of 39.5 MJ kg^{-1} (ED_{lip}) for fat and 23.5 MJ kg^{-1} (ED_{pro}) for lean body mass (protein) (Schmidt-Nielson, 1990), and growth efficiencies of 0.75 for lipid growth ($GE_{lip} = 1.33$), and 0.45 for protein growth ($GE_{pro} = 2.22$) (see Eqn. 2; Webster, 1985) were used to estimate energetic costs of depositing new tissues during production.

Energetic costs of production were predicted in MJ, using

$$P = \Delta M\left[P_{blu}P_{lip}ED_{lip}GE_{lip} + \left(1 - P_{lip}\right)\left(1 - P_w\right)ED_{pro}\right] \qquad \textit{Eqn. 2}$$

where $\triangle M$ is the daily change in mass in kg, P_{blu} is the proportion of the body that is blubber, P_{lip} is the proportion of blubber that is lipid, ED_{lip} is the energetic density of lipid in MJ kg^{-1}, GE_{lip} is the growth efficiency of lipid, P_w is the proportion of the lean body mass that is water ED_{pro} is the energetic density of protein in MJ kg^{-1}, and GE_{pro} is the growth efficiency of protein.

Energetic costs of resting metabolism and thermoregulation (E_m). Resting metabolic rates (RMR) measured for three adult Pacific white-sided dolphins were found to be seasonally constant, and approximately 3 times Kleiber's (1975) predictions of basal metabolic rates for terrestrial mammals (Chapter 2). I assumed RMRs for adult dolphins ranged from approximately 2.5-3.5 times Kleiber ($X = 2.5\text{-}3.5$), and were normally distributed around a mean of 3 times Kleiber (± 0.25 S.D. times Kleiber; from Chapter 2). I assumed that the resting metabolic rates of Pacific white-sided dolphin calves were elevated an additional 1.5 times Kleiber, and that the elevated metabolic rates of growing animals decreased linearly from 1.5 to 1.0 times Kleiber between the ages of 0-1 and 7-8 years old. This assumption was supported by data on killer whales, showing that juveniles had elevated rates of 1.2-1.3 times the basal rates of adults (Kasting *et al.*, 1989) and was consistent with the basal metabolic rates of juvenile phocid seals which were elevated by 1.4 times Kleiber (Innes *et al.*, 1987), and with modeling methods employed by Winship *et al.* (2002) to estimate elevated resting metabolism of sub-adults.

One of the requirements for measuring resting metabolism is that animals must meet be thermally neutral (Kleiber, 1975). Because I did not see any seasonal trends or trends related to changing pool temperature when measuring resting metabolic rates (Chapter 2) and because it is thought that Pacific white-sided dolphins inhabit areas based at least in part on ocean temperature (Ferrero *et al.*, 2002), I assumed there was no cost of thermoregulation (i.e., $E_{therm} = 0$). This assumption was supported by results from Costa (1999) which indicate that most dolphins select habitat well within their thermal neutral zone. Research suggests that at least some small temperate cetaceans have a modified proportion of lipid in their blubber as an adaption to cold temperatures, which indicates that harbour porpoise, and perhaps Pacific white-sided dolphins, common dolphins, and bottlenose dolphins, do not expend extra energy for thermoregulation in waters above 10°C (Worthy 1991 cited in, Worthy, 2001).

The combined energy cost of resting metabolism and thermoregulation was thus estimated using

$$E_m = X\,0.29288M^{.75} + E_{therm} \qquad \textit{Eqn. 3}$$

where E_m is the metabolic rate in MJ day^{-1}, X is a multiplier of resting metabolic rate that varies with age class, M is mass in kg, and E_{therm} is the cost of thermoregulation in MJ.

Activity (A). I estimated the cost of activity by assuming that total activity costs could be approximated using the cost of swimming (Cost of Transport). This assumption was made in the absence of data indicating the activities and associated energetic costs incurred by Pacific white-sided dolphins, and because regardless of activity the dolphins are typically swimming.

I estimated the total meters swum daily (*m*) based on average swimming speeds of Pacific white-sided dolphins. Mean (±S.D.) swimming speeds of Pacific white-sided dolphins VHF tagged in Monterey Bay, California, were 2.1 ± 0.61 m s^{-1} (Black, 1994), which approximates the mean cruising speeds of other coastal dolphin species (Würsig & Würsig, 1980). These data are nearly identical to the most efficient swimming speeds attained by bottlenose dolphins (*Tursiops truncatus*) trained to swim alongside a boat (swimming speed of 2.1 m s^{-1}) (Williams *et al.*, 1993). I used the mean and S.D. values for swimming speeds determined by Black (1994) to calculate the total number of meters swum in an 18 hour day, assuming that dolphins sleep for 6 hours a day (Lilly, 1964; Goley, 1999; Norris & Dohl, 1980). Although dolphins do swim while sleeping, their speed appears to be well below average swimming speeds (*pers. obs*.), and respiration rates of dolphins sleeping in a swim pattern are significantly lower than average daily respiration rates (Sekiguchi & Kohshima, 2003). I therefore considered the *COT* while swimming to be negligible, and that any activity cost incurred while sleeping would have been approximated within the resting metabolic rate measurements (Chapter 3). Therefore, I estimated a mean of 136,000 ± 40,000 (S.D.) meters swum per day by the dolphins.

I thus assumed activity could be approximated using the COT equation, and I estimated the total cost of transport based on Williams (1999)

$$COT = m\ 7.79\ M^{-.29} \qquad \textit{Eqn. 4}$$

where *COT* is the Cost of Transport in Joules kg^{-1}, *m* is total meters swum per day, and *M* is mass in kg.

Heat increment of feeding (E_{hif}). I estimated the proportion of gross energy intake that was discharged as heat due to the heat increment of feeding based on very limited cetacean data, because the heat increment of feeding has rarely been studied in cetaceans. I am unaware of any published records for any small cetacean species. Preliminary heat increment of feeding values have been indicated as well-below 30% of ingested energy (D.P. Costa pers. comm. cited in, Williams *et al.*, 1992),

However, recently the change in oxygen consumption of a bottlenose dolphin was graphed during and after it ate 1.4 kg of capelin (Yeates & Houser, 2008). At rest, the bottlenose dolphins consumed about 3.8 ml O_2 min^{-1} kg^{-1} and at its peak it consumed about 5.6 ml O_2 min^{-1} kg^{-1} (Yeates & Houser, 2008). I estimated the total heat increment of feeding of this bottlenose dolphin using this graph of the rate of oxygen consumption from the time its meal was consumed until 250 minutes after the meal (when oxygen consumption rates returned to baseline levels). I integrated the area under the curve to calculate total oxygen consumption after feeding (~37 ml O_2 kg^{-1}), and converted it to total energetic cost. My estimate of the heat increment of feeding was 15% of ingested energy (~.75 kJ), based on a diet of capelin (with an assumed energetic density of 5.0 kJ g^{-1}; Anthony *et al.*, 2000)) —

which was consumed by the dolphin prior to oxygen consumption measurements (Yeates & Houser, 2008).

Heat increment of feeding has been measured as 4.7-9.0% of gross energy intake in seals consuming herring (*Clupea harengus*) (Markussen *et al.*, 1994). Elephant seals expressed a heat increment of feeding of 11-13% of total energy intake when eating herring (Gallivan & Ronald, 1981), and in Steller sea lions the heat increment of feeding varied from 9.9 – 12.4 % of total intake, depending on meal size (Rosen & Trites, 1997). As a model input, I used uniformly distributed values between 0.5 and 0.15 to represent proportion of *GER* allocated to the heat increment of feeding of Pacific white-sided dolphins in all life stages.

Fecal and urinary digestive efficiency (E_{f+u}). Fecal and urinary digestive efficiency (E_{f+u}) varies with diet. In general, diets low in lipids (i.e. shrimp or squid) have a lower efficiency whereas diets high in lipids (i.e. herring, salmon, other fatty fish) have a higher efficiency (Lawson *et al.*, 1997a; Lawson *et al.*, 1997b; Williams *et al.*, 1993). No data were available to predict the fecal and urinary digestive efficiencies separately for white-sided dolphins; however data did exist to predict the combined fecal and urinary digestive efficiency as a proportion of total energy intake.

A digestive efficiency of 0.90-0.95 was indicated for cetaceans eating marine animal or fish-based diets (Lockyer, 2007). Pinnipeds consuming a diet of herring or squid also showed digestive efficiency values of ~0.90-0.97 (Keiver *et al.*, 1984; Fadely *et al.*, 1990; Fisher *et al.*, 1991; Lawson *et al.*, 1997b). I therefore assumed digestive efficiency of Pacific white-sided dolphins was uniformly distributed between 0.90 and 0.97.

Energy costs associated with gestation. The total energetic cost of gestation was predicted by

$$Gestation = 18.42\, bm^{1.2} \qquad Eqn.5$$

where *Gestation* is in MJ day^{-1}, and *bm* is mass at birth (kg) (Brodie, 1975; Lockyer, 2007). Pacific white-sided dolphins' length at birth has been estimated to be between 90-105 cm Iwasaki and Kasuya (1997). I used the post-natal equation ($mass = 0.000035\ length^{2.82}$) (Heise, 1997b) to estimate birth mass from estimated lengths. I predicted that mass at birth ranged from 11 to 18 kg, and was uniformly distributed. I then added the estimated gestation costs to the *GER* of resting adult dolphins.

Energy costs associated with lactation. To account for the energetic costs of lactation I used two independent methods. I first assumed the mother needed to provide all of the calories needed by the calf to meet its daily energetic requirements for 365 days. This assumes that my model predictions of calf requirements are reasonable. The overall conversion of total energy intake to milk in lactating humans is 83% of energy consumed (Prentice & Prentice, 1988) and in grey seals is 85% (Anderson & Fedak, 1987). I assumed an 84% conversion in Pacific white-sided dolphins. Therefore, a lactating dolphin would need to consume an additional 119% of the calf's total food requirements to meet its requirements through milk calories, which, in the case of Pacific white-sided dolphins is 160% of resting female consumption. Previous research indicates the energetic requirements of a lactating female marine mammal are 130 - 190% of the energetic requirements of resting females, as roughly approximated in northern fur seals, long-finned pilot whales, bottlenose dolphins, and minke whales (Perez & Mooney, 1986; Lockyer, 2007; Kastelein *et al.*, 2002; Lockyer, 1993)

Because my primary method to estimate lactation costs relied on the accuracy of the model estimates of calf energy requirements, I used a second method to calculate lactating female energy requirements. I used the lactation period (estimated at 12 months), combined with the energetic density of milk, the efficiency of conversion from total energy intake to milk, and an estimate of the biomass of milk produced each day of the lactation period, to estimate lactation costs. I was not able to find literature regarding the caloric content of Pacific white-sided dolphin milk; however the energetic density of spinner dolphin (*Stenella longirostris*) milk was ~12 MJ kg^{-1} (Pilson & Waller, 1970) and common dolphin (*Delphinus delphis*) milk was 14.3 MJ kg^{-1} (Oftedal, 1997). I assumed the caloric content of Pacific white-sided dolphin milk was uniformly distributed between 12 and 14.3 MJ kg^{-1}. Based on an 84% conversion from total food intake to milk, an adult dolphin would need to consume ~120% more calories that it needed to produce in milk, therefore it would need to consume 14.4 to 17.2 MJ of food for each kg of milk produced. Odontocetes typically produce 0.30 to 0.90 kg of milk per day (Oftedal, 1997), I used assumed a uniform distribution of energetic requirements per kg of milk produced (14.4 to 17.2 MJ kg^{-1} of milk) and a uniform distribution of the mass of milk produced (0.30 to 0.90 kg day^{-1}) and multiplied them to estimate the caloric costs of lactation. This method increased lactating female requirements by ~120% of resting requirements.

