A MULTIPLE TROPHIC LEVEL APPROACH TO ASSESS ECOLOGICAL CONNECTIVITY AND BOUNDARY FUNCTION IN MARINE PROTECTED AREAS: A BRITISH COLUMBIA EXAMPLE.

By

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ABSTRACT

In this study, I present a multiple trophic level approach to assess connectivity and boundary delineation in six marine protected areas (MPAs) off the west coast of Vancouver Island, British Columbia. Through examination of three trophic levels that constitute a gray whale's (*Eschrichtius robustus*) food chain, I show that the existing set of marine reserves is ecologically functional for gray whales during their summer foraging bouts. Patterns in the distribution and levels of primary production throughout the study area show that each marine reserve, and the intervening areas, are connected by similar levels of chl *a*. There was no significant difference in chl *a* levels among park or non-park areas. The dispersal capacity of the gray whales primary prey item, *Holmesimysis sculpta*, in this part of their foraging range is suppressed with genetic evidence suggesting limited demographic exchange between two distant sites. To account for this, I argue that the life history characteristics and habitat preferences of *H. sculpta* are not indicative of widespread dispersal. In addition, I document the movement patterns of individual gray whales and show that they require multiple feeding sites over large spatial scales in order to find sufficient prey patches. Foraging locations for gray whales, based on the average foraging depth, suggest that the current configuration of the existing park boundaries can be altered, and that the addition of a new MPA at Nootka Island can increase the proportion of feeding gray whales inside park boundaries. The results show that the province of British Columbia has coincidentally established a network of MPAs for foraging gray whales in this part of their foraging range. By taking a multiple trophic level approach to assess connectivity and boundary delineation, the efficacy of networks of marine reserves can be tested using a wide ranging coastal cetacean.

Supervisor: Dr. D.A. Duffus (Department of Geography)

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CHAPTER 1

INTRODUCTION

The efficacy of marine reserves (analogous to marine protected areas, marine sanctuaries, marine conservation areas, etc.) is predicated on their ability to meet predetermined conservation objectives (Brailovskaya 1998, Agardy 2000, Jamieson & Levings 2001, Sala *et al.*2002). One of the most common objectives is to enhance commercially important marine species for continual harvesting (Brailovskaya 1998, Dayton *et al.*2000, Apostolaki *et al.*2002). The assertion that setting aside areas free from extraction (i.e., fishing/harvesting) will provide a surplus, or catalyze a 'spillover' effect of individuals to adjacent areas is common in the literature (Roberts 1995, Hastings & Botsford 1999, 2003, Jamieson & Levings 2001, Rogers-Bennett *et al.*2002). However, documentation of fishery enhancements as a result of the establishment of marine protected areas (MPAs) with fishing prohibitions is rare, and is generally documented in sedentary or sessile marine species common to coral or rocky reefs systems (Roberts 1995; 1998, Hatings & Botsford 1999, Dayton *et al.*2000, Sanchez Lizaso *et al.*2000). Other ecological objectives of MPAs are the maintenance/enhancement of biodiversity, the protection of unique habitats, and the protection of endangered/threatened species (Vanderkift & Phillips 1998, Hooker *et al.*1999, Jamieson & Levings 2001, Botsford *et al.*2003).

Whether the objective is the enhancement of fish stocks or the maintenance of biodiversity, the success of MPAs requires an understanding of the organism(s) in question and the ecological processes taking place. However, placement of marine reserves often occurs in the absence of sufficient knowledge of the ecological processes that affect targeted species (Agardy 2000). This *ad hoc* approach to marine reserve design has undermined the utility of MPAs and has recently invoked much discussion in regard to whether or not MPAs serve any purpose other than providing a false sense of security when it comes to protecting marine species (Halpern 2003). One of the main issues is that of design; how do we effectively design MPAs to meet conservation objectives? Clearly, the objectives of a MPA must be explicit in order for the design to be effective, however, the objectives of many conservation agencies, especially in Canada (both at the federal and provincial/state levels) are ambiguous (Jamieson & Levins 2001, Dunham *et al.*2002). It is readily apparent that there are two fundamental problems in MPA design; unclear objectives and insufficient knowledge of the ecological domain that encompass that which is to be protected.

Since the inception of MPAs, design flaws mostly stem from adopting design principles from terrestrial reserves (Carr *et al.*2003). There are inherent differences between marine systems and terrestrial systems, for example; dispersal, disturbance, scales of connectivity/movement, population structure, life histories of organisms and the management of these systems. Therefore, it should come as no surprise that by implementing similar design principles from terrestrial reserves that we encounter several problems (Carr *et al.* 2003). The one commonality between these two systems is the conservation objectives which again, are often vague, but at least the ecological understanding of terrestrial ecosystems is far more advanced than marine systems and this may make certain tasks (eg., species protection) more easily accomplished.

An important caveat concerning MPA literature is the language that is commonly used. Terms or phrases such as 'ecological integrity', 'the maintenance of biodiversity', 'the sustainable management of commercial fisheries' and that MPAs provide 'important ecological services' has slowed the progress of marine conservation and MPA science. The underlying issue here is that these 'catch phrases' are difficult to define or attach any meaning to. Thus, to design MPAs based on meaningless or ambiguous terminology makes the task even more difficult. Again, this terminology stems from terrestrial conservation literature (Carr *et al.*2003) and has spilled over to marine conservation literature along with design flaws and other incompatibilities. What makes things more difficult in marine systems is our lack of understanding in regards to ecological processes and their effect on marine organisms. Rapid change and variability in marine ecosystems is pervasive and difficult to predict when compared to terrestrial systems and because of this lack of understanding the terminology should be clear and objectives definable.

This background sets the stage for the purpose of this thesis; to test the design of a network of six provincial MPAs on the west coast of Vancouver Island, British Columbia, Canada with a clear and definable set of objectives (Fig. 1.1, Table 1.1). A central issue in the design of MPAs and networks of MPAs is connectivity (Roberts 1997, Lockwood *et al.*2002, Thorrold *et al.*2002, Palumbi 2003) and because of the way in which the six MPAs in this study area were designed, ecological connectivity can be tested and measured. However, this requires some discussion on the theory behind marine park design and connectivity.

Marine Park Design and Connectivity in Marine Populations

The difficulty in designing and locating marine reserves is a result of nebulous marine boundaries (unlike their terrestrial counterparts), highly mobile/migratory speices and inherently variable oceanic processes (Duffus & Dearden 1993, Paisley 1995, Ballentine 1995, Agardy 2000, Garcia Charton 2000, Carr *et al.*2003). The optimal design and placement of marine reserves therefore hinges upon current scientific knowledge of the driving forces in oceanic production and the distribution and dispersal capabilities of marine organisms (Roberts 1998, Crowder *et al.*2000, Roberts 2000, Warner *et al.*2000, Sala *et al.*2002, Lockwood *et al.*2002). Source areas that contribute a disproportionate number of propagules to adjacent areas and sink areas that contribute little, but still maintain populations are important in MPA design (Ogden 1997, Roberts 1998, Crowder *et al.*2000). This premise supposes that if we can identify s*ource* areas then we should set aside these regions as ‘no-take’ reserves thus enhancing overall biomass of the desired species (Roberts 1998). A problem arises because research addressing source/sink dynamics is extremely difficult to test empirically and many socioeconomic factors (i.e., pressure by the fishing industry) take precedence over scientific investigation (Ogden 1997, Brailovskaya 1998). This leads into the concept of open versus closed populations and recent evidence suggests that many marine species, even those with long pelagic larval stages, may exhibit a degree of local retention (Swearer *et al.*1999, Jones *et al.*1999, Cowen *et al.*2000, Warner & Cowen 2002, Taylor & Hellberg 2003).

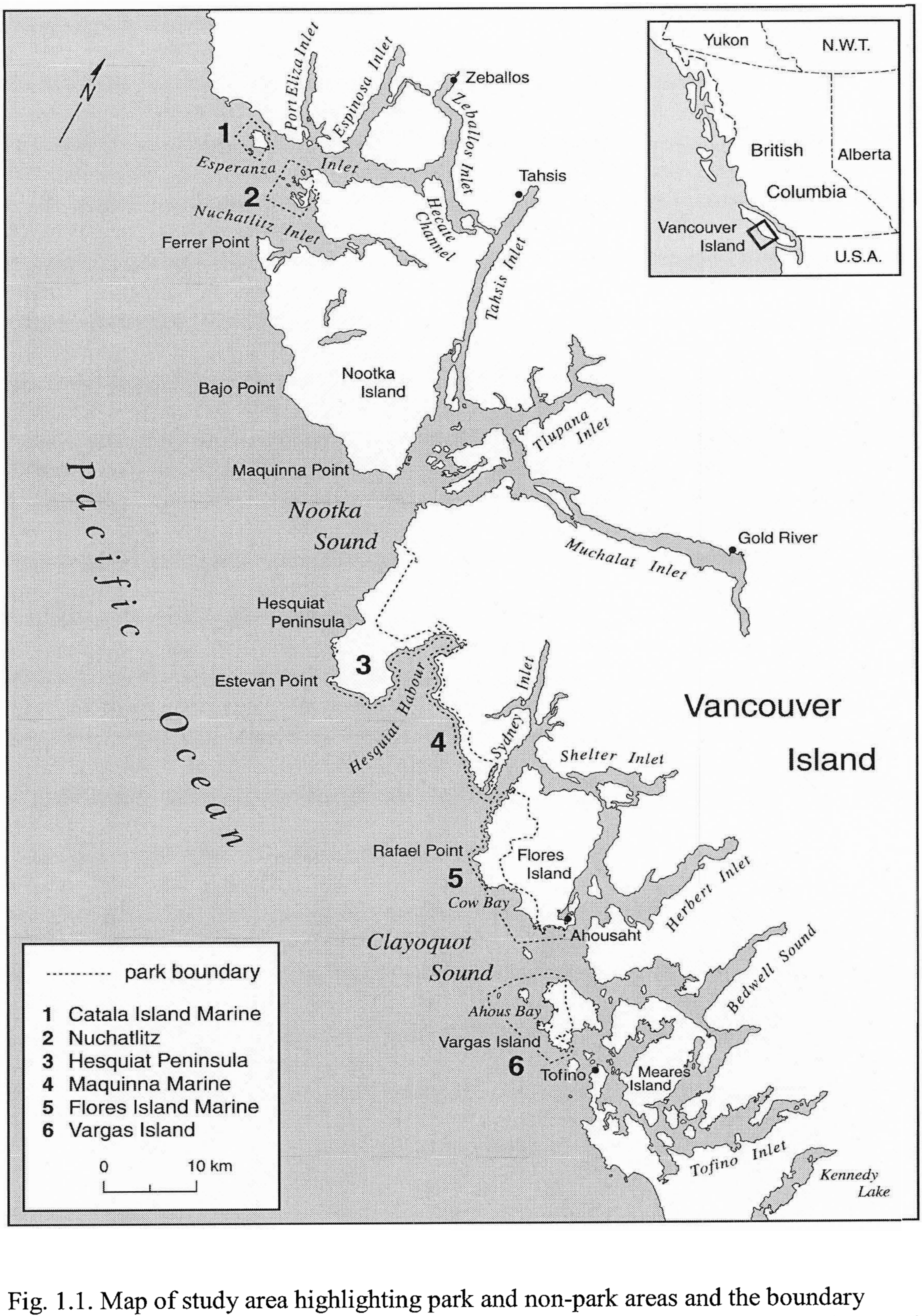

Fig. 1.1. Map of study area highlighting park and non-park areas and the boundary delineating the north and south portions of the study area. Non-park areas are shown with shaded areas.

Table 1.1. Location, date of establishment and size of each of the six MPAs in the study area.

Name	*Location*	*Marine Area*	*Land Area*	*Est. Date*
Vargas Island	49°11'N; 126° 01'W (Ahous Bay)	5,920 ha	50 ha	July 12, 1995
Flores Island Marine	49°16'N; 126°09'W (Cow Bay)	2,969 ha	4,145 ha	July 12, 1995
Maquinna Marine	49°22'N; 126°16'W (Hot Springs Cove)	1,398 ha	1,269 ha	January 7, 1955
Hesquiat Peninsula	49°26'N; 126°27W (Hesquiat Harbour)	1,210 ha	6,689 ha	July 12, 1995
Nuchatlitz	49°49'N; 126°58'W	1,663 ha	442 ha	April 30, 1996
Catala Island Marine	49°51'N; 127°03'W (Rolling Roadstead)	596 ha	255 ha	July 12, 1995

The passive dispersal of marine organisms by oceanic currents is thought to account for much of the dispersal capacity during the larval stage of an animal's development (Cowen *et al.*2000, Smith *et al.*2001, Largier 2003). The concept that marine populations are 'open' over ecological time scales is predicated on the spatial and temporal scales of oceanic currents (Roberts 1997, Odgen 1997, Cowen *et al.*2000, Palumbi 2003). However, there is mounting evidence that suggests otherwise. Given species life histories and specific behavioural traits, species may in fact maintain their natal position during developmental stages, for example, around a given bay or reef (Jones *et al.*1999, Taylor & Hellberg 2003). This has implications for the design and placement of marine reserves because source and sink areas may not function, via major current regimes, as previously expected (Roberts 1997, Jamieson & Levings 1997). Therefore, connectivity between networks of MPAs essentially relies on knowledge of dispersal and distributions of the species in question.

Quantifying larval dispersal/retention in marine populations has been, and is currently, a major difficulty in marine ecology (Thorrold *et al.*2002). Several techniques can be employed when trying to determine connectivity or retention among marine populations, including natural or artificial markers or a combination of them both (Thorrold *et al.*2002). Natural markers, both genetic and environmental, reveal the extent of genetic variation (i.e., gene flow) and variation in geochemical signatures. Artificial markers, such as fluorescent compound tagging, readily incorporate fluorescent compounds into calcified tissues in which specimens are then released and captured at a later date. Other artificial tagging methods include elemental tagging, which utilizes rare earth elements (REEs), radioactive isotopes and thermal markers. All of the above techniques can be used in the marine environment but some are more advantageous than others. A combination of techniques often yields the best results (Swearer *et al.*1999, Jones *et al.*1999, Thorrold *et al.*2002, Hellberg *et al.*2002, Talylor & Hellberg 2003).

Current literature suggests that the mean dispersal distance of the organism in question should dictate the minimum distance between reserves (Sala *et al.*2002, Lockwood *et al.*2002). This will allow for dispersal mechanisms to take place in an ecologically functional manner. The size of the reserve should also reflect the average dispersal and mobility of specific organisms (Lockwood *et al.*2002). However, the effective placement of reserves may not always yield any observable ecological benefits for some time (Boyd & Murry 2001, Shears & Babcock 2003) and this may give political/socioeconomic administrators rationale to stall or reject the implementation of MPAs (Ballantine 1995, Agardy 2000,). Furthermore, measuring the effectiveness of reserves becomes even more complex when assessing potential changes due to MPA establishment compared to natural oceanic variability (Garcia Charton *et al.*2000) and placement on the basis of focal species or specific taxonomic groups is often reflected in the socioeconomic value of the species (Vanderklift & Phillips 1998, Zacharias & Roff 2001, Dunham *et al.*2002). Determining the focal species can be a difficult choice and commercially exploited fish species or endangered/threatened species are often chosen since they are deemed most sensitive (Hooker *et al.*1999, Sala *et al.*2002, Hooker *et al.*2002, Hooker & Gerber 2004). It is also important to consider connectivity through the trophic spectrum as well since these interactions are essential to the distribution of species. Although trophic interactions in marine systems are complex (especially when we add the human dimension) (Jackson *et al.*2001) by focusing on a focal species it is possible to minimize this complexity (Fig. 1.2). Gray whales (*Eschrichtius robustus*), by being a relatively low trophic level predator (Pauly *et al.*2002), make a good candidate species to measure connectivity through different levels of their food web.

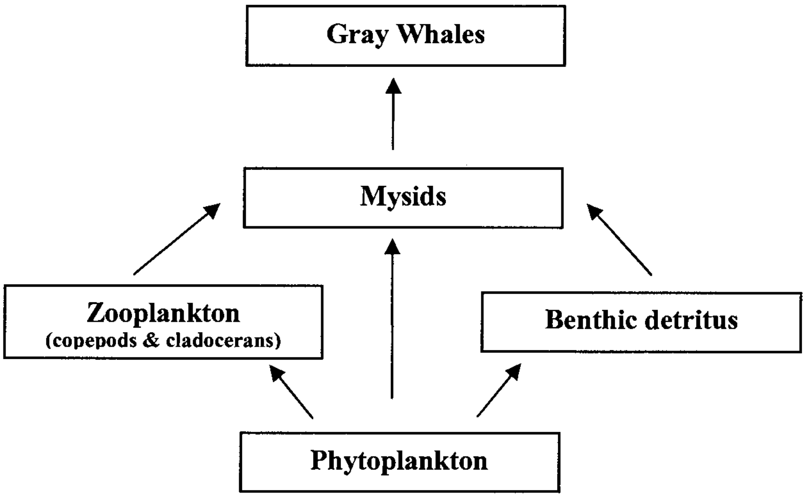

Fig. 1.2. Trophic diagram of a gray whales food chain highlighting relationship with primary production and mysids, their preferred prey item in this area (adapted from Hooker *et al.*2002).

Few studies have examined the efficacy of marine reserves in reference to marine mammals even though it is often suggested in the literature (Duffus & Dearden 1993, Agardy 2000, Sala *et al.*2002, Hooker & Gerber 2004). The overall aim of this research is to assess biological connectivity between this set of marine reserves using gray whale food chains and to determine whether or not the existing marine parks in this study area function as a network. Ancillary to this will be the examination of the current MPA boundaries with reference to the distribution of primary production and the spatial patterning of foraging gray whales. I will accomplish this by examining the important trophic levels that constitute a gray whale's food chain and how they can be incorporated into this set of MPAs. By using a muti-trophic level approach to measure connectivity, I present a novel approach to the future of marine reserve design with special emphasis on wide ranging predators.

Chapter two describes the underlying distribution and spatial/temporal variation in chlorophyll *a* [chl *a*] throughout the study area and inside and outside of the designated park boundaries. This is done because primary production is the foundation for upper trophic levels. Consequently, connectivity can then be measured by comparing mean levels of chl *a* among park areas. The third chapter will specifically examine the dispersal capacity of the gray whale's primary prey item (mysids), (Order *Mysidacea*), more specifically one single species of mysid (*Holmesimysis sculpta*). This is done on a molecular level measuring gene flow between distant populations in order to ascertain a degree of connectivity at this trophic level. Chapter four describes the movement patterns of the apex predator (gray whales) in this scenario in terms of connectivity between multiple park areas. The fifth, and final chapter, will incorporate the three research objectives together and illustrate how this multi-trophic level method can be used to measure connectivity among a set of marine reserves off Vancouver Island.

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CHAPTER 2

SPATIAL AND TEMPORAL VARIATION IN CHL *a* DISTRIBUTION AS A COMPONENT TO MARINE RESERVE DESIGN

INTRODUCTION

Depending on the objectives of any marine reserve network, connectivity can be quantified at various ecological scales and on a multitude of trophic levels. Designing marine protected areas for wide ranging species such as cetaceans requires an understanding of both their physical habitat requirements as well as their ecological requirements. Furthermore, life history characteristics of both predator and prey should be well understood in order to implement effective conservation measures (Duffus & Dearden 1992, Hooker *et al.*1999, Hooker & Gerber 2004). For the eastern Pacific gray whale (*Eschrichtius robustus*), and for many other baleen whales, there are three primary components to their life history. In the northern hemisphere, gray whales undergo an annual migration (1) and have latitudinal habitat partitioning in regards to breeding (2) and foraging (3) (Kim & Oliver 1989, Duffus 1996, Rugh *et al.*1999). Foraging habitat for gray whales is primarily characterized by high latitude coastal regions of the eastern Pacific Ocean and breeding occurs at lower latitudes of the eastern Pacific (Rice & Wolfman 1971, Nerini 1984, Kim & Oliver 1989). The ecological impetus for high latitude foraging in many cetaceans is primarily a result of increased oceanic production due to coastal upwelling, habitat structure and the availability of prey (Piatt *et al.*1989, Piatt & Methven 1992, Fiedler *et al.*1998, Croll *et al.*1998, Hooker *et al.*1999, Fauchald *et al.*2000, Benson *et al.*2002, Ingram & Rogan 2002, Mendes *et al.*2002).

The trophic linkages between elevated levels of primary production and increased zooplankton biomass are fairly well known (Mackas *et al.*1980, Durbin *et al.*1995, 2003) as is the importance of these linkages to higher level predators such as whales (Beardsley *et al.*1996, Fiedler *et al.*1998, Croll *et al.*1998, Fauchald *et al.*2000, Benson *et al.*2002, Baumgartner & Mate 2003). When viewed spatially, zooplankton distribution appears ephemeral or 'patchy' in nature (Fenchel 1998, Folt & Burns 1999) however, phytoplankton blooms can appear to be ubiquitous near coastal regions at large spatial scales (100s - 1000s of km) (Menge *et al.*1997, Wieters *et al.*2003, Gonzales-Silvera *et al.*2004). Traditionally, primary production has been viewed in this light, however recent studies (Menge & Daley 1997, Wieters *et al.*2003) have documented mesoscale variation (tens to hundreds of km) in chlorophyll *a* [chl *a*] levels (a proxy measure for net primary production). Oceanographic investigations on these topics have mainly been descriptive in nature and usually are correlated to physical forcing mechanisms such as sea-surface temperature and current dynamics (Mackas *et al.*1980, Engelsen *et al.*2002, Hirst & Bunker 2003, Baumgartner *et al.*2003).

Designing marine reserves traditionally has not been based on measures of chl *a* variation, as a component of their design, even though primary production forms the basis for all higher trophic levels (Nybakken 2001). Variation in primary production may also influence the structure of food webs (Menge & Daley 1997, Nybakken 2001, Wieters *et al.*2003). This is commonly referred to as bottom-up forcing in marine systems; whereas species assemblages are controlled by ecological processes such as upwelling and nutrient loading as opposed to top-down effects such as predation and other trophic interactions (Menge *et al.*1997, Shears & Babcock 2003). Trophic interactions of many top predators in the marine environment can be very complex (Jackson *et al.*2001); however gray whales operate on a relatively short food chain

(Dunham & Duffus 2001, 2002) rendering it plausible to measure connectivity from autotrophs (e.g. phytoplankton) to primary consumers (e.g. small omnivorous invertebrates) to secondary consumers (e.g. whales).

Gray whales are known to feed in nutrient-rich nearshore environments (Dunham & Duffus 2001, 2002), therefore the design and placement of a network of MPAs should reflect the ecological requirements of the species. Also, the spatial arrangement of these MPAs should also reflect the temporal variability in chl *a* levels over their summer foraging bouts. For a wide-ranging species such as a gray whale, whose distribution reflects that of certain coastal phytoplankton distributions, MPAs for foraging gray whales should cover similar spatial scales. Realistically, this could not be possible since gray whales do not forage throughout their entire range and setting aside such huge areas for gray whales would not be feasible. The most appropriate approach would be to design and place several marine reserves that are connected in terms similar production levels and are in known feeding locations for gray whales.

Quantifying connectivity in the marine environment, and applying it to marine reserve design, is difficult due to the dynamic and highly variable nature of oceanographic processes (both physical and biological) (Swearer *et al.*1999, Jones *et al.*1999, Cowen *et al.*2000, Smith *et al.*2001, Warner & Cowen 2002, Taylor & Hellberg 2003). Traditionally, connectivity has been measured through the movement and dispersal capabilities of the organism(s) in question and is more prevalent in terrestrial systems (Carr *et al.*2003). In marine systems it may be possible to measure connectivity through process oriented phenomena, like upwelling or oceanic production, since this is often what drives many species to aggregate in specific areas at specific times (Piatt *et* *al.*1989, Piatt & Methven 1992, Fiedler *et al.*1998, Croll *et al.*1998, Hooker *et al.*1999, Fauchald *et al.*2000, Benson *et al.*2002, Mendes *et al.*2002, Ingram & Rogan 2002).

The purpose of this chapter is to describe variation in chl *a* levels in known gray whale foraging grounds inside and outside of established provincial MPAs. Since the marine reserves under question were established with little ecological foresight, boundary function will be tested to see whether or not there exists any difference in chl *a* levels inside and outside park boundaries. Fine to coarse scale (tens to hundreds of km) spatial and temporal variation (days to months) in chl *a* will also be assessed over the entire foraging area and throughout the feeding season. Although several studies have documented correlations between cetacean abundance and distribution and enhanced production (e.g., Fiedler *et al.*1998, Croll *et al.*1998, Fauchald *et al.*2000, Benson *et al.*2002,), none have looked at the designation of marine reserves with reference to chl *a* distribution.

METHODS

Study Area

I sampled off the west coast of Vancouver Island during May to September of 2004. The study area is from the southeastern corner of Vargas Island to the northwestern tip of Catala Island spanning approximately 130 km (Fig. 2.1). Sampling occurred in both park and non/park areas. Out sites or 'non-park' areas were chosen based on previous photo-identification evidence suggesting that whales utilize areas such as Perez Rocks, Barcester Bay, Escalante Rocks and Bajo Reefs for foraging. Furthermore, through examination of reef structure, water depth and substrate, the non/park areas are similar to gray whale foraging areas in the southern portion of the study area which has been studied extensively (Duffus 1996, Dunham & Duffus 2001, 2002). Northern regions are defined as being north of Estevan Point and encompass Nootka Sound and southern regions are defined as all areas to the south of Estevan Point and encompass Clayoquot Sound (Fig. 2.2). A total of 14 sampling sites were established in both park and non-park areas (Table 2.1).

Sample Design

The coastline of each marine reserve was stratified into 0.5nm grids and 14 randomly placed nearshore stations were selected within the grid cells, in both park/non-park areas, and in the intervening areas between adjacent park boundaries. Upon selection of the nearshore stations, two additional stations were placed perpendicular to the shoreline, and offshore from the nearshore station in each sampling area. All stations were equal distances apart with the third station in each park being outside the designated boundary. Only two stations were placed in the non-park areas, one close to shore (approx. 20m) and one 500m offshore from the nearshore station perpendicular from the shoreline. In the areas between park boundaries only one station was randomly selected. Sampling coordinates were acquired using the Canadian Hydrographic Service Field Sheets No. 3603, 3673, 3674, 3675 and 3676 (2003). A total of 28 sampling stations were selected and marked using a Magellen *Colortrack* GPS to ensure repetitive sampling at the same locations. The random placement of the nearshore stations and subsequent placement of the remainder of the stations ensured adequate coverage of the entire study area.

