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MARINE MAMMALS IN THE HECATE STRAIT ECOSYSTEM

by

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ABSTRACT

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There is an increasing interest in the development of ecosystem-based resource management tools. An ecosystem approach to management is necessary to provide more comprehensive advice to fishery managers about the interaction between fisheries and the ecosystems of which they are a part. This report forms the basis of the marine mammal component of an ecosystem model being developed by Fisheries and Oceans Canada for the Hecate Strait / Queen Charlotte Sound area of the British Columbia coast. Hecate Strait is well suited as a case study area for developing such a model because of the extensive commercial fisheries database and because the biota and physical environment (oceanographic and benthic) are relatively well studied. The region is under steady pressure from recreational and commercial activities and the benefits from an ecosystem-based management model would accrue to many stakeholders. This report summarizes current and historical data on marine mammals – including population size, distribution (spatial and temporal), catch (commercial and aquarium), diet, consumption, and production – for the species most commonly seen in British Columbia's northern shelf waters. Data from 1950 to present day are included, although earlier information is used when necessary to elucidate current conditions. Issues relating to the incorporation of these data in ecosystem models, and the role of marine mammals in the Hecate Strait ecosystem, are discussed.

ecosystems
marine mammals
resource management
modeling
pop. dynamics

RÉSUMÉ

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L'élaboration d'outils de gestion écosystémique des ressources suscite de plus en plus d'intérêt. Une méthode de gestion écosystémique est nécessaire pour fournir aux gestionnaires des pêches des conseils détaillés sur les interactions entre les pêches et les écosystèmes dont elles dépendent. Ce rapport constitue le fondement de la composante mammifères marins du modèle écosystémique que Pêches et Océans Canada est en train d'élaborer pour la région du détroit d'Hécate et du bassin de la Reine-Charlotte (C.-B.). La vaste base de données existante sur la pêche commerciale dans le détroit d'Hécate et le fait que le biote et le milieu physique (océanographique et benthique) sont relativement bien connus font en sorte que cette zone se prête bien à une étude de cas visant à élaborer un modèle écosystémique. Cette zone subit de manière soutenue les répercussions d'activités récréatives et commerciales, et de nombreux intervenants tireront profit d'un modèle de gestion écosystémique. Sont résumées dans ce rapport les données historiques et actuelles (de 1950 à aujourd'hui) sur les espèces de mammifères marins les plus fréquemment observées sur la plate-forme du nord de la C.-B., y compris des données sur la taille, la distribution (spatiale et temporelle), le régime alimentaire, la consommation et la production des populations ainsi que sur les prises (commerciales ou destinées à des aquariums). Les données les plus anciennes sont utilisées au besoin pour mieux comprendre les conditions actuelles. Les problèmes liés à l'intégration de ces données dans les modèles écosystémiques et le rôle des mammifères marins dans l'écosystème du détroit d'Hécate sont abordés dans ce rapport.

PREFACE

The available data on marine mammal abundance, distribution, and diet are generally quite limited. Abundance estimates from designed surveys have wide confidence intervals, largely because of the patchy distribution of the animals and the high level of effort required to obtain a reasonable number of sightings. In addition, surveys are conducted primarily in summer months, making it difficult to conclude anything definitive about seasonal occupancy in any particular area. Diet data are limited primarily to opportunistically collected samples, making them extremely patchy in time and in space. Since most marine mammals appear capable of feeding on a range of prey species, the relative influences of preference and availability on diet composition remain unknown. The validity of extrapolating these diet data beyond their location and time of collection is therefore open to debate.

Nevertheless, the increasing popularity of ecosystem and other integrated models implies that assumptions and generalisations will be drawn from the available data regardless of their quality or relevance. I have therefore endeavored to maintain a clear separation between the source data and the consequent model parameters by clearly laying out the assumptions necessary to derive the necessary parameters from the data. These assumptions are purposely simplistic (and occasionally somewhat naive) emphasizing the limited knowledge we have on these species.

My objectives were twofold. First, I wanted to provide the best possible parameters on marine mammal diet and abundance for the Hecate Strait Ecosystem Project. I also wanted this report to serve as a comprehensive review of the available abundance, distribution, and diet data for British Columbia and the Pacific Northwest. I hope that by emphasizing and maintaining the distinction between the derived parameters and the available data I have achieved both.

I wish to emphasize that the abundance estimates for marine mammals in Hecate Strait have a low, unknowable degree of accuracy. They are no more than the application of educated guesses and speculative assumptions to estimates that already have large confidence intervals. It would therefore be a mistake to adopt these abundance estimates for other applications without further consideration.

INTRODUCTION

This report addresses the marine mammal component of the Hecate Strait Ecosystem Project. The project was conceived to examine the possibilities of using the Ecopath suite of tools for ecosystem-based fisheries management, a topic which is becoming increasingly relevant to resource managers. The traditional fishery management paradigm is based on single species biological reference points and stock assessments. An ecosystem approach provides more comprehensive advice to fishery managers by taking into account the direct and indirect effects of other species, and potentially environmental conditions, on the future of commercial stocks. Ideally, management targets need to account for the effects of large scale environmental forcing, biological interactions among species, and their effects at different life history stages, when considering commercial stock production and recovery times, particularly after periods of heavy exploitation.

Hecate Strait is well suited as a case study for developing ecosystem-based methods for fisheries management. It has been the subject of considerable research on the spatial and temporal distributions, abundance, and feeding habits of many commercial species. Numerous research cruises have been conducted to describe the physical habitat characteristics such as surficial geology and physical oceanography. Unfortunately, marine mammals have not been the subjects of any such research efforts until very recently.

This report summarizes available data on population size and distribution, catch (commercial and aquarium), diet, consumption, and production for marine mammals that frequent British Columbia waters. Time series of population abundance and catches are provided where available. Population estimates for Hecate Strait were largely derived from values reported for a much larger geographic area (i.e., eastern North Pacific). Assumptions used to derive local population estimates are clearly stated. Diet information is limited to that available for the eastern North Pacific, except where additional information serves to clarify diet assumptions. The diet data are summarized by species, or by larger taxonomic groups, particularly for less common prey species, or in cases of insufficient data. The focus of this report is from 1950 to present day, however earlier information is used when necessary to elucidate current conditions.

MARINE MAMMALS IN HECATE STRAIT

The Hecate Strait study area includes the strait itself, Dixon Entrance to the north, and Queen Charlotte sound to the south (Figure 1). The western extent of the study area was delimited by the 500 m depth contour. While the study area does not explicitly include the ecology of inlets or littoral waters, the use of these areas by marine mammals and some of their prey species is acknowledged. The region is used extensively by a number of marine mammal species including 5 species of baleen whales, 2 species of pinnipeds, and 4 species of odontocetes (toothed whales). Other marine mammals occur in the study area infrequently (beaked whales, fur seals, California sea lions) or on the periphery (sperm whales, sei whales), and are therefore considered minor players in the Hecate Strait ecosystem. Nevertheless, sighting and catch data are included for beaked whales where they are available.

Patterns of habitat use vary considerably. The large baleen whales are migratory, with the occurrence of blue, fin and sei whales peaking during the summer months. Humpback whale abundance also peaks during the summer, but the species is observed in British Columbia on a year-round basis. The migration of grey whales takes the majority of the population past the British Columbia coast in spring and fall, although some remain in British Columbia waters all summer. In contrast, little is known about the seasonal movements of minke whales. Steller sea lions exhibit strong seasonal movements that take them from rookeries during the breeding season (June-August) to more widely distributed haul-outs at other times of the year (Figure 2). Dall's porpoise, harbour porpoise and Pacific white-sided dolphins have all been observed in the study area, but there is little information on their spatio-temporal distributions. Harbour seals are increasingly common in British Columbia, occur on a year round basis, and appear to exhibit some site fidelity. Sea otters, while establishing a small presence in the study area, are not included in this analysis because of their relatively small numbers and primarily near shore distribution.

SIGHTING DATA

Marine mammal sighting data (Table 1) have been collected in British Columbia since 1957. These data are maintained by the Vancouver Aquarium Marine Science Centre as part of the British Columbia Cetacean Sighting Network in collaboration with the Department of Fisheries and Oceans. These data include sightings from studies conducted by Parks Canada in the Queen Charlotte Islands (Ford et al. 1994) as well as coast-wide data collected voluntarily from boaters.

Unfortunately, effort and sightability biases in these data complicate any analysis. It is difficult to assume equal sightability because some species (e.g., Dall's porpoise, Pacific white-sided dolphins) are more attracted to vessels than others. Meanwhile, sighting effort is biased towards areas frequented by boaters, and particular species (e.g., killer whales, grey whales). Nevertheless, the proportion of animals observed over all years likely gives some indication of the relative abundance of marine mammals in waters frequented by boaters. These proportions are used in partial support of the abundance estimates for minke and humpback whales.

MARINE MAMMAL ECOSYSTEM PARAMETERS

Marine mammal data for ecosystem models of the eastern North Pacific were first prepared by Trites and Heise (1996a, b), in support of mass balance models of the Alaska Gyre and the southern British Columbia shelf. The southern British Columbia shelf study area included Queen Charlotte Sound and the west coast of Vancouver Island, but none of the inside straits. The Alaskan Gyre study, while not explicitly defined, is assumed to represent the pelagic area, over abyssal depths, centered in the Gulf of Alaska. This information has been modified and updated for subsequent EcoPath models including Trites et al. (1999 – Bering Sea); Haggan et al. (1999 – Hecate Strait); Okey and Pauly (1999 – Prince William Sound); and Pitcher et al. (2002 – Northern British Columbia). This report represents the first comprehensive review of these parameters for British Columbia waters since Trites and Heise (1996a, b).

Biomass estimates are a function of animal size and abundance. Estimates of mean body weight for males and females of each species were based on the methods of Trites and Pauly (1998). This remains the most reliable and consistent method of estimating mean population body weights from a species' maximum length. Abundance and distributional estimates were based primarily on the latest status reports from the National Marine Fisheries Service (NMFS) and the Department of Fisheries and Oceans (DFO). Abundance was first estimated for the entire eastern North Pacific. Local (Hecate Strait) estimates were then based on simple distribution assumptions and additional data where available. However, abundance and distributional information for marine mammals is generally poor with rather large confidence intervals. Confidence intervals or other measures of uncertainty were included when they appeared in the source. Abundance estimates were subsequently derived for Hecate Strait as either a minimum value, or with a somewhat arbitrary range, based on the data and the assumed strength of the assumptions. These ranges are provided as a guide to the modeling process, not as a true confidence interval for the study area population.

Diet compositions for commercial whale species were based on stomach contents examined during the latter part of the whaling era (primarily 1960s and 1970s). Diet information for other species was based primarily on strandings (odontocetes), fecal analysis (pinnipeds), and direct observation (killer whales, Pacific white-sided dolphins).

Consumption rates (i.e., annual ration) for baleen whales were assumed to be 4% of body weight per day (Lockyer 1981). For small odontocetes and pinnipeds, consumption was calculated according to an allometric equation (Innes et al. 1987) based primarily on captive juvenile pinnipeds and modified by Trites and Heise (1996a). The daily ration R (kg/day) was given by:

$$R = 0.1 \cdot W_{i,s}^{0.8} \qquad \text{Equation 1}$$

Where W is the mean body weight in kilograms for species (*i*) and sex (*s*). The value of 0.1 was adjusted downward from the published value of 0.123 by Trites and Heise (1996a) to account for the difference between growth and maintenance.

CONSIDERATIONS FOR ECOSYSTEM MODELING

OCEANOGRAPHY AND PATCH DYNAMICS

Hecate Strait is part of the transition zone between the coastal downwelling domain (extending from the central to southeast coasts of Alaska) and the coastal upwelling domain located primarily off the coast of Washington and Oregon (Ware and McFarlane 1989). These two oceanographic domains likely contain somewhat different ecosystems, including different fish communities. The position of the transition zone is primarily a function of the North Pacific West Wind Drift, which bifurcates into the Alaskan Current – the southern portion of the Alaskan Gyre, and the California Current – part of the Central Pacific gyre.

These dynamic oceanographic conditions presumably influence the year to year structure of fish communities in the study area and, by extension, the distribution of most marine mammals. Understanding the underlying relationships between marine mammals and their prey in such a dynamic oceanographic region presents a significant challenge to the effective representation of marine mammals in an ecosystem model.

Marine mammals are some of the most wide-ranging predator species in marine ecosystems. As top predators capable of consuming significant amounts of biomass, their role in structuring ecosystems can be significant. However their interactions with prey species occur over a range of spatial and temporal scales, making it difficult to quantitatively evaluate these interactions and the corresponding ecosystem effects (Trites 2002). With the exception of a few species, marine mammals are generalist predators, well suited to exploiting prey patchiness due to their high mobility: Grey whales are capable of exploiting spring herring spawn; humpback and blue whales exploit euphausiid concentrations, transient killer whales search for pinniped pupping areas, and small cetaceans and pinnipeds likely take advantage of the seasonal pulses in forage fish. Therefore, prey distribution will clearly affect seasonal and annual occupancy.