I set up my Monte Carlo simulations (see next section) to alternate between estimates from the first and second methods of assessing costs of lactation so that model outputs would reflect error in both attempts of determining the cost of lactation.

4.3.2 Data analyses

Energetic needs were predicted for each day of life from birth to 45 years. I also grouped daily energetic requirements by life stage. To incorporate parameter uncertainty and individual variability, I ran 10,000 Monte Carlo simulations to estimate a distribution and range for average daily prey energetic requirements for each age class. Values used in Monte Carlo analyses are listed in Table 1.

Sensitivity analyses determined which model parameters were most sensitive to change. I allowed each major model parameter (*Production – P*, *Metabolism –* E_m *and A*, and *Assimilation –* E_{hif} and E_{f+u}, and *Gestation* and *Lactation* estimates) to run through the Monte Carlo analysis 10,000 times while keeping all other parameters at their mean values. This allowed me to determine which major parameters had the greatest effect on the *GER* prediction (e.g., Winship *et al.*, 2002).

Table 4.1 Bioenergetic model parameter values for Pacific white-sided dolphins (sources in text).

Name	Symbol	Equation	Value	Details
Fecal and urinary digestive efficiency	E_{f+u}	(1)	.90-.97	all animals
Heat increment of feeding	E_{hif}	(1)	.05-.15	all animals
Proportion of body growth that is blubber	P_{blu}	(2)	37.45 ± 6.13	calf
			29.62 ± 2.04	juvenile
			26.49 ± 2.46	adult
			25.81 ± 2.75	pregnant
			23.54 ± 3.97	lactating
Proportion of lipid in the blubber	P_{lip}	(2)	$.81 \pm .078$	all animals
Energetic density of lipid	ED_{lip}	(2)	9434 kcalkg^{-1}	all animals
Energetic density of protein	ED_{pro}	(2)	5613 kcalkg^{-1}	all animals
Growth efficiency of lipid	GE_{lip}	(2)	1.33	all animals
Growth efficiency of protein	GE_{pro}	(2)	2.22	all animals
Proportion of lean body mass that is water	P_w	(2)	0.73	all animals
Scaler to multiply times Kleiber predictions to estimate resting metabolic rate	X	(3)	$4.50 \pm .25$	0<1 years
			$4.31 \pm .25$	1<2 years
			$4.13 \pm .25$	2<3 years
			$3.94 \pm .25$	3<4 years
			$3.75 \pm .25$	4<5 years
			$3.56 \pm .25$	5<6 years
			$3.38 \pm .25$	6<7years
			$3.19 \pm .25$	7<8 years
			$3.00 \pm .25$	8+ years
Number of metres swum per day	m	(4)	$136{,}000 \pm 40{,}000$	all animals
Mass at birth	bm	(5)	11-18 kg	pregnant animals

4.4 Results

Model predictions indicate that the total daily energy requirements of Pacific white-sided dolphins increase rapidly from birth to sexual maturity (Fig. 4.2). The model predicts that they require ~30 MJ day^{-1} as calves and ~65 MJ day^{-1} once they are ~7 years and older. My model shows that the mass-specific (per kilogram) food requirements decrease rapidly from calves to adults (Fig. 4.3). Results indicate that dolphins require ~1.3 MJ kg^{-1} day^{-1} in their first year of life, and ~0.67 MJ kg^{-1}day^{-1}once they reached adulthood.

My model predicts that average daily energy requirements (mean ± S.D.) for calves are 32.5 ± 4.5 MJ day^{-1}. The model indicates that juveniles require about twice as much food as calves (60.6 ± 3.3 MJ day^{-1}), and that non-reproductive adults require slightly more energy than juveniles (65.0 ± 1.7 MJ day^{-1}). The model estimates of energetic costs of gestation were only marginally greater than the energetic requirements predicted for non-reproductive adults. The estimated energetic costs of lactation were about 140% higher than energetic costs of resting females (89.60 ± 15.21 MJ day^{-1}) (Fig. 4.4).

Model results illustrate that mass-specific (per kilogram) energetic needs of calves, juveniles, and lactating females were heightened when compared with other life stages. Calves require (mean ± S.D.) 1.25 ± 0.16 MJ kg^{-1} day^{-1}, juveniles require about 0.82 ± 0.05 MJ kg^{-1} day^{-1}, and lactating females require 0.92 ± 0.16 MJ kg^{-1} day^{-1}. The model indicates that non-reproductive adults and pregnant females have similar energetic requirements of about 0.66 ± 0.02 MJ kg^{-1} day^{-1} (Fig. 4.5).

Sensitivity analyses revealed that the most important model parameter was the estimate of metabolism, which includes estimates of resting metabolic rate and of activity costs/swimming speeds (Fig. 4.6). Changes in this estimate resulted in the greatest changes to total energy requirements. Growth was the second most sensitive parameter, and assimilation of food was the least sensitive to changes. These trends were consistent for dolphins in all life stages except for lactating females where the error associated with incorporating the two disparate methodologies overshadowed errors in other parameters (Fig. 4.6).

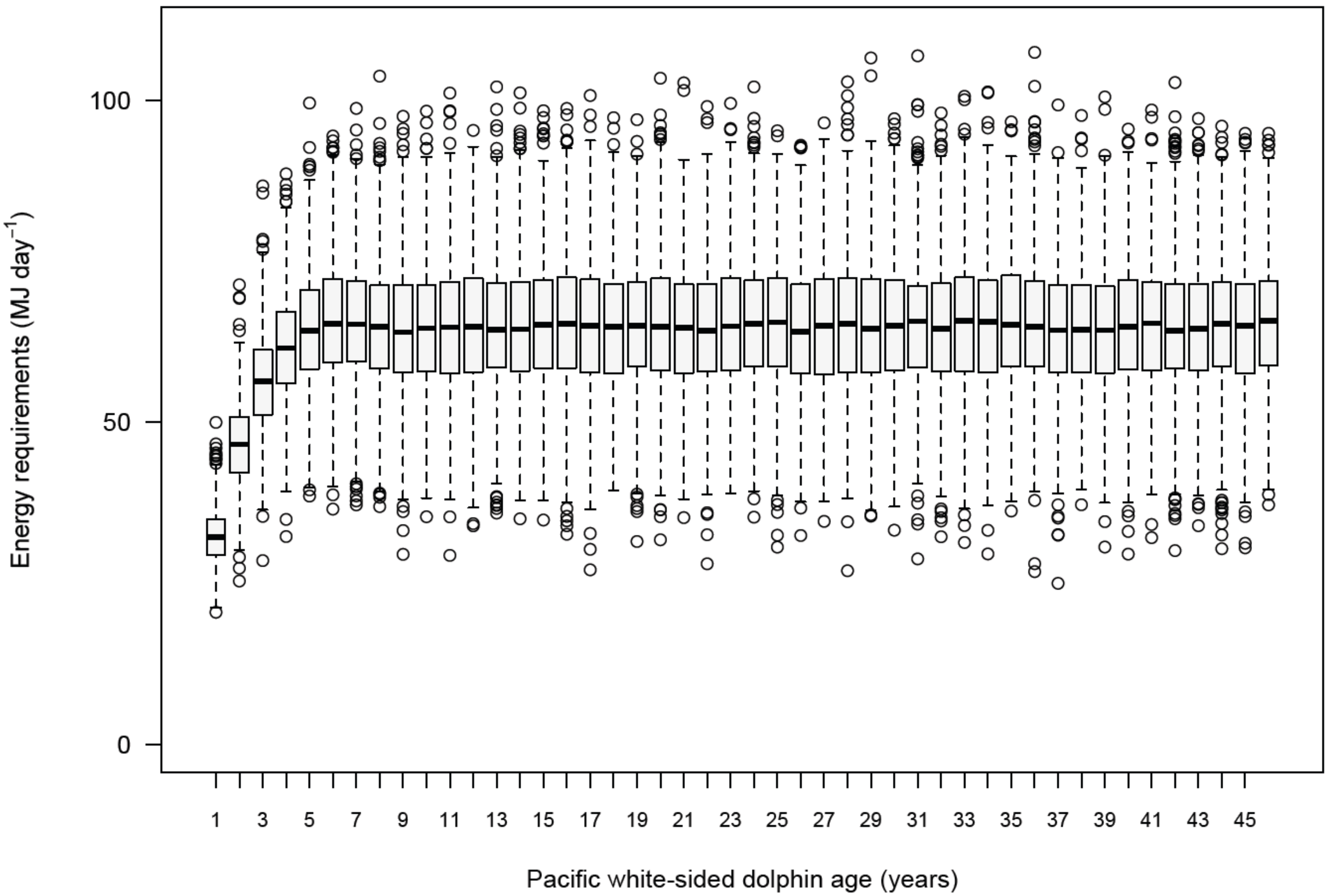

Figure 4.2 Daily gross energy requirements of Pacific white-sided dolphins aged 1-45 years old. Numbers on the x-axis represent age plus one day, for example, at x=1, the dolphins are between 1 and 364 days old. Bold lines in centre of boxes represent the median value, box edges represent the 25th and 75th percentiles of the data distribution and whiskers represent the range. Open circles represent model outliers.