Data Collection

A seven meter aluminum vessel was used to gain access to the sampling stations. At each station a Sea-Bird 19 plus CTD (Conductivity, Temperature, Depth) with an attached "Wet-Labs" (ECO-AFL) fluorometer was deployed. CTD casts recorded the physical/biological oceanographic parameters; depth, salinity, temperature and chlorophyll *a* via fluorescence, however only depth and chl *a* will be used for analysis in this study. A total of three full surveys (Vargas Island to Catala Island) and four partial surveys were completed (Vargas Island to Perez Rocks or Estevan Point) (Table 2.2). A total of 144 casts were made throughout the 2003 sampling season.

Data Analysis

All CTD data was processed using Sea-Bird Electronics data processing software package version 5.31a (Sea-Bird Electronics, Inc., 2004). CTD profiles were created using Sea-Birds Electronics "Plot39" version 1.0b (Sea-Bird Electronics, Inc., 1999). For statistical analysis all surveys were analyzed separately to examine spatial variation and pooled over the entire season to look at temporal variation. Since there is a sampling bias towards the southern portion of the study area, results will be given for both partial and full surveys as well as the aggregated results. Partial surveys were due to poor weather conditions that prohibited a full survey to be completed in less than eight days. Mean chl *a* levels of the upper 5 m of the water column are used for all statistical tests.

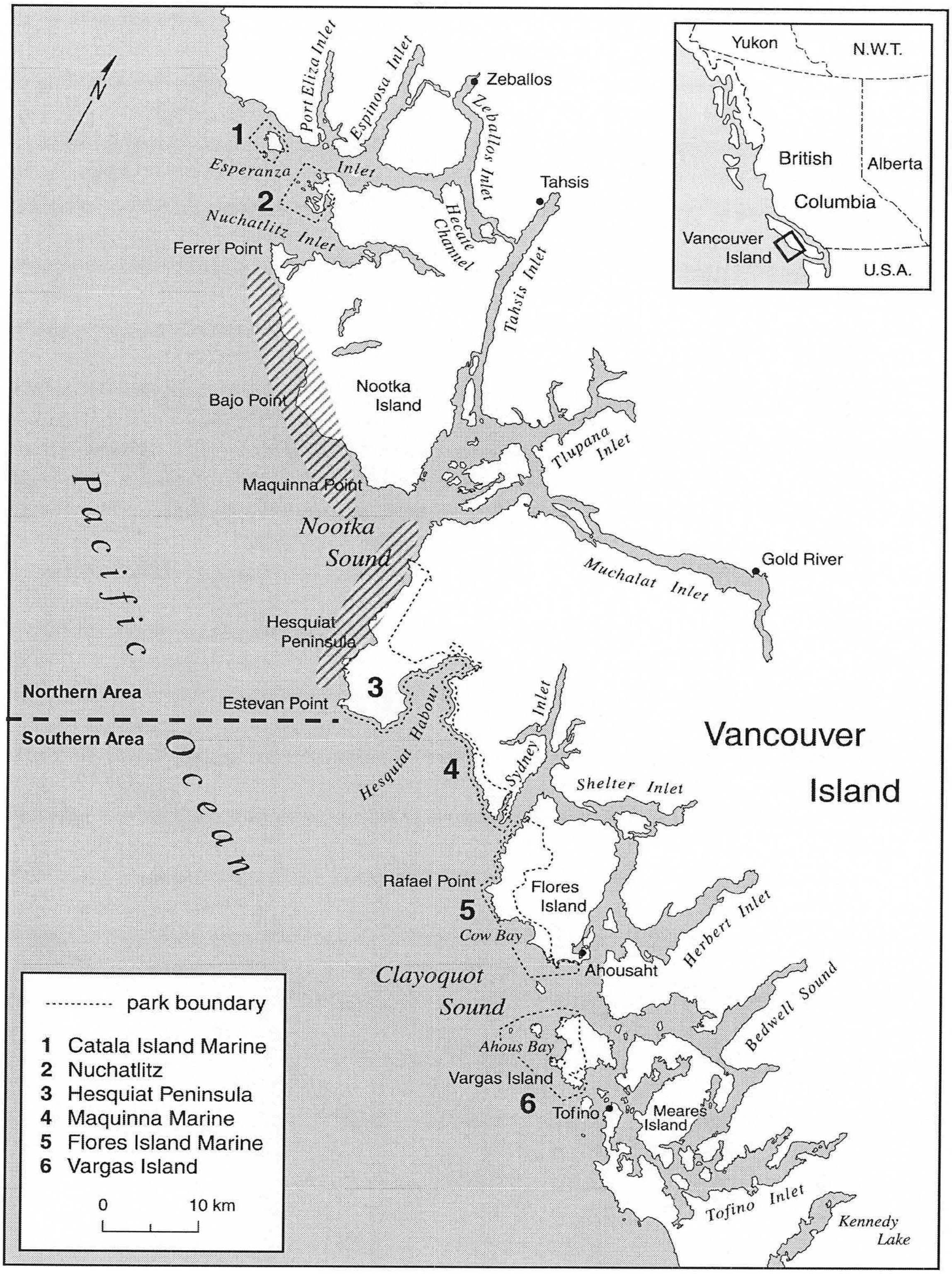


Fig. 2.1. Map of study area highlighting park and non-park areas and the boundary delineating the north and south portions of the study area. Non-park areas are shown with shaded areas.

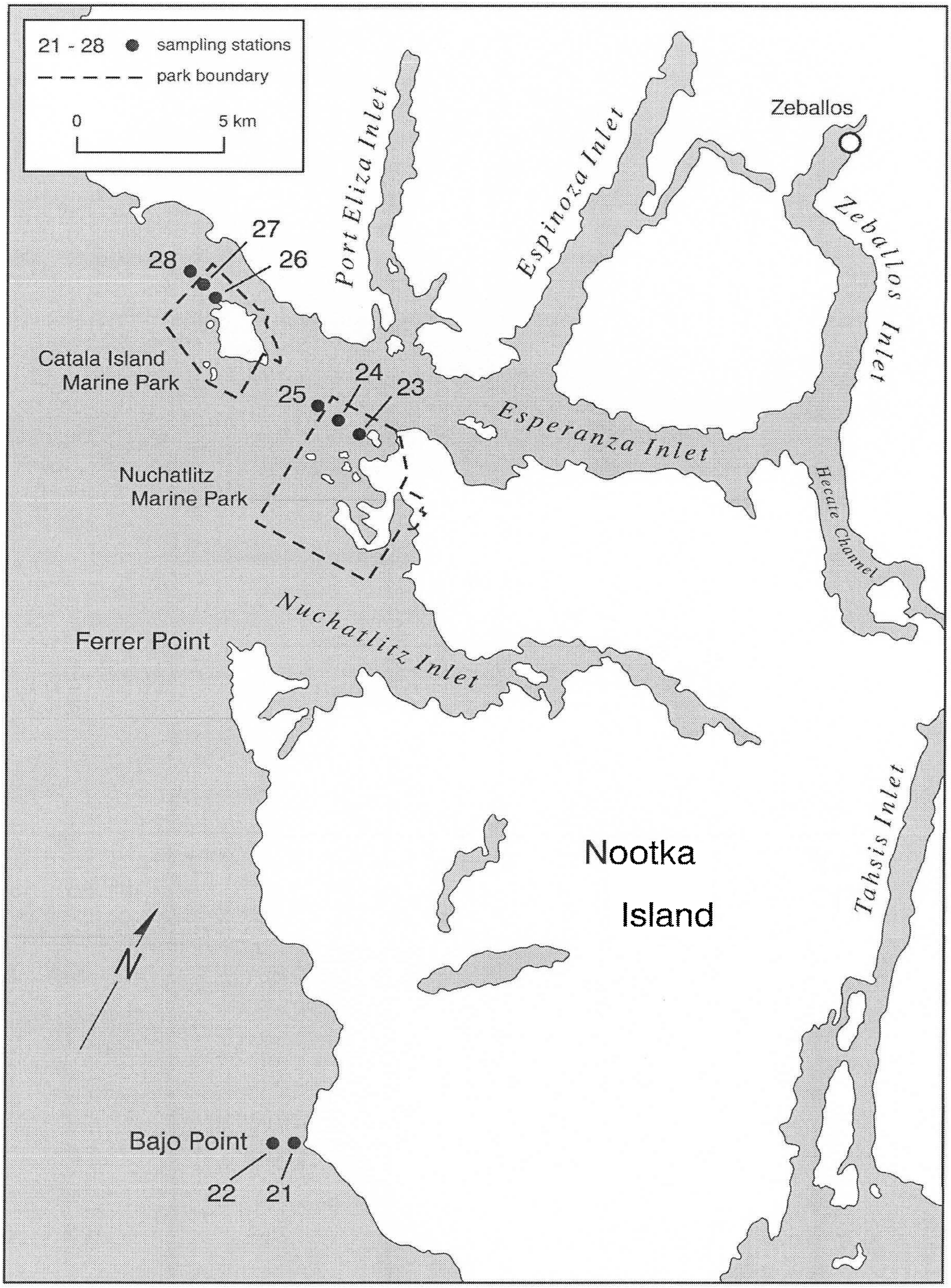


Fig. 2.2. Sampling locations for CTD casts in the northern portion of the study area.

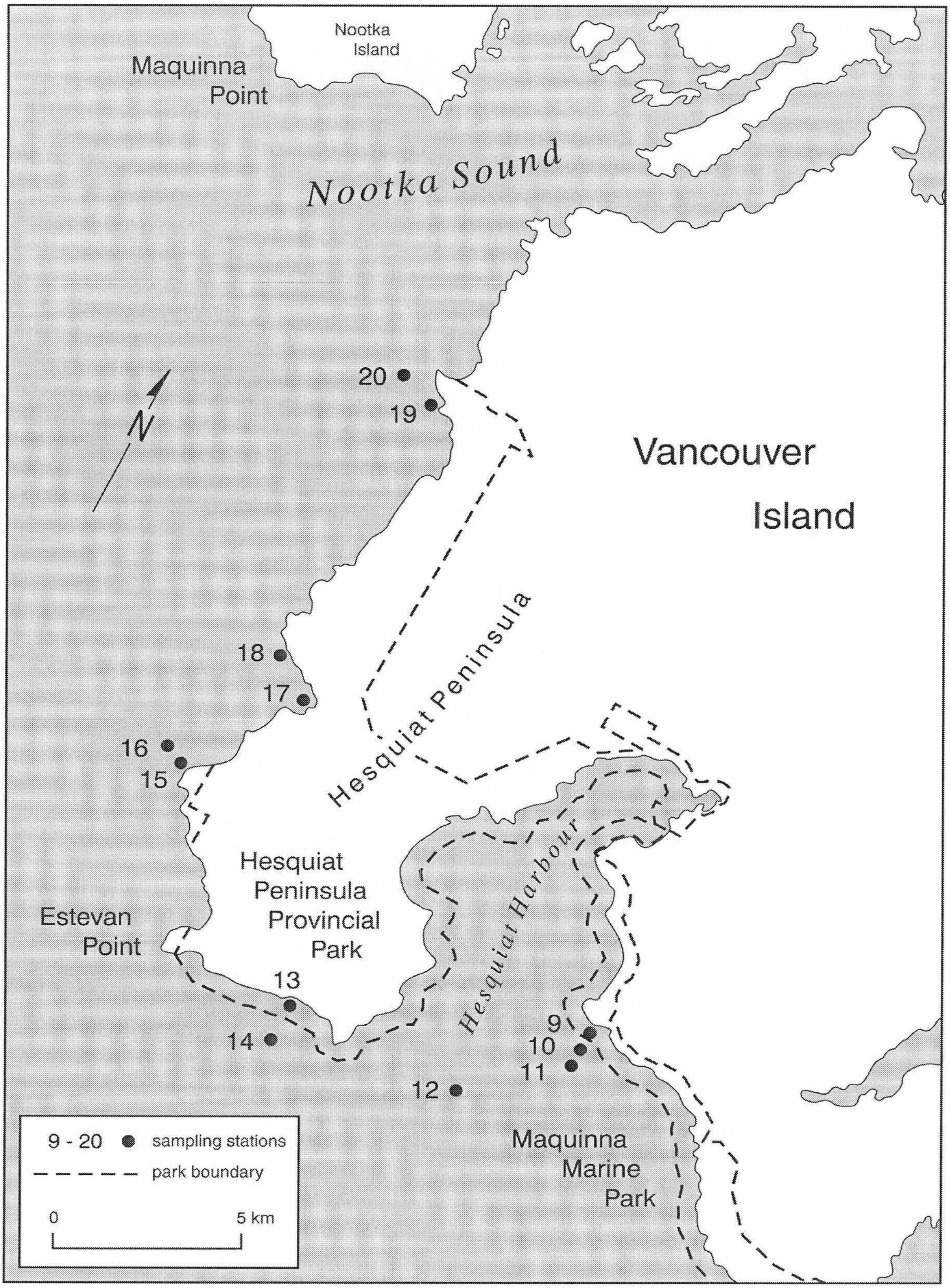


Fig. 2.3. Sampling locations for CTD casts in the middle portion of the study area.

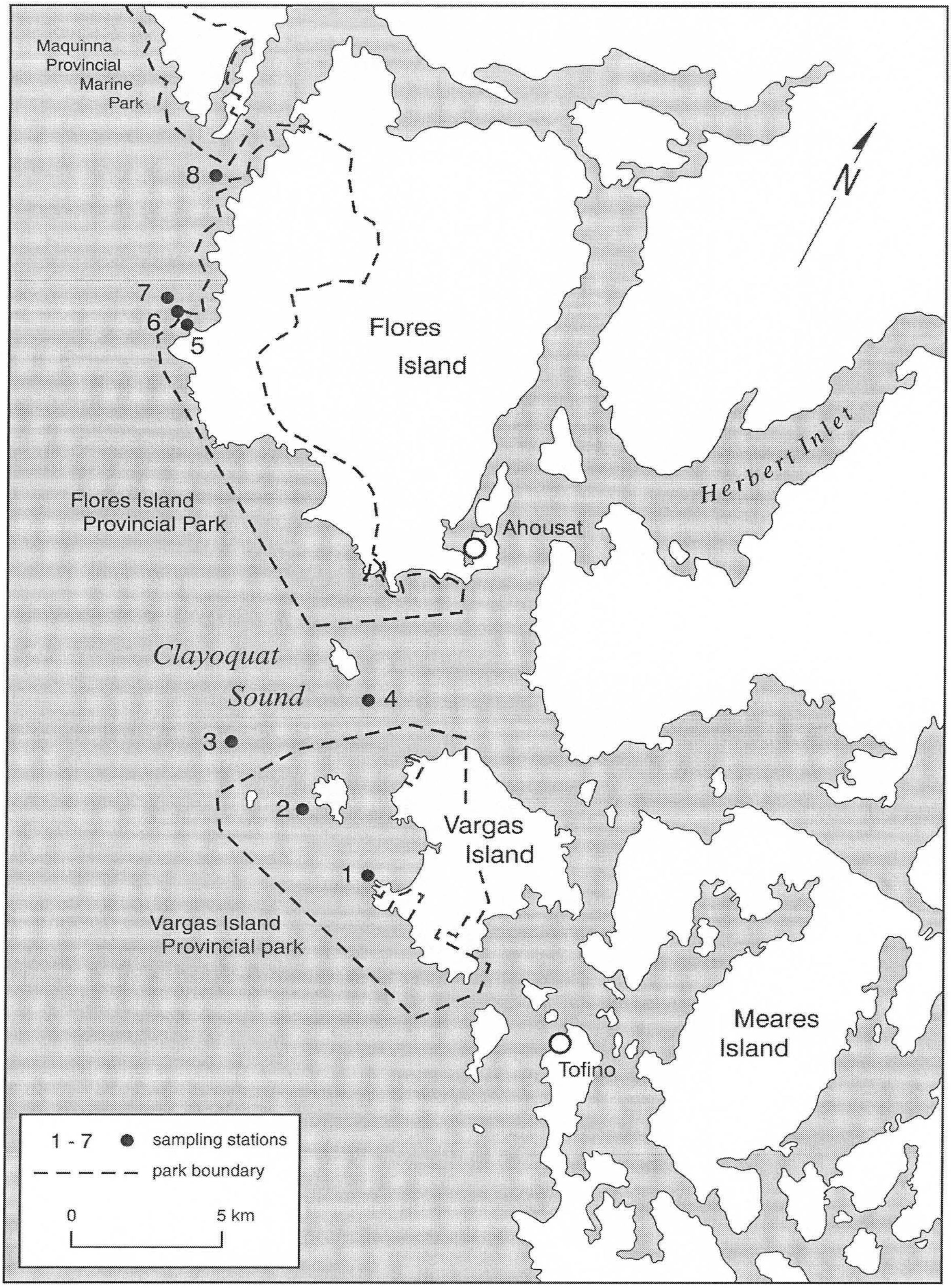


Fig. 2.4. Sampling locations for CTD casts in the southern portion of the study area.

Table 2.1. List of all sampling sites, both park and non-park and sampling region.

Site	*Location*	*Designation*	*Boundary Region*
1	Vargas Island	Marine Park	South
2	Vargas – Flores	Non-Park	South
3	Flores Island	Marine Park	South
4	Flores – Maquinna	Non-Park	South
5	Maquinna	Marine Park	South
6	Maquinna – Hesquiat	Non- Park	South
7	Hesquiat	Marine Park	South
8	Perez Rocks	Non-Park	North
9	Barcester Bay	Non-Park	North
10	Escalante Rocks	Non-Park	North
11	Bajo Reefs	Non-Park	North
12	Nuchatlitz	Marine Park	North
13	Nuchatlitz – Catala	Non-Park	North
14	Catala Island	Marine Park	North

Table 2.2. Timeline of dates and locations of both full and partial surveys.

Survey Number	*Date*	*Location*	*Survey Type*
1	01 June to 04 June	Vargas to Hesquiat	Partial
2	19 June to 22 June	Vargas to Hesquiat	Partial
3	30 June to 01 July	Vargas to Catala	Full
4	13 July to 16 July	Vargas to Catala	Full
5	28 July to 06 Aug	Vargas to Catala	Full
6	20 Aug to 23Aug	Vargas to Perez	Partial
7	07 Sept to 09 Sept	Vargas to Perez	Partial

RESULTS

1) Do mean chlorophyll *a* measurements differ between park and non-park areas?

For partial surveys (n = 4) an independent sample t-test yielded no difference in chl *a* levels between park and non-park areas (t = .231, df =57, p = .818). Similarly, full surveys (n = 3) also yielded no difference in chl *a* levels across park boundaries (t = -.977, df = 82, p = .331). When aggregated together (n = 7), all surveys again showed no difference between chl *a* levels across park boundaries (t = -.415, df = 141, p = .679)

(Table 2.3). Figure 2.5 illustrates the mean chl *a* levels for both partial and full surveys and figure 2.6 shows mean chl *a* levels for all surveys.

Table 2.3. Group statistics of chl *a* in both park/non-park areas for all survey types.

Survey Type	*Park Presence*	*N*	*Mean*	*Std. Deviation*	*Std. Error*	*t*	*df*	*p*
Partial Surveys								
	Non-Park	31	3.156	3.251	0.583	.231	57	**.818**
	Park	28	2.955	3.393	0.642			
Full Surveys								
	Non-Park	51	3.688	3.017	0.421	-.977	82	**.331**
	Park	33	4.349	3.059	0.532			
All Surveys								
	Non-Park	82	3.487	3.093	0.341	-.415	141	**.679**
	Park	61	3.709	3.267	0.418			

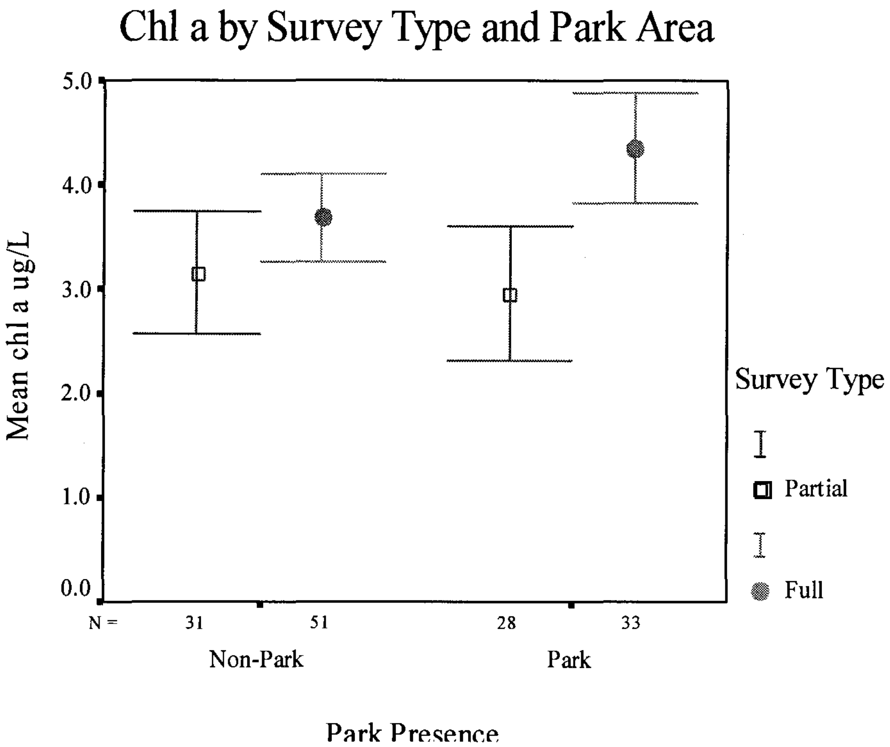


Fig. 2.5. Pooled mean chl *a* levels for partial and full surveys. Bars represent ±1 standard error.

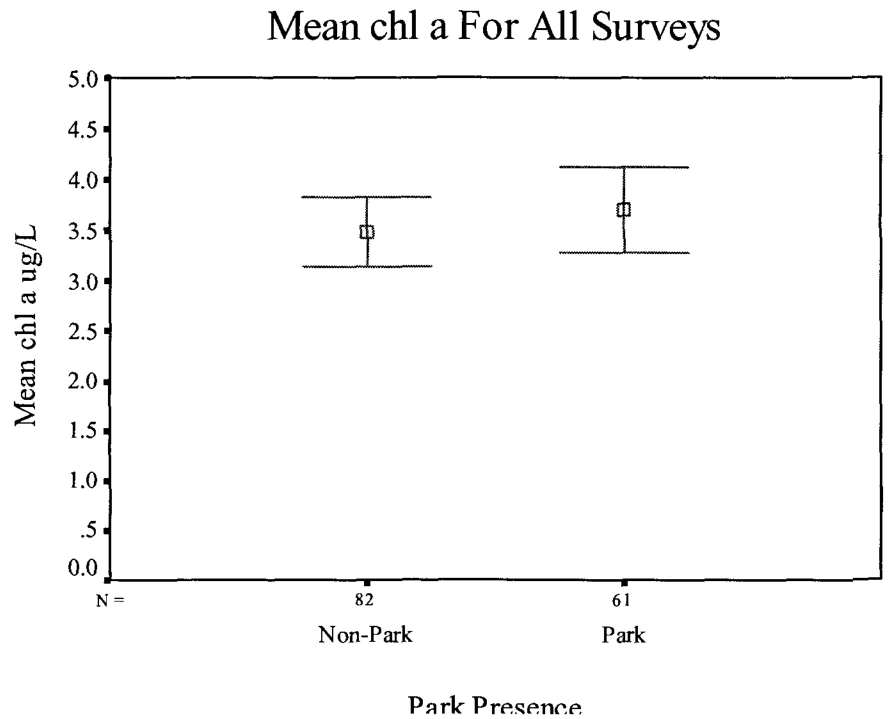


Fig. 2.6. Pooled mean chl *a* for all surveys. Bars represent ±1 standard error.

An independent t-test showed that there was also no difference in chl *a* levels due to survey type (t = -1.663 df= 141, p = .099) (Table 2.4). Figure 2.7 illustrates the mean chl *a* levels by survey type. For this test, equal variances were not assumed.

Table 2.4. Group statistics of chl *a* by survey type.

Survey Type	*N*	*Mean*	*Std. Deviation*	*Std. Error*	*t*	*Df*	*p*
Partial	59	3.061	3.294	.428	-1.663	141	.099
Full	84	3.948	3.087	.330			

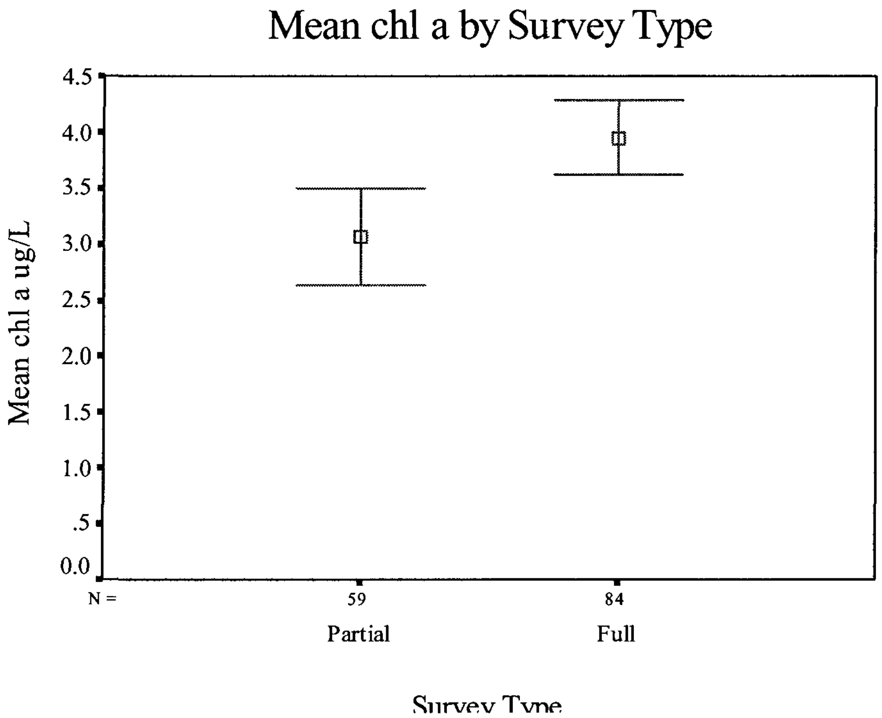
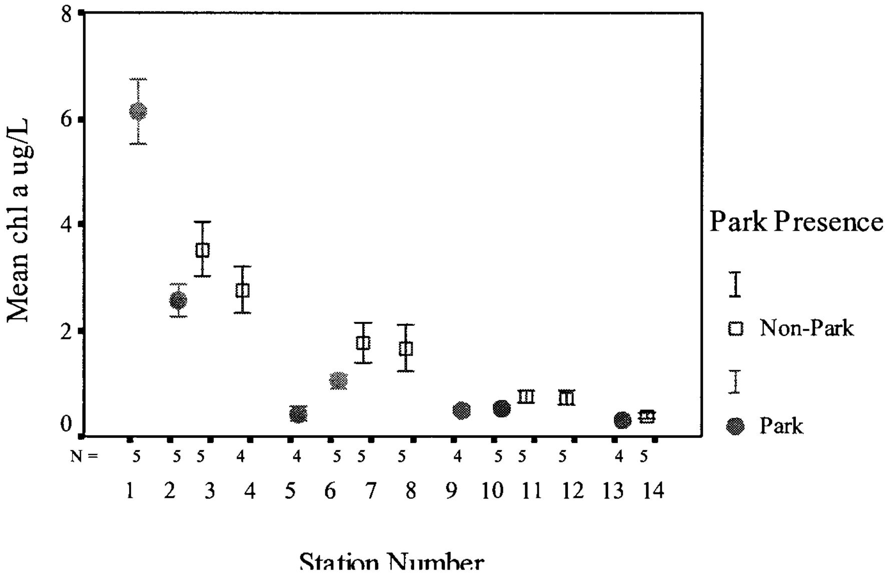


Fig. 2.7. Pooled mean chl *a* levels by survey type. Bars represent ±1 standard error.