Given the dynamic nature of the study area, and the presumed ability of marine mammals to adapt to changes in prey distributions, inter- and intra-annual fluctuations are an important aspect of ecosystem studies. However, while ecosystem models provide the ability to adjust diet preferences and population estimates on a proportional basis, few implementations support the representation of spatial or temporal patchiness. The importance of the ecosystem dynamics that consequently remain unrepresented is an open question that can only be answered through extensive testing of the model against some explicit representation of patch dynamics.

MARINE MAMMAL POPULATION TRENDS

The available information on the population trends of British Columbia's marine mammals may provide some insight into how their ecological role may have changed over time. These trends will assist with the time series fitting of the ecosystem model.

The grey whale population has shown a steady increase in numbers from 1950 until the early 1990s (SAR 2002), when the population appears to have reached historic abundance levels. For this study, the more important aspect is the resultant increase in the portion of the population that feeds in British Columbian waters vs. that which completes the northward migration. Given the recovery of this species over the last 50 years, it is reasonable to expect this recovery to have been logistic in shape. Similarly, the abundance of fin whales in the study area can be assumed to have recovered from near zero in 1954 to the estimated population size presented herein. Humpback whales also appear to be recovering in the study area, but it is premature to make assumptions about the shape of the recovery curves for these two species.

With little evidence to the contrary, it is reasonable to assume that minke whale and odontocete (toothed whale) populations (with the exception of killer whales) have been relatively stable from 1950 to present. The population level effects of killer whale removals in the 1960s remains unclear given the small population size and strong social structure. In spite of this assumed stability, the inter-annual and seasonal occurrence of odontocetes in the study area can also be assumed to be variable. Given the information contained herein, odontocetes can be listed according to decreasing habitat use variability as: Pacific white-sided dolphins >> transient killer whales > Dall's porpoise > harbour porpoise > resident killer whales. This qualitative knowledge may provide some guidance with respect to the flexibility of functional groups during the fitting of the model to time series data.

Abundance and removal estimates for Steller sea lions and harbour seals are some of the most accurate data presented here, and thereby provide an excellent set of constraints on the ecosystem model. If the resulting model can be made to reflect the impacts of the historic removals and subsequent recovery of these pinniped populations, it's potential use as a management tool will be enhanced.

FUNCTIONAL GROUPS

It is standard practice in ecosystem models to create functional groups containing a number of species. For marine mammals, it has become commonplace to create a baleen group including all large whales (i.e., grey, blue, fin, humpback, and minke whales). However since the characteristics of functional groups are proportional to the biomass of the constituents, this baleen group – which has always been dominated by grey whales – has presumably always behaved primarily as a benthic foraging group. If grey whale diet dominates the dynamics of the group, then it will be relatively insensitive to other prey species (e.g., euphausiids – the main prey for blue and humpback whales). Consequently, the baleen group may show little change in response to a reduction in euphausiids when in fact, humpback and blue whales could be significantly affected. The model would not reflect the loss of these euphausiid predators, and the corresponding increase in euphausiid availability would also be missed, potentially resulting in an erroneous increase in other euphausiid predators.

Thus, a key consideration in creating functional groups should be whether potential members play a similar ecological role. It is also essential to consider data availability and quality when creating functional groups to ensure that minimal information is lost. Species with more data can be more accurately parameterized, and it may be an advantage to avoid distorting relatively accurate information with assumptions for species where less information is available. Finally, given the high profile of certain charismatic species such as large whales, a model with fewer functional groups and more individual species – especially at higher trophic levels – is likely to be better received, particularly by the public.

For functional groups, a baleen group consisting of blue, fin and humpback whales is reasonable. The ecological role of these 3 species as zooplankton grazers is similar, but appears to be separated spatially with humpback whales closest to the shore and blue whales furthest away. It is recommended that grey whales be kept separate from the baleen group, and further divided into resident and migratory populations because the significant differences in diet and occupancy likely lead to different roles in the Hecate Strait ecosystem. For the purposes of a fisheries management model, the minke whale, Pacific white-sided dolphin, Dall's porpoise and harbour porpoise could reasonably be combined into a "small cetacean" group given their diet composition. Resident and transient killer whales should be maintained as their own groups.

Previous ecosystem models of the study area have combined harbour seals and Steller sea lions into a pinniped group. While this is an attractive idea, these species contribute significant biomass to the study area and display opportunistic feeding habits which may be relevant to the fisheries management model. Keeping the species separate would facilitate analysis of the model based on a sensitivity analysis of their diet composition. In addition, keeping the detailed time series data separate for each species would allow more accurate fitting of the model to time series data.

BALEEN WHALES

All of the large whale species were once found within 200 nmi of British Columbia. This includes the baleen species: blue (*Balaenoptera musculus*), fin (*Balaenoptera physalus*), sei (*Balaenoptera borealis*), humpback (*Megaptera novaeangliae*), North Pacific right (*Eubalaena japonica*), and grey (*Eschrichtius robustus*) whales. Sei, fin, blue, grey, and humpback whales all engage in extensive migrations between summer feeding grounds (north) and winter breeding grounds (south). Historically, these migrations brought them within reach of the coastal whaling stations (i.e., within 200 nmi of shore). While the sei whales appear to have migrated past British Columbia, subpopulations of fin, humpback, and possibly blue whales may have used sections of the British Columbia coast as feeding areas (Gregr et al. 2000). Today, the remnant population of North Pacific right whales has been seen primarily in the Bering Sea (SAR 2001e), while grey and humpback whales both make extensive use of coastal habitats (Darling et al. 1998, Pike and MacAskie 1969).

The smaller minke whale (*Balaenoptera acutorostrata*) was never hunted commercially by British Columbia coastal stations. Consequently, very little local information is available on the abundance or distribution of this species. Nevertheless, there is evidence the species occurred in British Columbia's inshore waters (Pike and MacAskie 1969).

For each species, available abundance and stock structure data were reviewed. This information was combined with historic catch distributions, and other assumptions as necessary, to derive the abundance parameters for this study. To further support the abundance estimates, the spatial distribution of georeferenced historic catches was summarized to provide an indication of what proportion of the commercial stocks were caught in the study area (Table 2).

BLUE WHALES

The current size and distribution of blue whale populations in the North Pacific remains unclear. Gambell (1976), cited in Breiwick and Braham (1984), estimated the pre-exploitation stock for the entire North Pacific at 4,900 (no coefficient of variation – CV) and 1976 stocks at 1,600 (1,400-1,900; no CV). Recent surveys by the NMFS have led to the recognition of only two stocks in US waters: A Hawaiian stock for which no population estimate is available; and a California/Mexico stock with an estimated population size of 1,940 (CV=0.15) (SAR 2000a). This estimate is a variance weighted averaged of line transect and mark recapture estimates. Perry et al. (1999) provide a minimum estimate of 3,300 for the entire North Pacific.

NMFS (1998) suggested that there may be as many as five subpopulations in the North Pacific. Gregr et al. (2000) elaborated on this and suggested that one of these subpopulations – the eastern Gulf of Alaska stock – may have used southeast Alaska and northern British Columbian waters as a feeding ground. The British Columbia catch record shows that 29% of the blue whales caught by coastal stations were potentially within the study area (i.e., in depths of 200 m or less, north of 51.5° N latitude - Table 2). However these catches were predominantly on the western edges of Dixon Entrance and Queen Charlotte Sound (near the shelf break).

Abundance and diet estimates

Assuming that: 1) there are five stocks in the North Pacific; 2) they contain the same number of animals; 3) the catch proportions (Table 2) reflect the proportion of this stock (29%) that may frequent the study area; and 4) using the most recent North Pacific population estimate of 3,300 animals, an abundance estimate for Hecate Strait of 3,300/5 * 0.29 = 191 animals can be calculated. However given that: 1) the majority of animals likely occur in exposed, shelf-edge regions outside the current study area; 2) the putative stock extends across the eastern Gulf of Alaska; and 3) the California/Mexico stock may currently represent closer to 2/3 of the North Pacific population, this estimate should be reduced, perhaps by 50-90% (to between 96 and 12 animals). Recent surveys suggest that the lower end of this estimate is more appropriate as two years of effort have produced only one sighting (J.K.B. Ford, personal communication. Pacific Biological Station, Nanaimo, BC, V9R 5K6). The abundance for Hecate Strait was therefore estimated at 25, with a range of 10-100 animals (Table 3).

The diet of blue whales (Table 4) is understood to be predominantly euphausiids. Diet composition was estimated according to Nichol and Heise (1992) who reported a diet of euphausiids (95%) and copepods (5%) based on the contents of 30 stomachs.

FIN WHALES

Large numbers of fin whales were taken only after modern whaling was introduced to the North Pacific at the turn of the 20th century. The 1974 North Pacific population was estimated at between 14,620-18,630 animals, down from a pre-exploitation estimate of 42,000-45,000 (Breiwick and Braham 1984). An estimated 8,520-10,970 animals were believed to occur in the eastern Pacific during the early 1970's (Perry et al. 1999). Gregr et al. (2000) supported previous suggestions (Pike and MacAskie 1969) that a subpopulation used British Columbian waters as a feeding ground. NMFS recognizes three stocks of fin whales in American waters: Hawaii, Alaska/Northeast Pacific, and California-Washington-Oregon (Ca/Wa/Or). The size of the Ca/Wa/Or stock was recently estimated at 1,236 animals (CV=0.20), with a minimum population of 1,044 (SAR 2001a). No estimate is available for the entire Alaska/Northeast Pacific stock. However a summer 1999 survey in the central Bering Sea yielded an estimate of 4,951 animals (CV=0.29) for that region (SAR 2001b).

Abundance and diet estimates

Combining the population estimates from the Ca/Wa/Or and Bering Sea surveys gives a minimum estimate of 5,995 animals for the eastern North Pacific stock. Assuming 6,000 animals, divided equally between Alaska, British Columbia, and Ca/Wa/Or, and using the study area proportion from Table 2 (12%) gives an estimate of (6,000/3) * 0.12 = 240. Two factors may warrant a reduction of this estimate. Commercial catches of this species moved progressively further offshore between the 1940s and 1967 (Gregr et al. 2000), indicating that inshore animals were the first to be caught. This inshore removal, combined with any degree of feeding site fidelity, would slow the recovery of the species in inshore waters. The study area abundance was therefore estimated at 200 (100-300) animals (Table 3).

Nichol and Heise (1992) described fin whale diet as euphausiids (75%), copepods (20%), and miscellaneous pelagic fish (5%). Based on a recent analysis of stomach contents (Flinn et al. 2002), the estimated diet composition was revised to include euphausiids (85%), copepods (10%), herring (*Clupea pallasii*) (3%) and small squid (2%) (Table 4).

SEI WHALES

Although 3% of the total British Columbia sei whale catch came from Hecate Strait (Table 2), this is primarily an offshore species whose occurrence in British Columbia coastal waters is unpredictable (COSEWIC 2003a). During the last years of the whale fishery (1950's to 1967), even fewer of these catches occurred in the study area (Nichol et al. 2002, Tables 5a, b). The study area abundance was therefore estimated as 0.

MINKE WHALES

While minke whales were never extensively exploited in the eastern North Pacific, the IWC does recognize three North Pacific stocks on the basis of this limited exploitation history: One in the Sea of Japan/East China sea; one in the western North Pacific (west of 180°), and one in the "remainder" of the Pacific. The "remainder" stock is divided into two stocks by NMFS: The Alaska stock and the Ca/Wa/Or stock (SAR 2001c).

The most recent population estimate for the Ca/Wa/Or stock is 631 (CV=0.45), with a minimum estimate of 440 (SAR 2000b). A recent survey in the Bering Sea provided an estimate of 936 (CV=0.35) animals for the central Bering Sea during summer. However this estimate cannot be extrapolated to the rest of the Alaskan stock (SAR 2001c).

At least some minke whales in the Ca/Wa/Or stock appear to establish home ranges, in contrast to the more migratory habits of the animals further north (Dorsey et al. 1990). These resident minke whales occur in the inland waters of Washington State (i.e., east of Cape Flattery) and in central California. They are considered by NMFS to be a separate stock because of apparent behavioural differences (SAR 2000b). The species occurs year round in California waters, and in the Gulf of California (SAR 2001c).

Trites and Heise (1996b) estimated the number of minke whales on the southern British Columbia shelf, at 100, with a range of 50 to 300, based on pure speculation (K. Heise, personal communication. Department of Zoology, University of British Columbia, Vancouver, BC, V6T 1Z4). Given that this species occurs in both Alaska and Ca/Wa/Or, it is likely that it also occurs with some frequency in the waters of Hecate Strait. According to Pike and MacAskie (1969), minke whales were frequently seen in inside waters. The sighting data (Table 1) suggest that minke whales are encountered by boaters almost as often as grey whales and harbour porpoise.