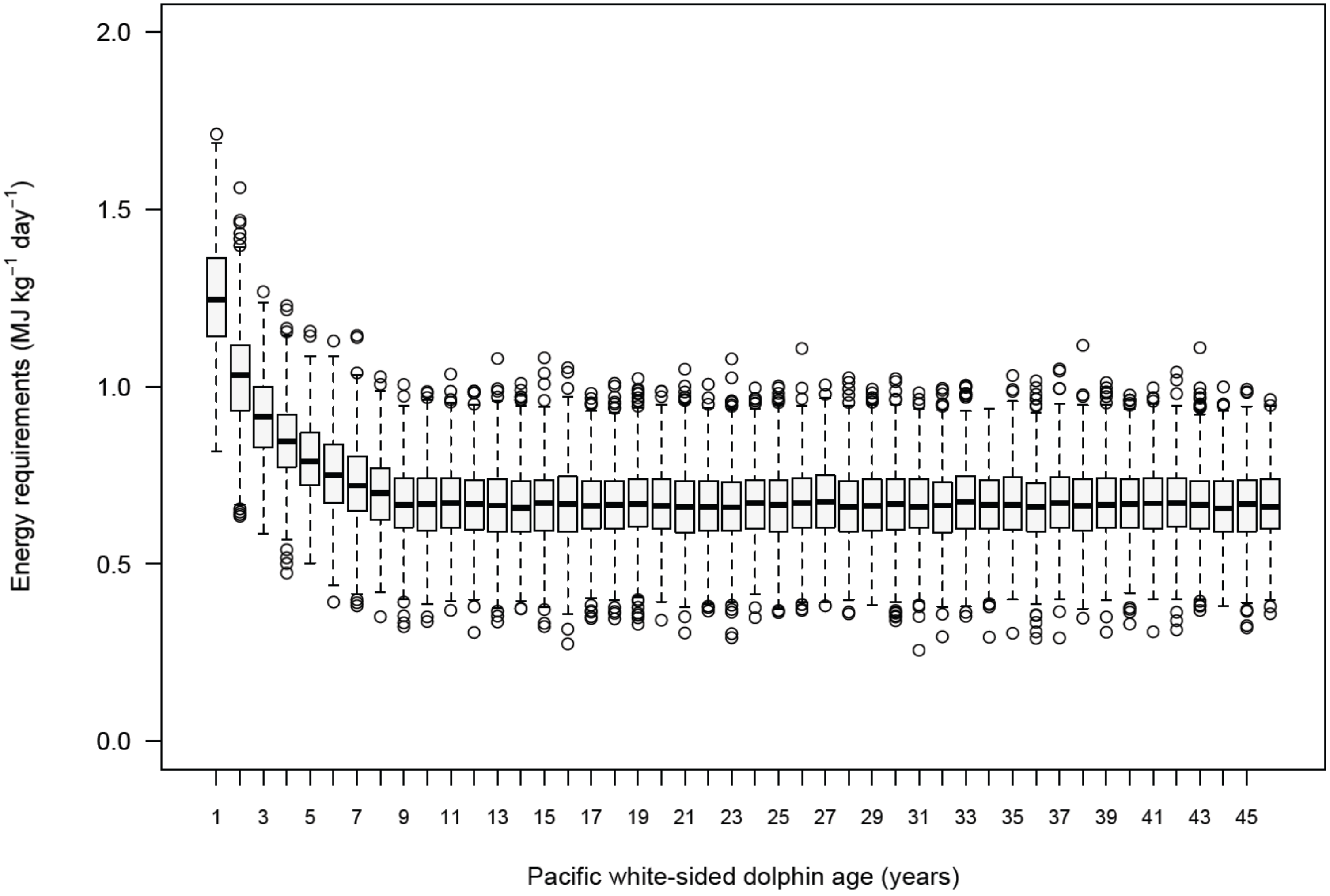

Figure 4.3 Daily mass-specific (per kilogram) energy requirements of Pacific white-sided dolphins aged 1-45 years. Numbers on the x-axis represent age plus one day, for example, at x=1, the dolphins are between 1 and 364 days old. Bold lines in center of boxes show median value, whiskers represent the range, and circles indicate model outliers.

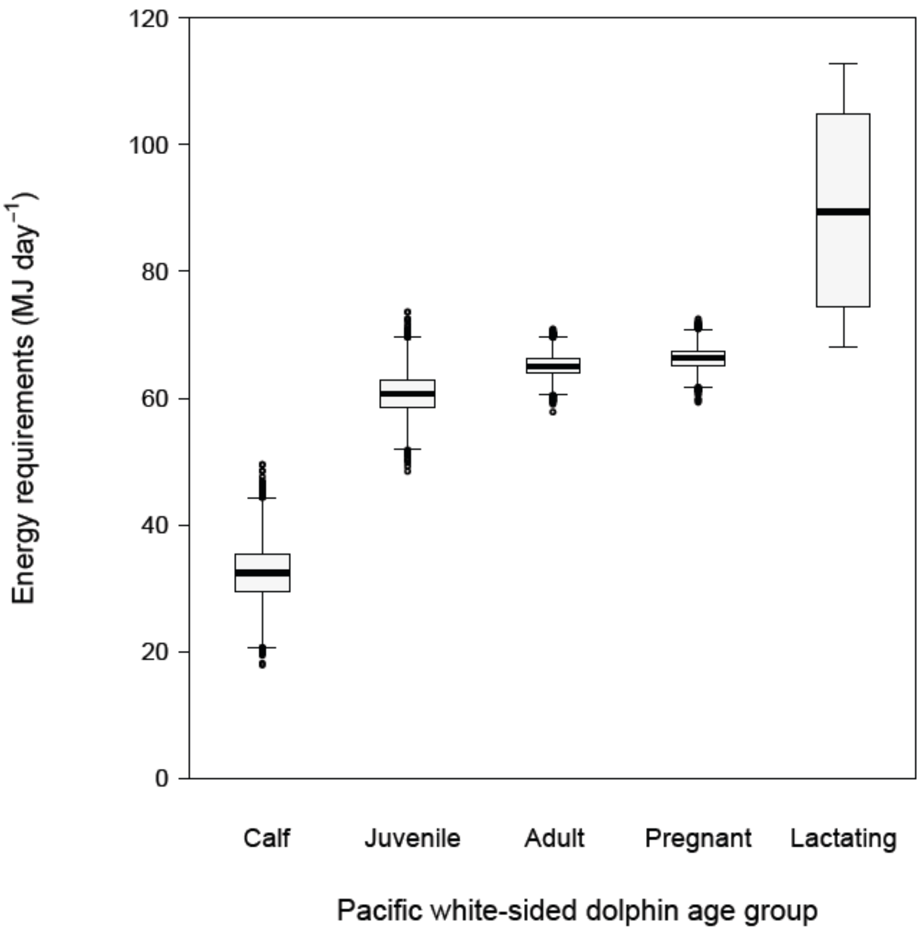

Figure 4.4 Total daily energy requirements for Pacific white-sided dolphin in each reproductive stage. Bold lines in centre of boxes represent the median value, box edges represent the 25th and 75th percentiles of the data distribution and whiskers represent the range. Open circles represent model outliers.

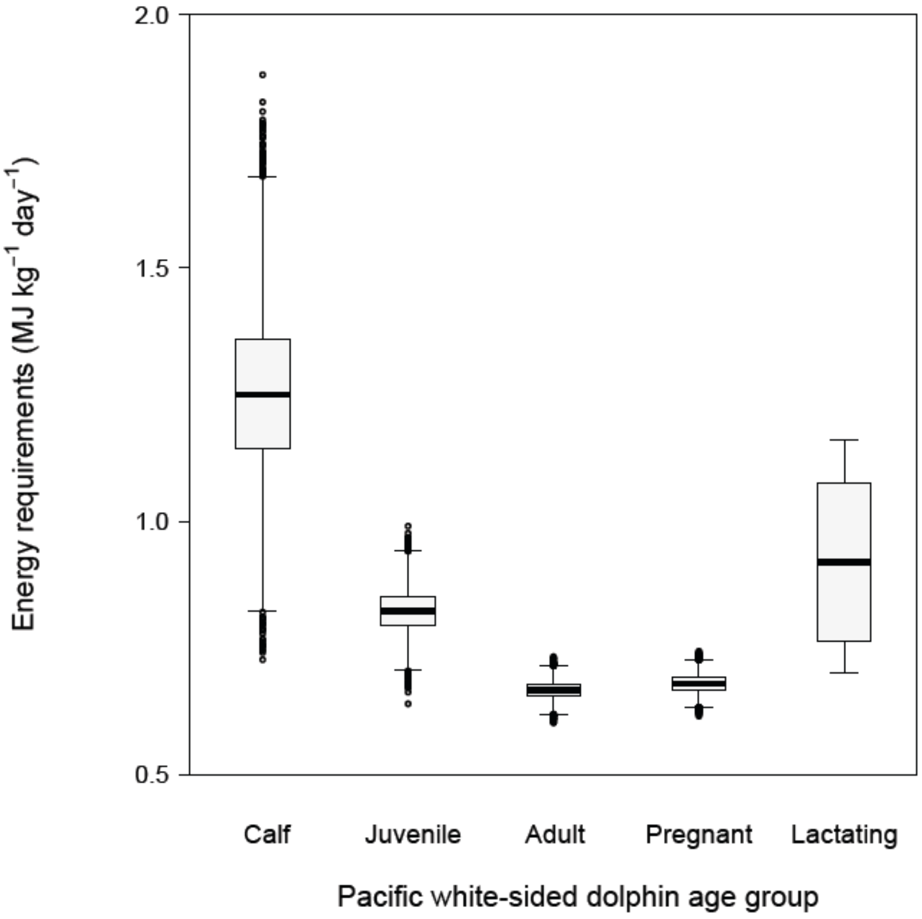

Figure 4.5 Per kg requirements for Pacific white-sided dolphin in each reproductive stage. Bold lines in centre of boxes represent the median value, box edges represent the 25th and 75th percentiles of the data distribution and whiskers represent the range. Open circles represent model outliers.