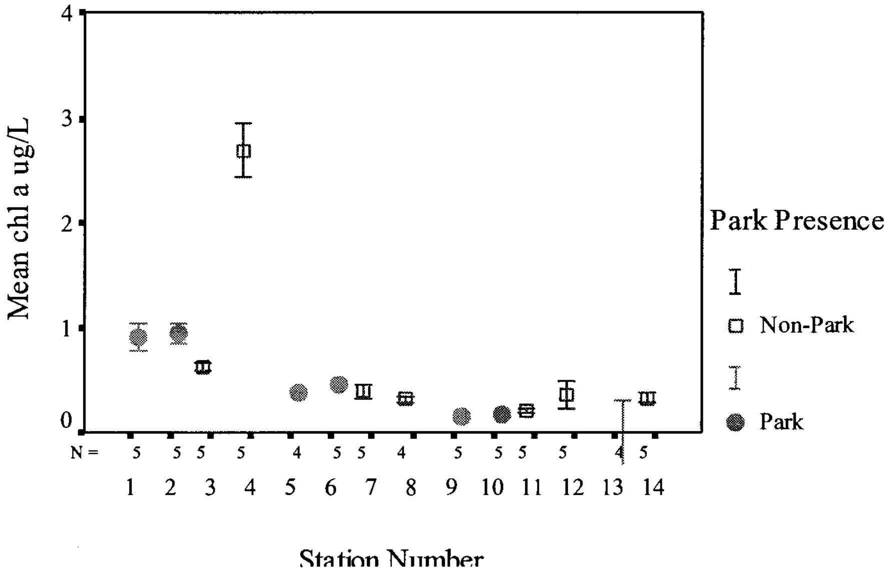
2) Is there a significant difference in chl *a* levels among stations {fine to coarse spatial scales (1 to 10000 m)}?

To illustrate fine scale variation in chl *a*, the upper 5m of the water column for each station are plotted across each survey (≤ 8 days). Mean chl *a* levels and standard deviations are given for both park and non-park areas (Fig. 2.8). Aggregated results across the entire season are shown in Figure 2.9. Results from ANOVA for all stations aggregated across the entire season show no significant differences (n = 28, df = 27, f = .486, p = .984). To meet the assumption of normality, a logarithmic transformation was carried out on the data.



Mean chl a by Station (South - North)

Survey 1

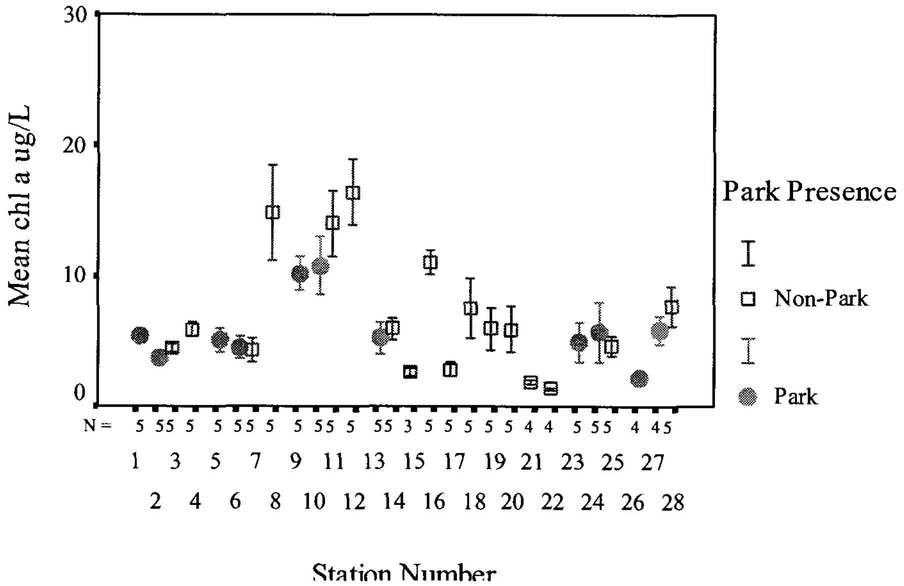


Mean chl a by Station (South - North)

Survey 2

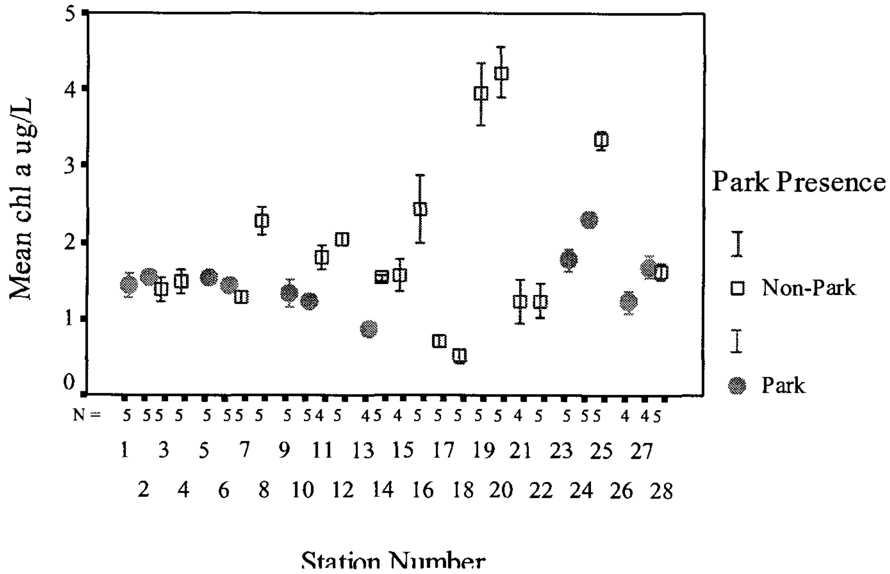
Mean chl a by Station (South - North)

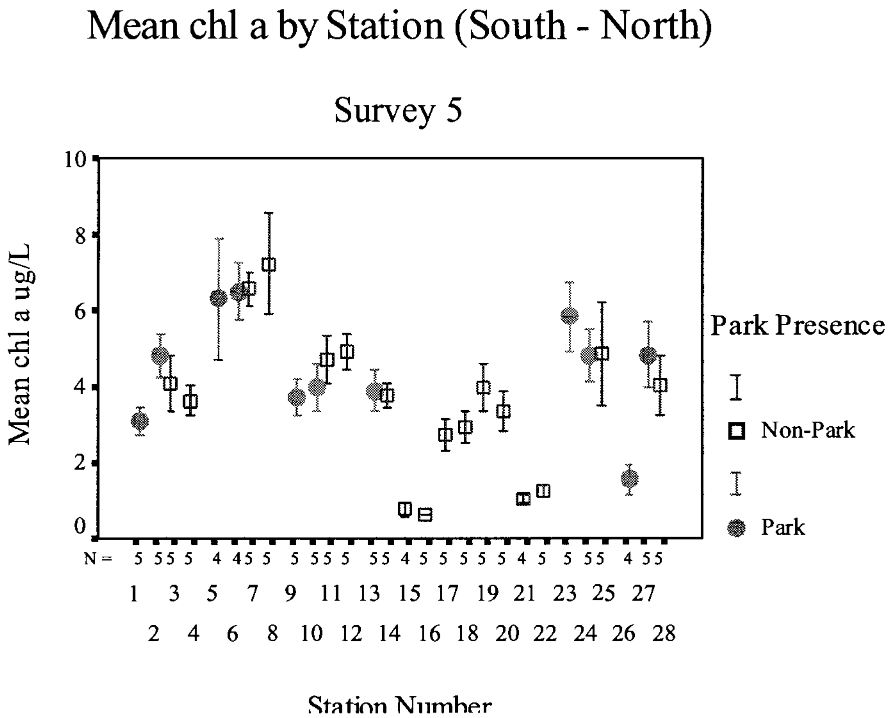
Survey 3

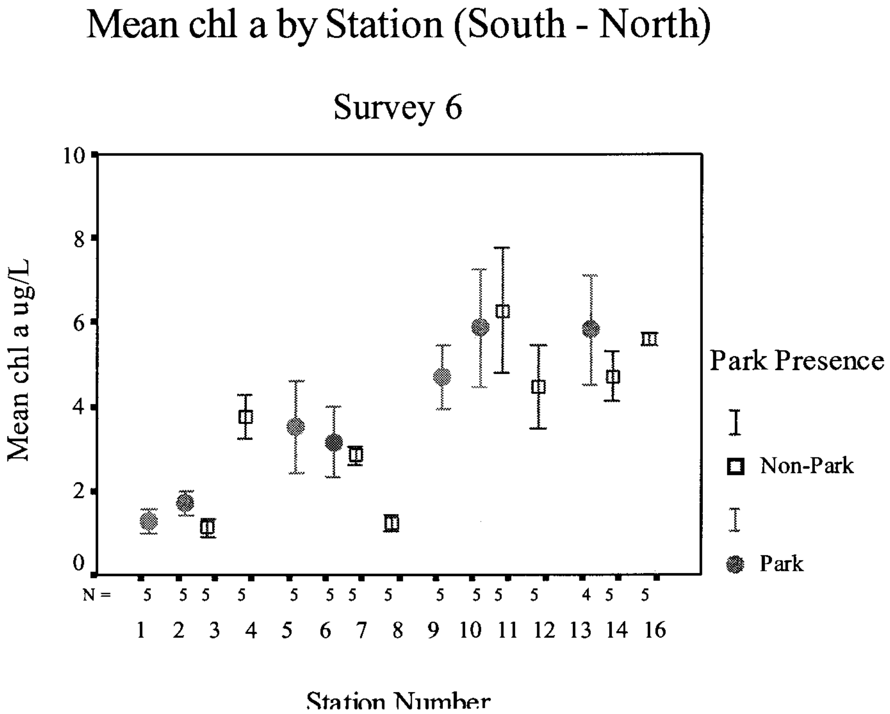


Mean chl a by Station (South - North)

Survey 4




Mean chl a by Station (South - North)
Survey 5
Mean chl a ug/L
10
8
6
4
2
0
N= 5 55 5 4 45 5 5 55 5 55 4 5 5 5 5 5 4 5 5 55 4 55
1 3 5 7 9 11 13 15 17 19 21 23 25 27
2 4 6 8 10 12 14 16 18 20 22 24 26 28
Station Number
Park Presence
Non-Park
Park


Mean chl a by Station (South - North)
Survey 6
Mean chl a ug/L
10
8
6
4
2
0
N= 5 5 5 5 5 5 5 5 5 5 5 5 4 5 5
1 2 3 4 5 6 7 8 9 10 11 12 13 14 16
Station Number
Park Presence
Non-Park
Park

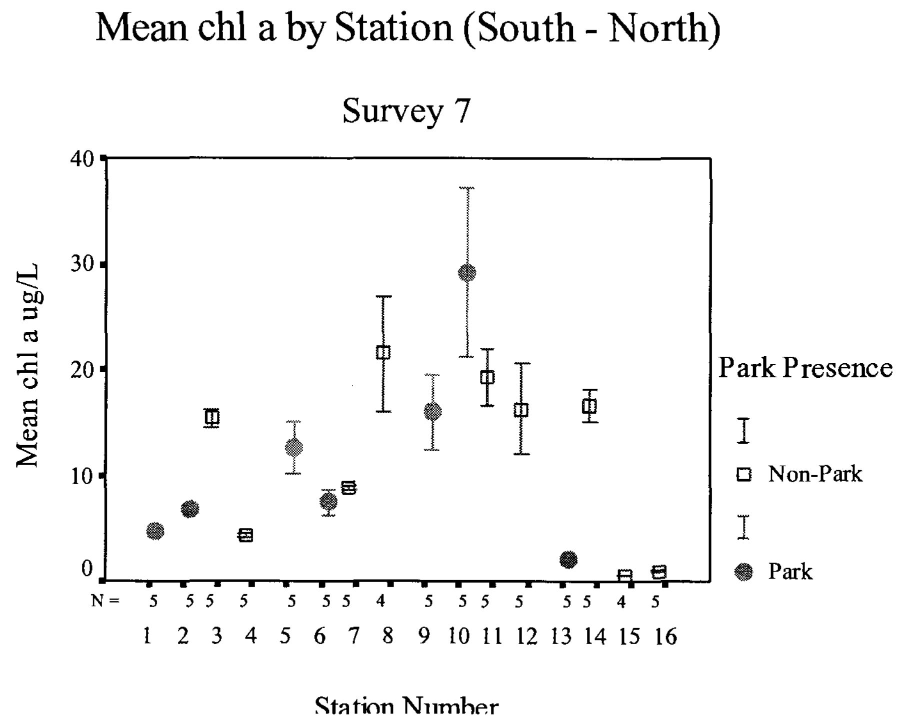


Fig. 2.8. Mean chl *a* levels and standard deviations by station (south – north) for surveys one through seven. Bars represent standard ±1 error.

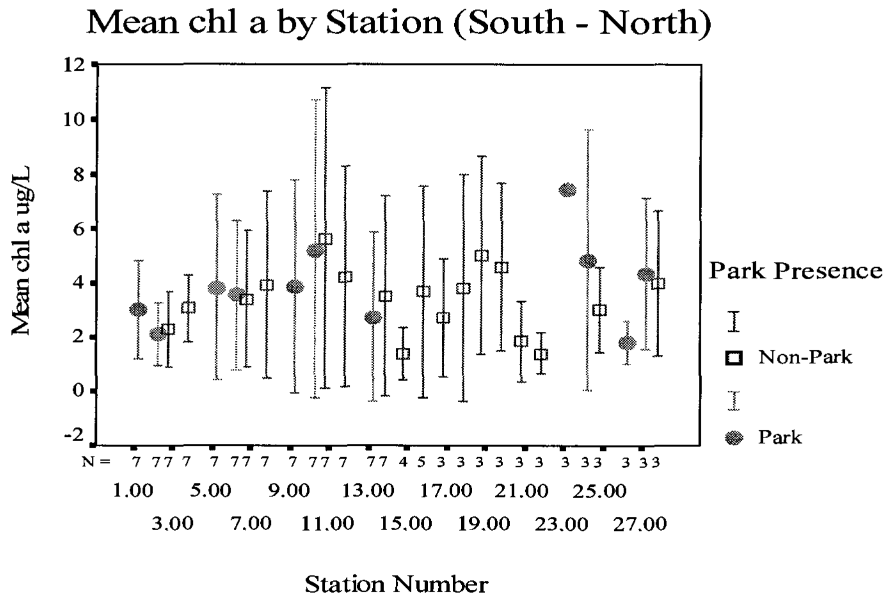


Fig. 2.9. Pooled mean chl *a* levels by station (south – north) for all surveys. Bars represent ±1 standard error.

3) Is there temporal variation in mean chl *a* values across the study area?

For aggregated surveys a one-way ANOVA indicated significant temporal variation (reported by survey number) (n = 7, f = 33.171, df = 6, p = .000). Associated post-hoc tests (Scheffe) indicate that surveys 1, 2 & 4 and 5 & 6 were all similar in mean chl *a* levels, survey three was significantly different from all others except survey seven (Fig. 2.10). To meet the assumption of normality, a logarithmic transformation was carried out on the data.

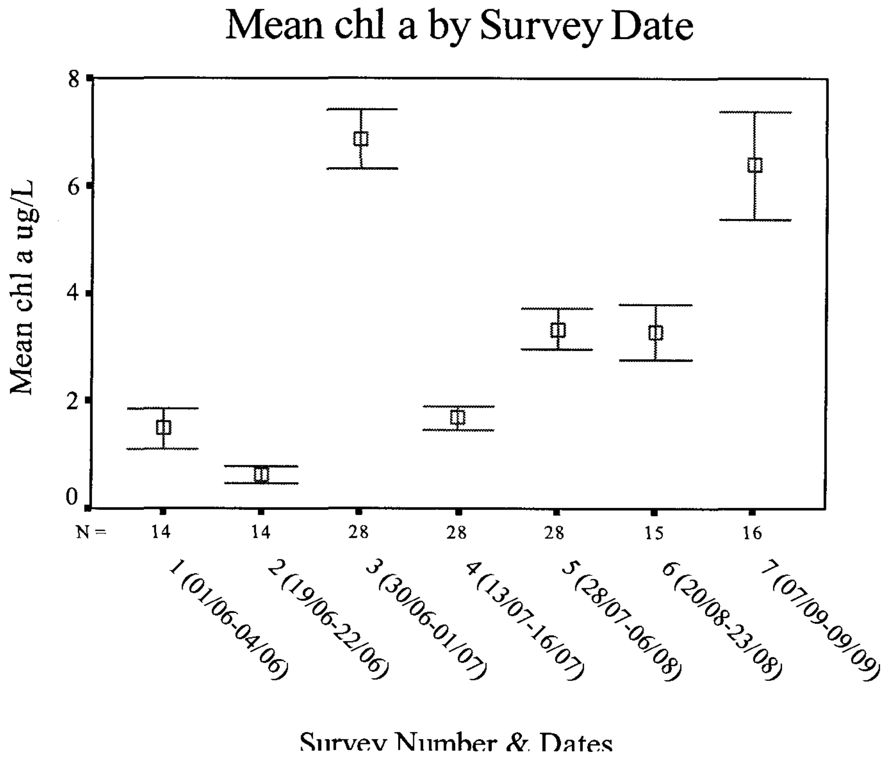


Fig. 2.10. Mean chl *a* levels across time (reported by survey number). Bars represent ±1 standard error.

DISCUSSION

Quantifying connectivity between MPAs based on chl *a* levels alone illustrates several problems inherent in marine reserve design. The fluid nature of marine ecosystems makes it difficult to assign boundaries with any ecological veracity. Unlike terrestrial systems, marine areas are in a constant state of change and variability is the norm (Carr *et al.*2003). Phytoplankton production in marine ecosystems is likely the most important biological factor in dictating the overall biomass and presence of many fish, invertebrate and marine mammal/bird species. Furthermore, the scale at which oceanographers traditionally measured primary production at far exceeds that of this study (1000s of km vs. 100s of km). Recent evidence suggests that primary production may not be as ubiquitous as previously thought (Mackas *et al.*1980, Menge & Daley 1997, Wieter *et al.*2003). Designing a network of marine reserves (to meet a specific goal) in areas of similar elevated production levels would therefore be optimal. Results from this study show that the six MPAs on the west coast of Vancouver Island had no significant spatial variation in chl *a* levels ($p = .679$) when compared to regions outside of park boundaries. Furthermore, even though there was a bias towards the southern boundary region, no significant differences occurred due to survey type ($p = .099$). This speaks to the issue of boundary delineation of MPAs in terms of ecological processes. Can we delineate marine reserve boundaries in terms of overall chl *a* levels?

In nearshore environments the influx of terrestrial derived nutrients (e.g. phosphorous and nitrogen) is substantially higher than offshore regions, and a mixed water column is more prevalent in nearshore waters (Nybakken 2001). These facts, coupled with coastal upwelling, leads to a more homogeneous distribution of chl *a* nearshore when compared to a patchy chl *a* distribution in the offshore regions. Boundary delineation on the basis of chl *a* distribution alone would not be plausible since coastal chl *a* distribution in this study area is fairly homogeneous over extended temporal scales. However, in some instances chl *a* has been shown to vary on fine spatial scales (e.g., Menge & Daley 1997, Wieter *et al.*2003) and in this study area short term (within one sampling period) fine scale (10s of km) variation, when aggregated over the entire season, was non-significant.

The existing set of marine reserves on the central portion of the west coast of Vancouver Island may be resilient to short term chl *a* variation only because they are spatially arranged over a large area. Within one sampling period (<= 8 days) there appears to be variation among different park areas based on graphical examination. However, this variation does not seem to persist in one single park area over longer temporal scales. When viewed at short temporal scales, chl *a* levels in park areas are spatially disjunct. This indicates that depending on the temporal scale at which chl *a* is examined, variability is either present or masked through time. This suggests connectivity at varying temporal scales, within a short time frame. Overall, when chl *a* values are aggregated over the entire summer season it appears ubiquitous and hence connected. One of the benefits of having several smaller reserves spread over larger spatial scales is their ability to incorporate oceanographic variability within protective boundaries. What remains to be determined is whether or not the persistence of this variability is more important than short term peaks in productivity when viewed further up in the food chain.

Menge & Daley (1997) demonstrated that mesoscale variation in chl *a* levels may have resulted in different benthic community structures at two different locations.

Although the sampling regime differed from that of this study (only two months of sampling) it does demonstrate the community effects of increased primary production at a mesoscale. The degree of the variation is likely an important factor; its effects at other trophic levels however, are beyond the scope of this study. Several years of chl *a* data would therefore be needed to ascertain any meaningful ecological consequences due to variation in primary production as it pertains to community structure.

An array of MPAs is essential for incorporating large scale ecological processes into conservation agendas. The timing and frequency of phytoplankton blooms, as well as their spatial patterning likely has great influence on zooplankton biomass and species distributions (Fiedler *et al.*1998, Croll *et al.*1998, Fauchald *et al.*2000, Benson *et al.*2002). Results from this study indicate that the six MPAs that were designed and placed off the west coast of Vancouver Island are spatially disjunct in regards to chl *a* distribution on short temporal scales (days to weeks). At longer temporal scales (weeks to months) however, oceanographic variability becomes evened out and appears ubiquitous and is statistically significant. The spatial arrangement of marine reserves is an important factor when quantifying degrees of connectivity. In the case of this set of marine reserves, depending at what temporal scale chl *a* distribution is viewed at, they may or may not be connected through an ecological process such as upwelling or chl *a* distribution. Boundary delineation in coastal marine reserves would be more efficient if based on the ecological requirements of the species in question rather than chl *a* distribution. Results from this study indicate no significant difference in chl *a* levels inside or outside the current set of reserves which is likely due to the proximity to the coastline and the extent as to which the Vancouver Island shelf extends offshore.

The purpose of this research was to determine whether or not the existing set of marine reserves is connected in terms of overall chl *a* distribution. Since primary production is a key component to the presence of all higher trophic levels it would be wise to place MPAs in productive regions of the coast. Also, given the objectives of this set of marine reserves, primary production is an important indirect variable to baleen whale foraging grounds and is a direct food source for their primary prey item at specific ontogenic stages (Viherluoto *et al.*2000, Viherluoto & Viitasalo 2001). The placement of reserves would not solely be dependent on phytoplankton production, but rather a suite of trophic interactions that are connected both spatially and ecologically.

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CHAPTER 3

MYSID POPULATION STRUCTURING AND DISPERSAL RELATIVE TO AN EXISTING SET OF MARINE RESERVES

INTRODUCTION

A major field of interest in marine ecology is the dispersal of marine organisms. Accurately measuring dispersal is difficult and many discrepancies have emerged concerning the process by which marine organisms are transported (Cowen *et al.*2000 Bradbury & Snelgrove 2001). Until recently, most marine larvae have been viewed as passive particles subject to physical oceanographic processes which ultimately influence their dispersal potential (Roberts 1997, Ogden 1997, Cowen *et al.*2000). However, recent evidence is suggesting that marine larvae can be locally retained even though they may have long planktonic larval durations (Jones *et al.*1999, Swearer *et al.*1999, Su Sponagle *et al.*2002, Palumbi 2003). The role of behaviour and the life history characteristics of specific taxonomic groups, coupled with physical oceanographic processes, is more likely a better predictor of larval dispersal. This is important because traditional larval dispersal models (ones that do not include behaviour and life history) may be overestimating transport distances for commercially important species which may have far reaching ecological consequences (Cowen *et al.*1997, Warner *et al.*2000, Lockwood *et al.*2002, Largier 2003).

This disparity has lead to a reevaluation of the concept of ‘open’ marine populations being the norm and now considerable attention is being paid to the idea of localized retention in marine populations (Su Sponagule *et al.*2002). The value in knowing degrees of connectivity in species populations reflects our ability to predict recruitment potential for specific geographic locations or the extent to which propagules are exported. This knowledge is therefore fundamental to the design and placement of marine reserves given a set of conservation objectives. There exist several techniques to quantify larval/invertebrate dispersal in the marine environment (e.g., artificial markers, natural markers, geochemical signatures, isotopes), although molecular markers provide an effective indirect means to estimate gene flow in natural populations and has proven useful in many situations (see Barber *et al.*2002, Mathews *et al.*2002, Jarman *et al.*2002, Palumbi 2003).