In Kawamura's (1980) detailed review of stomach contents from whale fisheries around the world, minke whales appear to be among the most euryphagous of the baleen species. The greatest diet diversity is observed in the North Pacific, likely due to the higher diversity of available prey. Kawamura (1980) lists a range of fish species in the minke whale diet including herring, saffron cod (*Eleginus gracilis*), Arctic smelt (*Osmerus mordax dentex*), capelin (*Mallotus villosus*), walleye pollock (*Theragra chalcogramma*), sandlance (*Ammodytes* spp.), Pacific cod (*Gadus macrocephalus*), rockfish (*Sebastes* spp.), Atka mackerel (*Pleurogrammus monopterygius*), sardines (*Sardinops* spp.), chum salmon (*Oncorhynchus keta*), Arctic cod (*Boreogadus saida*), and Pacific saury (*Cololabis saira*). Kawamura (1980) also noted that in the Bering Sea, fish prey increased in importance over zooplankton in coastal waters. Tamura and Fujise (2002) elaborated on the seasonal and geographical aspects of minke whale diet in the western North Pacific, and suggested that the seasonal and geographic changes in diet are a reflection of prey aggregations. From a total of 426 stomachs sampled between 1994 and 1999, the dominant prey found included Japanese anchovy (*Engraulis japonicus*) (43.7%), Pacific saury (36.5%), and euphausiids (17.1%), with 90.4% of the stomachs containing a single species. The diet of minke whales therefore seems to reflect local availability. Hoelzel et al. (1989) identified different feeding strategies associated with different feeding areas, further documenting the adaptability of minke whales to particular prey patches.

Abundance and diet estimates

There is little data available from which to estimate the abundance of this species in the study area. Abundance was therefore arbitrarily estimated at 200 (100-300), assuming: 1) the minimum population estimate for Ca/Wa/Or is 440 animals, and 2) that British Columbia has an equal number of animals, of which half may occur in the study area (Table 3). This estimate is very similar to that of Trites and Heise (1996b).

Minke whale diet for the southern British Columbia shelf was estimated by Trites and Heise (1996b) as euphausiids (30%), copepods (30%), herring (20%), and sandlance (20%). For this study, diet composition was expanded (Table 4) to include the range of schooling fishes mostly commonly found in the study area. The revised diet included: euphausiids (20%), copepods (5%), herring (15%), sandlance (10%), Pacific cod (5%), rockfish (5%), transient (pink – *O. gorbuscha* and chum) salmon (5%), gadids (5%), and other forage fish (30%).

HUMPBACK WHALES

Humpback whales were one of the first targets of the coastal whalers. The largest catches by British Columbian stations occurred between 1908 and 1917 (Gregr et al. 2000). While by 1925, the coastal whalers had turned their focus to other species, humpback whales continued to appear in the catch through the 1960's (Gregr et al. 2000, Table 5a).

It is estimated that a pre-1905, North Pacific population of about 15,000 humpback whales may have been reduced to as few as 1,000 animals prior to international protection after 1965 (Rice 1978). SAR (2001d) identified 3 stocks of humpback whales recognized by the NMFS in the North Pacific: The Ca/Wa/Or and Mexico stock; the Central North Pacific stock; and the

Western North Pacific stock. The Central North Pacific stock is believed to breed in Hawaiian waters and to use three feeding areas located around Kodiak Island, Prince William Sound, and southeastern Alaska (presumably including northern British Columbia).

Baker and Herman (1987) gave a mark recapture estimate for the Central North Pacific stock of 1,400 animals based on data collected between 1980 and 1983. Cerchio (1994 cited in Clapham et al. 1999) suggested that the size of this stock could be anywhere from 2,000 to 5,000 animals. Calambokidis et al. (1997) estimated this stock at 4,005 (CV=0.095), and provided the only recent basin-wide estimate of 6,000-8,000 animals. In northern British Columbia, 275 individual animals have been identified between 1992 and 1998, primarily around Langara Island (G. Ellis, personal communication, cited in SAR 2001d).

Over 900 animals have been individually identified in British Columbia waters as part of recent photo-id efforts (Ford, personal communication). However it is currently unclear how many of these animals use British Columbia waters on an annual basis. The majority of these animals have been identified at the northern (Dixon Entrance) and southern (Queen Charlotte Sound) edges of Hecate Strait.

Abundance and diet estimates

Based on the available data, it is clear that the humpback whale population in British Columbia has increased considerably over the last 2-3 decades. To support the time series fitting of the model, local abundance estimates were derived for two periods based on the estimates of 1,400 for 1980 (Baker and Herman 1987), and 4,005 for 1997 (Calambokidis et al. 1997).

Estimates of study area abundance were based on three assumptions: 1) The three feeding groups of the Central North Pacific stock are of equal size; 2) half of the southeastern Alaska/northern British Columbia feeding group occurs in British Columbia; and 3) the historical proportion of the catch from Hecate Strait (11%, Table 2) reflects the study area abundance. These assumptions applied to the 1980 estimate of 1,400 gave an abundance estimate of 1,400 / 3 / 2 * 0.11 = 26 animals. Applied to the 1997 estimate of 4,005, they gave an abundance estimate of 4,005 / 3 / 2 * 0.11 = 73 animals.

However, a number of factors confound these estimates. First, the distributional assumptions are completely arbitrary. While considerable effort is currently being applied to identifying size and distribution of the central North Pacific stock, there is currently no basis on which to make assumptions regarding it's relative distribution. Second, the whale fishery was prosecuted primarily in waters at and beyond the shelf break. The calculated proportion of whales in the study area (11%) is therefore likely biased downwards because animals migrating to Hecate Strait would have been intercepted prior to entering the study area. Finally, the large number (>900) of individuals photo-identified in British Columbia is a strong indication that a present day estimate of 75 animals is somewhat low.

With no clear basis for refining the initial estimates, it was further assumed that, given the success of the photo-id work, they represent minimum values. Abundance was therefore estimated at 25 (25-100) animals for 1980 and at 75 (75-300) animals for 1997.

Humpback whale diet (Table 4) was estimated according to Nichol and Heise (1992) who reported a diet of euphausiids (80%), copepods (10%), and herring (10%) based on the contents of 35 stomachs. This diet was also used for the southern British Columbia shelf (Trites and Heise 1996b).

RIGHT WHALES

Population estimates from 1984 indicate less than 200 individuals in the North Pacific (SAR 2001e). Historically, the population extended across the entire North Pacific Ocean above 35°N, primarily in continental shelf regions. Sightings have occurred as far south as Central Baja California and the Yellow Sea in the winter, and far north as the Bering Sea and the Sea of Okhotsk in the summer. Between 1910 and 1934, seven right whales were taken by British Columbia coastal whalers (Nichol et al. 2002). Only 29 reliable sightings occurred in the eastern North Pacific between 1900 and 1991 (NMFS 1991), and recent aerial surveys in the Bering Sea (1998-2000) have photographed only 14 individual animals (SAR 2001e). The eastern North Pacific population may number in the tens of animals (O and Ford 2003). The study area abundance was therefore estimated at 0.

GREY WHALES

The initial, unexploited population size of grey whales in the eastern North Pacific was likely 15,000-35,000 individuals (Breiwick and Braham 1984; Reilly 1992). Heavy harvesting reduced this population to commercial extinction by the 1900s. Today, with an estimated population size of approximately 21,000 animals, it is believed to have recovered to historic levels (SAR 2002). With population growth rate estimates ranging as high as 7.2%, NMFS has adopted an R_{max} of 4.7% for this species (SAR 2002). Recent estimates of abundance (Table 6) provide annual estimates from 1967 to 1995 based on an annual population growth rate of 2.5% (Buckland and Breiwick 2002). An annual production rate of 2.5% was therefore recommended for this species.

Grey whales migrate through the coastal waters of British Columbia in the spring and fall. The northward (spring) migration is close to shore, and inshore feeding appears to be common during this portion of the migration. The southbound (fall) migration appears to be further from shore, and little feeding has been observed (COSEWIC 2004).

A small portion of the population does not complete the migration to Alaska and spends the summer feeding off the British Columbia coast. Termed summer-resident grey whales, these animals appear to exhibit feeding site fidelity, and are seen along the entire west coast of Vancouver Island, and along British Columbia's central and north coasts (Figure 3) (COSEWIC 2004).

On Arctic feeding grounds the diet of grey whales is comprised almost exclusively (95%) of amphipods (*Ampelisca* spp., *Atylus* spp., and *Anonyx* spp.) (Nerini 1984). However the diet in British Columbia is more diverse. Resident grey whales consume mysid shrimp (primarily *Holmesimysis sculpta*, *Neomysis rayii*, and *Acanthomysis* spp.), porcelain crab larvae (*Pachycheles rudis*), and benthic ghost shrimp (*Callianassa californiensis*) as well as benthic amphipods (Family Ampeliscidae) (e.g., Dunham and Duffus 2002, Darling et al. 1998). Migratory animals, particularly late migrants, appear to consume primarily herring spawn to increase their energy reserves before completing the migration. The majority of this feeding is conducted in western Hecate Strait feeding areas (COSEWIC 2004).

Abundance and diet estimates

It is difficult to estimate either the migratory or summer-resident populations of Hecate Strait with any accuracy given the lack of information for much of British Columbia's central coast, and no quantitative information on the inshore diversion of the main migration. Given that work done primarily on the west coast of Vancouver Island and the south Central Coast has identified 71 summer-residents to date, the summer-resident population in Hecate Strait was estimated at 50-150 animals, with a point estimate of 75.

The proportion passing through Hecate Strait likely changes from season to season according to oceanographic conditions. With very limited information regarding the migratory diversion into Hecate Strait (COSEWIC 2004, Pike 1962), an abundance estimate of 300 (100-1000) animals in Hecate Strait is purely speculative.

The relationship between these present day estimates and the modeled time series of annual abundance for the entire eastern Pacific population (Table 6) is unknown. For the purposes of fitting a time series, one approach would be to assume that the migratory diversion and the summer-resident population is a constant proportion of the total eastern Pacific stock. While a non-linear relationship may be more likely from a biological perspective, there is no information from which to even begin to estimate the necessary parameters.

The diet estimate presented here was modified significantly from the more benthic diet proposed by Trites and Heise (1996b) for the southern British Columbia shelf. For migratory grey whales, diet was estimated as herring spawn (60%), crab larvae (20%), ghost shrimp (10%), and benthic prey (amphipods, polychaetes and molluscs) (10%). The diet for resident grey whales was estimated as mysid shrimp (60%), benthic prey (30%), ghost shrimp (5%), and crab larvae (5%) (Table 4).

BIOMASS, CONSUMPTION AND PRODUCTION

Baleen whale biomass (Table 3) was calculated according to Equation 2 where: A is abundance, W is the mean adult body weight in tonnes, and O is the annual occurrence, based on the portion of the year that the population is considered present in the study area.

$$B = A \cdot W \cdot O \qquad \text{Equation 2}$$

Abundance was based on the available data and the assumptions outlined above. Adult body weight was based on the maximum reported lengths of males and females, and assumes a sex ratio of 50%. These values were taken unmodified from Trites and Heise (1996a, b) and are based on methods subsequently published by Trites and Pauly (1998).

Occurrence for blue, fin and humpback whales is based on monthly trends in historic whaling records presented in Gregr et al. (2000). The monthly trends for these species are similar and show a steadily increasing number of animals from April to August and a marked decline in numbers in October. Occupancy for these species is therefore estimated to be from June to September (4/12 = 0.33).

The northward grey whale migrations extend over many months, with the majority of the animals passing through British Columbia waters between January and the end of May. Occupancy in the study area is estimated at about 2 months (Ford, personal communication). Summer-resident grey whales occupy British Columbia feeding grounds between March and November (Volker Deecke, personal communication. Marine Mammal Research Unit, University of British Columbia, 6248 Biological Sciences Road, Vancouver, BC, V6T 1Z4). This translates into occupancies of 2/12 (0.17) and 9/12 (0.75) for migrating and resident grey whales respectively.

Heise (personal communication) suggested that minke whales in British Columbia appear to be quite resident, implying behaviour more like animals from Ca/Wa/Or than those in Alaska. With no additional information, and allowing for some limited movement out of the study area, an occupancy of 9/12 (0.75) is arbitrarily assumed.

Trites and Heise (1996a, b) calculated sex-specific mean weights and daily rations according to Equation 1, and assumed sex ratios of 0.5 for all baleen species. While more accurate sex ratios are available from the historic whaling records (Nichol and Heise 1992, Gregr et al. 2000), this adjustment was considered unnecessary given the arbitrary nature of the abundance estimates. Table 3 therefore shows weights and rations for these species based on the means of the sex-specific values reported by Trites and Heise (1996a, b).

The Consumption/Biomass ratio can be calculated independently of the size of the study area according to Equation 3:

$$\begin{aligned} Q/B &= A_N * 365(r) / A_N * wt \\ &= 365 * r / wt \end{aligned} \qquad \text{Equation 3}$$

Where *A* is the annual abundance, corrected for seasonal shifts in distributions; *r* is the calculated daily ration; and *wt* is the mean weight of an individual.

The currently accepted maximum rate of population growth (R_{max}) for cetaceans is 4% (Reilly and Barlow 1986). Annual production was therefore estimated as half of R_{max}, or 2% for all baleen species (except grey whales, as noted above). This value was originally proposed by Trites and Heise (1996a, b), and is therefore consistent with all previous Ecopath studies of marine mammals in the North Pacific.

REMOVALS

Baleen whales were hunted in the eastern North Pacific by both a coastal and a pelagic whale fishery. The proportion of Hecate Strait animals removed by the pelagic fishery during their oceanic migration is difficult to estimate. However detailed records were kept by the coastal fishery (Nichol et al. 2002) for the time period of interest (1954 to present). These values can be considered the minimum numbers removed annually from the study area.