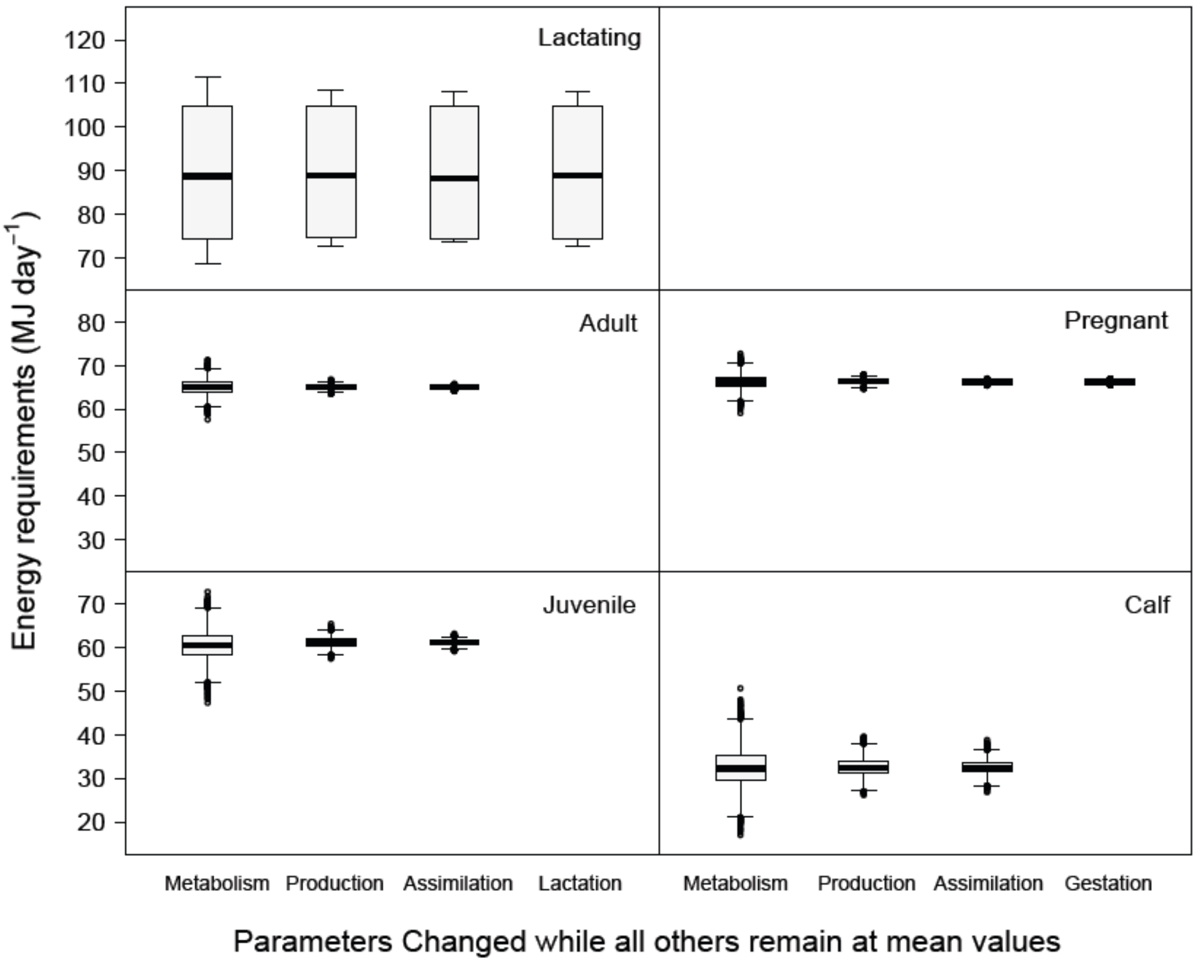

Figure 4.6 The effect of changes in model parameters on estimates of total energetic requirements of Pacific white-sided dolphins in different demographic groups. Bold lines in centre of boxes represent the median value, box edges represent the 25th and 75th percentiles of the data distribution and whiskers represent the range. Open circles represent model outliers. Note that y-axis scales vary but range is consistent (60 MJ)

4.5 Discussion

My model predicted the energetic requirements of Pacific white-sided dolphins at different ages and reproductive states. Combining model predictions with population demographics and diet parameters allows food requirements to be calculated for Pacific white-sided dolphins anywhere. These estimates of energetic requirements can be used to assist with the conservation of dolphins and the management of fisheries at local and global scales. However, applications of my model predictions for management or conservation are not without some caveats.

4.5.1 Study limitations

As with any model, my model is a simplified description of a complex system that comes with certain caveats. Most notably, some of the bioenergetic parameters are based on limited data and others were not estimated specifically from Pacific white-sided dolphins. However, they are the best data currently available and are consistent with values for related species of cetaceans or mammals of similar sizes.

I had assumed that dolphins inhabit areas within their thermal-neutral zone (Costa & Williams, 1999; Worthy, 2001), although I recognize that Pacific white-sided dolphins inhabit an extensive oceanic range (Stacey & Baird, 1991) and occur in both the cold waters of the Bering Sea and the warm waters off Southern California. It is therefore uncertain if the habitats within which dolphins could be presumed thermally neutral include all of their habitats. Thus, it is possible that dolphins expend some energy for thermoregulation in the temperature extremes of their habitat, which would increase their gross energy requirements.

Another assumption needing further scrutiny is the way in which the energetic costs of lactation were estimated. I first assumed my modeled energy requirements for calves were reasonable, and based the costs of lactation incurred by the mother on these model results. This method inferred lactation costs increased food requirements by 160% of food required by resting females. This result agreed with the bulk of studies regarding lactation costs in marine mammals – including the lactation costs of pinnipeds, mysticetes and bottlenose dolphins (Perez & Mooney, 1986; Lockyer, 2007; Kastelein *et al.*, 2002; Lockyer, 1993). However, the model-based estimates of lactation may be an over-estimate for Pacific white-sided dolphins. The daily energy needs of calves were modeled based in part on the modeled costs of activity—estimated by the Cost of Transport equation. This may be an over-estimate of energetic needs of calves, if they draft behind their mothers when swimming, which could lower their activity costs.

As a second means to avoid using the bioenergetics model results for calves, I used energetic densities of delphinid milks, and generalized estimates of quantities of milk produced daily by lactating dolphins, to determine the cost of lactation (Oftedal, 1997). This method inferred that the cost of lactation increased food requirements by about 120% the food requirements of resting females. The idea that the lactation cost would be low (~120% of resting) may have merit because the rate of growth of young dolphins is low. Pacific white-sided dolphin fetuses have often been measured in excess of 80 cm, and calves are born between 90 and 100 cm long (Ferrero & Walker, 1996; Heise, 1997). As such, the length at birth is about 50% of the asymptotic length of adults (~190 cm). The length at weaning is thought to occur between 125 and 130 cm – when animals are about 65% asymptotic adult length and are about a year old (8 to 16 months; Ferrero & Walker, 1996; Heise, 1997). Thus, the growth rate of calves is relatively slow when compared with both mysticetes and pinnipeds. Other similar-sized delphinds show similar trends in size at birth and size at weaning such as striped dolphins (*Stenella coeruleoalba*) that are born at about 90 cm (46% asymptotic length) and wean at about a 64% asymptotic length (Marsili *et al.*, 1997), and spinner dolphins (*Stenella longirostris*) that are 77 cm (44% asymptotic length) at birth and wean at about a year (75% asymptotic length; Perrin *et al.*, 1977). Furthermore, the cost of lactation in odontocetes is thought to be lower than in mysticetes and pinnipeds because the fat content of odontocete milk is surprising low (10-15% as opposed to ~50% in mysticetes and up to 80% in pinnipeds; Oftedal 1997), and mysticete milk is typically twice as energetically dense as odontocete milk (West *et al.*, 2007).

Using both methods to determine the costs of lactation indicates that lactating females required 140% more food than resting females. However, this estimate should be used with caution given the incomplete knowledge about the duration of lactation, caloric content of milk, and mass of milk actually produced in Pacific white-sided dolphins. There is also disparity between the results from these two methodologies. Such shortcomings regarding the cost of lactation in Pacific white-sided dolphins can be addressed with future research.

Despite potential errors in model assumptions, my model uses the best available information to estimate the food requirements of Pacific white-sided dolphins. The model estimates are considered reasonable, and are associated with rather large error bounds that reflect uncertainty (and individual variation) in the model parameters. Further refinement of the mean estimates will require additional study to refine some of the important model parameters.

4.5.2 Energetic requirements

Total energy requirements of Pacific white-sided dolphins were generally high, and varied for dolphins in different life-stages. Calves required the least energy in terms of total consumption (~32.5 MJ day^{-1}), but required the most energy when their needs were expressed relative to their body size (~1.25 MJ kg^{-1} day^{-1}). Juveniles, adults, and pregnant females required similar total energy intake (~61–67 MJ day^{-1}). However, per kg requirements of juveniles (~0.82 MJ kg^{-1} day^{-1}) were greater than per kg requirements of non-reproductive adults (~0.67 MJ day^{-1}). The energetic costs of growth, or production, likely inflate the food requirements of juveniles and calves. Lactating females required the highest total energy intake (~90 MJ day^{-1}; ~0.92 MJ kg^{-1} day^{-1}) to sustain their basic requirements and those of a calf.

My model predictions were consistent with studies of cetaceans growing up in aquaria, which indicate that per kg requirements decrease as dolphins age, and level out once they reach maturity (Kastelein *et al.*, 1994; Kastelein *et al.*, 2000; Kastelein *et al.*, 2003a) and follow the general mammalian pattern of mass-specific energy requirements being elevated in sub-adult animals. My predicted per kg requirements were also consistently elevated for growing and lactating animals, which suggests it is most important for them to acquire adequate, high-quality prey in these life stages.

The predicted energetic requirements for non-reproductive adult Pacific white-sided dolphins were generally higher than estimates of other similar sized small cetaceans inhabiting temperate waters. For example, the energetic requirements of Dall's porpoise (*Phocoenoides dalli*) were ~0.25 MJ kg^{-1} day^{-1}, or about 1/3 of my estimate for Pacific white-sided dolphins (Ohizumi & Miyazaki, 1998). Killer whale (*Orcinus orca*) energetic requirements were estimated at ~0.17 MJ kg^{-1}day^{-1} or about 1/4 the per kg requirements of white-sided dolphins (Sigurjonsson & Vikingsson, 1997) and as ~0.21 MJ kg^{-1}day^{-1} (males) and 0.25 MJ kg^{-1}day^{-1} (females) (Noren, 2010). The only small cetacean that comes close to

Table 4.2 Gross energetic requirements estimated for small, temperate cetaceans in the wild.

Species	Mass (kg)	MJ day^{-1}	MJ kg^{-1} day^{-1}	Source
Harbour porpoise	39	21	0.54	Sigurjonsson & Vikingsson, 1997
Pacific white-sided dolphin	95	64	0.67	This study
Pacific white-sided dolphin	95	65	0.68	adapted from Sigurjonsson & Vikingsson, 1997
Dall's Porpoise	108	27	0.25	Ohizumi & Miyazaki, 1998
Pacific white-sided dolphin	190	65	0.34	Sigurjonsson & Vikingsson, 1997
Killer whale	2350	400	0.17	Sigurjonsson & Vikingsson, 1997
Female Killer whale	3338	763	0.25	Noren, 2010
Male Killer whale	4434	876	0.21	Noren, 2010

having the energy requirements of a Pacific white-sided dolphin is the harbour porpoise (*Phocoena phocoena*) at 0.54 MJ kg^{-1}day^{-1} (Sigurjonsson & Vikingsson, 1997) (see Table 3.2).