Genetic Techniques and Their Insights on Dispersal

The genetic variation across a species' range provides an indirect means of tracking marine larvae and other propagules. Genetic markers that are not subject to selection and mutation have been used successfully to infer connectivity in marine populations (Hellberg *et al.*2002). Widespread dispersal can be detected through homogeneity in gene frequencies (Flowers *et al.*2002) as well as evidence supporting sharp genetic breaks which may indicate suppressed larval exchange (Barber *et al.*2002). However, because it only takes a small number of migrants infiltrating a neighboring population to induce genetic similarities, specific source locations cannot be elucidated through genetic analysis (Palumbi 2003). Perhaps the most alluring attribute of this technique is that it allows for empirical evidence to be presented without inferring too much about process oriented drivers in dispersal. For example, sharp genetic breaks were discovered in populations of mantis shrimp (*Haptosquilla pulchella*) in the Indo-West Pacific Ocean even though the physical oceanographic conditions (prevailing currents) suggested widespread dispersal. Genetic similarities between populations in close proximity to each other revealed limited dispersal and more retentive characteristics

(Barber *et al.*2002). Why this occurs remains elusive, but it most likely is a result of larval behaviour which is not yet understood for this species (Barber *et al.*2002). Similarly, a study on pelagic Caribbean reef fish yielded evidence of localized retention even though the species were wide-spread and occupied similar habitats (Taylor & Hellberg 2003). Genetic variation seems to be a powerful tool to estimate the degree to which populations are open or closed, however it is not without its own set of limitations (Slatkin 1987, Palumbi 2003).

The utility of genetic techniques depends on the question being asked. If populations exhibit homogeneity in gene frequencies, the only thing that can be gained is that gene flow exists to some extent (Slatkin 1987). The problem rests on a temporal scale. Gene flow is detectable on evolutionary time scales, therefore the information gleaned through genetic analysis may not be useful on ecologically relevant time scales which management decisions are made (Palumbi 2003). Unlike other direct methods of measuring dispersal, genetic evidence cannot pinpoint source locations or sink areas for marine populations. Homogeneity in gene frequencies can only infer some degree of dispersal through genetic exchange. Albeit useful, sharp genetic breaks provide more valuable information since a lack of genetic exchange between populations may indicate a lack of dispersal from either distant or nearby populations (Palumbi 2003). Genetic techniques to measure dispersal are also useful to quantify connectivity between marine reserves (Barber *et al.*2002, Thorrold *et al.*2002, Palumbi 2003). In the context of this experiment, gray whales (*Eschrichtius robustus*) feed directly on mysids (Order *Mysidacea*) in part of their foraging range, so the design of marine protected areas

(MPAs) for this species would benefit greatly from information pertaining to the dispersal capacity of their prey.

Quantifying larval dispersal or retention in the marine environment is difficult and the techniques involved are often expensive and time consuming (Thorrold *et al.*2002). At best, novel approaches are gaining insight as to where larvae are coming from (source areas) and where larvae are ending up (sink areas), but no single technique is without limitation (Thorrold *et al.*2002, Largier 2003, Palumbi 2003). For the purpose of this chapter, genetic techniques are used to ascertain the dispersal potential of one species of mysid (*Holmesimysis sculpta*) off central Vancouver Island. *H. sculpta* is the dominant mysid species in this area (Patterson, 2004) and is a targeted prey species for eastern Pacific gray whales that forage in this region (*Eschrichtius robustus*) (Dunham & Duffus 2000, 2001).

Mysids are a small shrimp-like crustaceans often referred to as 'opossum shrimp' because gravid females carry their young in marsupia below the thoracic region (Mauchline 1980, Kozloff 2000). They are generally found above the benthos (<1m), mainly around rocky reefs in amongst kelp and eel grass beds, and are characterized as hyperbenthic swarmers (Mauchline 1980, Ohtsuka 1984, Kim and Oliver 1989, Kaartvedt 1989, Stearns & Dardeau 1990, Twinning *et al.*2000). Information pertaining to their dispersal is limited and mysids do not have a pelagic larval stage; rather, they give birth to live young resembling adult mysids (Kozloff 1990). Twinning *et al.*(2000) demonstrated that *Mysidium gracile* exhibit a high degree of retention always returning to the same swarm in the exact location after nightly vertical migrations into the water column to feed. Similarly, Kaartvedt (1989) found that the horizontal dispersal of mysid species (*Boreomysis megalops, Lophogaster typicus, Leptomysis gracilis* and *Schistomysis ornate*) was severely limited by their behaviour even in migrations occurring from depths of over 100 m to the surface in Norwegian fjords. This may indicate that a relatively high degree of retention occurs within mysid populations rather than wide spread dispersal as is the norm for many other invertebrate species (Roberts 1997, Cowen *et al.*2000). Off the central coast of Vancouver Island, gray whales feed extensively on dense swams of mysids and their distribution reflects that of their targeted prey (Dunham & Duffus 2001, 2002). Therefore, when designing a set of marine reserves for foraging gray whales it would be important to understand the dispersal potential of the prey species. The premise for this portion of the thesis is to illustrate connectivity (or not) at the middle portion of a gray whale's food chain. By examining gene flow between two geographically distant (~80km) populations of mysids within an existing framework of MPAs I will demonstrate connectivity, or lack thereof, at this trophic level.

METHODS

Study Area

I sampled off the west coast of Vancouver Island during May to September of 2004. The study area ranged from the southeastern corner of Vargas Island to the northwestern tip of Catala Island spanning approximately 130 km. Sampling occurred in both park and non/park areas (Fig. 3.1). Out sites or 'non-park' areas were chosen based on previous photo-identification evidence suggesting that whales utilize areas such as Perez Rocks, Barcester Bay, Escalante Rocks and Bajo Reefs for foraging. Furthermore, through examination of reef structure, water depth and substrate, the non/park areas are similar to gray whale foraging areas in the southern portion of the study area (Duffus

1996, Dunham & Duffus 2001, 2002). Northern areas are defined as being north of Estevan Point and encompass Nootka Sound and southern areas are defined as all areas to the south of Estevan Point and encompass Clayoquot Sound (Fig. 3.1). A total of 14 sampling sites were established (Table 3.1).

Sample Design

Fourteen randomly placed nearshore stations were selected in both park/non-park areas and in the intervening areas between adjacent park boundaries. Upon selection of the nearshore stations, two additional stations were placed perpendicular from the shoreline, moving offshore form the nearshore station in each sampling area. All stations were equal distances apart with the third station in each park being outside the designated boundary. Only two stations were placed in the non-park areas, one close to shore (approx. 20m) and one 500m offshore from the nearshore station perpendicular from the shoreline. In the areas between park boundaries only one station was randomly selected. Sampling coordinates were acquired using the Canadian Hydrographic Service Field Sheets No. 3603, 3673, 3674, 3675 and 3676 (2003). A total of 28 sampling stations were selected and marked using a Magellen *Colortrack* GPS to ensure repetitive sampling at the same locations (Figs. 3.2, 3.3, 3.4). In addition to the randomly placed stations, opportunistic mysid sampling was conducted near foraging whales to ensure mysid capture. This occurred in both park and non-park areas.

Data Collection

A seven meter aluminum vessel was used to gain access to the sampling stations. I conducted plankton tows with a 2 x 20 cm diameter bongo-style plankton net, 80 cm long, with a 500 μm mesh size. To be most efficient at capturing mysids, I would drop the net until it hit the seafloor and drag it along the bottom bouncing it as it was towed along. At each station two tows would be conducted within a 100m radius of the station centre point. Opportunistic sampling also occurred in the vicinity of foraging whales within the designated park boundaries and in the non-park sites. Once a foraging whale was located we would slowly approach it and deploy the plankton net in the exact location of the foraging whale. Foraging whales were determined through observations on the animal's behaviour. For example, multiple dives in a single location with no apparent linear movement would have been characterized as foraging. Once mysids were captured they would be sieved and stored in 70 - 95% ethanol. Three full surveys (Vargas Island to Catala Island) and four partial surveys were completed (Vargas Island to Perez Rocks or Estevan Point) (Table 3.2). A total of 282 plankton tows were conducted yielding 52 samples from all sites except Nuchatlitz Marine Park where no mysids were captured.

DNA Extraction, Primer Design and Sequencing.

For genetic analysis, 17 mature mysids (*H. sculpta*) were selected from two sampling locations that were the greatest distance apart (~80km) (Table 3.3, Fig. 3.5). Mature adult mysids were identified to species using Kathmann *et al.*(1989). Tissue from each individual mysid (0.5cm^2) was used for DNA extraction. We used a universal mitochondrial cytochrome *b* primer; 151F (458) 5`-TGT GGR GCN ACY GTW ATY AC T AA-3` and 270R (820) 5`- AAN AGG AAR TAY CAY TCN GGY TG-3` (see Merrit *et al.*1998) for molluscan taxa to amplify *H. sculpta* DNA and subsequently design a specific mt cyt *b* primer for *H. sculpta*. DNA extractions were performed with a 5% Chelex® (BioRad), 0.2% SDS, 0.1 mg/ml Proteinase K solution for 30min at 55°C, followed by 10min at 95°C (Nelson *et al.* 1998). A fragment of approximately 350 base pairs (bp) of the mt cyt *b* locus was amplified via the polymerase chain reaction using primers 151F and 270R (Merrit *et al.*1998). Each 50µl reaction consisted of 5µl reaction buffer solution (Tris-Cl, KCI, $\{NH_4\}_2$ SO_4, 1.5mM $MgCl_2$, pH 8.7) using 24 pmol of forward and reverse primer resulting in 80 µM of each nucleotide/1.25µ *Taq* (Qiagen). PCRs were carried out in a PTC 100 Thermal Cycler (MJ Research) and began with an initial denaturation of 15 min at 95°C, a step-down PCR at 4 cycles starting at 94°C/30 sec; 49°C/90 sec; 53°C/90 sec; 72°C/90 sec and 40 cycles starting with 94°C/30 sec; 49°C/90 sec; 72°C/2 min and finishing with a final extension of 5 min at 72°C.

For cloning purposes, PCR reactions (50µl) were loaded on 7% 19:1 acrylamide:bis-acrylamide gel and ran at 100V for 20 hrs in 2x TAE buffer (stained). PCR product was extracted from the gel in 0.5M ammonium acetate, 10mM magnesium acetate tetrahydrate, 1mM EDTA, pH 8.0, and dissolved in TE pH 8.0 to a final volume of 10µl. PCR extractions were loaded into a pCR2.1 vector (Invitrogen) and transformed into TOP10 electrocompetent cells (Invitrogen). Single clones were selected and grown in LB+AMP+X-Gal+1PTG plates. Plasmid preparations of selected colonies were isolated and grown on LB media with 100µg/ml ampicillin using QIAprep Spin Miniprep Kit (Qiagen). Two different clones were sequenced with forward primer (M13) using a ABI™ 3700 DNA Analyzer with BigDye© ver. 3.0. terminator chemistry. BLAST™ was used to identify which clone was mt cyt *b*, and Primer3™ was used to design 4 forward and 4 reverse primers which were all aligned using CLUSTALW™. To optimize PCR product, 16 primer combinations were tested using the above methods. Once the selected primer set was identified, we used QIAquick 96 PCR Purification Kit (Qiagen) to purify the PCR product.

Samples were sequenced using forward primer (3F) 5` GAT ATG AGG GGG AGT AAC TAA AGG 3` and reverse primer (3R) 5` AGA TAT TGT CCA ATG AAT TTG AGG 3` in one direction using a ABI™ 3700 DNA Analyzer with **BigDye©** ver. 3.0. terminator chemistry. Sequences were read in SeqMann™ resulting in 175 bp fragments. ARLEQUIN software was used to estimate population structuring and dispersal.

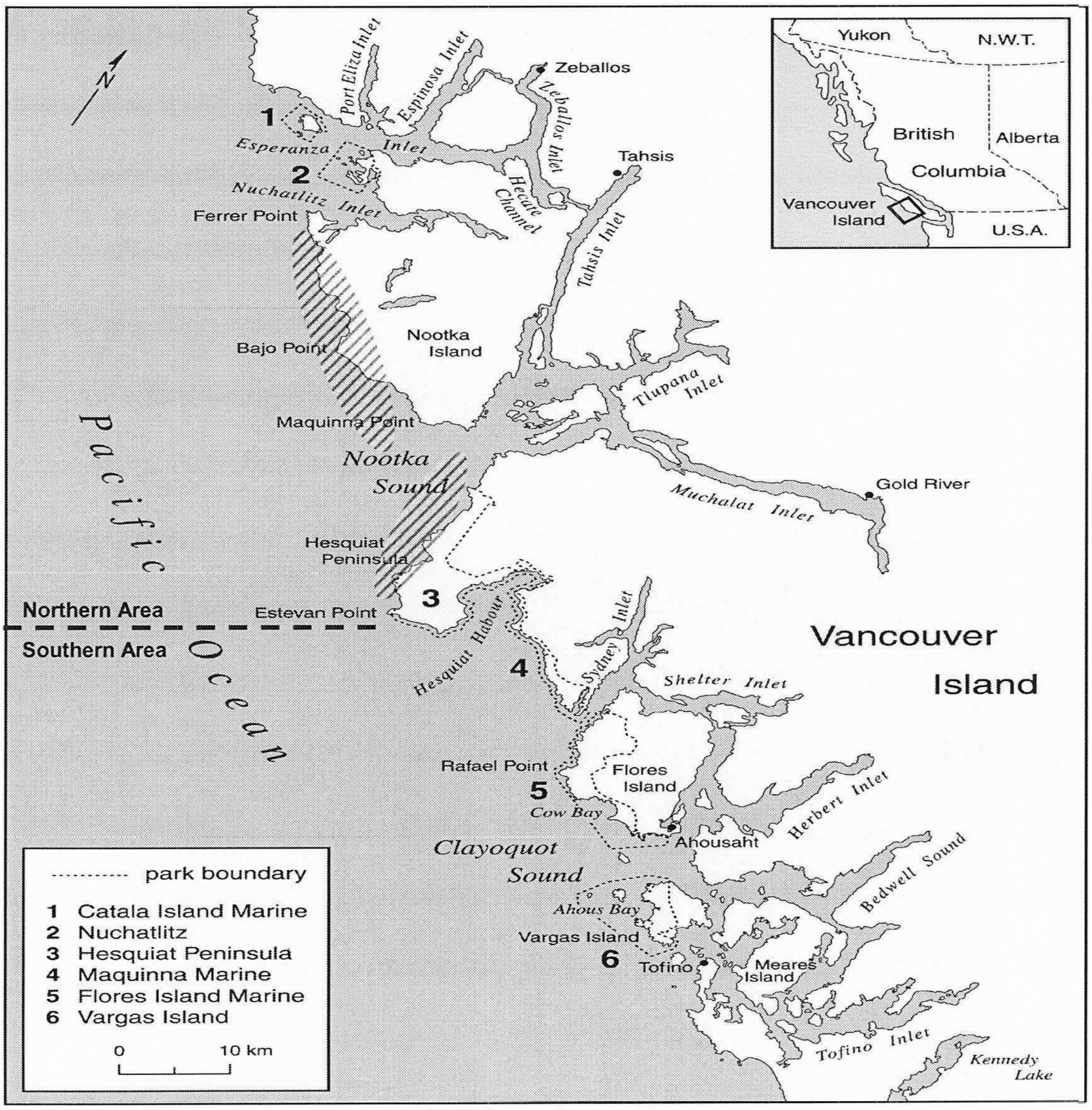

Fig. 3.1. Map of study area highlighting park and non-park areas and the boundary delineating the north and south portions of the study area. Non-park areas are shown with shaded areas.

Table 3.1. List of all sampling sites, both park and non-park and sampling region.

Site	*Location*	*Designation*	*Boundary Region*
1	Vargas Island	Marine Park	South
2	Vargas – Flores	Non-Park	South
3	Flores Island	Marine Park	South
4	Flores – Maquinna	Non-Park	South
5	Maquinna	Marine Park	South
6	Maquinna – Hesquiat	Non- Park	South
7	Hesquiat	Marine Park	South
8	Perez Rocks	Non-Park	North
9	Barcester Bay	Non-Park	North
10	Escalante Rocks	Non-Park	North
11	Bajo Reefs	Non-Park	North
12	Nuchatlitz	Marine Park	North
13	Nuchatlitz – Catala	Non-Park	North
14	Catala Island	Marine Park	North

Table 3.2. Timeline of dates and locations of both full and partial surveys.

Survey Number	*Date*	*Location*	*Survey Type*
1	01 June to 04 June	Vargas to Hesquiat	Partial
2	19 June to 22 June	Vargas to Hesquiat	Partial
3	30 June to 01 July	Vargas to Catala	Full
4	13 July to 16 July	Vargas to Catala	Full
5	28 July to 06 Aug	Vargas to Catala	Full
6	20 Aug to 23Aug	Vargas to Perez	Partial
7	07 Sept to 09 Sept	Vargas to Perez	Partial

Table 3.3 Dates and locations of mysid samples for genetic analysis.

Date	*Location*	*Latitude*	*Longitude*	*Park*	*N*
22 June 04	Vargas Island	49°11.158N	126°01.817W	Marine Park	9
16 July 04	Bajo Reefs	49°36.805N	126°49.784W	Non-park	8

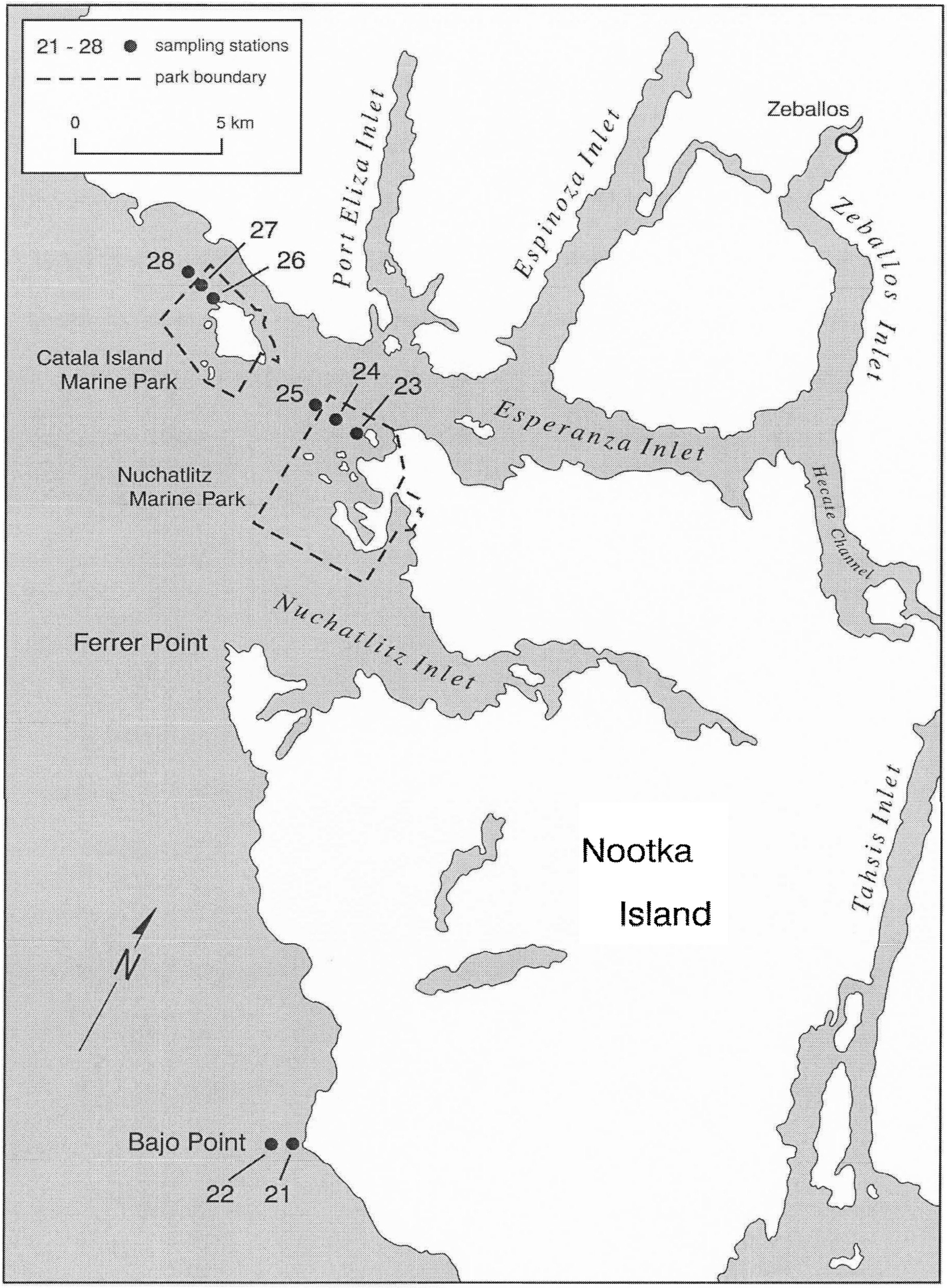

Fig. 3.2. Sampling locations for plankton tows in the northern portion of the study area.

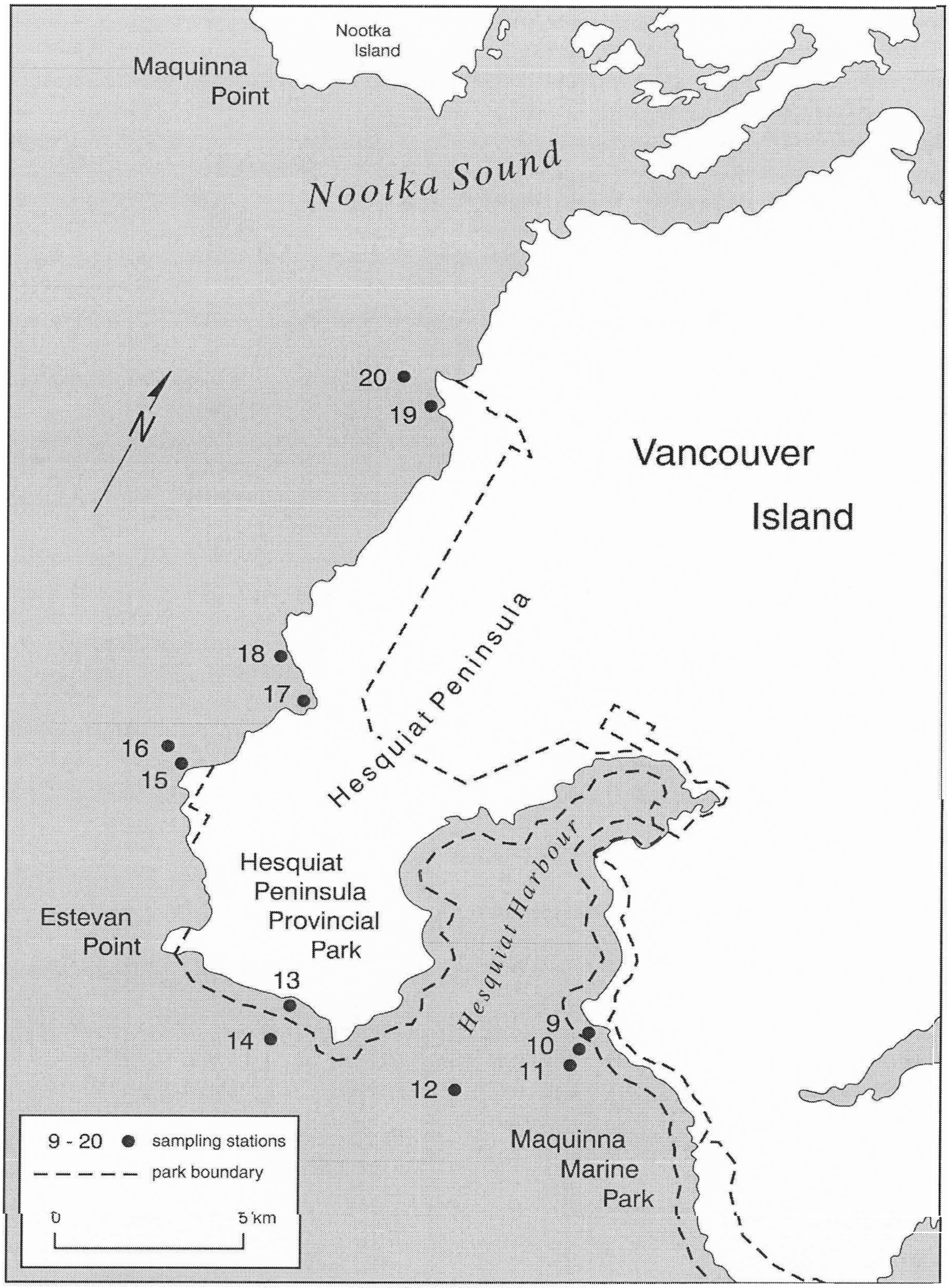

Fig. 3.3. Sampling locations for plankton tows in the middle portion of the study area.

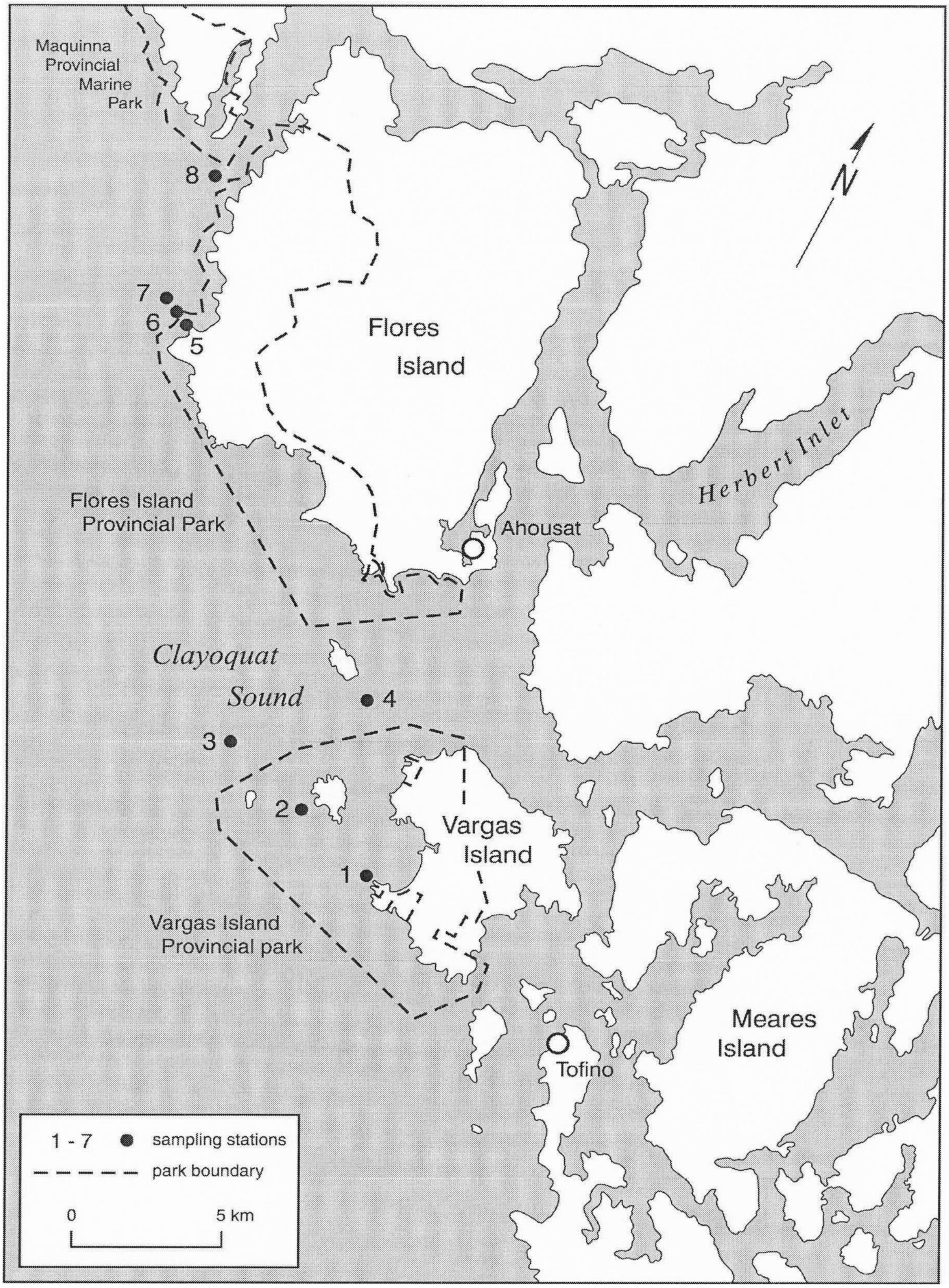

Fig. 3.4. Sampling locations for plankton tows in the southern portion of the study area.