Coastal whalers removed at least 9,828 animals from British Columbia waters between 1948 and 1967 (Table 5a). The majority of animals taken were fin (34%), sei (28%) and sperm (28%) whales. These animals were all taken by vessels operating from the whaling station located at Coal Harbour, on the west coast of Vancouver Island (Gregr et al. 2000, Nichol et al. 2002).

To estimate the proportion of kills that occurred in the study area, the catch data was subset based on the geographic coordinates reported for each whale kill. The subset (Figure 4, Table 5b) contains those animals killed above 50.75° latitude, and in waters less than 1000 m deep. Although the 1000 m contour extends somewhat beyond the boundary of the study area (Figure 1), given the mobility of these species it can be assumed that Table 5a contains minimum removals from the study area for those species that frequent Hecate Strait (the 500 m contour was not part of the available oceanographic data set). Sperm, sei and beaked whales collectively comprised 56% of the total catch (Table 5a), but only 24% of the catch in the study area subset (Table 5b). Furthermore, the the majority of these catches were near the 1000m boundary. This supports the assertion that these three species do not play a major role in the ecology of the study area.

Coastal whaling ceased in British Columbia in 1967, and all species were protected from whaling by the International Whaling Commission by 1986. However whaling on a small scale (100s of animals) was recently (1994) resumed by the Japanese in the western North Pacific and is expected to continue (Government of Japan 2002).

TOOTHED WHALES

The odontocetes are a diverse group of animals ranging from the large, deep water sperm whale (*Physeter macrocephalus*) to the much smaller coastal dolphins and porpoises. This group also includes the pelagic beaked whales. Species which occur regularly in Hecate Strait include killer whales (*Orcinus orca*), Pacific white-sided dolphins (*Lagenorhyncus obliquidens*), Dall's porpoise (*Phocoenoides dalli*), and harbour porpoise (*Phocoena phocoena*). Sperm whales are regularly found on the edge of the study area, near the shelf break.

Baird's (*Berardius bairdii*), Stejneger's (*Mesoplodon stejnegeri*), and Cuvier's (*Ziphius cavirostris)* beaked whales are three ziphiids whose ranges include the offshore waters of British Columbia. However very little information is available on these, or other beaked whale species as they are primarily found in the open ocean. Although SAR (1999a) shows the range of Baird's beaked whale well offshore, 25 Baird's beaked whales were nevertheless taken by British Columbia whaling stations (Table 5a), and sightings have been reported throughout the summer off the west coast of Vancouver Island, with abundance peaking in August (Pike and MacAskie 1969). Evidence of Cuvier's beaked whale is British Columbia comes almost exclusively from strandings obtained from the central and west coasts, and the Queen Charlotte Islands (Pike and MacAskie 1969). SAR (1999b) shows the range of this species extending further inshore than that of Baird's beaked whales, including portions of the study area. Stejneger's beaked whales are the least understood of these three species in British Columbian waters. SAR (1999c) shows the range off British Columbia as intermediate between the other two species. Pike and MacAskie (1969) describe two strandings of *M. stejnegeri*, and two of *M. carlhubbsi*, an even lesser known species. Thus, while these species may occasionally be seen in on-shelf waters (Table 1), their ecological role in Hecate Strait is likely not significant.

SPERM WHALES

Sperm whales comprised almost a third (28%) of the total commercial catch by British Columbia coastal whaling stations between 1948 and 1967 (Table 5a), and 79% of the catch from the Queen Charlotte Island stations at Rose Harbour and Naden Harbour between 1933 and 1943 (Pike and MacAskie 1969). At least 6,158 sperm whales were removed by British Columbia coastal whaling between 1908 and 1967 (Nichol et al. 2002). While the majority of the animals were taken at or beyond the shelf break, habitat characterization suggests that males may occasionally use the deeper waters that extend into Hecate Strait at the south end of Moresby Island (Gregr and Trites 2001).

The IWC recognizes an eastern and a western stock in the North Pacific, while NMFS has divided the eastern stock into 3 management populations: 1) Alaska (North Pacific); 2) Ca/Wa/Or; and 3) Hawaii (SAR 2001f). Rice (1989) estimated that a pre-exploitation North Pacific population of 1,260,000 was reduced to 930,000 by the late 1970s. Recent estimates for the western North Pacific stock – 102,112 (CV=0.155), and the eastern temperate North Pacific –

39,200 (CV=0.60), are cited in SAR (1998a). However both current and historic abundance estimates for sperm whales are considered unreliable SAR (2001f).

Trites and Heise's (1996a) estimated a diet of large squid (80%), small squid (5%) and ragfish (*Icosteus aenigmaticus*) (15%) based on data from 501 stomachs reviewed by Nichol and Heise (1992). In a more detailed analysis of a larger (n=697) sample, Flinn et al. (2002) found a significant difference between the diets of males and females, with North Pacific giant squid (*Moroteuthis robusta*) dominating the diet for both sexes, but fish (primarily ragfish and rockfish, *Sebasetes* spp.; but including dogfish, *Squalus acanthias*; lamprey, *Lampetra* spp.; skate, *Rajidae* spp.; and hake, *Merluccius productus*) were more predominant in the male diet. Historically, males remained closer to shore later in the summer, while females moved further from shore (Gregr et al. 2000). The male diet is therefore of more interest to this study.

Abundance and diet estimates

The coastal whale fishery preferentially removed nearshore animals – the mean distance from shore for male sperm whale catches increased from less than 10 miles in the late 1940s to over 75 miles by 1967 (Gregr et al. 2000). This suggests that very few sperm whales were left in the study area post-exploitation. While portions of the study area appear to contain suitable sperm whale habitat (Gregr and Trites 2001), the degree to which these areas may have been re-occupied is unknown. Considering that sperm whales are most commonly observed outside the study area at and beyond the shelf break, an arbitrary abundance of 50 (10-150) animals was estimated (Table 7a).

While considerable year-to-year variation is apparent (Flinn et al. 2002), diet composition for male sperm whales in the study area was estimated as: large squid (60%), ragfish (15%), rockfish (10%), small squid (5%), and miscellaneous fish (10% – distributed equally among dogfish, lamprey, skates and hake) (Table 8a) (Flinn et al. 2002).

KILLER WHALES

Killer whales in British Columbia occur in 4 distinct groups: Northern residents, southern residents, transients and offshores (Ford et al. 2000). The resident, fish-eating populations are the most studied, as they re-occur predictably in the inside passages around Vancouver Island in the summer months. Marine mammal eating transients do not exhibit any apparent seasonal behaviour. The offshore group is the least studied, has been rarely observed in the study area, and is believed to feed on fish in the vicinity of the continental shelf (Ford et al. 2000). The southern resident community frequents primarily the waters around southern Vancouver Island. Therefore, only the northern resident and transient groups are assumed to influence the ecology of Hecate Strait.

COSEWIC (2003b) estimated the 1999 transient population at 219 individuals. No trend information is available. The northern resident population increased from the 1970s, after the cessation of live-captures, to 219 individuals in 1997. Since then, the population has declined somewhat, to a current (2002) population of 206. (Table 7b, Ford, personal communication).

Ford et al. (1998) showed both a considerable diversity in resident killer whale prey, and a clear preference towards chinook salmon (*Oncorhynchus tshawytscha*). From a total of 152 observations of resident killer whale-prey interactions (kills or harassment events), 96% involved salmon, while the remaining 4% involved Pacific herring, yelloweye rockfish (*Sebastes ruberrimus*), Pacific halibut (*Hippocampus stenolepis*), and unidentified flatfish. The salmon portion was comprised of chinook (65%), pink (17%), chum (6%), coho (*O. kisutch*) (6%), sockeye (*O. nerka*) (4%), and steelhead (*O. mykiss*) (2%). Data collected from the stomachs of 12 stranded animals show a pattern similar to the field observations, however the stomach of an animal stranded in December contained lingcod (*Ophiodon elongatus*), greenlings (*Hexagrammos* spp.), and seven species of flatfish. This demonstrates the potential for diversity in the diet. Of note was the very low occurrence of Pacific herring, which was observed in only 2 of the 152 interactions, and did not appear in any of the stranding stomachs.

Ford et al. (1998) observed 193 interactions between transient marine mammals and their prey. Interactions were observed with 9 species of marine mammals. The most highly represented were harbour seals (*Phoca vitulina*) (53%), Steller sea lions (*Eumetopias jubatus*) (13%), Dall's porpoise (12%) and harbour porpoise (11%). Interactions with Pacific white-sided dolphins, grey and minke whales were rarely observed. While transients were occasionally seen interacting with sea birds, the rarity of these interactions suggests they are not ecologically significant.

<u>Abundance and diet estimates</u>

Given the available information, a population of 220 (200-240) transients and 210 (200-225) residents was estimated for the study area (Table 7a). There is no population trend data for transients, but annual population estimates are available for northern residents from 1975 (Table 7b; Ford, personal communication).

There is no evidence of seasonal migrations, but residents are clearly associated with salmon aggregations in the summer months, while associations of transients with harbour seal pupping areas are apparent (Ford and Ellis 1999). Seasonal changes in distribution are difficult to assess because less observational effort is applied in winter months. However, residents are more common in nearshore waters in summer than in winter. The range of northern residents (Ford et al. 2000) appears largely contained within the study area, at least during summer months. Any estimates for transients, or winter occupancy by residents are complete speculation (Ford, personal communication). Trites and Heise (1996b) estimated an occupancy of 1/5 for transients on the southern British Columbia shelf. For this study, arbitrary annual occupancy estimates of 60% by northern residents and 10% by transients were proposed.

Trites and Heise (1996a, b) estimated killer whale diets based on stomach content analyses conducted by Barrett-Lennard et al. (1995). In the Alaskan gyre, for resident killer whales, summer diet was estimated as salmon (80%), small (10%) and large (10%) pelagic fishes. The estimated winter diet contained less salmon (60%), and an increased number of small and large pelagic fishes (20% each). The transient diet for the Alaskan gyre was described as toothed whales (50%), baleen whales (40%), and pinnipeds (10%) in summer and toothed whales (60%) and pinnipeds (40%) in winter (Trites and Heise 1996a). For the southern British Columbia shelf, a year-round resident killer whale diet was estimated as resident salmon (65%), transient salmon (15%), sharks (15%), and herring (5%), while the year-round transient diet was estimated as pinnipeds (75%), porpoises (20%) and baleen whales (5%) (Trites and Heise 1996b).

The observational samples of resident killer whale diets are strongly biased towards summer months, when killer whales congregate in near shore waters in pursuit of salmonid prey, and conditions for data collection are most suitable (Ford et al. 1998). It may well be that demersal prey are more important at other times of the year, when salmonids are less available. Given the seasonality associated with salmonids and the observed diet diversity, a diet of chinook (45%), transient salmon (pink and chum) (10%), other salmon (5%), Pacific halibut (10%), rockfish (*Sebastes* spp.) (10%), hexagrammids (10%), small squid (5%), and other demersals (5%) was estimated (Table 8a).

The dominance of harbour seals in the diet of transient killer whales is likely a function of their abundance and ease of capture (Ford et al. 1998). Prey handling times were significantly longer, and success rates lower for observed attacks on Steller sea lions. In addition, while the number of interactions observed with transients was roughly equal for both Dall's and harbour porpoise, attacks on harbour porpoises were almost twice as likely to succeed (Ford et al. 1998). The limited number of observed interactions with baleen whales may be due to the spatial bias in sampling (two-thirds of the transient interactions were observed off northwestern or southeastern Vancouver Island). Interactions with baleen whales may be more common in less accessible waters (Ford et al. 1998), and at other times of the year. The relative availability of marine mammal prey (e.g., the abundance of harbour seals, the limited number of baleen whales) is also a likely factor affecting diet. Diet composition for transient killer whales was therefore estimated as harbour seals (58%), harbour porpoise (15%), Steller sea lions (10%), Dall's porpoise (10%), minke whale (5%) and grey whale (2%) (Table 8a).

DALL'S PORPOISE

Dall's porpoise are widely distributed in the North Pacific, having been sighted from 28°N to 65°N. Throughout most of the eastern North Pacific, they are present year round, although there may be some winter movements offshore (SAR 2000c). This species is currently divided by NMFS into two stocks (Alaska, and Washington to California) for management purposes. It is expected that a more detailed stock structure will emerge when data become available. The current population estimate for the Alaskan stock is 83,400 (CV=0.097), while the Ca/Or/Wa stock is estimated at 117,545 (CV=0.45) SAR (2000d). However it is acknowledged that these population estimates are biased upward because of vessel attraction.