The total energy requirements of Pacific white-sided dolphins estimated by Sigurjonsson and Vikingsson (1997) (~65 MJ day^{-1}) were nearly identical to my model predictions. However their per kg estimates were only ~0.34 MJ kg^{-1}day^{-1} based on a mean weight of 190 kg, which seems far too heavy for an adult Pacific white-sided dolphin (see, Ferrero & Walker, 1996; Heise, 1997b; Trites & Pauly, 1998). Using the commonly accepted mass estimate of 95 kg for adult Pacific white-sided dolphins (Heise, 1997b), the weight-adjusted consumption estimates of Sigurjonsson and Vikingsson (1997) would be about 0.68 MJ kg^{-1}day^{-1} and much closer to my model predictions of ~0.67 MJ kg^{-1}day^{-1} (Table 4.2).

The question naturally arises whether my higher food intake estimates for Pacific white-sided dolphins genuinely reflected higher requirements or whether the model overestimated their energetic needs. The food intake of Pacific white-sided dolphins in aquaria is greater than that of other small captive cetaceans (Table 4.3). For example, non-reproductive adult Pacific white-sided dolphins consumed about 7% of their body weight daily while in aquaria, on a diet of herring, salmon, capelin and squid (Chapter 3). This was more than twice the relative biomass consumed by Amazon river dolphins (*Inia geoffrensis*) (3% bodyweight) on a diet of primarily trout and carp (Kastelein *et al.*, 1999). An adult bottlenose dolphin (*Tursiops truncatus*) consumed only 2% of its bodyweight in herring, mackerel and squid (Kastelein *et al.*, 2002). In contrast, an adult dusky dolphin (*Lagenorhynchus obscurus*) consumed slightly more biomass (on a presumably lower-energy diet) than Pacific white-sided dolphins—about 10% bodyweight, while consuming hake, cephalopods, and teleost fishes (Kastelein *et al.*, 2000). Collectively, these data indicate that Pacific white-sided dolphins have elevated energetic needs, even in aquaria, when compared with other small cetaceans. The exception to this trend is that the closely related dusky dolphin, with similar ecological patterns, and living in the wild in a temperate habitat, consumes about the same energy per day despite slight variations in biomass consumed (Table 4.3).

In general, the estimated energetic requirements of Pacific white-sided dolphins in the wild were 1.5 times higher than food consumption of white-sided dolphins in captivity (Chapter 3). This difference is due to the energetic cost associated with activity, which are higher for wild dolphins than for those housed in aquaria. Indeed, activity budgets constructed for captive Pacific white-sided dolphins indicate they spend the bulk of their time (60-80% of their time) resting (Javdan, 2010; and see Appendix 1), whereas activity budgets constructed for wild Pacific white-sided dolphins indicate that resting only accounts for ~3% of their activity budget although it should be noted that the survey design in this case included only daylight hours (which likely precluded inclusion of sleeping) and that active dolphins are easier to detect than resting ones (Black, 1994).

Table 4.3 Food intake biomass measurements for non-growing adult small cetaceans in aquaria.

Species	Mass (kg)	Daily Food Intake (kg)	%Bodymass	Diet	Source
Dusky dolphin	70	7.0	10	hake, cephalopods, teleost fishes	Kastelein *et al.*, 2000
Pacific white-sided dolphin	116	8.5	7	40% herring, 40% capelin, 10% salmon, 10% squid	Chapter 2
Amazon river dolphin	145	3.6	2	trout and carp	Kastelein *et al.*, 1999
Bottlenose dolphin	225	4.7	2	herring, mackerel, squid	Kastelein *et al.*, 2002

4.5.3 Ecological implications

In the coastal waters of British Columbia, sightings of Pacific white-sided dolphins have increased markedly since the 1980s (Heise, 1997; Chapter 4). Pacific white-sided dolphins are now regularly found in areas containing several culturally and commercially important fish species. Recent stomach contents obtained from 15 stranded or by-caught animals on the BC coast indicate that salmon and sardine are the most important prey (of all prey that composed more than 10% of the diet by biomass) (Table 4.4). Herring are also important (Table 4.4), and were the most common prey observed in diets of Pacific white-sided dolphins during the 1990s (Heise, 1997). These prey species are consistent with the observation that Pacific white-sided dolphins primarily consume high-energy prey throughout their range (Stroud *et al.*, 1981; Walker *et al.*, 1986; Miyazaki *et al.*, 1991; Walker & Jones, 1993; Black, 1994; Heise, 1997; Morton, 2000; Kitamura *et al.*, 2008).

One useful application of my bioenergetics model to fisheries management is to estimate the prey-base required by populations of Pacific white-sided dolphins in different areas. I made very preliminary estimates of how much food dolphins require using my model predictions, limited diet analyses (n=15 dolphins) and limited information obtained from the literature regarding dolphin population-sizes. Based on limited dietary information, I assumed the diet of dolphins in the North Pacific was composed primarily of high-energy fish. For dolphins consuming prey in BC waters, I based my calculations on a diet of salmon and sardine, although I suspect herring was under-represented in my small dataset. Since salmonids and sardine together only comprised 80% of the biomass consumed, I also included generic high-energy fish in the diet of BC dolphins.

According to the bioenergetic model, an average Pacific white-sided dolphin (mean mass 78 kg; Trites & Pauly (1998) would require ~62 MJ day^{-1}. This single dolphin would therefore consume ~10 kg of a generic, high-energy fish if consuming only that prey. If consuming a more realistic, mixed-species diet, the dolphin would consume ~7.8 kg of salmon, 1.3 kg of sardine, and 2 kg of generic high-energy fish to meet its prey requirements (assuming prey energy densities of 5 kJ g^{-1} wet weight for salmonids—Logerwell & Schaufler (2005); 8 kJ g^{-1} for sardines—Rosa et al. (2010), and ~6 kJ g^{-1} for other high-energy fish—Anthony et al. (2000)).

However, the entire North Pacific population of 1 million dolphins (95% CIs of ~200,000–4,000,000—Buckland et al. (1993) or ~100,000–7,000,000—Miyashita (1993)) would consume ~10,000 tons of high-energy fish of a mix of species daily. Of this total, the ~25,000 dolphins that reside along part of the coast of British Columbia (95% CI of ~12,000–52,000—Williams & Thomas (2007)), would consume ~200 tonnes of salmon, 32 tonnes of sardine, and 50 tonnes of other high-energy fish daily. And of the BC total, the 150 dolphins residing in the Strait of Georgia (based on anecdotal suggestions) would consume 1170 kg of salmon, 195 kg of sardine, and 300 kg of generic high-energy fish per day. All of these estimates of consumption are based on a gross over-simplification of the population demographics and diets of Pacific white-sided dolphins, but are included as examples of how my model can be used to inform fisheries management once diet and population parameters are better understood.

Table 4.4 The number of stomachs, number of prey, length of prey, estimated biomass of prey and estimated total biomass of prey consumed by 15 Pacific white-sided dolphins (n=15 stomachs) by-caught or stranded in BC Waters between 1999 and 2009.

Common name	Species or family name	Taxa ID'd	No. of stom-achs	Total no. of prey	Modal length of indiv. (cm)	Biomass of indiv. (low est.) (g)	Biomass of indiv. (high est.) (g)	Total mean biomass (number of indiv. X mean biomass) (g)	Proportion of total biomass
Salmon(4)/ Steelhead(1)	Salmonidae	family	5	5	46-90	2116	16718	47084.0	0.6370
Sardine	*Sardinops sagax*	species	4	71	16.0-35.0	31	326	12672.8	0.1714
Hake	*Merluccius productus*	species	2	14	40.0-50.0	359	648	7052.4	0.0954
Mackerel	*Scomber japonicus*	species	2	6	30.0-39.0	352	749	3302.8	0.0447
Herring	*Clupea pallasi*	species	10	504	8.8-9.5	4	5	2312.7	0.0313
Northern Smooth-tongue	Bathylagidae	family	4	18	10.6-18.0	9	41	446.9	0.0060
Sablefish	*Anoplopoma fimbria*	species	2	7	22.4-24.3	101	130	807.9	0.0109
Pollock	*Theragra chalco-gramma*	species	2	22	8.9-10.0	6	8	148.8	0.0020
Capelin	*Mallotus villosus*	species	2	56	5.0-7.0	1	2	64.8	0.0009
Capelin(1)/ Eulachon(1)	Osmeridae	family	2	24	5.0-7.0	1	2	27.8	0.0004
Lampfish	Myctophidae	family	3	51	No estimate	Data not available	n/a	n/a	n/a
Cephalopod	Squid/ Octopus	family	4	8	Medium	Data not available	n/a	n/a	n/a
Shiner perch	Embiotocidae	family	3	5	11.0-15.0	Data not available	n/a	n/a	n/a

4.5.4 Future research

My model predictions were most sensitive to changes in resting metabolic rates and activity, which indicates that data for these parameters are the most informative for predicting energetic requirements, at least within the parameter ranges I used. I suspect that varying each parameter by a fixed rate (i.e. 10% of the mean) would yield different results, since boundaries would not be broader for any specific parameter, however some parameters are less likely to include broad variation than others (i.e. metabolism is unlikely to vary only 10% among individuals even without accounting for model uncertainty, whereas digestive efficiency is unlikely to vary more than 10%).

Assuming my sensitivity analyses reflects true susceptibility of model predictions to metabolism and activity estimates, these parameters would be the most important to study. My use of tagged dolphin swimming speeds from Black (1994) were based on data from three animals and assumptions that the cost of transport (*COT*) could approximate the costs of activity. Detailed movement data of Pacific white-sided dolphins, including respiration rates, activity states, and swimming speeds, would greatly improve food intake estimates (e.g., Williams & Noren, 2009). In addition, measurements of oxygen consumption of captive animals in various activity states that approximate activities performed by wild dolphins could also improve the activity parameter (e.g., Williams *et al.*, 1993; Kriete, 1995; Fahlman *et al.*, 2008). Future research should focus on determining the energetic costs of various activities, and the activity budget of this species in the wild, to better estimate the food requirements of Pacific white-sided dolphins at the individual level.

At the population level, the ability to apply individual requirements in an ecological context is limited by a lack of information on population structure of dolphins, a lack of confidence or thoroughness in population counts of dolphins, and a lack of knowledge regarding the seasonal diets of Pacific white-sided dolphins. The population structure could be further investigated through genetic analyses of dolphins in various geographic regions (e.g., Hayano *et al.*, 2010). Current population counts of dolphins in various areas are currently limited by attraction of dolphins to the research vessels leading to potential positive bias in counts, the lack of coverage of much common dolphin habitat, and the lack of seasonal and annual repetition of the same survey tracks (e.g., Buckland *et al.*, 1993;

Williams & Thomas, 2007; Ford *et al.*, 2010a). Aerial surveys may be a cost effective alternative to survey more dolphin habitat and cover more ground quickly. Finally, a continuous long-term study of the diet of Pacific white-sided dolphins could be undertaken by fisheries managers to better-predict ecosystem level impacts exuded, or experienced by, Pacific white-sided dolphins (e.g., Ford & Ellis, 2006). Given the paucity of information regarding the population demographics and diets of Pacific white-sided dolphins, my research provides a first estimate of prey requirements that can be refined and used for conservation and fisheries management.