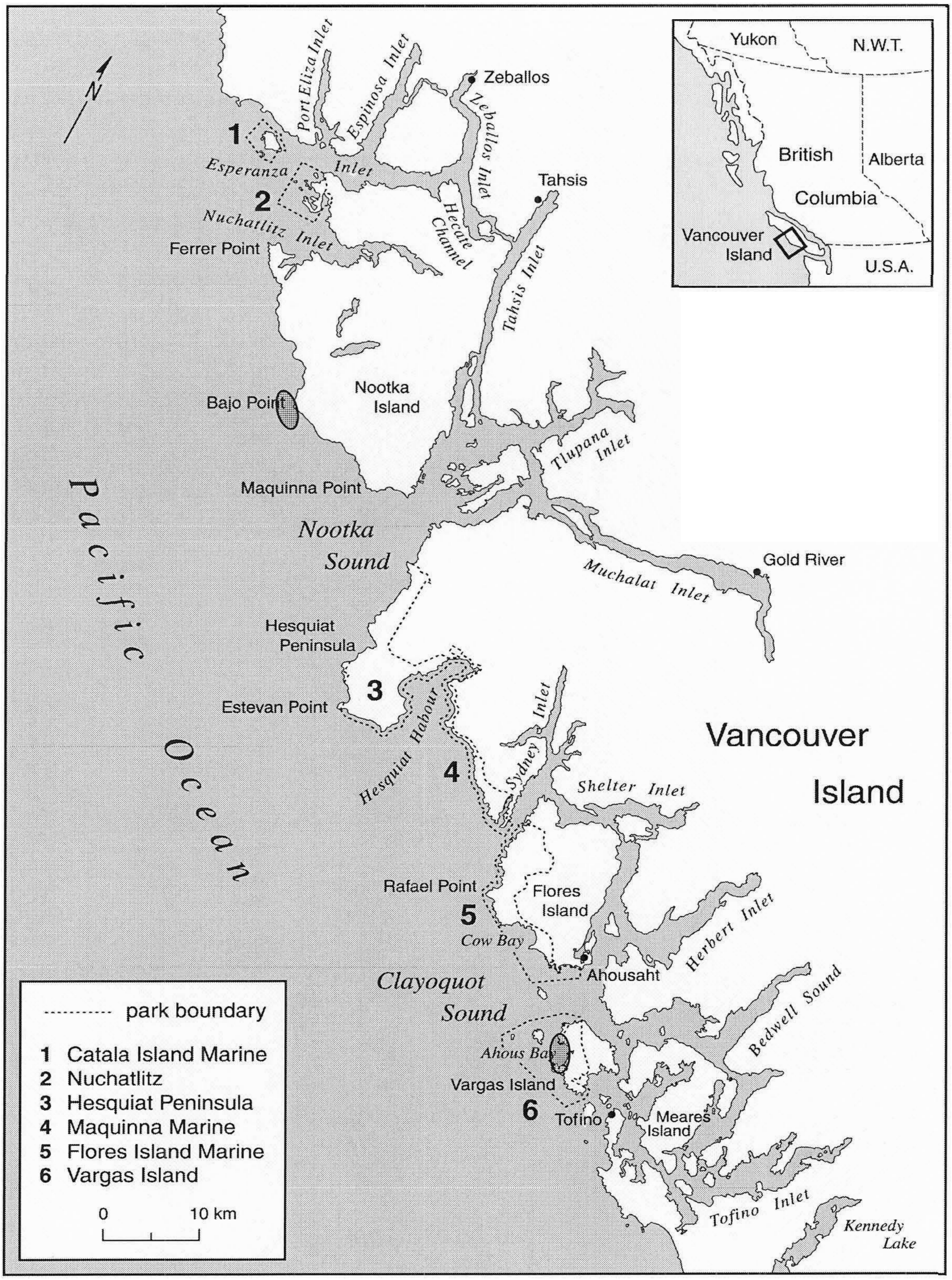

Fig. 3.5. Study area with circles indicating approximate locations of mysid samples used for genetic comparisons.

RESULTS

Technical problems with the sequencing machine and the contamination of some of the samples resulted in uneven and small sample sizes for both Vargas Island and Bajo Reefs. However, successful sequences were analyzed from both Vargas Island (n = 9) and Bajo Reefs (n = 8) and were compared to illustrate potential genetic structuring. Through comparing each population (region) two distinct haplotypes were apparent (Table 3.4, Fig. 3.6). There was one variable site at 163 bp that differed between populations. The population pairwise differentiation test was non-significant (p = .292 @ 30000 Morkov steps). However, estimates of gene flow (F_{ST} = .114, p = .079) suggest limited dispersal. Migration rates, the effective population size and rate of migration (N_em), of 3.87 migrants per generation between Vargas and Bajo Reefs are estimated. Sequences from the mt cyt *b* fragment were entered into gene bank and close matches were made with two other species of mysid; *Neomysis americana* and *Neomysis integer*. Species found in the Atlantic and Baltic regions respectively.

Table 3.4. Relative Haplotype Frequencies for Vargas and Bajo Reefs.

Haplotype	*Bajo Reefs*	*Vargas Island*
1	.556	.875
2	.444	.125

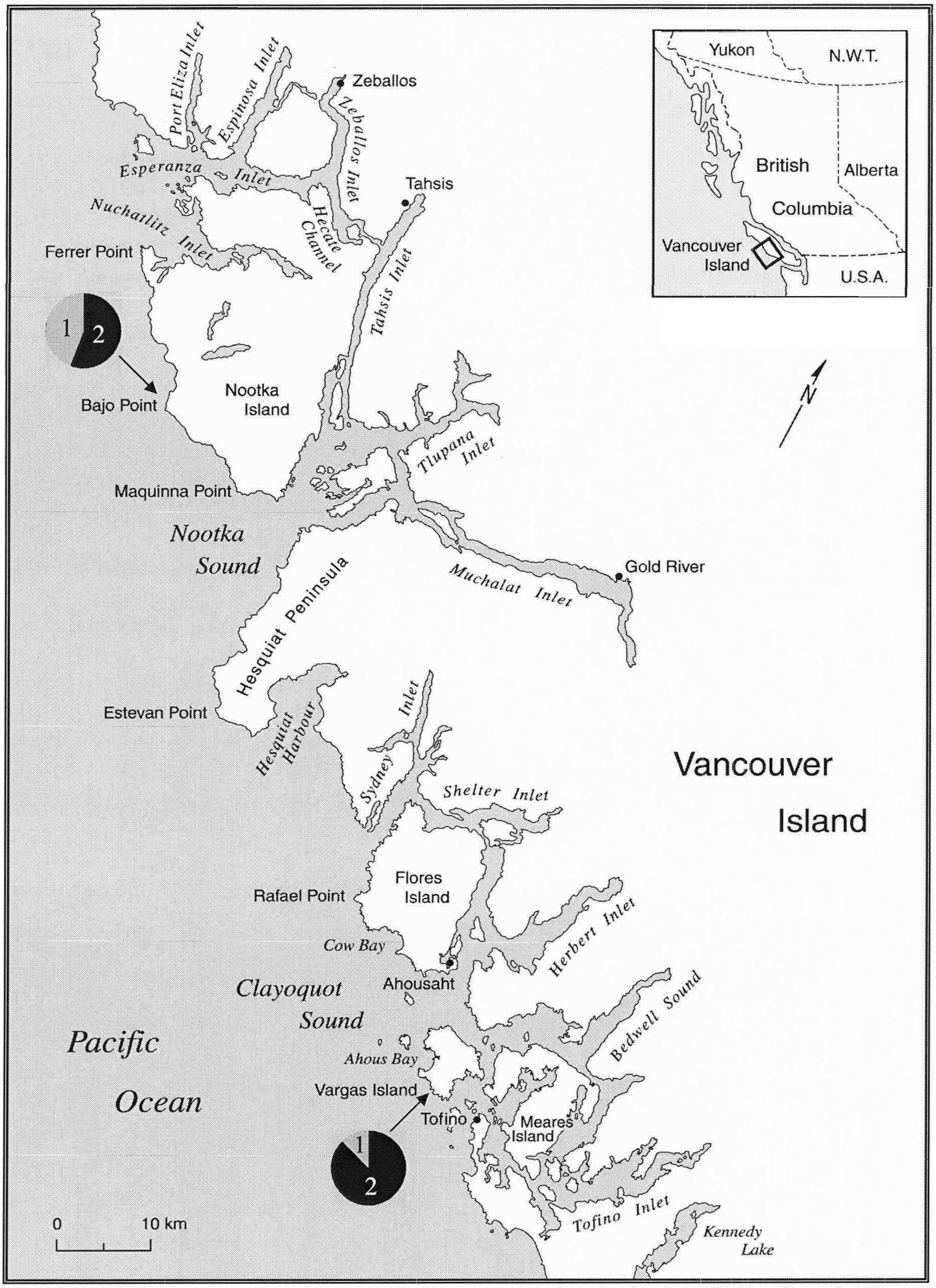

Fig. 3.6. Pie diagrams illustrating haplotype frequencies for both Bajo Reefs and Vargas Island. Light grey represents haplotype 1 and black represents haplotype 2.

DISCUSSION

Results from this study reveal the first attempt to describe the dispersal potential and population structure of *H. scupta* off the west coast of Vancouver Island. Although preliminary, the genetic differentiation found in *H. sculpta* at one single loci can be used to suggest limited gene flow and suppressed population exchange at geographic scales less than 100 km. Limited gene flow in marine environments at this scale are rare and were first described by Avise (1992) in studies with horseshoe crabs along the SE coast of the United States. Sharp genetic breaks in species have also been found in the Indonesian Archipelago with mantis shrimp (Barber *et al.*2002), black tiger prawns and starfish in the western Pacific (Williams & Benzie 1998, Duda & Palumbi 1999) and in other fish species (Avise 1992). The role of dispersal in marine organisms is important when determining levels of recruitment from adjacent populations (Swearer *et al.*1999, Jones *et al.*1999) and when designing marine reserves that are set up to maintain localized populations (Barber *et al.*2002). *H. scuplta*, being a primary prey item for gray whales (Dunham & Duffus 2001, 2002) in this part of their foraging range, is a critical component the whale's food web and therefore an important link to understanding connectivity throughout their trophic spectrum.

Evidence as to why *H. scupta* may have limited dispersal and exhibit genetic differentiation at small spatial scales is likely due to their life history characteristics and habitat preferences. As noted earlier, mysids do not have a pelagic larval stage; instead young are born resembling adult mysids and exhibit similar behavioural characteristics (Mauchline 1980, Kozloff 2000). Pelagic larval durations (PLDs) may have a profound effect on the dispersal capacity in many marine organisms since directional movement is highly variable depending on the specific life stage of the organism in question (Bradbury & Snelgrove 2001, Su Sponaugle *et al.*2002). This can also be verified through genetic analyses that focus on gene flow (Palumbi 1996, 2003). Even thought there is evidence of suppressed larval exchange in some species with long PLDs, it is not the norm (Barber *et al.*2002, Taylor & Hellberg 2003, Palumbi 2003). As mysids are characterized as being hyperbenthic (within 1m of the benthos) (Mauchline 1980, Kozloff 2000) and are found in nearshore environments which are highly dynamic, other explanations to account for limited dispersal can be made through the examination of nearshore oceanography and behaviour.

Other species of mysids have exhibited vertical migrations in fjords (Kaartvedt 1989) and in tropical systems (Twinning *et al.*2000) and in both of these examples there was evidence of limited horizontal dispersal. In most cases, the benthic boundary layer is less subject to strong horizontal velocities than the rest of the water column and as particles move up the water column they may be subjected to increased horizontal movement. Some of the better known studies documenting vertical migration and the effects on larval transport have been done in estuaries (Stearns & Dardeau 1990, Su Sponaugle *et al.*2002). The timing of vertical migrations with tidal fluxes, frontal circulations and wind driven surface transport can greatly influence local retention and self-recruitment (Smith *et al.*2001, Bradbury & Snelgrove 2001, Houde 2001, Su Sponaugle *et al.*2002). The potential of being dispersed passively through advection may decrease because current velocities are diminished near the benthos and may be impeded by other obstacles such as kelp, which is common in nearshore mysid habitat (Mauchline 1980, Kozloff 2000). Although it is postulated that organisms that undergo vertical migrations off the Vancouver Island shelf are advected further offshore during the late spring, summer, and autumn months (Makas 1992, Smith *et al.*2001) it is not fully understood whether or not nearshore oceanographic processes would result in similar patterns since current velocities are fairly turbulent and not unidirectional (Kopach 2004).

It is clear that there are many variables that contribute to the dispersal potential of many marine organisms and the debate over which process, physical or biological, most influences larval dispersal and retention is ongoing. Genetic investigation is an indirect method of measuring the degree to which populations are related over time and space; however it does not provide a great deal of explanation as to how organisms are dispersed (Palumbi 2003). Nonetheless, genetic differentiation in the context of this study, suggest that other mechanisms are responsible for suppressed migration rates and gene flow. However, no matter what the explanation is, the genetic results indicate the potential for heterogeneous mysid population structuring which indicate a barrier to demographic exchange. Mysids constitute the middle portion of a grays whale's food chain and the results indicate that at this level there exists a degree of disconnectedness between the current configuration of MPAs.

Connectivity, in this sense, is absent due the lack of demographic exchange between sites. However, if more sites were selected on finer spatial scales there may exist a gradient in gene frequencies, rather than sharp genetic breaks, which would allow for further investigation on the dispersal capacity of *H. sculpta*. Because one of the defining characteristics of an ecologically functional system of reserves is connectivity, it could be said that these six MPAs do not meet this condition. However, connectivity may be present at other trophic levels, for example, patterns in primary production which is a main driver in zooplankton patchiness (Folt & Burns 1999) and the spatial distribution of the predator in this scenario. Even if the biophysical correlates to dispersal or retention in *H. sculpta* are not fully understood, an understanding of some of the mechanisms taking place can still enhance our abilities to measure connectivity among marine zooplankton spatially. Understanding key behavioural traits and life history characteristics of the species in question and by linking them with physical oceanographic processes, can help investigators chose the appropriate techniques in order to measure larval dispersal and make better management decisions concerning the placement of marine reserves.

The purpose of this study was to measure the dispersal capacity of *H. sculpta* within the framework of an existing network of reserves. Since mysids are a primary prey item for gray whales in this part of their foraging range (Dunham & Duffus 2001, 2002), this component of their food chain is vital to the whales' distributional patterns and presence off the coast of Vancouver Island. If *H. sculpta* exhibit suppressed population exchange at finer spatial scales, than the placement of marine reserves in their associated habitats is crucial because of their limited capacity to recruit from nearby population sources. At this spatial scale, *H. sculpta* seem to show little gene flow based on the F_{ST} values given and therefore represent discontinuity at this trophic level.

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CHAPTER 4

GRAY WHALE FORAGING DISTRIBUTION PATTERNS, CONNECTIVITY AND THE DESIGN OF MARINE PROTECTED AREAS

INTRODUCTION

Animal movement and their utilization of different habitat types as a product of their life history has been a topic of intense interest in ecology, conservation and many other related disciplines. Understanding the linkages between these areas throughout an animal's range has also been of strong interest, but more importantly, these linkages are crucial for effective conservation initiatives that target discrete foraging areas, stopover sites and breeding sites for the species in question (Muriuki *et al.*1997, Hobson 1999, Apostolaki *et al.*2002, Webster *et al.*2002, Becker & Beissinger 2003, Hooker & Gerber 2004). In highly mobile or migratory species, like birds and marine mammals, specific areas used for foraging, resting and breeding can be highly predictable. If these areas are altered in anyway it may be detrimental to species survival (Clapham *et al.*1999, Apostolaki *et al.*2002, Baird *et al.*2002, Moore & Clarke 2002, Webster *et al.*2002). Foraging areas can also be highly variable dependent on the availability of prey and variability in oceanographic conditions. For many cetaceans, especially baleen whales, foraging regions are located in nutrient rich waters that can support the prey biomass necessary for large marine mammals and these areas may change on varying spatial and temporal scales (Piatt *et al.*1989, Piatt & Methven 1992, Fiedler *et al.*1998, Croll *et al.*1998, Hooker *et al.*1999, Fauchald *et al.*2000, Benson *et al.*2002, Mendes *et al.*2002, Ingram & Rogan 2002).

Gray whales (*Eschrichtius robustus*) feed on a variety of prey types at high latitude coastal temperate waters in the northeast Pacific (Kim & Oliver 1989, Duffus 1996, Rugh *et al.*1999). Tracking gray whale movement can provide information regarding life history traits which may be useful in initiating effective conservation initiatives. For example, in many species of migratory or highly mobile birds and mammals the linkages discovered through tracking movement patterns in a variety of species have been beneficial in identifying breeding and foraging habitats (Muriuki *et al.*1997, Hobson 1999, Webster *et al.*2002, Ingram & Rogan 2002, Becker & Beissinger 2003, Gillanders *et al.*2003, Rendall *et al.*2004). Subsequently, by setting these areas aside, free from development, resource extraction and other forms of human use it may be beneficial for species survival, fecundity and overall fitness (Muriuki *et al.*1997, Hooker & Gerber 2004). Although, the migratory and foraging behaviour of many bird species are different than that of a terrestrial or marine mammals, the same principles of tracking movement as a tool for conservation applies. Using gray whales as a focal species for conservation through the implementation of marine reserves, it may be possible to design and manage marine reserves better through documenting their foraging and movement patterns.

Focal species conservation has its own suite of limitations (see Zacharias & Roff 2001), but nonetheless, for a species that utilizes a wide variety of habitats, has foraging plasticity and a large foraging range it would behoove us to reconsider the utility of focal species studies, especially in marine systems. For example, many connectivity (or dispersal) studies done in marine systems are single species experiments (Jones et al., 1999, Cowen et al., 2000, Lockwood et al., 2002, Largier 2003). Whether it's pertaining to commercial fisheries or zooplankton studies, the sheer difficulty in measuring dispersal in marine environments almost forces the use of a single species approach. Also, by choosing a species that operates on a short food chain, like gray whales (Pauly *et al.*1998), it decreases the complexity of marine food web dynamics which are commonplace (Jackson *et al.*2002).

The advantage of using gray whales as a focal species for connectivity studies is that they are relatively (compared to many other baleen whales) well understood in terms of habitat use, foraging ecology, life history and population dynamics (Rice & Wolfman 1971, Nerini 1984, Kim & Oliver 1989, Rugh 1999). Several known breeding areas have been identified in the Gulf of California and off the Baja peninsula in Mexico (Rice & Wolfman 1971, Findley & Vidal 2002), their migratory route is well established and monitored and primary, secondary and tertiary feeding grounds have been identified (Kim & Oliver 1989, Rugh 1999, Dunham & Duffus 2001, 2002). As a consequence, many protected areas have been established at known gray whale breeding sites, however virtually no protected areas have been specifically designed for gray whales on their foraging grounds. Gray whales may prove a useful surrogate to measure connectivity in marine environments at various trophic levels and they also can be used to test the efficacy of networks of marine reserves for other coastal cetacean species.

The design and implementation of networks of marine reserves is not a new concept (Ballentine 1995, Roberts 1998). However, the utility of MPA networks is difficult to measure because measuring connectivity in marine environments is complex and many species exhibit large scale distributions (eg., sharks, marine mammals, marine birds, many marine invertebrates and pelagic fish species). The optimal design and placement of marine reserves therefore hinges upon current scientific knowledge of the driving forces in oceanic production and the distribution and dispersal capabilities of marine animals (Roberts 1998, Crowder *et al.*2000, Roberts 2000, Warner *et al.*2000, Warner & Cowen 2002, Sala *et al.*2002, Lockwood *et al.*2002). Commonplace in MPA research is the concept of source/sink population dynamics with reference to commercial fisheries (Ogden 1997, Roberts 1998, Crowder *et al.*2000). This premise supposes that if we can identify s*ource* areas then we should set aside these regions as 'no-take' reserves thus enhancing overall biomass of the desired species (Roberts 1998). A problem arises because source/sink dynamics are extremely difficult to test empirically and many socioeconomic factors (i.e., pressure by the fishing industry) take precedence over scientific investigation (Ogden 1997, Brailovskaya 1998). With the exception of designing marine reserves for the protection of commercially important fish stocks, very few have been established to protect cetacean species or known cetacean foraging grounds (Hoyt 2005).

In Clayoquot and Nootka Sound, British Columbia, gray whales' aggregate along the rocky coastline and bays to forage during boreal summers (Dunham & Duffus 2001, 2002). Gray whales are characterized as selective foragers taking advantage of several prey types whenever in abundance (Duffus 1996, Dunham and Duffus 2001, 2002). Main prey items include hyperbenthic mysids (Order *Mysidacea*), pelagic porcelain crab larvae (4 spp. of the family *Porcellanidae*), benthic ghost shrimp (*Callianassa californiensis*) and benthic amphipods (family *Ampeliscidae*) (Dunham & Duffus 2001). Dunham & Duffus (2001, 2002) determined mysids to be the preferred prey type in this area and the dominant species was *Holmesimysis scupta*. Subsequent examination of mysid swarms and species assemblages revealed similar results (Patterson 2004). Gray whale conservation has been mainly through the cessation of commercial hunting, legislative protection and the establishment of marine reserves on their breeding grounds (Rice & Wolfman 1971, Findley & Vidal 2002). However, virtually no marine reserves have been established for gray whale foraging grounds. In Canada, the province of British Columbia designed and established six MPAs that encompass much of the foraging area utilized by gray whales in these regions. Even though these MPAs were not established with the foraging habits of gray whales in mind (the fact that they encompass important foraging grounds is purely coincidental), they are a useful set of reserves to test for connectivity in a large marine predator.

The purpose of this chapter is to examine ecological connectivity between an existing set of six provincial MPAs off the west coast of Vancouver Island through tracking the movement of individual whales over the foraging season. The design and placement of each individual park will be assessed in terms of the distribution and spatial location of foraging animals with reference to boundary allocation. Out-sites (or non-park areas) will also be examined in terms of their importance as gray whale foraging grounds that are not included in the existing set of reserves. The gray whale represents the final trophic level in this scenario, making the measurement of connectivity complete by coupling measurements of connectivity with the two previous chapters that targeted other aspects of the gray whales' trophic spectrum. The design and implementation of an effective network of marine reserves off Vancouver Island for gray whales may then be possible when examined through ecological linkages rather than an *ad hoc* administrative approach.

METHODS

Study Area

The study area ranged from the southeastern corner of Vargas Island to the northwestern tip of Catala Island spanning approximately 130 km (Fig. 4.1) encompassing both park and non/park areas. Out sites or 'non-park' areas were chosen based on previous evidence suggesting that whales utilize areas such as Perez Rocks, Barcester Bay, Escalante Rocks and Bajo Reefs as foraging. Furthermore, through examination of reef structure, water depth and substrate, the non/park areas are similar to gray whale foraging areas in the southern portion of the study area which has been studied extensively (Duffus 1996, Malcolm & Duffus 2000, Dunham & Duffus 2001, 2002). In total there are 11 foraging sites/areas examined in this study (Table 4.2). Northern regions are defined as being north of Estevan Point and encompass Nootka Sound and southern regions are defined as all areas to the south of Estevan Point and encompass Clayoquot Sound.

Sample Design

A line transect was established to survey for foraging gray whales along the entire coast line from the southwestern corner of Vargas Island to the northwestern tip of Catala Island (Fig. 4.2). For each gray whale survey, at least four observers were onboard the vessel in order to cover the entire 360°. Observers scanned the horizon for whales and upon encountering individual animals, photographs were taken of both the left and right flanks of the whale; photographs of the dorsal tail flukes were taken opportunistically. Surveys were conducted in a one-way direction to minimize duplicate sampling.

Additional distributional data for foraging gray whales at Flores Island Marine for 2002, 2003 and 2004 followed the same protocol.

Data Collection

Whale transects were carried out in a seven meter aluminum vessel. A Canon D60 digital camera with a Canon 80mm-300mm lens was used to take all photographs. Associated Canon software was used to retrieve photographs and upload them to a computer. When required, Adobe Photoshop 7.0® was used to enhance the contrast of the photographs. ArcMap® was used to plot whale locations with reference to MPA boundaries. A total of three full surveys (Vargas Island to Catala Island) and four partial surveys were completed (Vargas Island to Perez Rocks or Estevan Point) (Table 4.1). Partial surveys were due to poor weather conditions that prohibited a full survey to be completed in less than eight days. The transect line spanned both park and non-park areas (Table 4.2).

Table 4.1. Timeline of dates and locations of both full and partial surveys.

Survey Number	***Date***	***Location***	***Survey Type***
1	01 June to 04 June	Vargas to Hesquiat	Partial
2	19 June to 22 June	Vargas to Hesquiat	Partial
3	30 June to 01 July	Vargas to Catala	Full
4	13 July to 16 July	Vargas to Catala	Full
5	28 July to 06 Aug	Vargas to Catala	Full
6	20 Aug to 23Aug	Vargas to Perez	Partial
7	07 Sept to 09 Sept	Vargas to Perez	Partial

Table 4.2. List of all park/non-park areas (foraging areas) intersected by the transect route.