Houck and Jefferson (1999) detail the diversity of prey species observed in the stomachs of Dall's porpoise, which includes 46 species of fish and 20 species of cephalopods. Norris and Prescott (1961 cited in Houck and Jefferson 1999) observed that the prey items were all less that 25cm in length. Various studies (cited in Houck and Jefferson 1999) also showed that different prey items dominated in different geographic locations. For example, in Monterey Bay, hake (*Merluccius productus*), rockfish, and market squid (*Loligo opalescens*) comprised 85% of the diet in one year, while another study off Japan found that lanternfish (Myctophidae) accounted for over 70% of the food items. Stroud et al. (1981) also reported considerable diet diversity in specimens collected between 1964 to 1968 in coastal waters from California to the Strait of Juan de Fuca. The 9 stomachs examined contained 9 different species of fish and 3 species of squid. Walker et al. (1998) examined stomach contents from 22 Dall's porpoise stranding in the inland waters of southern British Columbia and Washington state between 1991 and 1997, the majority of which (21/22) were collected in spring (March-May). These samples contained predominantly blackbelly eelpout (*Lycodopsis pacifica*) (63%), followed by walleye pollock (21%), Pacific herring (7%), hake (6%), eulachon (*Thaleichthys pacificus*) (1.3%), market squid (1.2%), and sandlance (0.6%). Although Walker et al. (1998) noted that temporal bias (towards spring) was the reason for the dominance of eelpout, there is insufficient information to develop seasonal diet estimates for Dall's porpoise.

Abundance and diet estimates

Trites and Heise (1996b) estimated the number of Dall's porpoise on the southern British Columbia shelf at 1,000 (300-3,000). Assuming that 10% of the Alaskan stock is found in British Columbia waters, and dividing British Columbia waters into 4 regions based on North Coast, South Coast, inside and outside waters, and assuming an equal distribution of animals among these regions would imply a study area population of 0.10 * 83,400 * 0.25 = 2,085 animals. This is within the range suggested by Trites and Heise (1996b) for the southern British Columbia shelf. Given the speculative nature of the assumptions, the estimate of Trites and Heise (1996b) was retained for this study area (Table 7a).

The diet for this species is clearly more diverse than that originally proposed by Trites and Heise (1996b) which included herring (40%), sandlance (30%) and small squid (30%). Considering the results from Walker et al. (1998), and that Hecate Strait is on the periphery of the range for hake, the diet composition proposed by Trites and Heise (1996b) was modified to include herring (30%), pollock (30%), eelpout (10%), small squid (10%), eulachon (10%), and sandlance (10%) (Table 8b). It is important to note, however, that a number of other diets could be proposed with equal confidence.

HARBOUR PORPOISE

Harbour porpoise primarily frequent coastal waters, and are known to occur year-round in southern British Columbia (SAR 2000e). While evidence for stock boundaries and size remain somewhat equivocal, four stocks are currently recognized between Washington and California, and three in Alaska, although these may more accurately be referred to as management units (SAR 2000f). Harbour porpoise appears to occur at lower densities in Alaskan waters relative to the U.S. West Coast (SAR 2000e), suggesting that densities may decrease with increasing latitude.

An aerial survey in 1997, provided a corrected abundance estimate of 10,508 (CV = 0.274) animals in the eastern Gulf of Alaska (ranging from Dixon Entrance to Cape Suckling and offshore to the 1,000 fathom depth contour (SAR 2000f). Aerial surveys of southern British Columbia, Washington and Oregon from shore to a depth of approximately 200 m provided a corrected estimate of 44,644 (CV = 0.38) (SAR 2000e).

Harbour porpoise are believed to forage primarily on small schooling clupeoid and gadid fishes, typically ranging from 10-30 cm in length (Read 1999). Walker et al. (1998) examined the contents of 26 harbour porpoise stomachs collected from stranding in the inland waters of southern British Columbia and Washington from 1990 and 1997. The dominant prey were identified as small squid (55%), eelpout (19%), hake (12%), and Pacific herring (12%), with Pacific sanddab (*Citharichthys sordidus*), pollock, eulachon and sandlance contributing between 1% and 3% each.

Abundance and diet estimates

Trites and Heise (1996b) estimated harbour porpoise abundance on the southern British Columbia shelf at 1,000 (150-1,500). When compared to the results of the NMFS surveys reported above, this estimate seems rather low. Based on the assumption that the coastline in the study area is (conservatively) about one third of what was surveyed as part of the 1997 Gulf of Alaska survey, British Columbia's central coast was assigned a third (3,403 animals) of the population estimated for the Gulf of Alaska. Since this is primarily an inshore species, it was further assumed that 25% of the Central Coast population occurs outside the study area (i.e., on the west coast of the Queen Charlotte Islands). This gave an estimated abundance for Hecate Strait of 2,500 (1,000-4,000) animals (Table 7a).

While the temporal bias in Walker et al.'s (1998) stomach data complicates the interpretation of the results, two generalizations can be made: First, squid seem to be a more important prey item to harbour porpoise than to Dall's porpoise; and second, harbour porpoise appears to be the more generalist of the two species.

The diet described by Trites and Heise (1996b) was similar to Dall's porpoise and consisted of herring (40%), sandlance (30%), small squid (20%) and miscellaneous demersals (10%). For this report, this diet was revised to include small squid (30%), herring (30%), sandlance (10%), pollock (10%), eelpout (5%), eulachon (5%), and miscellaneous demersals (10%) (Table 8b). However, as with Dall's porpoise, many other diet compositions could be proposed with equal confidence.

PACIFIC WHITE SIDED DOLPHIN

This species is found throughout the temperate North Pacific, and on the east coast ranges from California to the Aleutian Islands. It occurs on the high seas and continental margins of British Columbia and Alaska, and is known to enter inshore passes (SAR 2000g). NMFS recognizes two stocks in the eastern North Pacific: The North Pacific stock extending northward from the British Columbia-Washington border, and the Ca/Wa/Or stock extending southward to Mexico (SAR

2000g). However geographic stock boundaries appear dynamic and poorly understood, likely because the distribution of the species is highly variable, apparently in response to changing oceanographic conditions at both seasonal and annual time scales (SAR 2000h).

Minimum population estimates are 26,880 and 17,475 for the North Pacific and Ca/Wa/Or stocks respectively (SAR 2000g, SAR 2000h). SAR (2000g) additionally provides an abundance estimate of 25,825 (CV = 0.49) for the Ca/Wa/Or population.

In a study that spanned 14 years, Morton (2000) found that the abundance of Pacific white-sided dolphins varied seasonally and annually in the Broughton Archipelago – just to the south of the Hecate Strait study area. The highest abundances were observed in winter. Seasonal movements of this species have also been reported in other areas. Brownell et al. (1999) cited studies describing peaks in abundance off California between February and April, and in May off Oregon and Washington, and suggested that this is strongly indicative of seasonal north-south movements.

Morton (2000) noted a correlation in the increased annual abundance of the species around Vancouver Island with an increase in water temperature, and an increased abundance of anchovy (*Engraulis* spp.) and Pacific sardines. Heise (1996) reviewed the historic occurrence of Pacific white-sided dolphins in British Columbia and concluded that this species may now be the most abundant cetacean in the coastal waters of British Columbia.

Northern anchovy (*Engraulis mordax*), Pacific whiting (*Merluccius productus*), and Pacific saury were the most common fishes observed in the stomachs of 44 specimens collected off the U.S. west coast between 1964 and 1972 (Stroud et al. 1981). Brownell et al. (1999) reported the occurrence of 40 families of fishes and 13 families of cephalopods in Pacific white-sided dolphin stomachs based on a review of the literature. A considerable difference was noted between coastal and offshore regions. The most commonly observed prey species in coastal studies included northern anchovy, Pacific hake, Pacific saury, juvenile rockfish, horse mackerel (*Trachurus symmetricus*) and market squid (Brownell et al. 1999).

From remains collected during 92 encounters with foraging animals, Heise (1997a) observed a prey composition of herring (59%), salmon (30%), gadids (6%), shrimp (3%) and capelin (1%). An additional analysis of stomach contents from 11 strandings also identified pollock, sablefish (*Anoplopoma fimbria*) and smelt (*Osmerus mordax dentex*). It appears that in some circumstances, the species did not consume a particular prey item that was in abundance (Heise 1997a), suggesting that diet may be a function of selection as well as availability.

Abundance and diet estimates

Trites and Heise (1996b) estimated the abundance of Pacific white-sided dolphins on the southern British Columbia shelf at 2,000 (1,000-3,000). However recent studies have documented an increased abundance in British Columbia's near shore waters (Heise 1997a, Morton 2000), and provided more detailed diet information (Heise 1997a).

The true annual occurrence of this species in the study area is likely to be highly variable, and dependent on oceanographic conditions and prey availability. To estimate the abundance in the study area, it was assumed that British Columbia has approximately half the amount of habitat for this species compared to the Alaskan study area of SAR (2000g). Subsequently, assuming equal distribution in the 4 coastal regions described for Dall's porpoise gives a minimum estimate of 3,360 (26,880 /2 /4). The study area abundance was therefore estimated at 3,000 (2,000-4,000) (Table 7a). This is higher than the estimate for the southern British Columbia shelf Trites and Heise (1996b), but may be justified because Hecate Strait is a much larger study area.

Trites and Heise (1996b) estimated a diet composition of herring (40%), sandlance (30%), transient salmon (10%), rockfish (10%) and (presumably small) squid (10%). Given that this study area is considerably further north than where most stomach data were collected, the diet was revised to more closely reflect Heise (1997a), and includes: Herring (40%), sandlance (20%), rockfish (10%), transient salmon (10%), small squid (5%), gadids (5%), pollock (2%), sablefish (2%), smelt (2%), capelin (2%), and shrimp (2%). (Table 8a). As with the other small odontocetes, this represents just one of many equally plausible diet compositions.

BIOMASS, CONSUMPTION AND PRODUCTION

Heise (1997b) estimated the finite population growth rate for Pacific white-sided dolphins at between 0.94% and 1.02%. Olesiuk et al. (1990a) estimated the growth rate of the northern resident killer whale population at 2.92% between 1973 and 1987. However for the purposes of this study, a value of 2% was recommended following Trites and Heise (1996a, b), and based on the currently accepted maximum rate of population growth (R_{max}) for all cetaceans of 4% (Reilly and Barlow 1986). This will ensure consistency both within the current study, and with past ecosystem models.

The species weights reported by Trites and Heise (1996b) derived from a length-based relationship were retained (Table 7a). For all species except killer whales and sperm whales, sex ratios were assumed to be 0.5, and daily ration was calculated according to Equation 1. For killer whales, a female-biased sex ratio of 0.64:0.36, and consumption rates of 85 kg/day for residents and 73 kg/day for transients were reported by Barrett-Lennard et al. (1995) (Table 7a). The same weights and sex ratios were used for both residents and transients. It was assumed that only male sperm whales occur in the study area.

Seasonal occupancy of the study area by odontocetes is likely to depend on many factors, and vary significantly from year to near. Nevertheless, sperm whale occupancy was arbitrarily estimated at 0.5 to account for any offshore movement and their peripheral distribution. The study area occupancy of killer whales was estimated at 0.90 for residents and 0.20 for transients based on the discussion above. Dall's porpoise occupancy was arbitrarily estimated at 0.80 to account for the possibility of some offshore movement in winter. Occupancy was estimated as 1.0 for harbour porpoise and 7/12 (0.58) for Pacific white-sided dolphins (Table 7a).

REMOVALS

Sperm whales were a major target of commercial whaling for centuries. Their take by coastal whalers is included along with the other commercial species (Tables 5a, b). There is no evidence that dolphins or porpoises have ever been commercially exploited in the eastern North Pacific. However there is a history of live captures of killer whales and Pacific white-sided dolphins for aquaria, and minimal interactions with commercial fisheries persist.

Annual mortality of Dall's porpoise from fisheries interaction is estimated at less than 50 in the Alaska Stock (SAR 2000d) and less than 5 for the Ca/Wa/Or Stock (SAR 2000c). For harbour porpoise, SAR (2000e) estimates annual mortality in the Or/Wa coast stock at 12.4 (CV=0.46) animals due to interactions with a marine set gillnet fishery. SAR (2000f) estimates annual mortality in the Alaska Stock at 3 animals, based entirely on self-reported fisheries data. Mortality of Pacific white-sided dolphins due to fishing interactions is minimal, with estimates well below 5 animals per year for either the North Pacific or Ca/Or/Wa Stocks (SAR 2000g; SAR 2000h). A total of 128 Pacific white-sided dolphins were taken by in a live-capture fishery off California between the late 1950's and 1993 (SAR 2000h). In spite of this, the mortality of these species attributable to human interactions is relatively low. Given the apparent size of these stocks, direct mortality due to human interactions is unlikely to be ecologically significant.

Olesiuk et al. (1990a) summarizes the historical kills and live-capture fishery of killer whales. The view of killer whales as a pest species persisted into the 1970's. As a result, the animals were subject to occasionally lethal harassment by the air force, the DFO, and commercial fishers (Olesiuk et al. 1990a). No estimates of mortality are available, but bullet wounds were evident in up to 25% of the animals taken during the British Columbia live-capture fishery. The live-capture fishery took a total of 68 animals from British Columbia waters between 1962 and 1975, mostly from the southern resident community (Olesiuk et al. 1990a). A small number were taken from the northern resident (n=15) and transient (n=2) communities (Table 9).

PINNIPEDS

Steller sea lions and harbour seals are the principal pinniped species found in Hecate Strait. While California sea lions are occasionally seen in these higher latitudes, and seem to have extended their range further north in recent years, significant numbers are not observed north of Vancouver Island (P.F. Olesiuk, personal communication. Pacific Biological Station, Nanaimo, BC, V9R 5K6). Fur seals have been observed passing through the inside waters, and may have been present in larger numbers historically (Olesiuk, personal communication). The influence of these two species on the Hecate Strait ecosystem is considered negligible.