Chapter 5: Conclusion

5.1 Research summary

The main goals of my research were to 1) assess the spatial distribution of Pacific white-sided dolphins in coastal British Columbia, 2) assess the resting metabolic rates of this species, and 3) determine the energetic requirements of different demographic groups of Pacific white-sided dolphins. My research provides baseline information of the spatial ecology and food requirements of a relatively understudied yet abundant species.

Spatial distribution of Pacific white-sided dolphins was mapped based upon sightings obtained opportunistically and from scientific surveys. Observer effort associated with the respective data sets was modeled and adjustments were made to assess sightings density per unit effort of groups of Pacific white-sided dolphins on the BC coast over the past 54 years, and seasonally over the past 8 years. My findings indicate a southward range shift from the 1950s to 2010, and seasonal movements from offshore to nearshore waters concurrent with the timing of the herring spawn on the BC coast from 2002-2010.

The range shift of white-sided dolphins in BC may have increased their overlap with human activities and could put them at risk for entanglement and by-catch, or could mean increased competition with fisheries for common prey-resources (i.e. sardine, herring, and salmon fisheries). Seasonal movements to nearshore waters may well be prey-driven, and dolphins may rely on seasonal prey-pulses of high-energy prey to nearshore habitats to meet their energetic requirements. This would be especially likely if dolphins exhibited seasonally varied metabolic rates that might drive heightened food requirements in some times of the year, or if dolphins had particularly elevated energetic requirements which may indicate a need for high-quality, high-energy food in order to meet metabolic demands.

To estimate the food requirements of wild dolphins, I first used open-circuit gas respirometry to assess metabolism of three captive dolphins at the Vancouver Aquarium. I measured resting metabolic rates and total energy intake for the dolphins twice monthly for one year to develop baseline energetic requirements for this species, and to deduce whether seasonal changes in metabolism of food intake occur because such changes may act as potential drivers of seasonal changes in distribution. Average resting metabolic rates measured for Pacific white-sided dolphins were somewhat elevated when compared with resting metabolic rates measured for other small cetaceans, and were constant throughout the year despite an increase in food intake in the fall. I was unable to attribute changes in food intake adequately to confirm whether the trend was a phenomenon of a limited sample size, of residing in captivity (for example if aquaria priorities influenced food intake), or whether it would be expressed in the wild.

I used my measured average and seasonally constant resting metabolic rates to inform a generalized bioenergetics model to assess the food requirements of Pacific white-sided dolphins globally, regionally, and locally. My model included estimates of the assimilation efficiency (i.e. it accounted for proportion of energy left over after fecal and urinary processes), and the metabolizable energy available for use in Pacific white-sided dolphins. Of the metabolizable energy, I partitioned my model to assess energy used in production (i.e. growth, gestation, lactation) and metabolism (i.e. maintenance, activity).

My model revealed that total energy requirements of white-sided dolphins are high relative to other small cetaceans. The estimated energetic requirements of Pacific white-sided dolphins in the wild were 1.5 times higher than food consumption of white-sided dolphins in captivity. This difference is due to energetic costs associated with activity, which are higher for wild dolphins than for those housed in aquaria. Activity budgets constructed for captive Pacific white-sided dolphins indicate they spend the bulk (60-80%) of their time resting (Javdan, 2010; and see Appendix 1), whereas activity budgets constructed for wild Pacific white-sided dolphins indicate that resting only accounts for only ~3% of their activity budget (Black, 1994). Comparing the food intake of Pacific white-sided dolphins with that of other cetaceans in aquaria also showed that they had elevated food requirements compared with other small captive cetaceans (Kastelein *et al.*, 1999; Kastelein *et al.*, 2002).

Combining energetic requirements with spatial distribution of white-sided dolphins in coastal British Columbia may give some indication of the biomass of fish they require on a local or regional scale, which has implications for fisheries management. The elevated food requirements I predicted for Pacific white-sided dolphins appear to be reflected in both aquaria and in other bioenergetics models, and could indicate a reliance of Pacific white-sided dolphins on high-energy prey. Should this be the case, it is possible that populations of Pacific white-sided dolphins could a) be prey-linked in their distribution patterns, or b) be reliant on specific types of prey in some seasons and experience nutritional stress when these prey items are absent or rare.

Pacific white-sided dolphins are considered to be abundant and are listed by COSEWIC as “not-at-risk”. However, my combined research suggests that white-sided dolphins may be faced with increased conservation risks associated with their high energy requirements and change in distribution. Dolphins that rely on seasonally aggregating schools of high-energy fish such as herring, and are increasingly reliant on near-shore habitats where overlap with human use is high, could be exposed to collisions with boats, heightened levels of underwater noise, by-catch, urban run-off and contaminants, or susceptibility to low prey-availability or competition with fisheries.

5.2 Study limitations

5.2.1 Spatial distribution of white-sided dolphins in BC

I was unable to precisely quantify observer effort for the opportunistic dataset. The effort model constructed by Smith *et al.* (2006) for the opportunistic sightings lacked sufficient data to compare total sightings density per unit effort values between seasons. The spatial extent covered by the DFO survey data varied between some years and seasons, and the lack randomized or replicated survey tracks with equidistant spacing made common spatial analyses techniques inappropriate for my research (Ford *et al.*, 2010a). Despite these drawbacks, the extensive research into the modeled observer effort for opportunistic sightings, and the repeated visits to the same grid cells in the surveyed sightings allowed a novel evaluation of spatial use of the BC coast by dolphins to be made.

Another weakness in my study is that the spatial extent of the sightings data did not encompass the full range of habitats used by white-sided dolphins in BC waters. Effort associated with the scientific survey data was limited in waters beyond 50 km of the shelf-break (Ford *et al.*, 2010a) and effort associated with the opportunistic data was sparse in areas far offshore (Smith *et al.* 2006). Implications of my spatial analyses should therefore be considered preliminary until data are such that quantitative line-transect sampling can be conducted over a larger spatial extent.

5.2.2 Resting metabolic rates and food intake of captive dolphins

The extent to which my resting metabolic rate measurements of captive animal are representative of dolphins in the wild is uncertain. For example, the lack of seasonal variation in pool temperatures (typically between 10°C and 15°C) may have falsely implied seasonal consistency in metabolic rates when cooler temperatures (such as those experienced by dolphins in the wild) may have induced metabolic depression or elevation. In addition, one of the dolphins exhibited a strong training effect whereby measurements were artificially inflated early in the study, and decreased as the study went on. This further limited my sample size (from 3 to 2 study animals), and raises questions about whether or not other behavioural responses to my research may have induced elevated metabolic rates that went unnoticed. Ideally a future study would include monitoring of the heart rate of the study animals, which could help deduce whether or not metabolic rates are being measured when dolphins are truly in a restful state. Although physically the dolphins I studied were at rest, the may have been active psychologically. Having heart rate measurements concurrent with activity budgets and resting metabolism measurements would greatly improve many studies of cetacean metabolism.

I am also uncertain whether seasonal increases in food intake in the captive dolphins in fall are indicative of similar trends in the wild, given that the behaviours and activities of dolphins in aquaria do not necessarily mimic those of wild dolphins. Although the reproductive season may have been related to decreases in mass in summer (perhaps due to an increase in sexual activity in summer and lack of extra food consumption due perhaps to hormones), the strength of that correlation could not be tested due to a lack of information on seasonal hormones and activity budgets. Another possible explanation for the increase in food in fall was that a high-energy prey-pulse occurs in summer in the wild (on the coast of Japan where the three study animals were by-caught). Such a pulse in prey may supplement the energy consumption of wild dolphins and in turn may prevent summer mass-loss and associated compensatory food intake in fall.

Despite these shortcomings, the data collected from the three individuals represents the most comprehensive energetics study conducted to date with Pacific white-sided dolphins, and the only cetacean energetics study that has spanned multiple seasons and examined both resting metabolic rates and total calories ingested. As such, it provides a starting point upon which further energetic studies of small cetaceans can build.

5.2.3 Food requirements of wild dolphins

My model, as with any model, is a simplified description of a complex system that comes with certain caveats. Most notably, some of the bioenergetic parameters are based on limited data and others were not estimated specifically from Pacific white-sided dolphins. However, they are the best data that are currently available and are in line with values for related species of cetaceans or mammals of similar sizes.

I had assumed that dolphins inhabit areas within their thermal-neutral zone (Costa & Williams, 1999; Worthy, 2001), although I recognize that Pacific white-sided dolphins inhabit an extensive oceanic range (Stacey & Baird, 1991) and occur in both the cold waters of the Bering Sea and the warm waters off Southern California. It is therefore uncertain if the habitats within which dolphins could be presumed thermally neutral include all of their habitats. Thus, it is possible that dolphins expend some energy for thermoregulation in the temperature extremes of their habitat, which would increase their gross energy requirements.

Another assumption needing further scrutiny is the way in which the energetic costs of lactation were estimated. My model predictions regarding the energetic costs of lactation should be used with caution given the incomplete knowledge about lactation period, caloric content of milk, and mass of milk actually produced by Pacific white-sided dolphins.

Despite potential errors in model assumptions, my model uses the best available information to estimate the food requirements of Pacific white-sided dolphins. The model estimates are considered reasonable, and are associated with rather large error bounds that reflect uncertainty in some of the model parameters. Further refinement of the mean estimates will require additional study.

5.3 Research applications

Spatial information about fisheries can now be combined with seasonal dolphin hot-spots to mitigate incidents of by-catch and entanglement. My results may further contribute to determining areas of important or perhaps critical habitat for Pacific white-sided dolphins. My results can also be used to determine the extent of overlap between dolphins and prey, which, if combined with daily prey requirements of Pacific white-sided dolphins and local or seasonal diet information, can be used to provide estimates of daily biomass consumption in specific areas along the BC coastline.

My measurements of captive resting metabolic rate were combined with other physiological parameters in a bioenergetics model and used to predict the total energetic requirements of Pacific white-sided dolphins at different ages and reproductive states. Combining model predictions with population demographics and diet parameters allowed for food biomass requirements to be calculated for Pacific white-sided dolphins anywhere. These estimates of energetic requirements can be used to assist with the conservation of dolphins and the management of fisheries at local and global scales.

5.4 Future research

My research shows decadal and seasonal changes in areas used by dolphins, which may reflect a change in the distribution and abundance of prey. Identifying important, or even critical, habitat for Pacific white-sided dolphins will require further research into what drives the hot-spots I identified. Long-term data sets to document seasonality in distribution, prey requirements, and other drivers of cetacean distributions are therefore needed to better define the habitat needs of Pacific white-sided dolphins and other small cetaceans.