Site	*Location*	*Designation*	*Boundary Region*
1	Vargas Island	Marine Park	South
2	Flores Island	Marine Park	South
3	Maquinna	Marine Park	South
4	Hesquiat Peninsula	Non-Park	South-North
5	Perez Rocks	Non-Park	North
6	Barcester Bay	Non- Park	North
7	Escalante Rocks	Non-Park	North
8	Bajo Reefs	Non-Park	North
9	West Nootka Island	Non-Park	North
10	Catala Island	Marine Park	North
11	Nuchatlitz	Marine Park	North

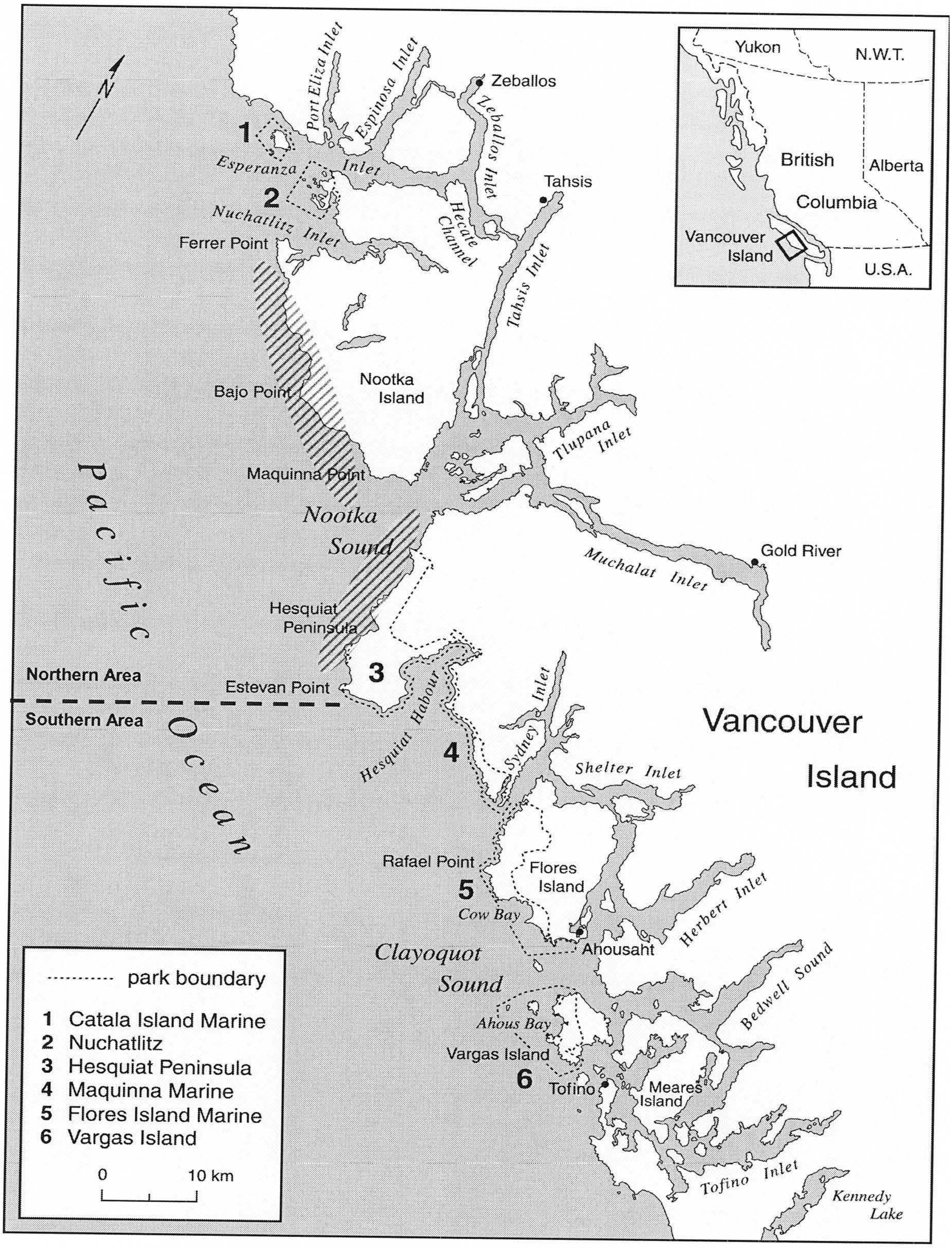

Fig. 4.1. Map of study area highlighting park and non-park areas and the boundary delineating the north and south portions of the study area. Non-park areas are shaded.

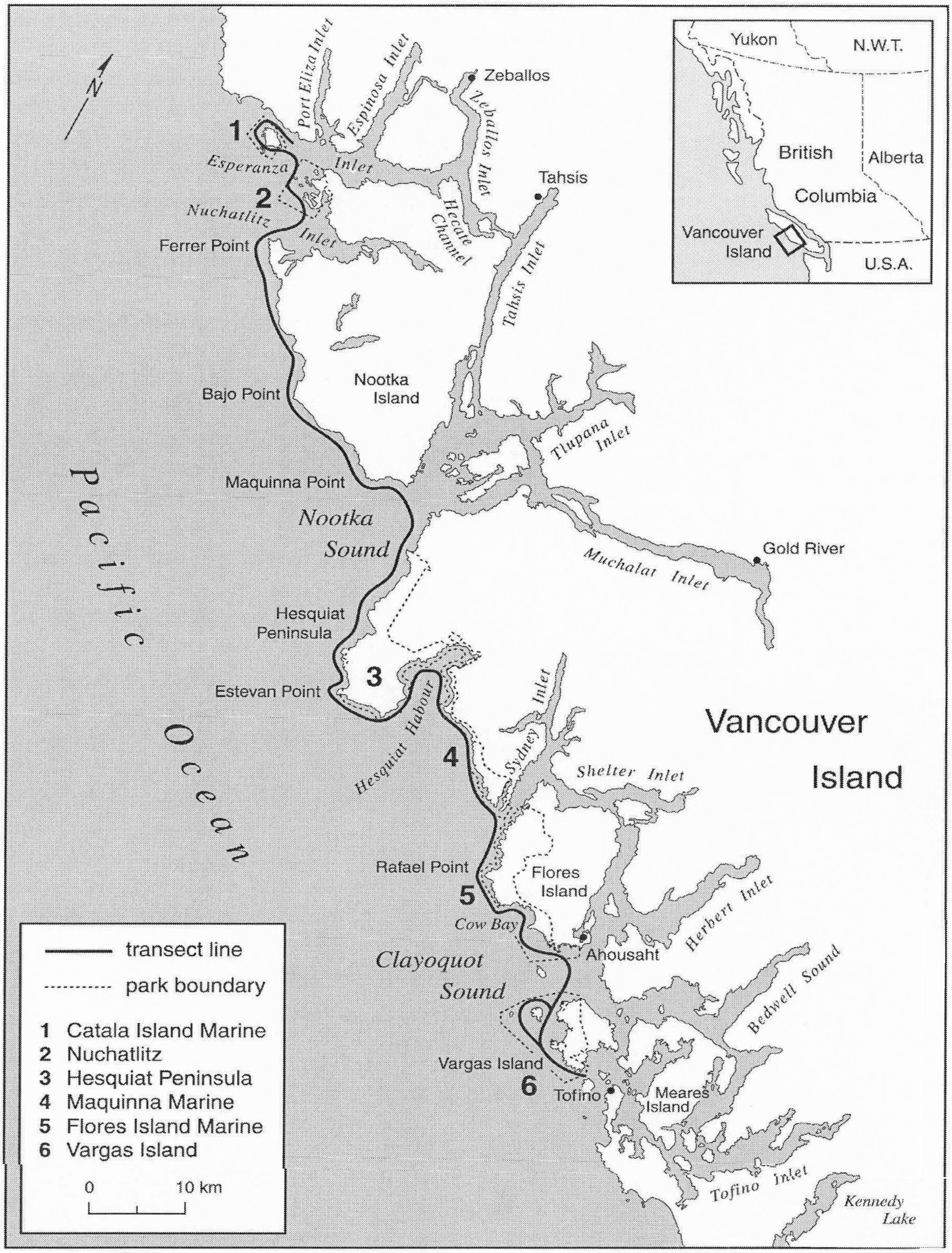

Fig. 4.2. Map of study area showing the transect line through all park/non-park areas.

RESULTS

Connectivity

A total of 66 individual whales were identified in the 2003 season and 17 individuals were re-sighted at more than one foraging site. In total there were 114 foraging encounters throughout the 2003 season. The distance traveled between different foraging sites for the 17 re-sighted whales ranged between 2.6 km and 104 km (Table 4.3, Fig 4.3). Of these 17 individuals only four were re-sighted between park areas alone (Table 4.3). Connectivity between non-park areas were higher than park areas alone (park = 4.9%, non-park = 53.7%, both = 41.5%) (Fig. 4.4) and connectivity between the northern and southern areas and the northern area alone were highest (south = 12.2%, both = 43.9%, north = 43.9%) (Fig. 4.5). Figure 4.6 illustrates connectivity through the 17 re-sighted whales among foraging sites, both park and non-park.

Table 4.3. Summary data for all individual re-sighted whales at all foraging sites. Whales re-sighted only in park areas are shaded gray.

Whale #	*Number of foraging sites frequented*	*Number of Re-sights*	*Minimum Distance Traveled (km)*	*Maximum Distance Traveled (km)*
1	2	9	7.94	25.6
2	3	3	4.01	18.1
3	3	4	2.6	29.8
4	4	4	10.1	38.2
5	2	3	26.3	28.0
6	4	4	13.5	104
7	2	2	8.5	8.5
8	2	2	95.1	95.1
9	2	2	31.3	31.3
10	2	2	75.3	75.3
11	2	2	50.8	50.8
12	2	2	52.1	52.1
13	3	3	8.47	18.3
14	2	2	13.6	13.6
15	2	2	22.7	22.7
16	2	2	51.3	51.3
17	2	2	50.4	50.4
Average	**2.4**	**4.1**	**30.08**	**41.96**

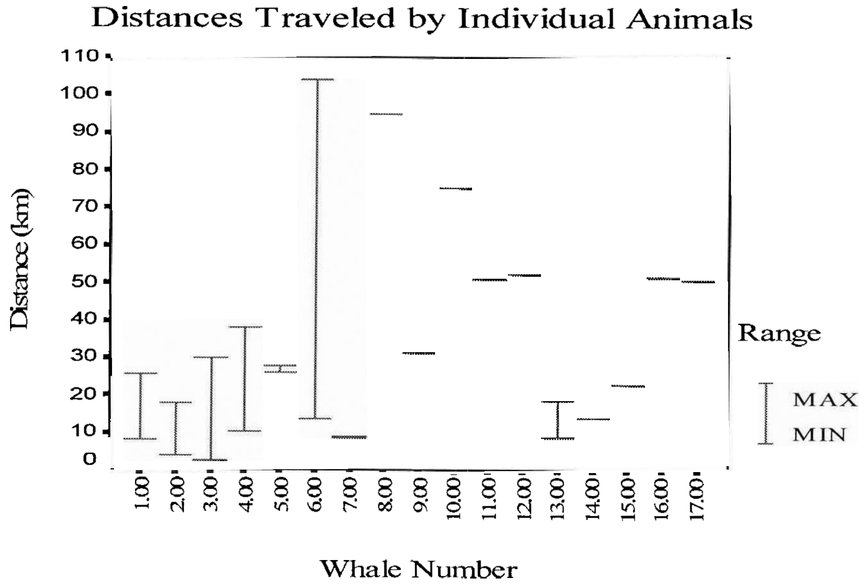

Fig. 4.3. Distances traveled by re-sighted whales (n = 17) for all surveys.

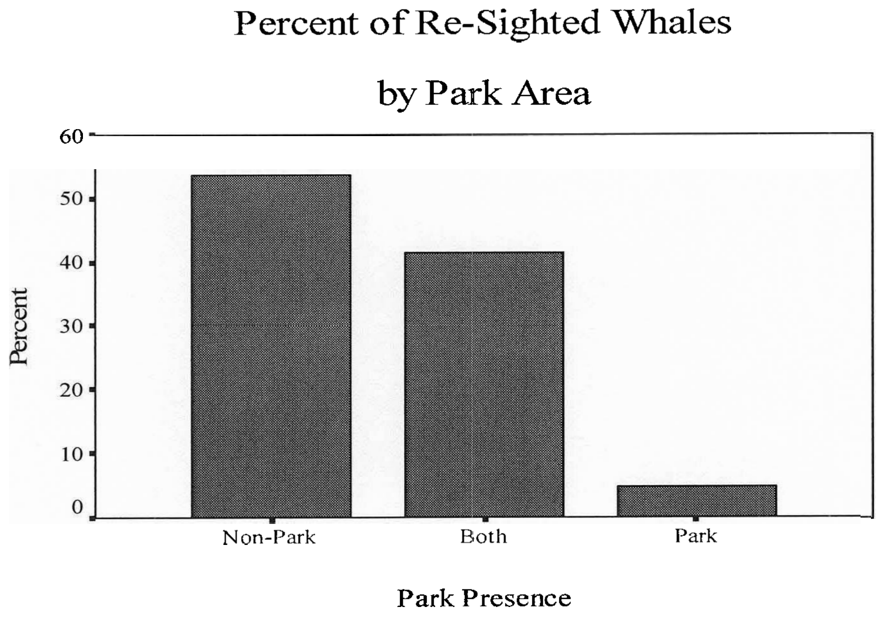

Fig. 4.4. The proportion of re-sighted whales (n=17) by park area for all surveys.

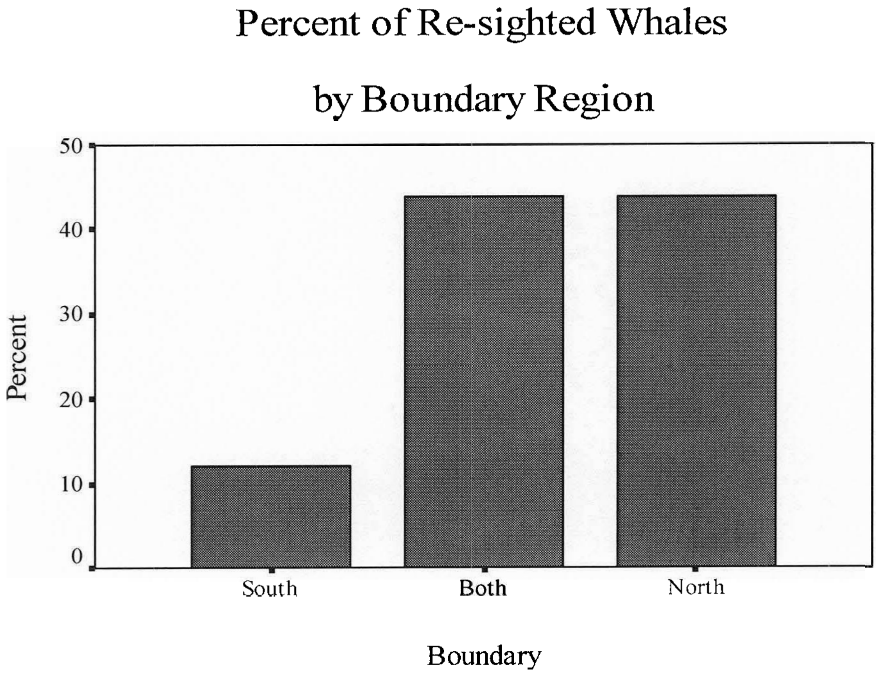

Fig. 4.5. The proportion of re-sighted whales (n = 17) by boundary region (northern and southern areas; see Fig. 4.1) for all surveys.

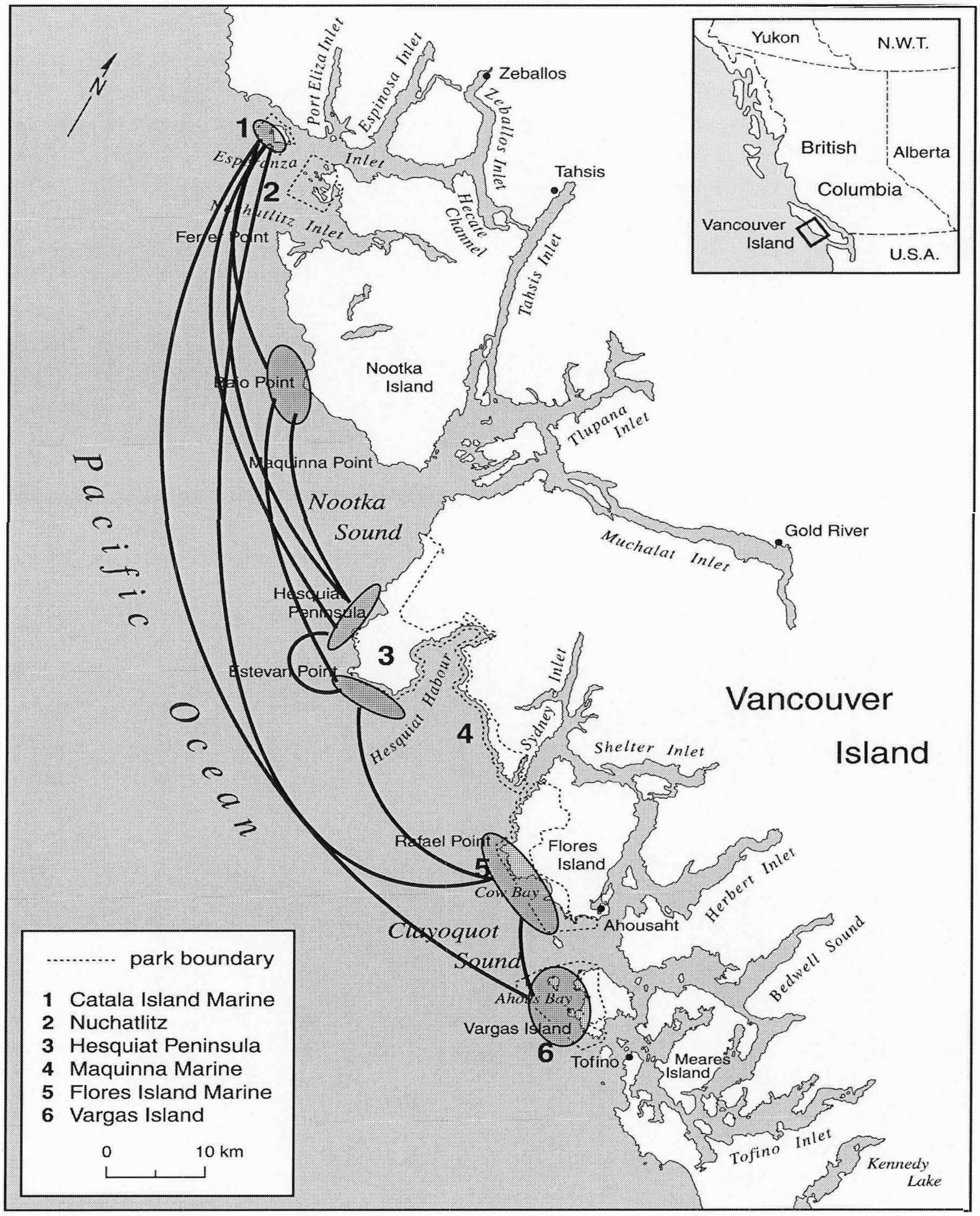

Fig. 4.6. Circles illustrate foraging sites and lines show which foraging sites were connected for all 17 re-sighted whales. Lines are not scaled to show the number of whales.

Boundary Delineation

For all 114 foraging whale encounters 37% (n = 42) were found within park boundaries and 63% (n = 72) were outside park boundaries (Figs. 4.7, 4.8, 4.9, 4.10, 4.11). Based on the park boundaries on the western side of Flores Island, Maquinna Marine and Hesquiat Peninsula, it appears that the park boundaries follow the 10m depth contour or are approximately 500m from the shoreline (Figs. 4.12, 4.13, 4.14). Figure 4.15 shows the 10m contour for Nuchatlitz and Catala Island. Foraging whales were seen in all established MPAs except for Nuchatlitz Marine Park (Table 4.4). Even though the boundaries of the given set of MPAs were not based on depth, data on the mean foraging depths for all 114 whales in 2003 (n= 107, mean=14.43, SD=7.52) exceed the designated park boundaries when they are in depths of <10m. Mean tidal fluctuations in this study area are 3.4m with a high tidal range of 4.1m and a low of 0.0. Therefore, the average foraging depth for whales with the tidal amplitude accounted for equals approximately 10-11m.

I experimented with boundary alterations using the 10m contour as an indicator of gray whale foraging habitat. This approach to boundary delineation is based on ecological data rather than an administrative *ad hoc* approach. By buffering the 10m contour line by 500m an additional 23 foraging locations are added to the parks on the western edge of Flores Island, the western shores of Hesquiat Peninsula and at Catala Island Marine (Figs. 4.16, 4.17, 4.18). This increases the percentage of foraging encounters inside the park boundaries from 37% to 57% (Figs. 4.19 and 4.20). I used a 500m buffer because in several cases it extended to the shoreline (Figs. 4.12 and 4.13) or it extended to the existing park boundaries (Fig. 4.14). The addition of a marine park off the west coast of Nootka Island will add another 30 foraging encounters (Fig. 4.10 and Table 4.4). A total of 68 additional foraging encounters are added within park boundaries with the addition of a 500m buffer around the 10m contour line. If the 10m contour is used as an indicator of gray whale foraging habitat, the park boundaries around Flores Island, Maquinna Marine, Hesquiat Peninsula and Catala Island and an additional MPA off Nootka Island would have to be adjusted.

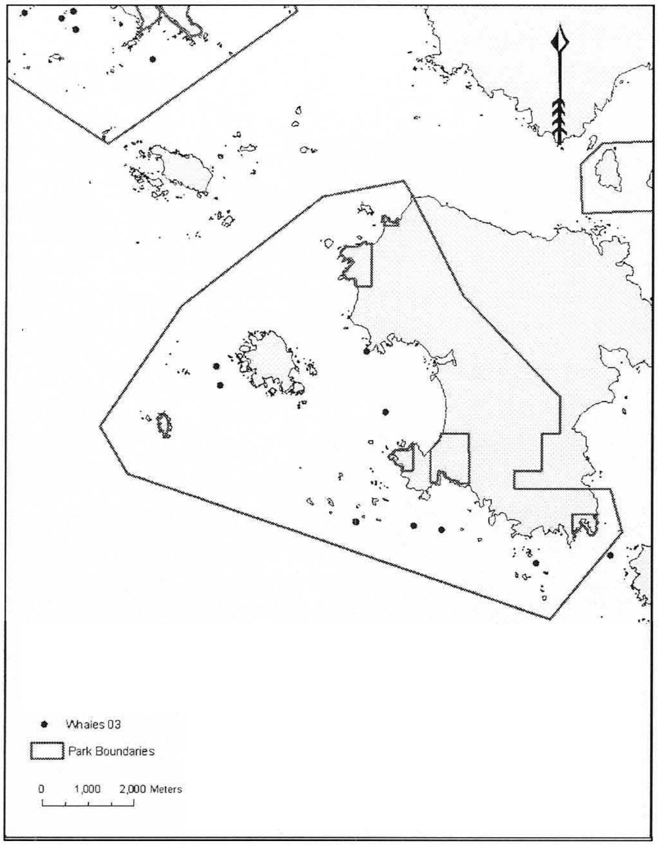

Fig. 4.7. Whale distribution at Vargas Island Marine.

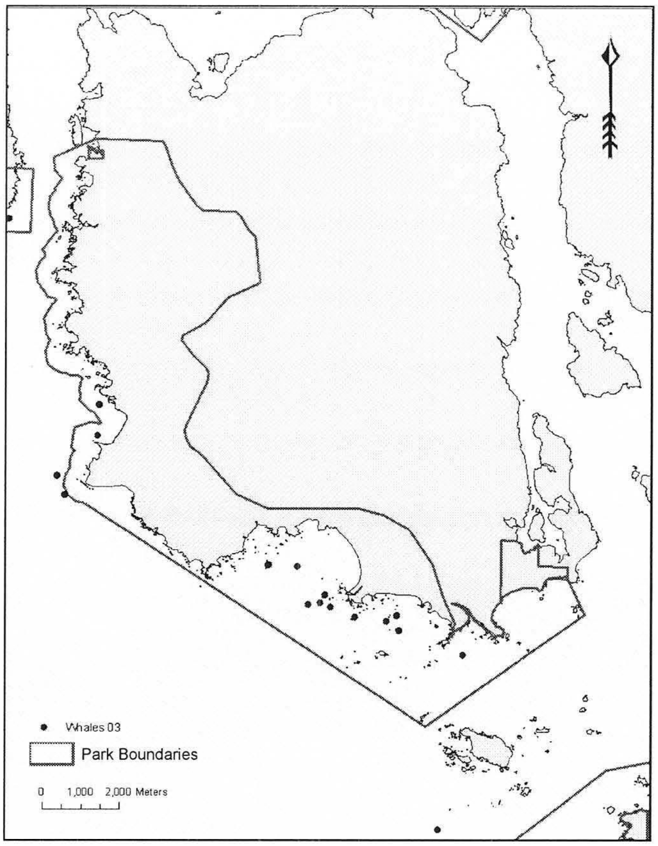

Fig. 4.8. Whale distribution at Flores Island Marine.