Control programs primarily in the 1950's and 1960's collected a significant amount of detail on the populations of harbour seals and Steller sea lions in British Columbian waters. As a result, reasonably accurate time series data of abundances and removals are available. Improved Steller sea lion diet information is also available based on recent work in northern British Columbia and southeast Alaska.

The diets of pinnipeds appear to be the most diverse among marine mammals, in terms of prey composition. While this may be partially a function of better data obtained through recent scat analysis techniques, there is evidence of a diverse diet that varies by season and location, for both Steller sea lions and harbour seals. Consequently, the diet data, particularly for Steller sea lions, are presented in more detail than for the cetacea.

STELLER SEA LIONS

British Columbia's Steller sea lions are part of a trans-boundary stock that extends into southeast Alaska. The minimum population estimate for this stock (31,005) was based on counts from 1994, with 9,277 of these animals surveyed in British Columbia (SAR 2001g). In spite of the significant recovery of this species, the productivity rate is still assumed to be the theoretical maximum for pinnipeds (i.e., 12%). Minimum estimated mortality from fishing interactions in both U.S. and Canadian waters was 2.65 animals per year (SAR 2001g).

Bigg (1985) summarized the results of 9 surveys conducted between 1913 and 1982. Olesiuk (2003) summarized the results of an additional 5 province-wide surveys conducted between 1971 and 2002. Counts of pups and non-pups increased at an average rate of 3.2% per year through the 1970s. Since the mid-1980's, this rate has increased to 7.6% (pups), and 4.7%. (non-pups). No change was observed in the rookery structure, but the number of year-round haulout sites increased from 12 to 21. The size of the 2002 British Columbia population, during breeding season, was estimated at between 18,400 and 19,700 animals. The proportion of the population (pups and non-pups) found on rookeries has consistently been about 60%. This suggests rookery occupancy during breeding season is a good indicator of total abundance Olesiuk (2003).

Seasonal diet composition was obtained for southeast Alaska (Winship and Trites 2003) and for northern British Columbia (A.W. Trites, unpublished data. Marine Mammal Research Unit, Fisheries Centre, University of British Columbia, 6248 Biological Sciences Road, Vancouver B.C. V6T 1Z4) (Tables 11a, b). Winship and Trites (2003) provided a breakdown of the southeast Alaska diet into four seasons. Diet composition for northern British Columbia was available for summer only, based on data from a single season. Some obvious differences in diet were apparent. Specifically, the proportion of rockfish and forage fish was much higher in the British Columbia diet, while gadids were much less prevalent. This difference in diet between two adjacent areas – southeast Alaska and northern British Columbia – may be related to different prey assemblages on either side of Dixon Entrance, at the north end of the study area.

Abundance and diet estimates

To develop a time series of abundance estimates, the rookery site counts from Bigg (1985) were combined with the census results from the 1971 through 2002 surveys (Olesiuk 2003). The rookery counts were scaled upwards to match the census data on the assumption that they represent 60% of the total British Columbia population (Table 10).

During summer, a small proportion of non-breeding animals may be found at the more exposed haulout (non-rookery) sites outside the study area (Figure 2). However it appears that the majority of these animals, and perhaps even some from the Forrester rookery complex just north of Dixon Entrance, seek refuge from winter storms in the more sheltered waters of Hecate Strait (Trites, personal communication). Thus, the proportion of the British Columbia population in the study area was estimated as 80% in summer (April-September) and 90% in winter (October-March).

While the rookeries in the Scott Group, at Cape St. James, and at Forrester Island are at the boundaries of the study area, the ecosystem influences of animals at these sites on Hecate Strait are likely significant. This is because the rookeries are located at what are presumably highly productive areas, where the shelf and inland waters intersect. This provides animals at these sites the opportunity to intercept prey as it enters or leaves Hecate Strait.

The diet proposed by Trites and Heise (1996b) (Table 11c), was based on the initial work of Trites and Calkins (unpublished data) in southeast Alaska, and provides greater diet resolution than more recent estimates (i.e. Winship and Trites 2003; Trites unpublished data). Based on these three studies (Tables 11a, b, c), a study area specific estimate of summer and winter diets was subjectively defined (Table 11d).

HARBOUR SEALS

NMFS recognizes 3 separate stocks of harbour seals (*Phoca vitulina*) in Alaska based primarily on recent population trends. These are the Bering Sea Stock, the Gulf of Alaska Stock and the Southeast Alaska Stock (SAR 1998b). Burg et al. (1999) identified two distinct populations in British Columbia – one in southern British Columbia and one northern British Columbia / southeast Alaska – based on genetic analyses. Additionally, they suggested that at least 3 populations exist in the North Pacific.

The Southeast Alaska stock appears to contain a stable population with a minimum estimated size of 35,226 animals. The net productivity rate is assumed to be 12%, the theoretical maximum for pinnipeds. Fisheries interactions are estimated to account for a minimum mortality of 36 animals per year, while a subsistence harvest in Alaska has averaged 1,749 animals per year between 1992 and 1996 (SAR 1998b).

Harbour seals are common in coastal areas, inlets and estuaries throughout British Columbia. Historic culls, bounty kills, and pelt harvests eventually caused a severe decline in population by the late 1960's (Olesiuk et al. 1990b). Since protection in 1970, a tenfold increase in the British Columbia population was observed from the early 1970s (9000-10,500) to 1988 (75,000-88,000). This implies a population growth rate of 12.5% (Olesiuk et al. 1990b).

Trites and Heise (1996b) based diet information on scat analysis from "non-estuary" sites in the Strait of Georgia (Olesiuk et al. 1990b). Recent analyses of scats collected from 1990 through 1999 in southeast Alaska (Jemison 2001) showed that pollock, arrowtooth flounder (*Reinhardtius stomias*) and herring, followed by other gadids, dominate the diet. However this diet composition should be treated with caution as the majority of the samples were collected at a single site (Olesiuk, personal communication). In the North Atlantic, Brown and Pierce (1998) analysed scats from the UK and found a predominance of sandlance and gadids, although at different times of the year: Sandlance were important in spring and early summer, while gadids were dominant in winter. Pelagic species (herring, garfish (*Belone belone*) and mackerel) were important in late summer and fall.

<u>Abundance and diet estimates</u>

Olesiuk (personal communication) generously summarized harbour seal population estimates (Table 12) – including removals (Table 9) – since 1950 for the DFO statistical areas (1-10) that occur within the study area (Figure 5). These data were based on an analysis of historical data, and a population growth model.

The diet reported by Trites and Heise (1996b) was modified to reflect the more detailed information available (Table 13). In particular, the proportions of sandlance and flatfish were increased, and hake was removed, since the study area is on the periphery of the range of this prey species. However harbour seals are believed to be extremely opportunistic, and diet can be expected to vary significantly by season and location according to local prey availability (Olesiuk, personal communication).

BIOMASS, CONSUMPTION AND PRODUCTION

Biomass for Steller sea lions (Table 10) was estimated using an adult weight of 197 kg. This was based on an assumed sex ratio of 0.6 female, and weights of 214 kg (male) and 186 kg (female). For harbour seals, biomass (Table 12) was calculated using an adult weight of 62 kg, based on an assumed sex ratio of 0.5 female, and weights of 69 kg (male) and 55 kg (female). Weights were obtained according to Trites and Pauly (1998).

Consumption was calculated according to Equation 1, resulting in daily rations of 6.85 kg/day for Steller sea lions and 2.72 kg/day for harbour seals. Q/B ratios calculated according to Equation 3 were 12.7 $year^{-1}$ and 16.0 $year^{-1}$ respectively.

The maximum rate of population growth for pinnipeds is believed to be about 12% (Small and DeMaster 1995). The P/B ratio in past Ecopath models of Hecate Strait used a value of half the maximum, or 6%, for both these species. However, to achieve the abundances estimated in Table 12, a harbour seal growth rate of 12.5% was used (Olesiuk, personal communication). Based on survey data, Steller sea lion populations appear to have grown at a rate of 3.2% between 1971 and 2002 (Olesiuk 2003). Thus, for this study, growth rates of 12.5% and 3.2% were recommended for harbour seals and Steller sea lions respectively.

REMOVALS

Both Steller sea lions and harbour seals were the subject of control programs in the mid-1900s because of their perceived impact on commercial fish stocks. Steller sea lions culls were conducted by fishery management agencies from 1913 to 1968 (Bigg 1985). These programs reduced the population to 25-30% of peak levels observed in the early 1900s (Olesiuk 2003) and involved organized kills and commercial takes for meat, blubber and hides. Sea lions were culled primarily on rookeries between 1912 and 1939, on non-rookeries between 1940 and 1958, and on both types of sites from 1959 through 1968 (Bigg 1985). Additional mortality is attributed to the Canadian Air Force and Navy during the late 1930's and early 1940's.

Culls and pelt harvests of harbour seals are believed to have killed between 200,000 and 240,000 animals in British Columbia. The population experienced a severe decline during 1963-1969 because of unsustainable commercial harvests (Olesiuk et al. 1990b). In 1970, both species were protected in Canada under the federal Fisheries Act.

Removals for both species are summarized in Table 9. These should be considered minimum values as kills were likely often unreported, and both Steller sea lions and harbour seals continue to be subject to predator control programs at finfish aquaculture sites. However the number of removals (hundreds for sea lions and thousands for harbour seals since 1990) is small relative to the population sizes, and the locations are usually well removed from the study area (around Vancouver Island) (Jamieson and Olesiuk 2001). These removals were therefore not considered significant for this study.

CONCLUSIONS

A significant amount of research has been completed since Trites and Heise's (1996a, b) last review of marine mammals in the eastern North Pacific. Stock assessment reports by the NMFS and the DFO have contributed broadly to the abundance and distribution estimates, while local field studies have improved the available information on diet composition for pinnipeds, killer whales, and Pacific white-sided dolphins.

The species considered as part of this report include 5 species of baleen whales, 2 species of pinnipeds, and 5 species of odontocetes. Other marine mammals occur in the study area infrequently (fur seal, California sea lion) or on the periphery (sei whale), and are consequently considered minor players in the Hecate Strait ecosystem.

The available data on abundance and diet were summarized to provide a comprehensive review of the data available for the northeast Pacific in general, and British Columbia specifically. These data were then combined with sometimes speculative assumptions to derive regional estimates for the Hecate Strait study area. The clear distinction between data and estimated parameter values should extend the utility of this report to researchers interested in developing regional estimates for any area from Washington State through southeast Alaska, and to those simply looking for a review of available data.

The detailed information that is emerging on pinniped diets provides strong evidence that, at least for some marine mammal species, their diet is a reflection of availability as much as preference. Pinnipeds, along with minke whales, may be the most generalist feeders among the marine mammals, followed by the smaller odontocetes. Killer whales, the larger baleen species, and perhaps Pacific white-sided dolphins, appear more closely associated with specific prey types. The balance between availability and preference represents a major challenge to ecosystem models.

The accuracy with which marine mammals (and other species) are represented in ecosystem models would ideally be determined by an explicit confrontation between the assumptions on which parameter estimates are based and the available data. However given the lack of abundance and distributional data (which is slow in coming and expensive to collect) other approaches to model validation are needed. Numerical methods to explore the stability of ecosystem models and the relative effects of various parameters would be useful as a first step in identifying potentially fatal flaws in ecosystem models. Methods of sensitivity analysis, goodness of fit, identification of high and low leverage data, and testing the strength of key assumptions are long overdue. These analyses are essential if ecosystem models are to move beyond exploratory analyses and become operational tools suitable for management.

EPILOGUE

The marine mammal parameters proposed in this report have been entered into the Hecate Strait EcoPath model. An interesting result has emerged from the portion of the model dealing entirely with marine mammal data: transient killer whales and their prey. Transient killer whales were described as feeding principally on harbour seals (58%), with the rest of the diet made up of Steller sea lions (10%), harbour porpoise (15%), Dall's porpoise (10%), minke whale (5%) and grey whales (2%). The occupancy for the assumed population (220 +/- 20) of transient killer whales was estimated at 0.20. This translates into the entire transient population being present in the study area for 2 months of the year, or 440 "killer whale months".

During the trophic balancing of the model, it quickly became apparent that the needs of the transient killer whales far exceeded the prey biomass available. For example, to support the presumed 440 killer whale months, the production of harbour seals would have to be increased from the proposed value of 12.5% to a much less realistic 25%.

Balancing trophic models requires the ecological parameters to be adjusted, but the selection of which parameters to change is quite subjective. Ideally, the confidence associated with each parameter - abundance, occupancy, production - for all groups involved would be assessed, and the estimates ranked according to their reliability. However this is not possible, because the confidence associated with most of the parameters is simply not known.

One approach to balancing this portion could be to reduce transient occupancy to 0.042. This is the equivalent of the entire population being in the study area for just 2 weeks out of the year, or similarly about 9 animals being in the study area year round – a total of about 110 killer whale months. This approach is attractive because it requires only a single parameter to be changed. This is likely better than trying to "rachet up" the available biomass by adjusting various parameters for several prey species.