At the population management level, the ability to apply individual food requirements in an ecological context is limited by a lack of information on stock structure of dolphins, a lack of confidence or thoroughness in population counts of dolphins, and a lack of knowledge regarding the seasonal diets of Pacific white-sided dolphins. The stock structure could be further investigated through genetic analyses of dolphins in various geographic regions (e.g., Hayano *et al.*, 2010). Current population counts of dolphins in various areas are limited by the affinity of dolphins to the research vessels, the lack of coverage of much common dolphin habitat, and the lack of seasonal and annual repetition of the same survey tracks (e.g., Buckland *et al.*, 1993; Williams & Thomas, 2007; Ford *et al.*, 2010a). Aerial surveys may be a cost effective alternative to survey more dolphin habitat and cover more ground quickly. Finally, a continuous long-term study of the diet of Pacific white-sided dolphins could be undertaken by fisheries managers to better-predict ecosystem level impacts exerted or experienced by Pacific white-sided dolphins (e.g., Ford & Ellis, 2006).

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Appendicies

Appendix A Oxygen trace

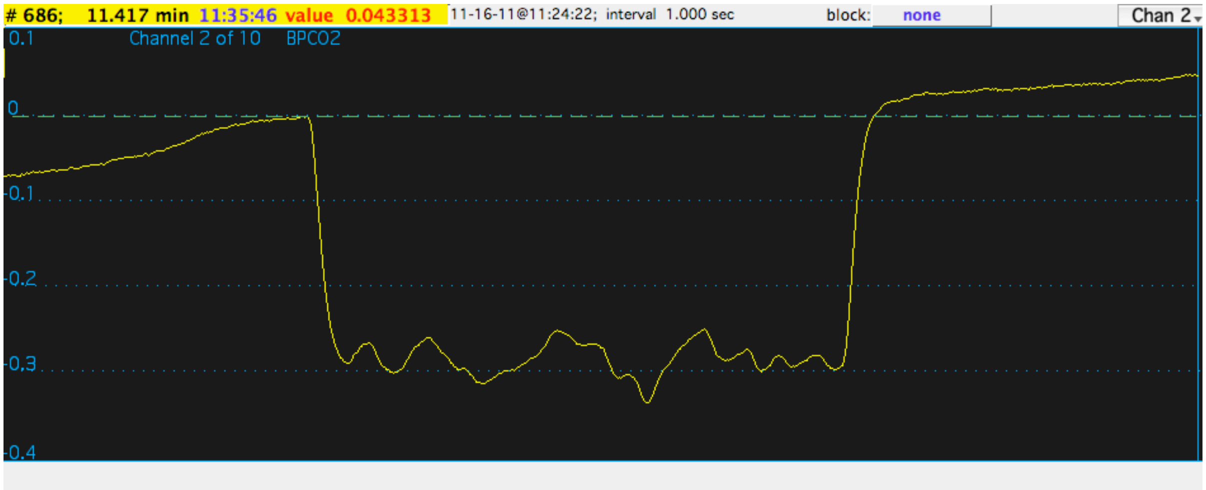

Figure A.1. Oxygen trace of Pacific white-sided dolphin M001 on 16 November 2011. This sample was randomly selected to show how resting metabolic rates were determined from oxygen consumption rates. The y-axis is oxygen concentration and the x-axis is time from 0 to 15 minutes. The first drop in oxygen consumption occurred at 2 min 45 seconds when the flow was turned on; and the second vertical line occurred at 10 minutes when the air flow was turned off and the trial ended.

Appendix B 24-hr ethograms and activity budgets

Two observers were stationed at the dolphin pool at the Vancouver Aquarium to simultaneously record dolphin behaviour at the underwater viewing (to see movements underwater) and from an outer pool deck looking down at the pool surface. Every 15 minutes, each observer recorded the instantaneous activity level of each individual (n=3 dolphins). Activity levels were ranked as 1, 2, or 3. ***Activity level 1*** constituted low energy, specifically <1 fluke stroke per second. This encompassed all surface resting activity, gliding through the water and very slow swimming. ***Activity level 2*** constituted mid energy output, greater than 1 but less than 2 fluke stroked per second. This encompassed mid-speed swimming in the habitat. ***Activity level 3*** constituted greater than 2 fluke strokes per second, as well as any breaching, leaps, tail-slaps, or show-performances. A histogram of frequencies of each activity level for each individual are presented below (Figure B.1) and the raw data are presented in Table B.1.

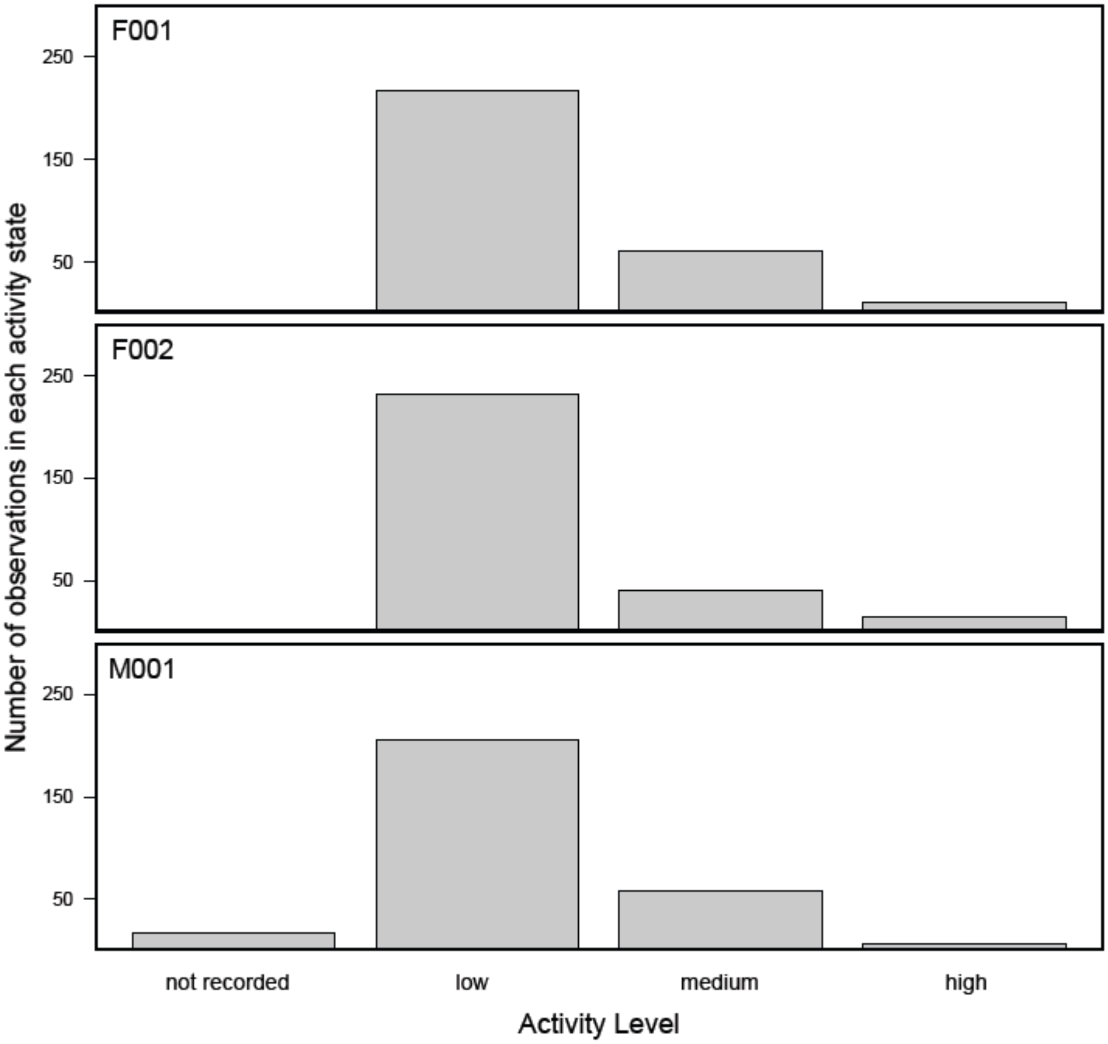

Figure B.1 Summary of proportion of time spent in each of three activity states (low, medium and high) for each individual studied at the Vancouver Aquarium (n=3).

Table B.1 Dolphin observations collected every 15 minutes over 24 hours. Activity state 1=low, 2=medium, and 3=high.

Date	Time	F001 Actiivty	F002 Activity	M001 Activity
30-Jan-12	9:15	1	1	1
30-Jan-12	9:30	1	2	1
30-Jan-12	9:45	1	2	2
30-Jan-12	10:00	2	2	1
30-Jan-12	10:15	2	1	3
30-Jan-12	10:30	2	1	1
30-Jan-12	10:45	1	1	1
30-Jan-12	11:00	1	1	2
30-Jan-12	11:15	2	1	1
30-Jan-12	11:30	2	1	1
30-Jan-12	11:45	2	1	1
30-Jan-12	12:00	2	1	2
30-Jan-12	12:15	2	1	1
30-Jan-12	12:30	1	1	1
30-Jan-12	12:45	1	1	1
30-Jan-12	13:00	1	2	1
30-Jan-12	13:15	2	1	1
30-Jan-12	13:30	1	1	2
30-Jan-12	13:45	2	1	1
30-Jan-12	14:00	2	1	2
30-Jan-12	14:15	1	1	2
30-Jan-12	14:30	2	1	2
30-Jan-12	14:45	2	1	2
30-Jan-12	15:00	2	1	2
30-Jan-12	15:15	1	1	2
30-Jan-12	15:30	2	1	2
30-Jan-12	15:45	1	1	2
30-Jan-12	16:00	1	1	2
30-Jan-12	16:15	1	1	2
30-Jan-12	16:30	1	1	2
30-Jan-12	16:45	1	1	2
30-Jan-12	17:00	2	2	1
30-Jan-12	17:15	2	2	1
30-Jan-12	17:30	1	1	1
30-Jan-12	17:45	2	2	1
30-Jan-12	18:00	1	1	2
30-Jan-12	18:15	2	2	2
30-Jan-12	18:30	1	1	1
30-Jan-12	18:45	1	1	1
30-Jan-12	19:00	1	1	2
30-Jan-12	19:15	1	1	1
30-Jan-12	19:30	1	1	1
30-Jan-12	19:45	1	1	1
30-Jan-12	20:00	1	1	1