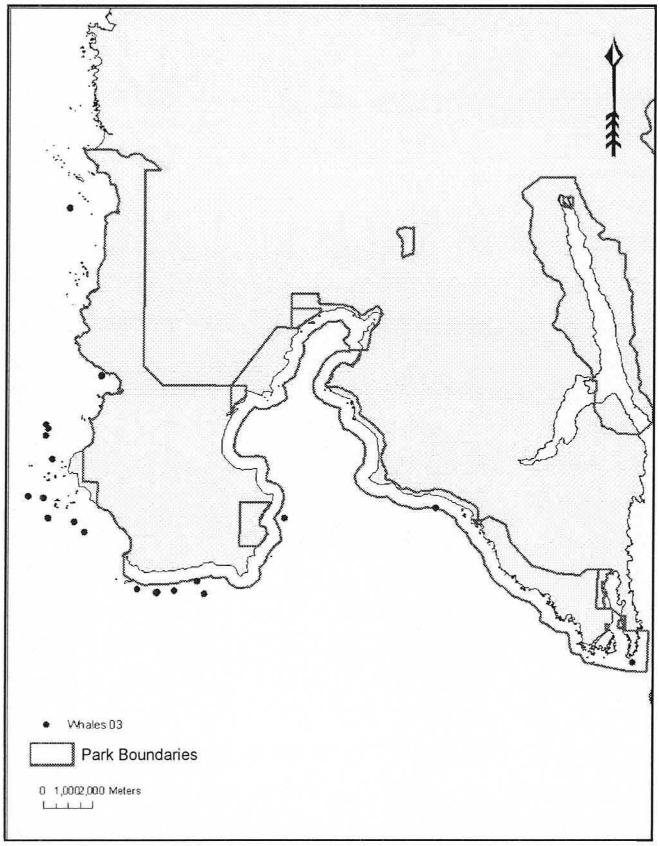

Fig. 4.9. Whale distribution at Maquinna Marine and Hesquiat Peninsula.

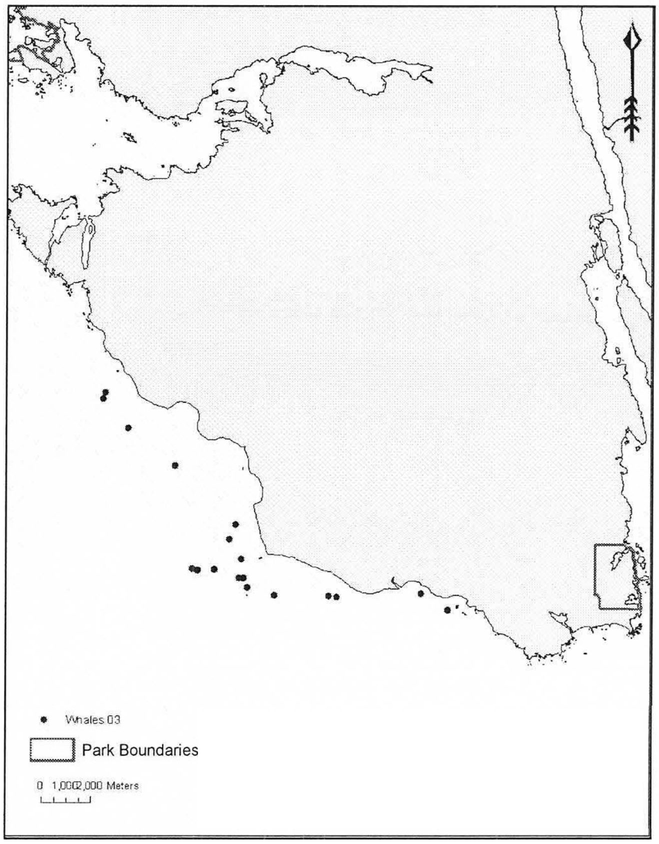

Fig. 4.10. Whale distribution at Nootka Island.

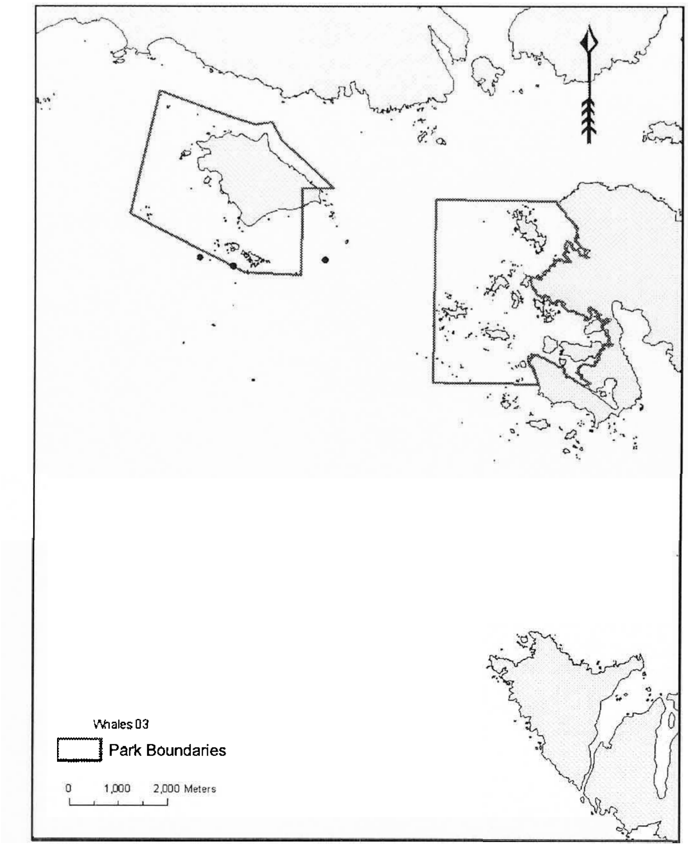

Fig. 4.11. Whale distribution at Nuchatlitz and Catala Island Marine.

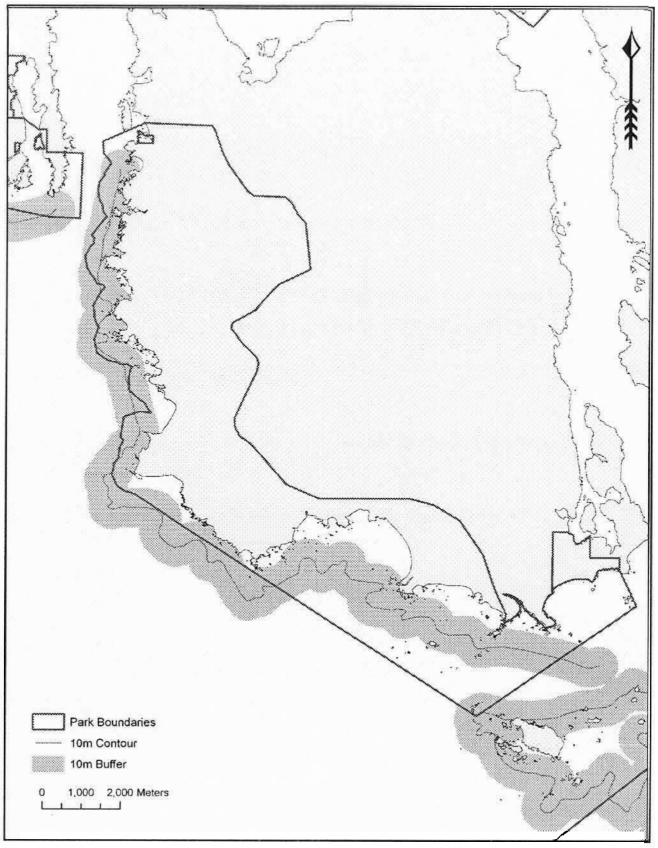

Fig. 4.12. Ten metre contour and 500m buffer at Flores Island Marine.

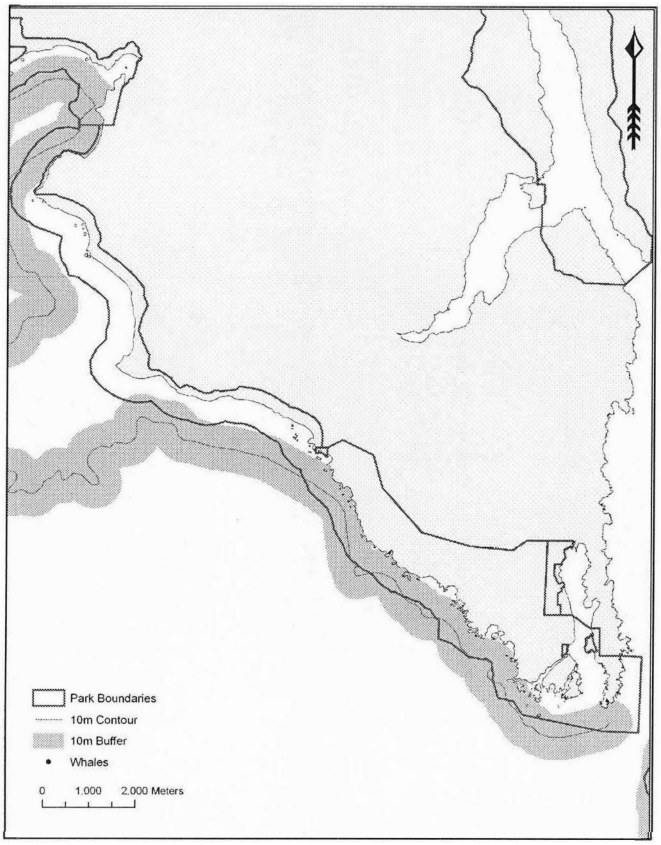

Fig. 4.13. Ten metre contour and 500m buffer at Maqunna Marine.

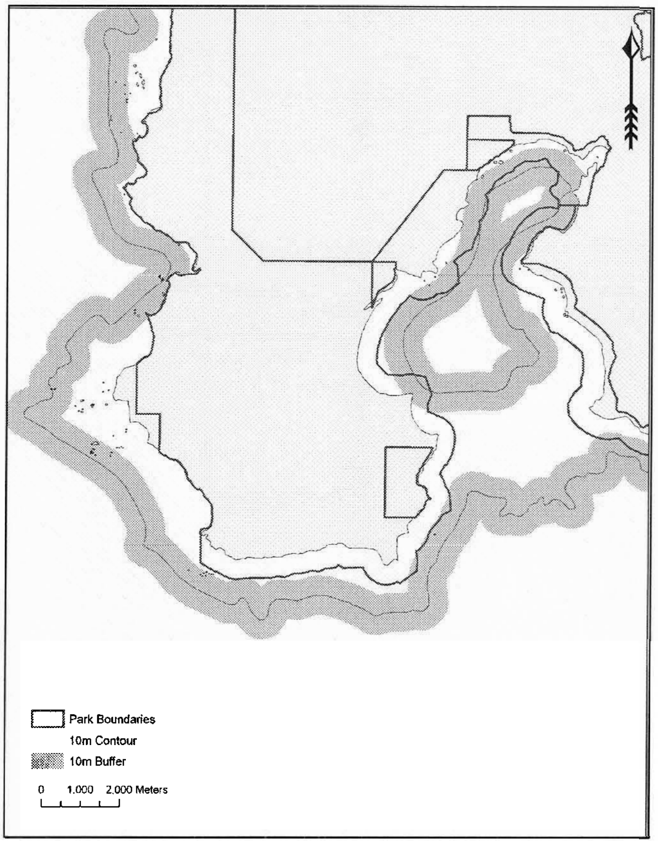

Fig. 4.14. Ten metre contour and 500m buffer at Hesquiat Peninsula.

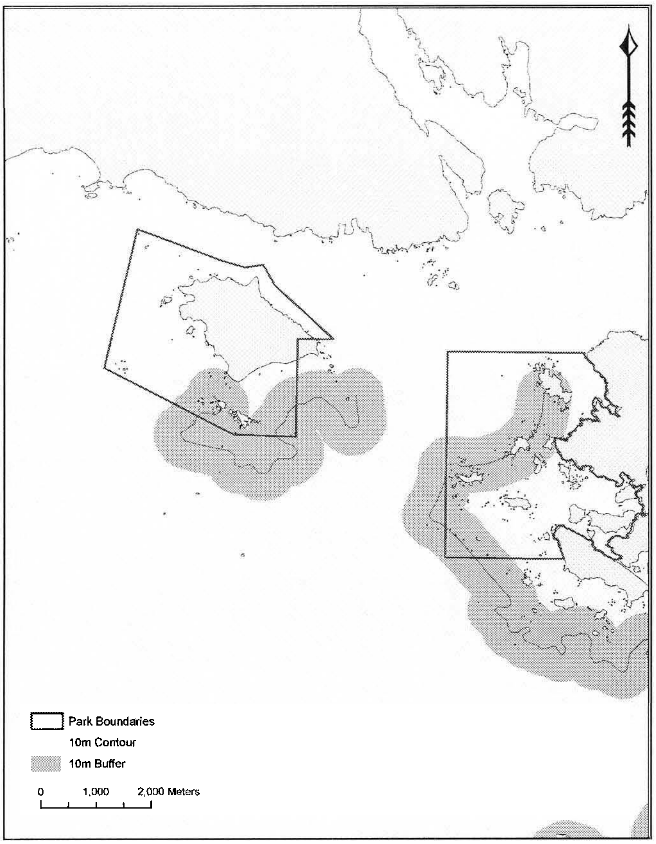

Fig. 4.15. Ten metre contour and 500m buffer at Nuchatlitz and Catala Island.

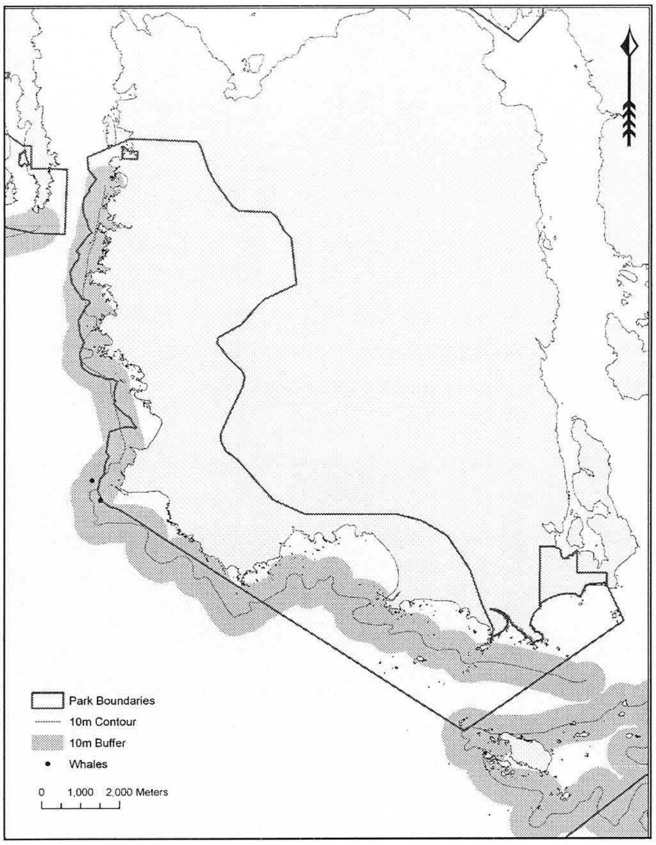

Fig. 4.16. Ten metre contour and 500m buffer at Flores Island Marine with foraging whale sightings (single circles indicate multiple whales).

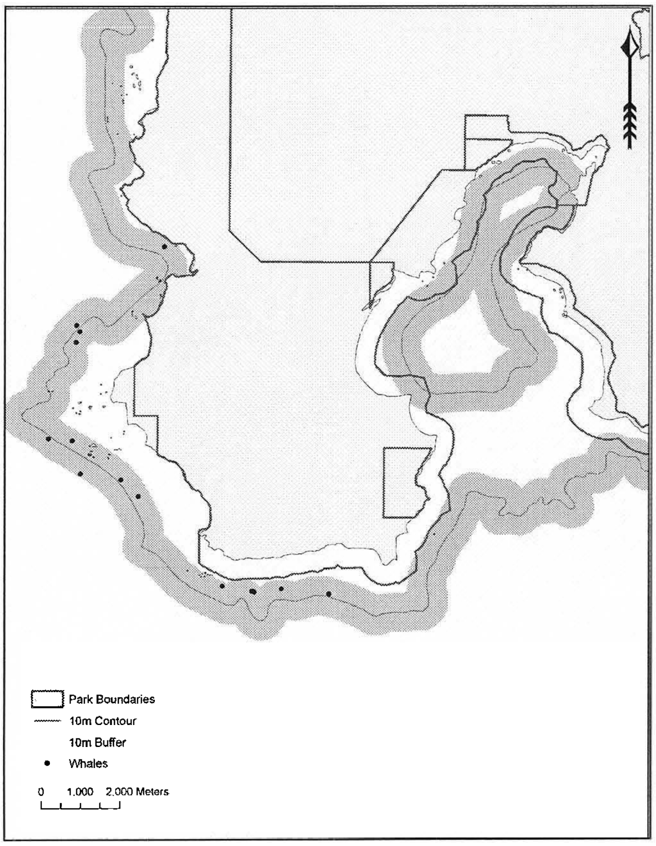

Fig. 4.17. Ten metre contour and 500m buffer at Hesquiat Peninsula with foraging whale sightings (single circles may indicate multiple whales).

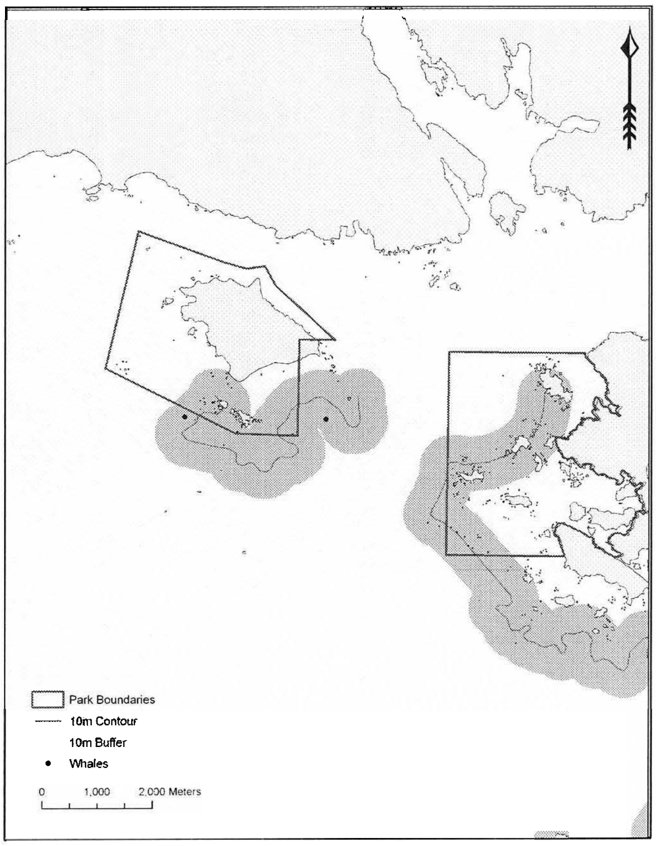

Fig. 4.18. Ten metre contour and 500m buffer at Catala Island Marine with foraging whale sightings (single circles may indicate multiple whales).

Table 4.4. Number of foraging whale encounters by foraging area. Totals include whales both inside and outside the boundary areas for MPAs.

Site	*Location*	*Designation*	*Number of Whales*	*Boundary Region*
1	Vargas Island	Marine Park	11	South
2	Flores Island	Marine Park	36	South
3	Maquinna	Marine Park	3	South
4	Hesquiat Peninsula	Non-Park	9	South-North
5	Perez Rocks	Non-Park	18	North
6	Barcester Bay	Non- Park	1	North
7	Escalante Rocks	Non-Park	2	North
8	Bajo Reefs	Non-Park	17	North
9	West Nootka Island	Non-Park	11	North
11	Nuchatlitz	Marine Park	0	North
10	Catala Island	Marine Park	6	North

To further illustrate the boundary issue, I experimented further with additional data on foraging whale locations during the summer of 2002, 2003 and 2004 (n = 886) at Flores Island Marine. The current boundary configuration shows that 73% of the whales are inside the designated park boundary (Table 4.5, Figs. 4.19, 4.20, 4.21). Slight adjustment of the boundaries with regards to bathymetry at Flores Island Marine can dramatically increase the proportion of whales found within park boundaries (Figs. 2.22, 4.23, 4.24). With the addition of the 10m buffer an additional 104 foraging encounters would be added to the 2002 season, 28 to 2003 and 80 to 2004. This would increase the total percentage of foraging whale encounters inside park boundaries from 73% to 97%.

Table 4.5. Number of foraging whales inside and outside designated boundaries at Flores Island Marine for 2002, 2003 and 2004.

Year	*N*	*Inside*	*Outside*
2002	455	337	118
2003	153	123	31
2004	278	184	64
Total	**886**	**644**	**242**

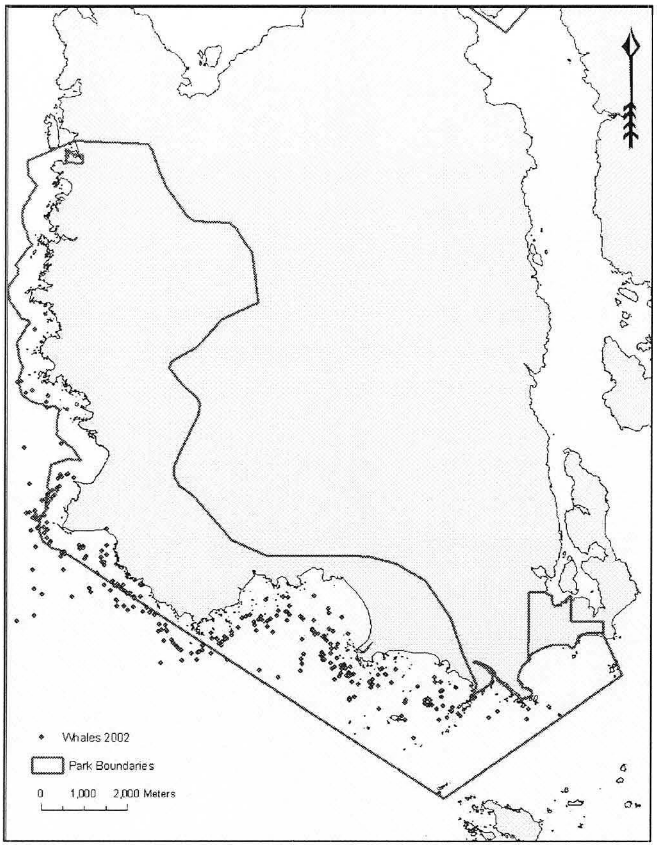

Fig. 4.19. Distribution of whales at Flores Island, 2002.

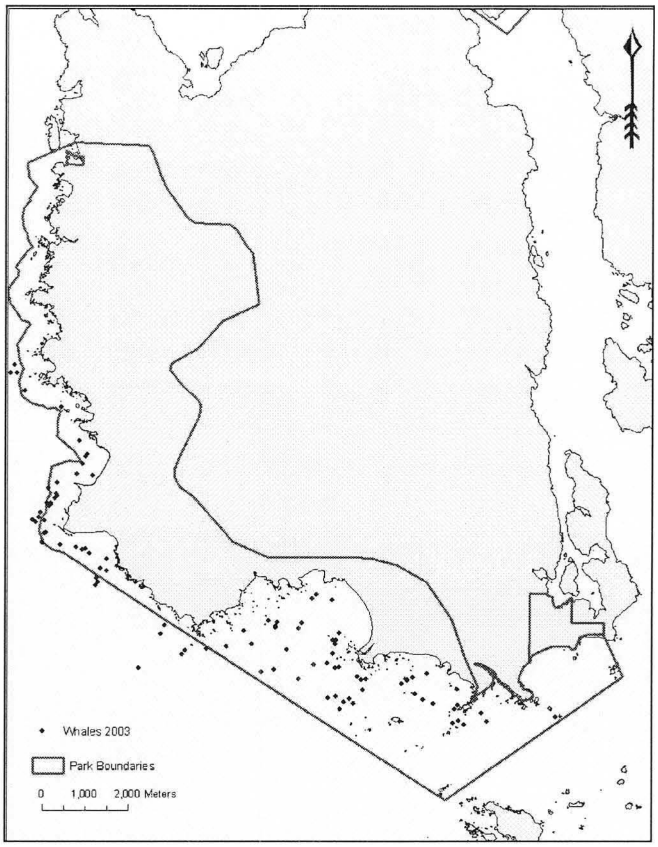

Fig. 4.20. Distribution of whales at Flores Island, 2003.

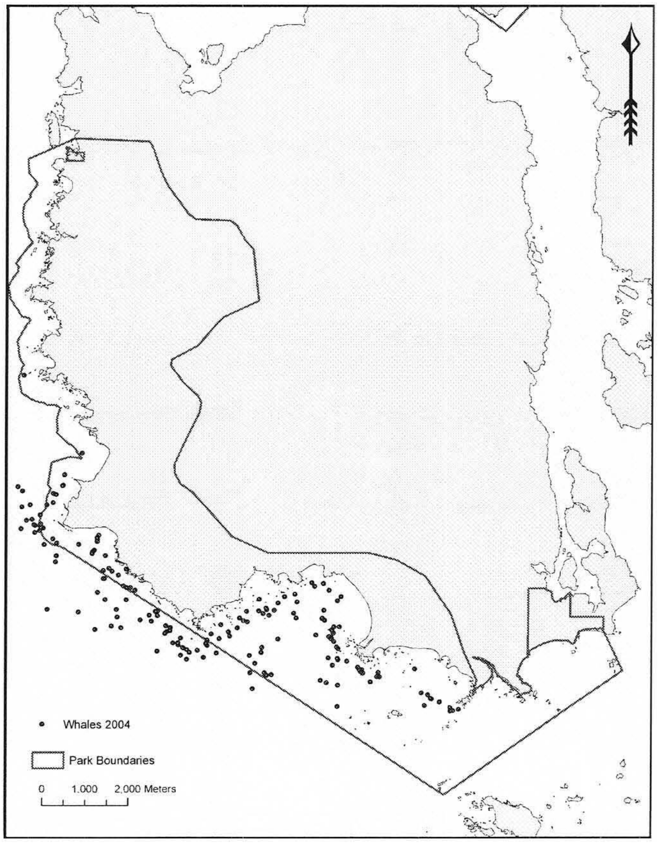

Fig. 4.21. Distribution of whales at Flores Island, 2004.