This brief description of the balancing necessary to make the best available marine mammal data self-consistent shows that the balancing of trophic models is rather arbitrary, and highlights the size of the implicit confidence intervals, particularly for wide-ranging species. However it also suggests that a mass balance approach might be applied to explore hypotheses about the seasonal distributions of marine mammals. By assessing the trophic consequences of various distributional scenarios, reasonable hypotheses about marine mammal distributions may be developed, while at the same time improving the parameterization of trophically-based ecosystem models.

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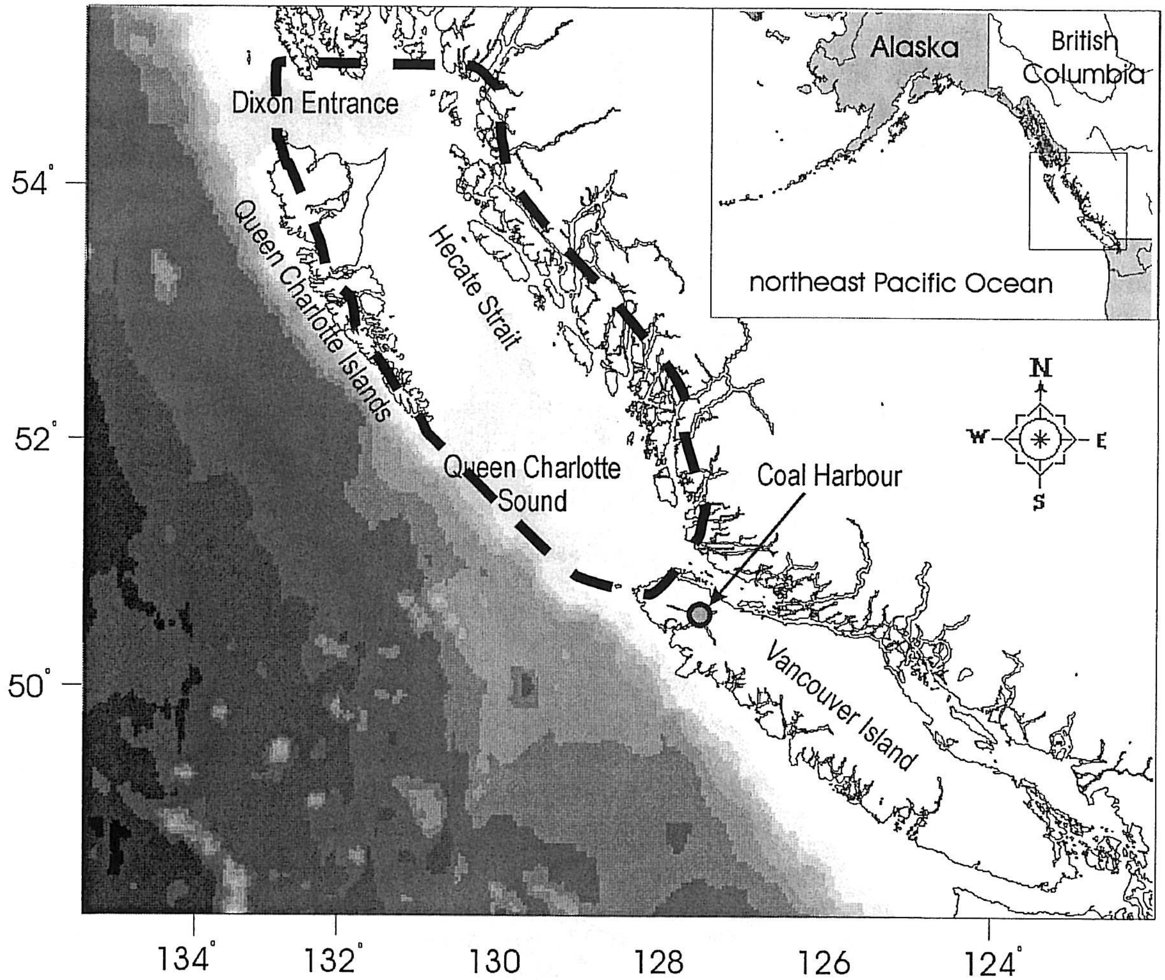

Figure 1: Map of British Columbia coastal waters showing the approximate boundaries of the study area. Bathymetry is shaded from shallow to deep (light to dark) using 200 m bathymetric contours.

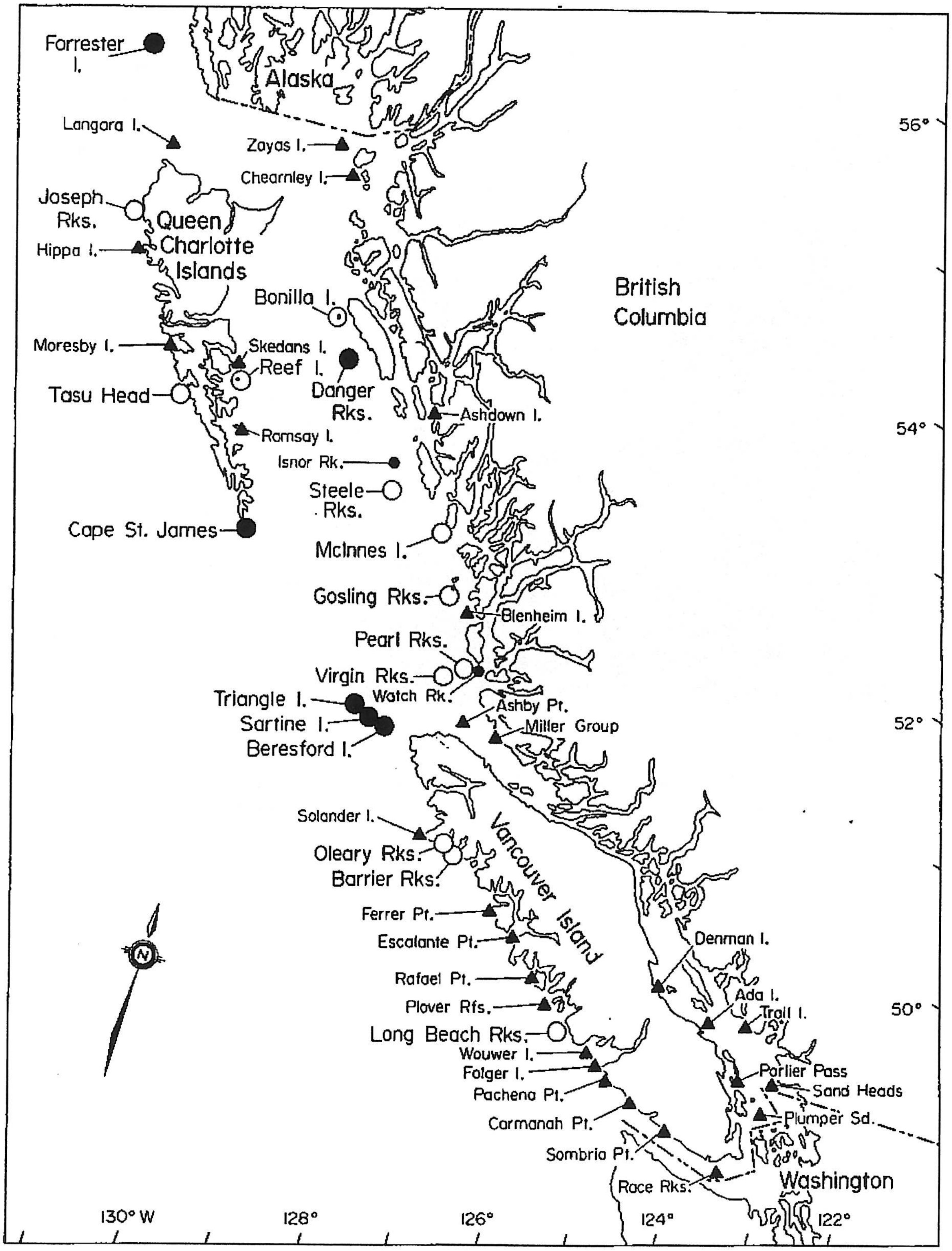

Figure 2: Locations of current rookeries (●), year-round haulouts (○) and winter sites (▲) (>= 50 individuals) of Steller sea lions in British Columbia (reproduced from Bigg 1985).

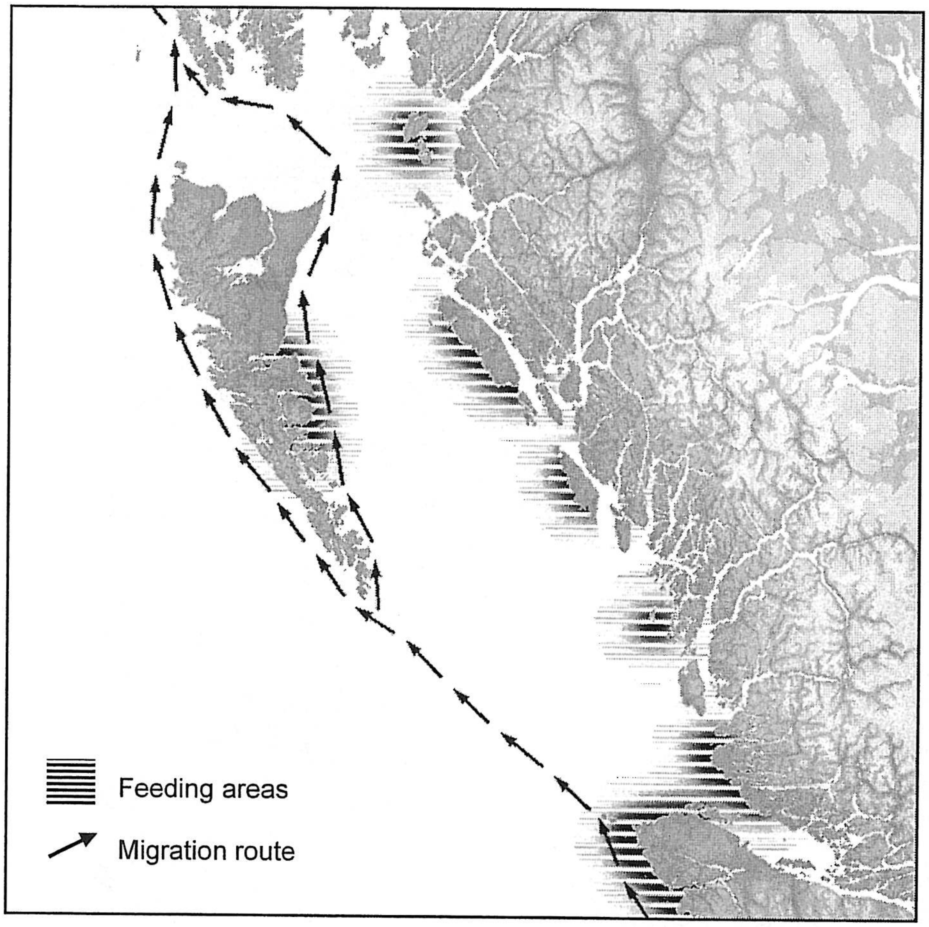

Figure 3. Map of coastal British Columbia showing the migration route and known feeding sites of grey whales (reproduced from COSEWIC 2004).

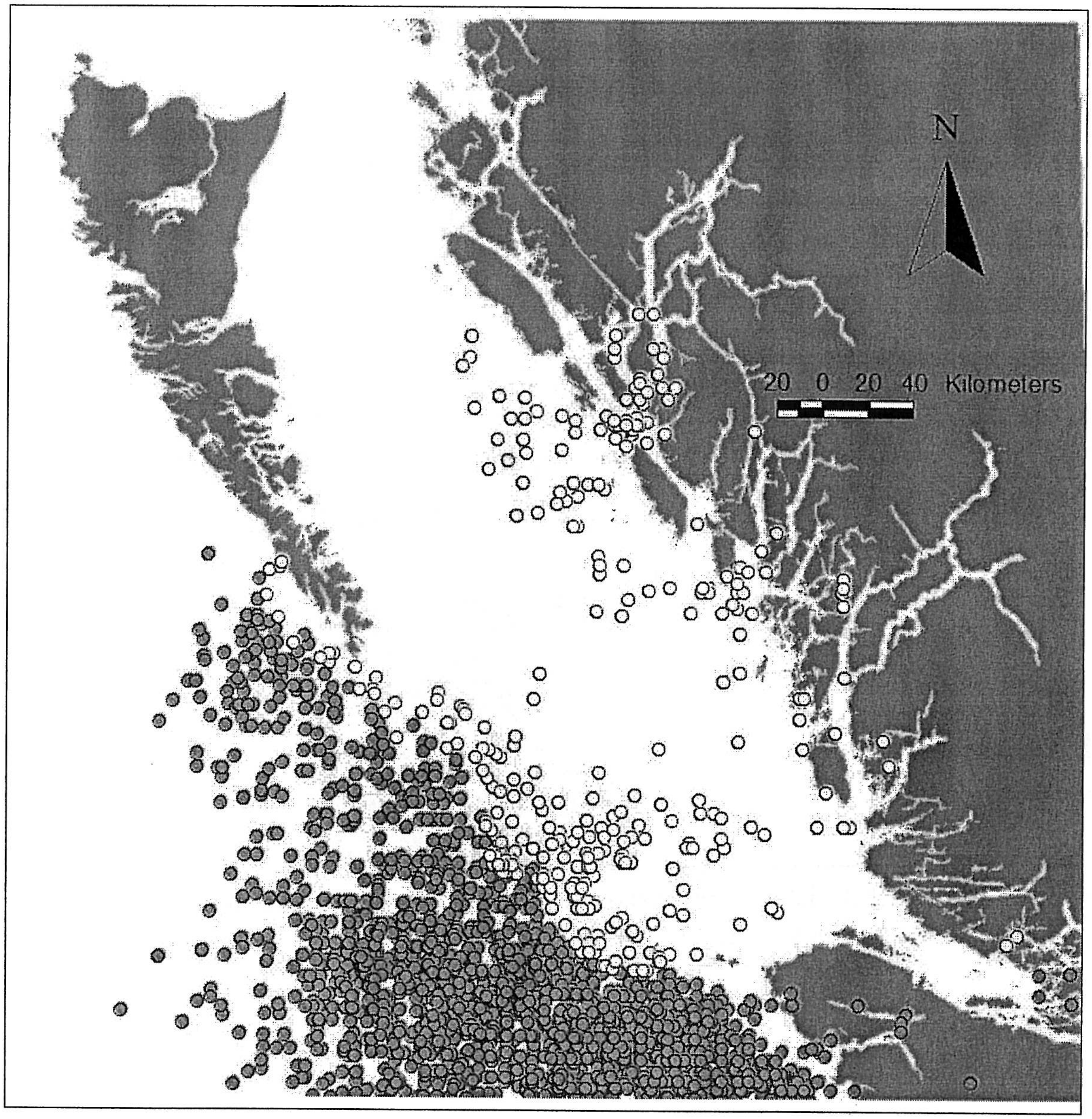

Figure 4. Locations of all catches by coastal whaling stations in the vicinity of Hecate Strait between 1948 and 1967. White circles show those catches estimated to be within the study area. See text and Tables 5a, b for details.