Date	Time	F001 Actiivty	F002 Activity	M001 Activity
30-Jan-12	20:15	1	1	1
30-Jan-12	20:30	1	1	1
30-Jan-12	20:45	1	1	1
30-Jan-12	21:00	1	1	2
30-Jan-12	21:15	1	2	1
30-Jan-12	21:30	1	2	1
30-Jan-12	21:45	1	2	1
30-Jan-12	22:00	1	2	2
30-Jan-12	22:15	1	1	2
30-Jan-12	22:30	1	1	2
30-Jan-12	22:45	2	2	1
30-Jan-12	23:00	1	1	1
30-Jan-12	23:15	1	1	1
30-Jan-12	23:30	1	1	1
30-Jan-12	23:45	1	1	1
31-Jan-12	0:00	1	1	1
31-Jan-12	0:15	1	1	1
31-Jan-12	0:30	1	1	2
31-Jan-12	0:45	1	1	2
31-Jan-12	1:00	2	2	2
31-Jan-12	1:15	2	2	1
31-Jan-12	1:30	1	1	1
31-Jan-12	1:45	1	1	1
31-Jan-12	2:00	1	1	1
31-Jan-12	2:15	1	1	1
31-Jan-12	2:30	1	1	1
31-Jan-12	2:45	3	3	1
31-Jan-12	3:00	1	1	1
31-Jan-12	3:15	1	1	2
31-Jan-12	3:30	1	1	2
31-Jan-12	3:45	1	1	1
31-Jan-12	4:00	1	1	2
31-Jan-12	4:15	1	1	1
31-Jan-12	4:30	1	1	1
31-Jan-12	4:45	1	1	1
31-Jan-12	5:00	1	1	1
31-Jan-12	5:15	1	1	1
31-Jan-12	5:30	1	1	2
31-Jan-12	5:45	1	1	1
31-Jan-12	6:00	1	1	1
31-Jan-12	6:15	1	1	1
31-Jan-12	6:30	1	1	1
31-Jan-12	6:45	1	1	1
31-Jan-12	7:00	1	1	1
31-Jan-12	7:15	2	2	1
31-Jan-12	7:30	1	1	1
31-Jan-12	7:45	2	1	1

Date	Time	F001 Actiivty	F002 Activity	M001 Activity
31-Jan-12	8:00	2	1	1
31-Jan-12	8:15	2	1	1
31-Jan-12	8:30	2	2	1
31-Jan-12	8:45	2	3	2
31-Jan-12	9:00	3	3	1
01-Feb-12	9:20	1	2	1
01-Feb-12	9:35	1	1	1
01-Feb-12	9:50	2	1	2
01-Feb-12	10:05	1	1	2
01-Feb-12	10:20	2	1	1
01-Feb-12	10:35	2	1	1
01-Feb-12	10:50	1	1	2
01-Feb-12	11:05	1	1	2
01-Feb-12	11:20	1	1	1
01-Feb-12	11:35	1	1	2
01-Feb-12	11:50	1	1	1
01-Feb-12	12:05	1	1	1
01-Feb-12	12:20	1	1	1
01-Feb-12	12:35	2	1	2
01-Feb-12	12:50	1	1	2
01-Feb-12	13:05	3	3	1
01-Feb-12	13:20	3	1	1
01-Feb-12	13:35	1	2	2
01-Feb-12	13:50	1	2	2
01-Feb-12	14:05	2	2	1
01-Feb-12	14:20	2	1	1
01-Feb-12	14:35	2	1	1
01-Feb-12	14:50	1	2	3
01-Feb-12	15:05	1	1	2
01-Feb-12	15:20	2	1	1
01-Feb-12	15:35	3	3	2
01-Feb-12	15:50	2	1	1
01-Feb-12	16:05	1	1	1
01-Feb-12	16:20	1	1	2
01-Feb-12	16:35	-	-	-
01-Feb-12	16:50	2	1	-
01-Feb-12	17:05	2	3	-
01-Feb-12	17:20	1	1	-
01-Feb-12	17:35	2	2	-
01-Feb-12	17:50	2	1	-
01-Feb-12	18:05	1	1	-
01-Feb-12	18:20	1	1	-
01-Feb-12	18:35	1	1	-
01-Feb-12	18:50	1	1	-
01-Feb-12	19:05	1	1	1
01-Feb-12	19:20	1	2	1
01-Feb-12	19:35	1	1	1

Date	Time	F001 Actiivty	F002 Activity	M001 Activity
01-Feb-12	19:50	1	1	1
01-Feb-12	20:05	1	1	1
01-Feb-12	20:20	1	1	1
01-Feb-12	20:35	1	1	1
01-Feb-12	20:50	1	1	1
01-Feb-12	21:05	1	2	1
01-Feb-12	21:20	1	1	1
01-Feb-12	21:35	2	2	1
01-Feb-12	21:50	1	2	1
01-Feb-12	22:05	1	1	1
01-Feb-12	22:20	1	1	1
01-Feb-12	22:35	1	1	1
01-Feb-12	22:50	1	1	1
01-Feb-12	23:05	1	1	1
01-Feb-12	23:20	1	1	1
01-Feb-12	23:35	1	1	1
01-Feb-12	23:50	1	1	1
02-Feb-12	0:05	1	1	1
02-Feb-12	0:20	1	1	2
02-Feb-12	0:35	1	1	1
02-Feb-12	0:50	1	1	1
02-Feb-12	1:05	1	1	1
02-Feb-12	1:20	1	1	1
02-Feb-12	1:35	1	1	1
02-Feb-12	1:50	1	1	1
02-Feb-12	2:05	1	1	1
02-Feb-12	2:20	1	1	1
02-Feb-12	2:35	1	1	1
02-Feb-12	2:50	1	1	1
02-Feb-12	3:05	1	1	1
02-Feb-12	3:20	1	1	1
02-Feb-12	3:35	1	1	1
02-Feb-12	3:50	1	1	1
02-Feb-12	4:05	1	1	1
02-Feb-12	4:20	1	1	1
02-Feb-12	4:35	1	1	1
02-Feb-12	4:50	1	1	1
02-Feb-12	5:05	1	1	1
02-Feb-12	5:20	1	1	1
02-Feb-12	5:35	2	2	1
02-Feb-12	5:50	1	1	1
02-Feb-12	6:05	1	1	2
02-Feb-12	6:20	3	3	2
02-Feb-12	6:35	2	2	2
02-Feb-12	6:50	3	3	2
02-Feb-12	7:05	2	2	2
02-Feb-12	7:20	1	2	1

Date	Time	F001 Actiivty	F002 Activity	M001 Activity
02-Feb-12	7:35	1	1	1
02-Feb-12	7:50	1	2	2
02-Feb-12	8:05	1	2	1
02-Feb-12	8:20	1	2	1
02-Feb-12	8:35	2	2	1
02-Feb-12	8:50	2	1	1
02-Feb-12	9:05	2	1	1
03-Feb-12	9:25	1	1	-
03-Feb-12	9:40	1	1	-
03-Feb-12	9:55	2	2	-
03-Feb-12	10:10	1	1	-
03-Feb-12	10:25	1	1	1
03-Feb-12	10:40	1	1	1
03-Feb-12	10:55	1	2	2
03-Feb-12	11:10	2	1	3
03-Feb-12	11:25	2	1	1
03-Feb-12	11:40	2	1	1
03-Feb-12	11:55	1	1	1
03-Feb-12	12:10	1	1	1
03-Feb-12	12:25	1	1	-
03-Feb-12	12:40	1	1	-
03-Feb-12	12:55	2	1	1
03-Feb-12	13:10	3	3	-
03-Feb-12	13:25	1	1	-
03-Feb-12	13:40	1	1	1
03-Feb-12	13:55	1	1	1
03-Feb-12	14:10	1	1	1
03-Feb-12	14:25	1	1	1
03-Feb-12	14:40	1	1	2
03-Feb-12	14:55	1	1	1
03-Feb-12	15:10	2	1	2
03-Feb-12	15:25	3	3	3
03-Feb-12	15:40	1	3	3
03-Feb-12	15:55	1	1	3
03-Feb-12	16:10	1	1	1
03-Feb-12	16:25	1	1	2
03-Feb-12	16:40	1	1	2
03-Feb-12	16:55	1	1	1
03-Feb-12	17:10	1	1	2
03-Feb-12	17:25	2	3	1
03-Feb-12	17:40	3	3	1
03-Feb-12	17:55	2	1	1
03-Feb-12	18:10	1	1	1
03-Feb-12	18:25	1	1	1
03-Feb-12	18:40	1	1	1
03-Feb-12	18:55	2	2	2
03-Feb-12	19:10	1	1	1

Date	Time	F001 Actiivty	F002 Activity	M001 Activity
03-Feb-12	19:25	1	1	1
03-Feb-12	19:40	3	3	1
03-Feb-12	19:55	2	3	1
03-Feb-12	20:10	1	1	1
03-Feb-12	20:25	1	1	1
03-Feb-12	20:40	1	1	1
03-Feb-12	20:55	1	1	1
03-Feb-12	21:10	1	1	1
03-Feb-12	21:25	1	1	1
03-Feb-12	21:40	1	1	1
03-Feb-12	21:55	1	1	1
03-Feb-12	22:10	1	1	1
03-Feb-12	22:25	1	1	1
03-Feb-12	22:40	1	1	1
03-Feb-12	22:55	1	1	1
03-Feb-12	23:10	1	1	1
03-Feb-12	23:25	1	1	1
03-Feb-12	23:40	1	1	1
03-Feb-12	23:55	1	1	1
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04-Feb-12	0:25	1	1	1
04-Feb-12	0:40	1	1	1
04-Feb-12	0:55	1	1	1
04-Feb-12	1:10	1	1	1
04-Feb-12	1:25	1	1	1
04-Feb-12	1:40	1	1	1
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04-Feb-12	3:25	1	1	1
04-Feb-12	3:40	2	2	1
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04-Feb-12	4:10	1	1	1
04-Feb-12	4:25	1	1	1
04-Feb-12	4:40	1	1	1
04-Feb-12	4:55	1	1	1
04-Feb-12	5:10	1	1	2
04-Feb-12	5:25	1	1	1
04-Feb-12	5:40	1	1	1
04-Feb-12	5:55	1	1	1
04-Feb-12	6:10	1	1	1
04-Feb-12	6:25	1	1	1
04-Feb-12	6:40	1	1	1
04-Feb-12	6:55	1	1	1

Date	Time	F001 Actiivty	F002 Activity	M001 Activity
04-Feb-12	7:10	2	2	1
04-Feb-12	7:25	1	1	1
04-Feb-12	7:40	1	1	1
04-Feb-12	7:55	1	1	1
04-Feb-12	8:10	1	1	1
04-Feb-12	8:25	1	1	1
04-Feb-12	8:40	1	1	1
04-Feb-12	8:55	1	1	1
04-Feb-12	9:10	1	2	1