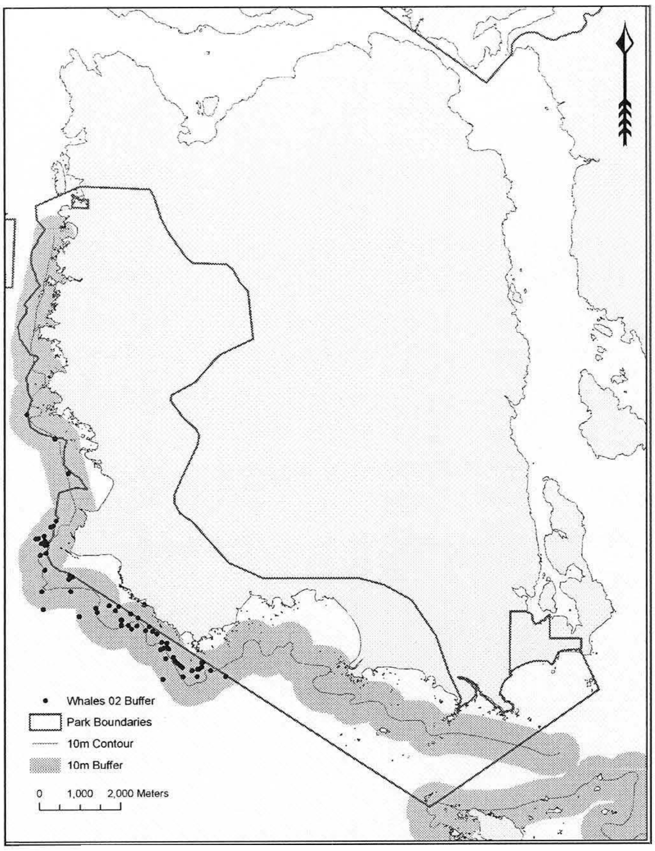

Fig. 4.22. Distribution of whales at Flores Island outside park boundaries with buffered 10m contour. 2002.

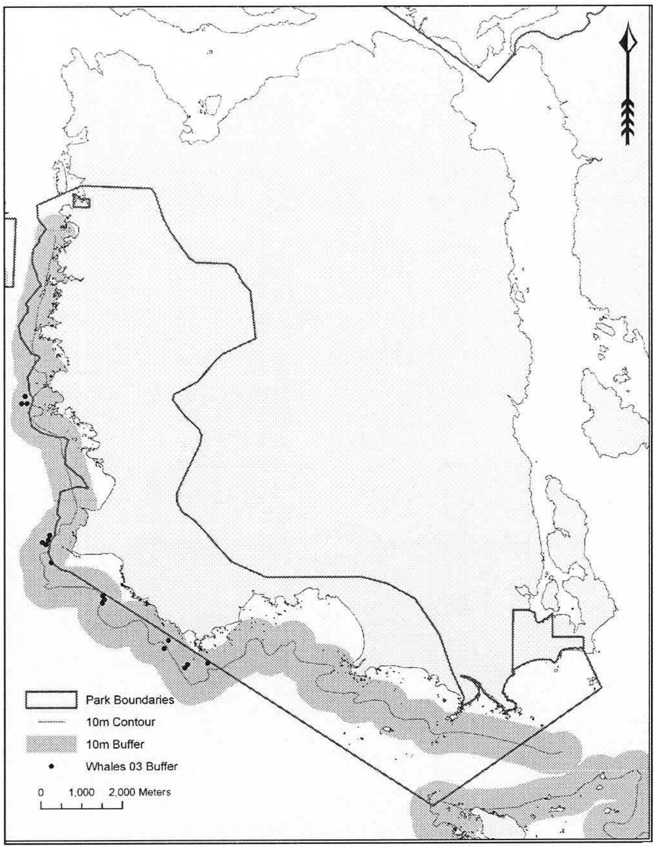

Fig. 4.23. Distribution of whales at Flores Island outside park boundaries with buffered 10m contour. 2003.

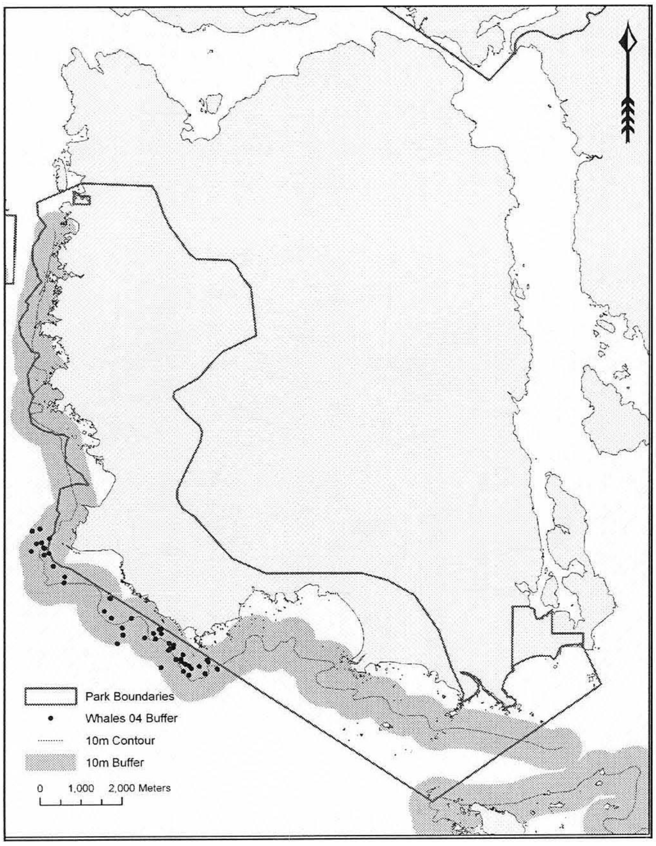

Fig. 4.24. Distribution of whales at Flores Island outside park boundaries with buffered 10m contour. 2004.

DISCUSSION

Based on individual gray whale movement, there is connectivity between reserve sites and if boundaries at the existing set of reserves are minimally altered they will include close to 100% of foraging whale encounters. In terms of connectivity between all foraging sites and MPAs alone, the data show the necessity for a multitude of MPAs in the form of a network over any single reserve scenario. Gray whales exert a substantial amount of top-down pressure on localized prey populations and this becomes apparent through the examination of their movement patterns (Patterson 2004). Therefore, no single MPA in one region could provide the protection necessary for this predator-prey relationship. Networks of marine reserves have been advocated in the past (Ballantine 1995), however, there are few examples of effective networks of MPAs in North America or worldwide (Hoyt 2005). Because of the mobility of many marine species, especially cetaceans, important life history characteristics that are associated with habitats, which are identifiable, (i.e., breeding grounds, foraging grounds, nursery grounds, stop-over sites for migratory birds) may be used to identify candidate MPAs sites. Measuring connectivity has been a difficult task in marine systems and has mainly been attempted with larval fish and marine invertebrate species (Jones *et al.*, 1999, Swearer *et al.*, 1999, 2002, Palumbi 2003) which is both technically challenging and expensive (Thorrold *et al.* 2001, Palumbi 2003). Identifying cetacean habitats and connectivity between habitats is also a difficult task; however, because of the ability to track individuals, it is possible to do so (Ingram & Rogan 2002, Rendall *et al.* 2004).

Gray whales, like many baleen whales, are explicitly linked to productive regions of the eastern north Pacific during summer foraging bouts (Kim & Oliver 1989, Duffus

1996, Dunham & Duffus 2000, 2001) and it is clear that they have the capacity to move over large spaces (100s to 1000s of km) in search of prey. Given this, the MPAs off the west coast of Vancouver Island should be spatially arranged to incorporate the variability in movement by individual gray whales. By strategically designing marine reserves at targeted foraging areas over large spatial scales (100s of km) it provides a degree of resilience to the spatial variability in gray whale foraging patterns, the spatial distribution and abundance of their prey and the underlying process of oceanographic production. By measuring connectivity via the movement patterns of gray whales, it gives a degree of functionality to this set of MPAs based on a clear objective – the objective being a network of marine protected areas for foraging gray whales. The results show that there is connectivity between the existing set of reserves off the west coast of Vancouver Island but, the spatial distribution of foraging whales also provides evidence of connectivity among foraging areas outside the park boundaries which may warrant the addition of a new MPA and the reconfiguration of existing park boundaries.

Slight alterations to park boundaries at Flores Island, Maquinna Marine, Hesquiat Peninsula and Catala Island based on both the geographic location of foraging whale encounters and the average foraging depth (mean = 14.43m) will increase the number of foraging encounters inside park boundaries. By adding a 500m buffer around the 10m depth contour, the number of foraging whales inside park boundaries increase by 20% based on data in 2003. Although the spatial location of foraging gray whales is highly variable, additional data for 2002, 2003 and 2004 (n = 886) at Flores Island Marine show similar trends. Alterations to park boundaries at Flores Island with reference to these data would increase the number of foraging whale encounters inside parks boundaries by 24%

making the total equal 97%. The total number of foraging whale encounters would also rise with the addition of a new MPA on the west coast of Nootka Island and the same 500m buffer around the 10m contour line would apply.

A major gap in the existing set of MPAs in this study area is found between the western shores of Hesquiat Peninsula and the northwestern tip of Nootka Island. Alterations to Hesquiat Peninsula Provincial Park can increase the number of foraging whales inside its park boundaries; however, there are no MPAs off the west coast of Nootka Island and in the 2003 season there were 28 encounters with foraging whales in this area, second in numbers only to Flores Island Marine. The distribution of foraging whales at Nootka Island is mainly in and around a reef complex (Bajo Reef) that extends approximately 3 nautical miles offshore from the coast (Fig. 4.25). By buffering the 10m contour line in this area and designing another MPA in this vicinity, 64% of the whales at Nootka Island would be included within park boundaries (Fig. 4.26). It should be noted that Bajo reef is divided into two sections, an inner reef and an outer reef, however the data for this study only included whales that were using the inner reef as foraging grounds. Whales were observed at the outer reef, likely in the same numbers, but no data was gathered for specific geographic locations. Therefore, by including the outer reef into any proposed MPA at Nootka Island will undoubtedly increase the number foraging whales within protected boundaries at this site. Connectivity studies coupled with distributional data on any species in marine systems provide an ecological basis for designing MPAs. In most cases, especially with the six MPAs in this study, boundary allocation and reserve placement is done fairly haphazardly, is based on anecdotal

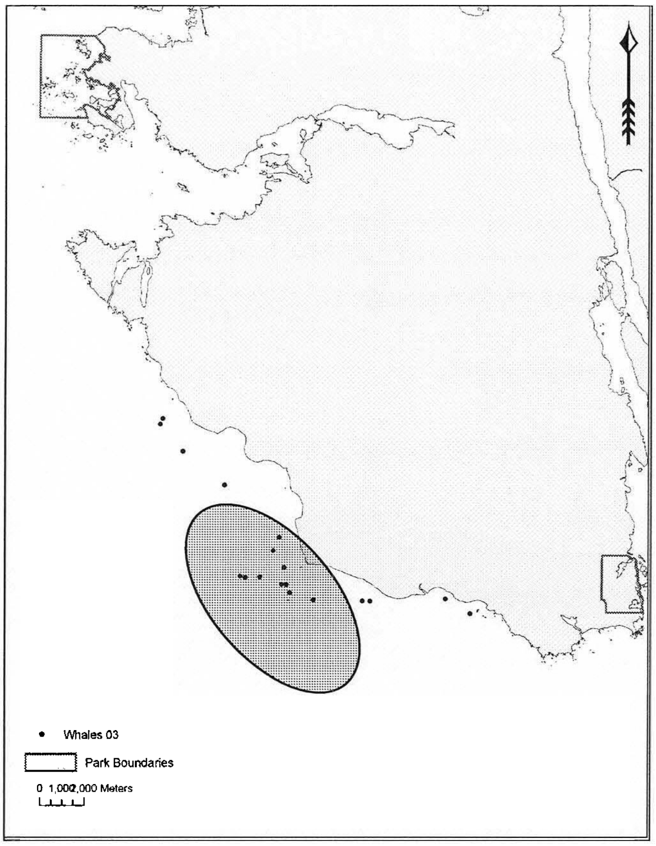

Fig. 4.25. Distribution of whales at Nootka Island. Circle highlights Bajo Reef complex (single dots may indicate multiple whales).

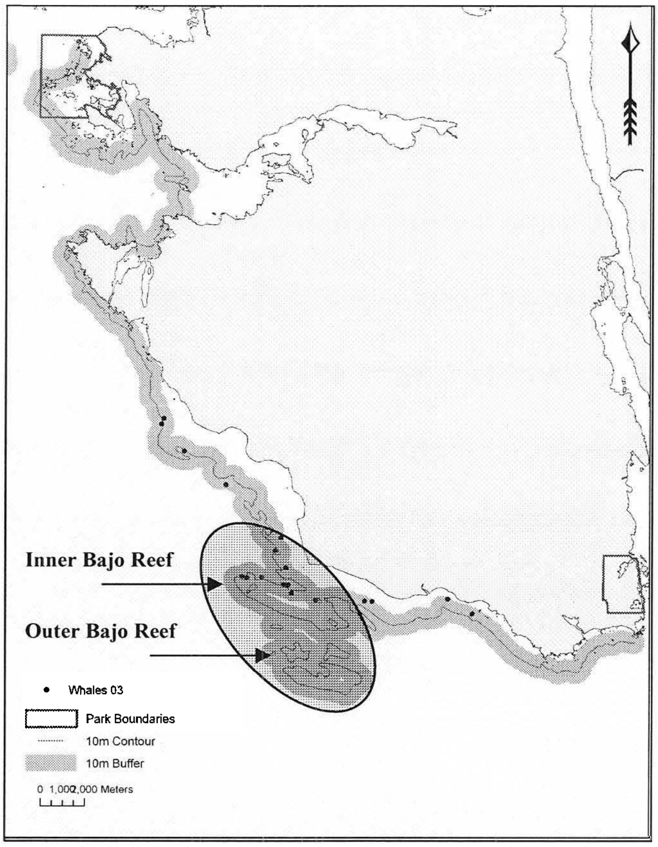

Fig. 4.26. Distribution of whales at Nootka Island with 500m buffer around the 10m contour line. Circle highlights Bajo Reef complex (single dots may indicate multiple whales).

ecological data and is often wrought with vague objectives and limited ecological foresight (Dunham *et al.*2002).

The six MPAs highlighted here were not designed to protect gray whale foraging habitat but, coincidentally they do encompass important gray whale foraging grounds. They also, based on their configuration along the coast, provide a good example of a network of MPAs if the main objective is to protect and secure gray whale foraging grounds from any form of anthropogenic disturbance. Many MPAs are designed to enhance commercial fisheries and to protect the representative habitats of any given region (Brailovskaya 1998, Vanderkift & Phillips 1998, Dayton *et al.*2000, Jamieson & Levings 1997, 2001, Apostolaki et al., 2002, Hastings & Botsford 1999). This, however, does not lend any utility to connectivity issues and networking reserves because protecting representative habitats on the basis of securing biodiversity may give a disjunct, disconnected configuration of reserves. Networking reserves may necessitate using a single species (or like species) approach because many life history traits and individuals' habitat utilization would be similar. For example, many dispersal and connectivity studies using advection (current) models or reserve siting algorithms use a single species approach because multiple species approaches require information on a multitude of variables that would influence their dispersal capacity or movement patterns, and these may not be well understood or known (Cowen et al., 2000, Smith *et al.*2001, Lockwood et al., 2002, Largier 2003). Also, for a hyper-mobile species like a gray whale (and many other cetacean species) even some of the largest reserves scenarios may not serve any utility (Gerber *et al.*2005).

The purpose of this study was to show that the current configuration of six MPAs off the west of Vancouver Island can function as a network to protect gray whale foraging habitat. Based on ecological data on connectivity and the spatial distribution of foraging whales, an additional MPA should be added off the west coast of Nootka Island and the park boundaries at Flores Island, Hesquiat Peninsula and Catala Island Marine should be reconfigured based on a 500m buffer around the 10m contour line. This would increase the proportion of foraging whale encounters inside the protected areas. The network can also provide resilience to both physical and biological variability in marine systems, which is common, but more data is needed to illustrate this point further. Data on gray whale foraging distributions coupled with the dispersal capacity of their prey and the underlying patterns in primary production will enable us to better design MPAs for gray whales specifically, and may also provide a framework for other cetacean species.

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CHAPTER 5

FINAL DISCUSSION AND CONCLUSION

The goal of this thesis is threefold: 1) to assess the connectivity, or lack thereof, among an established set of MPAs at three trophic levels within a gray whale's (*Eschrichtius robustus*) food web; 2) to evaluate the efficacy of the existing set of MPAs for foraging gray whales in terms of their location and boundary allocation and; 3) to offer recommendations as to how these existing MPAs could be altered in order to fulfill a specific goal which is to have a network of ecologically functional marine reserves for foraging gray whales. It should be noted that there are some underlying assumptions made throughout the thesis that could not be properly tested. The assumptions are fairly intuitive: 1) that primary production, based on overall chl *a* values, throughout the study area is an important component to gray whale foraging habitat and therefore an important process to consider in the design of MPAs; 2) that the whales' primary prey type (*Holmesimysis sculpta*), forage directly on phytoplankton throughout their range and is an important component to mysid population dynamics and; 3) that the spatial distribution of gray whales in this part of their foraging range is dictated primary by fluctuations in the above two assumptions. Therefore, any design scenario for MPAs with the objective of protecting gray whale foraging grounds should incorporate ecological data that focuses on elucidating these variables in order to be effective.

In chapter 2, variation in chl *a* throughout the study area is used as a variable to measure connectivity and boundary function in the six targeted MPAs. It is determined that although there is significant spatial variation in chl *a* levels among MPAs at short temporal scales, it becomes non-significant over longer temporal scales. Because of this, a problem arises when using primary production as a measure of connectivity. Under certain circumstances there may or may not be connectivity via this process due to chl *a* variability. Also, there was no significant differences in chl *a* between park and non-park areas. Even though fluctuations in primary production is an important variable to higher trophic levels (Menge & Daley 1997) it is difficult to ascertain whether or not it can be used to measure connectivity between MPAs or used in boundary delineation. Nonetheless, it should be considered in MPA design when focusing on specific species since persistent differences in primary production at discrete geographical locations may have an effect on community assemblages, including mammalian predators like cetaceans (Menge & Daley 1997, Croll *et al.*1998, Benson *et al.*2002).

The most important component in a gray whale's food chain is their main prey item, mysids (*H. sculpta*). Interestingly, *H. sculpta* populations may not be connected at this level in the food chain. Chapter 3 provides evidence of limited gene flow and suppressed dispersal capacity in *H. sculpta*. This suggests that *H. sculpta* may only inhabit discrete geographic locations within this part of their range and may have a restricted capacity to recruit from nearby populations. In this sense, the function of the network of reserves in this scenario fails to meet the criteria of connectivity. However, if *H. sculpta* cannot disperse enough to recolonize other foraging areas (or parks), then by having a multitude of MPAs like the configuration seen in this study, may protect against any potential degradation of existing mysid habitat. Further genetic analysis is needed to elucidate finer scale differentiation which can help in defining mean dispersal distances in this species (Palumbi 2003).

Chapter 4 focuses explicitly on animal movement and distribution to measure connectivity and delineate MPA boundaries. It demonstrates that not only is the existing set of MPAs connected by the apex predator in this scenario but, the current boundaries do not encompass all of their foraging patterns. It is not surprising that gray whales move such distances in search of food, given their annual migration route and their metabolic demands, but they do provide a sufficient measure of connectivity in marine systems during their annual feeding bouts. Foraging activity can be incorporated within park boundaries at an extremely high percentage (97%) with only slight alterations to the existing park boundaries and the addition of one new MPA at Nootka Island. Reconfiguration of the existing reserve boundaries can be done based on depth and the spatial locations of foraging whales. By using the average foraging depth, which is ecological evidence, it provides an easy way to enforce park boundaries through any future management strategies that may be undertaken by BC Parks.

There are 124 provincial marine parks in British Columbia with statutory powers given through the Ecological Reserves Act, Park Act, Protected Areas of British Columbia Act, Wildlife Act, Land Act and the Environment and Land Use Act (Duffus & Dearden 1993, Dunham *et al.*2002). In addition to the above mentioned provincial acts, the Ocean's Act and the Fisheries Act set forth by the federal government of Canada supercede all other Acts with regards to oceanic species and their associated management and protection (Duffus & Dearden 1993, Jamieson & Levings 2001, Dunham 2002). Environment Canada and Parks Canada also have legislation pertaining to the protection of marine species which are set forth through the Canada Wildlife Act, Migratory Birds Convention Act, the National Parks Act and the National Marine Conservation Areas Act (see Jamieson & Levings 2001 for details). All of these pieces of legislation have common mandates that they follow (ie., to protect and conserve representative habitats, endangered or threatened species, unique habitats and areas for scientific research), however, there are exceptions. For example, the Canada Wildlife Act and the Migratory Birds Act focus heavily on migratory/marine birds and the National Parks Act and the National Marine Conservation Areas Act highlight and promote public education and awareness in natural areas by providing opportunities for recreation (Duffus & Dearden 1993, Jamieson & Levings 2001).

Clearly, the legislative bodies and government agencies that coordinate the implementation and dictate the rationale for MPA establishment is convoluted and inefficient. The result is a system of provincial MPAs that, for the most part, have been established on an *ad hoc* basis but, nonetheless, they do exist. The six MPAs in this thesis are used to illustrate the potential of the existing system of MPAs on the west coast of Vancouver Island to function as a viable network for foraging gray whales. According to BC Parks all six of the MPAs primary objectives are to protect natural features, including all biota, with special emphasis on marine mammals, except Maquinna Marine. Maquinna Marine's primary objective is to promote the use and ensure safe access to the naturally occurring hot springs which are located within the park boundaries. Not only is the park culturally significant, but there are also user and moorage fees for park visitors that are enforced by the BC Parks Service (Dunham *et al.*2002). The objectives of the remaining five parks, prior to their establishment, were not to protect gray whale foraging habitat, which is evident by their boundary delineation. However, as a product of circumstance, slight alterations can be made to the park boundaries to fulfill this goal.

With the addition of a new MPA off the west coast of Nootka Island, which would incorporate the Bajo Reef complex, a more functional and connected system of reserves is foreseeable.

Gray whales are sensitive to many forms of anthropogenic disturbance including acoustic noise from seismic testing, oil and gas exploration, ship collisions, entanglement in fishing gear and habitat alteration (Rugh *et al.*1999, Baird *et al.*2002, COSEWIC 2004). They are listed as a species of 'special concern' under the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) mainly because of their successful recovery after the cessation of commercial whaling (Rugh *et al.*1999, Baird *et al.*2002). Current estimates for the eastern Pacific gray whale population are ~18,000 individuals (COSEWIC 2004). Even though the eastern gray whale population is thought to have reached historic levels, there still remains a need for protection through the establishment of marine reserves that target discrete foraging areas off Vancouver Island.

The evidence provided in chapter's 2, 3 and 4 supports the premise that networks of reserves are better suited in marine systems over single large reserves due to the scale at which gray whales disperse to forage, the variability in oceanographic production and the structure of nearshore mysid populations. Networks not only provide a degree of resilience to any potential change in the system, but they can also incorporate the inherent variability in oceanic systems within protective boundaries. For example, if gray whales were not present in the southern portion of the study area, due to a lack of sufficient prey, they may be present in the northern half of the study area. In effect, some parks may lay 'fallow' in terms of gray whale foraging activity either within a season or between years (unpublished data). Networks also provide resilience to human use of these areas. The secondary objective for the majority of these provincial parks focuses on recreational activities, which include whale watching, sport fishing and boating.

In the southern half of the study area, mainly in and around Clayoquot Sound, there is a thriving whale watching industry (Malcolm 2003). Both Flores Island and Vargas Island are host to several whale watching expeditions per day throughout the summer months. It is difficult to ascertain any disturbance to the whales foraging behaviour as a result of vessel interactions (Bass 2000), however it may become a management concern if the industry continues to grow without any limitations or park regulations and enforcement. Based on the data on average foraging depth and boundary delineation, an easy way to enforce entry into park areas would be to limit the number of vessels crossing the 10m contour line at any given time, especially on the western shores of Flores Island and in Cow Bay. At a larger scale, potential disturbance can be minimized with the addition of an MPA at Nootka Island and the extension of the Hesquiat Peninsula's western boundaries to include Perez Rocks and Barcester Bay since these areas receive virtually no recreational boaters or whale watchers. Therefore, the network of reserves can provide increased recreational opportunities in the south and act as refugia for foraging whales north of Estevan point. Consequently, this network of parks can fulfill all of the mandates pertaining to BC Parks, which has traditionally been a difficult task in protected area management and design. In addition, this research illustrates the importance of collecting ecological data on the species that we strive to protect before we establish conservation initiatives as well as the importance of elucidating connectivity through the trophic spectrum.

In the context of this thesis the use of the term 'foraging habitat' or 'important foraging areas' may invoke broader ecological consequences for gray whales. By definition, 'habitat', refers to the suite of physical and biological variables a species uses for survival and reproduction (Allaby 1998). This thesis only focuses on a portion of a gray whales' habitat - foraging habitat. However, as habitats in dynamic oceanic environments are difficult to define, gray whales do exhibit habitat partitioning in regards to breeding and foraging (Rice & Wolfman 1971, Nerini 1984, Kim & Oliver 1988, Rugh *et al.*1999). Whether or not these specific foraging areas are important to the overall fitness of the entire eastern gray whale population remains to be seen. It is probably unlikely. When viewed at finer spatial scales, discrete foraging areas may have more pronounced ecological consequences to these localized feeding aggregations of gray whales. If specific foraging areas off Vancouver Island were degraded by any means, how would that affect the local feeding aggregations of whales, if at all? It is likely that whales would simply move to other areas, however if the degradation of existing foraging areas were left unchecked and persisted, other effects on gray whale population dynamics may have greater influence (ie., density dependence, competition or increased predation). Essentially, there may be a reduction in their foraging range which would likely be a negative effect on their capacity to acquire resources.

The overarching goal of this thesis is to provide an example of a functional ecological network of marine reserves for foraging gray whales, regardless of their initial design. This thesis presents a multi-trophic level approach to measure connectivity and delineate boundaries for a network of marine reserves off Vancouver Island. Many studies of connectivity in marine systems focus only on one aspect of this phenomenon (usually with a single species) and rarely situate the species within the trophic spectrum. Independent studies on primary production, invertebrate dispersal and distribution, and cetacean distribution are useful and important, but they are rarely linked together to make more effective MPAs. Not only does this study offer a new approach to marine reserve design, it uses a wide ranging cetacean to illustrate the utility and potential of multi-trophic level studies in marine conservation. By choosing relevant trophic levels within a gray whales' food web and by measuring connectivity at each of these components, it gives a more full understanding of how these mechanisms operate within a framework of marine reserves. Although this method is tailored to a highly coastal cetacean, it may be applied to other wide ranging species in marine environments.

Marine reserves, albeit difficult to successfully implement, can minimize potential disturbances to gray whale foraging grounds through enforcement and proper management of human activities. It cannot be overemphasized that the success of MPAs in fulfilling conservation goals is mainly a result of political will and scientific certainty. In reality, BC marine parks only exist on paper, with little or no enforcement and a management regime that is largely nonexistent; nonetheless, they provide a foundation for future management and enforcement if need be.

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