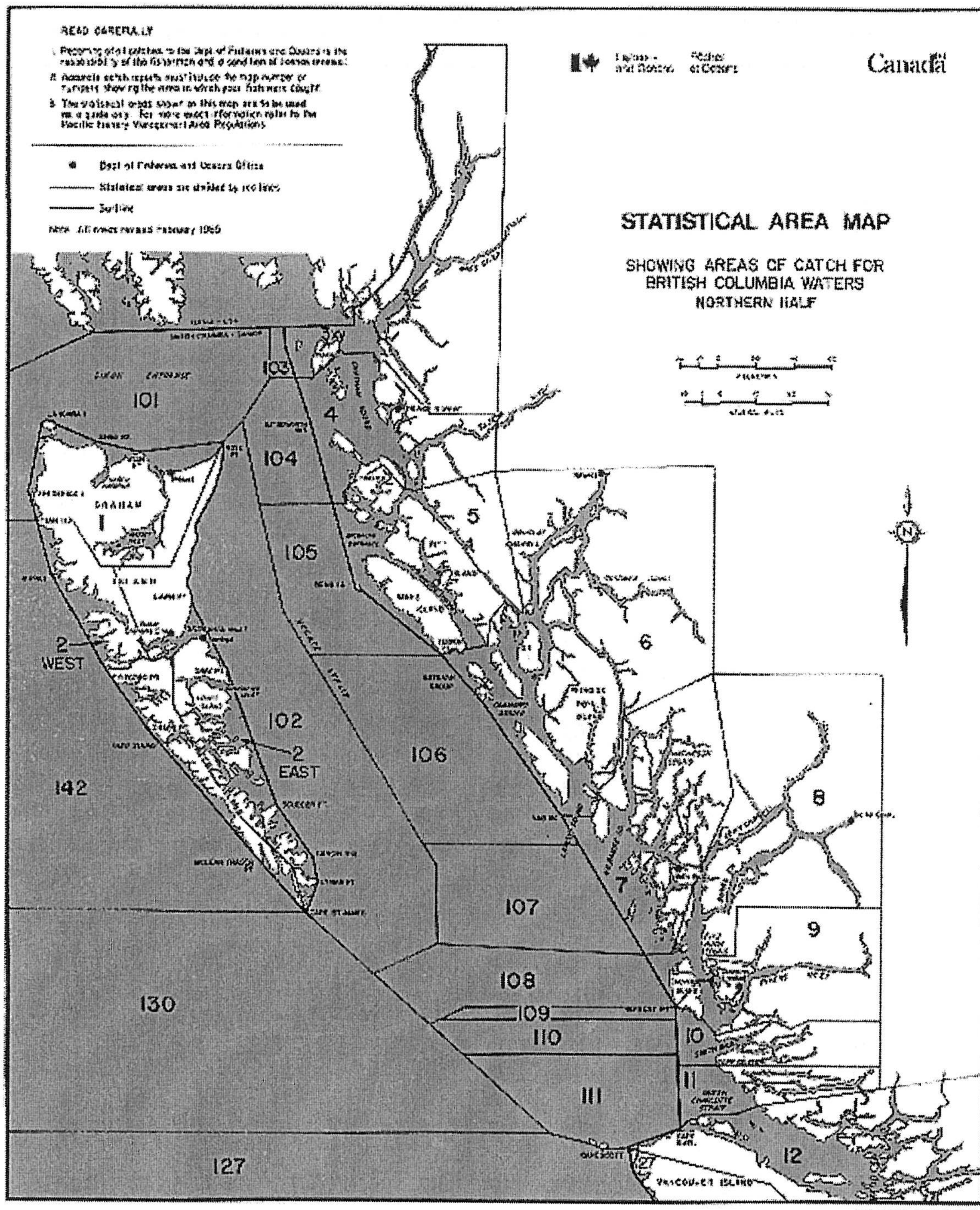

Figure 5: DFO Statistical areas in Hecate Strait. From http://www-sci.pac.dfo-mpo.gc.ca/sa/Commercial/Maps/nc_map_e.htm. Accessed March 2003.

Table 1: Summary of sighting data collected for British Columbia waters since 1957.

Year	Total	BW	FW	SW	HW	GW	MW	SPW	KW	DP	HP	PWD	BKW
1957	1												1
1958	8								8				
1959	8								7				1
1960	6								5			1	
1961	2								1				1
1968	1												1
1969	2								1				1
1971	4					1			3				
1972	3								3				
1973	7								6				1
1978	5					2			2				
1979	2											1	
1980	6					5			1				
1981	1											1	
1982	7					5			2				
1983	14				1	1			8	3		1	
1984	22	1			10				4	7			
1985	4		1			1			2				
1986	8					4			4				
1987	11				1	1	1		7				
1988	17				3	3	1	1	4	2		2	
1989	53	1	1	1	21	6	2		10	2	1	7	1
1990	128		1		85	5	1		23	3	1	9	
1991	138				63	3	11	3	33	3	9	12	1
1992	188		4		48	6	13	4	41	33	21	17	1
1993	182			1	36	5	28	1	42	13	23	33	
1994	135		7	1	56	10	5	3	11	10	1	31	
1995	186		6	1	100	14	1	1	15	15	2	31	
1996	79		1		47	5	1		10	3	1	11	
1997	88	1	3		51		2		19	2		10	
1998	41				20		3	1	9	1	2	5	
1999	29				11	3	3		7	1		4	
2000	13								13				
1998	11				7				4				
1999	27				8	5			9	2	3		
2000	31				10	8	1		10			2	
2001	319		3		150	9	5		74	34	13	19	
2002	298	1	1		138	17	5	1	53	26	17	39	
2003	3				1				2				
Total	2088	4	28	4	867	119	83	15	453	160	94	236	9
Proportion (%)		0.2	1.3	0.2	41.5	5.7	4.0	0.7	21.7	7.7	4.5	11.3	0.4

BW = blue whale; FW = fin whale; SW = sei whale; HW = humpback whale; GW = grey whale; MW = minke whale; SPW = sperm whale; KW = killer whale; DP = Dall's porpoise; HP = harbour porpoise; PWD = Pacific white-sided dolphin; BKW = beaked whale.

Table 2: Proportion of the georeferenced British Columbia catch (1908-1967), by species, that was at or above 51.5° N, and at a depth of 200 m or less – i.e., the proportion that could be considered within Hecate Strait.

Species	Total	On-shelf	On-shelf & North	"Hecate Strait" proportion
Blue	282	91	83	29%
Fin	3932	581	484	12%
Sei	2966	123	99	3%
Humpback	853	239	97	11%
Minke	1	0	0	0%
Grey	11	5	0	0%
Right	4	3	3	75%
Sperm	3335	380	277	8%
Baird's	29	2	2	7%

Table 3: Biomass estimates for baleen whales in Hecate Strait.

Species	Range	Abundance[1] estimate	Weight[1] (kg)	Biomass[2] (tonnes)	Occurrence[1] (months/12)	Biomass (tonnes/year)	Ration (kg/day)	Q/B ratio
Blue	10-100	25	102740	2569	0.33	856	4110	14.6
Fin	100-300	200	55590	11118	0.33	3706	2224	14.6
Humpback (1985)	25-100	25	30410	760	0.33	253	1216	14.6
Humpback (2000)	75-300	75	30410	2281	0.33	760	647	14.6
Grey (resident)	50-150	75	16180	1214	0.75	910	647	14.6
Grey (migratory)	100-1000	300	16180	4854	0.17	809	263	14.6
Minke	100-300	200	6570	1314	0.75	986	4110	14.6

1. See text for derivation of values.
2. Metric tons = 1,000 kg

Table 4: Diet composition estimates for baleen whales occurring in Hecate Strait.

Prey species	Euphausiids	Copepods	Squid	Herring	Sandlance	Pacific cod	Rockfish	Transient salmon	Gadids	Other forage fish	Herring spawn	Benthic prey	Mysid shrimp	Ghost shrimp	Crab larvae
Blue	0.95	0.05													
Fin[1]	0.85	0.10	0.02	0.03											
Humpback	0.80	0.10		0.10											
Grey (resident)[1]												0.30	0.60	0.05	0.05
Grey (migratory)[2]											0.60	0.10		0.10	0.20
Minke	0.20	0.05		0.15	0.10	0.05	0.05	0.05	0.05	0.30					

1. based on Flinn et al. (2002).
2. based on Darling et al. (1998), Dunham & Duffus (2002), and V. Deecke, personal communication.

Table 5a: Minimum number of baleen whales removed annually from British Columbia waters between 1948 and 1967.

Year	Total	BW	FW	SW	HW	GW	MW	RW	SPW	BBW
1948	97		21		62				14	
1949	241	2	98	3	74				64	
1950	299	4	145	21	92				36	1
1951	410	9	208	5	50	1		1	135	1
1952	459	16	240	21	60				122	
1953	517	8	181	14	46	10			254	4
1954	606	11	149	132	103				208	3
1955	586	11	119	129	37				287	3
1956	363	15	167	37	28				115	1
1957	623	15	280	93	48				183	4
1958	764	8	570	39	39				106	2
1959	843	28	369	182	28				236	
1960										
1961										
1962	681	26	155	316	16				167	1
1963	546	30	217	145	24				127	3
1964	847	12	140	593	10				92	
1965	827	9	81	589	18				130	
1966	682		134	351					195	2
1967	437		100	88			1		248	
Totals	9828	204	3374	2758	735	11	1	1	2719	25

BW = blue whale; FW = fin whale; SW = sei whale; HW = humpback whale; GW = grey whale; MW = minke whale; RW = right whale; SPW = sperm whale; BBW = Baird's beaked whale.

Table 5b: Minimum number of baleen whales removed annually from the area North of 50.75°, and at depths less than 1000m, between 1948 and 1967.

Year	Total	BW	FW	SW	HW	SPW	BBW
1948	4				4		
1949							
1950							
1951							
1952	104	2	72	3	9	18	
1953	65	1	20		5	38	1
1954	79	1	46	1	21	10	
1955	60		33	1	3	23	
1956	49	2	34	1	6	6	
1957	25		8	1	9	7	
1958	18		4		8	5	1
1959	36	1	24		1	10	
1960							
1961							
1962	9	1	3	1	1	3	
1963	114	5	95	10	2	2	
1964	9		7		2		
1965	47		36	1	10		
1966	36		24	8		4	
1967	1					1	
Totals	656	13	406	27	81	127	2

BW = blue whale; FW = fin whale; SW = sei whale; HW = humpback whale; SPW = sperm whale; BBW = Baird's beaked whale.

Table 6: Annual population estimates for eastern Pacific grey whales from 1967 to 1995 (Buckland and Breiwick 2002)

Year	Count	Biomass (t)	Year	Count	Biomass (t)
1967	12921	209062	1982	--	--
1968	12070	195293	1983	--	--
1969	12597	203819	1984	21443	346948
1970	10707	173239	1985	20113	325428
1971	9760	157917	1986	--	
1972	15099	244302	1987	20869	337660
1973	14696	237781	1988	--	--
1974	12955	209612	1989	--	--
1975	14520	234934	1990	--	--
1976	15304	247619	1991	--	--
1977	16879	273102	1992	17674	285965
1978	13104	212023	1993	23109	373904
1979	16364	264770	1994	--	--
1980	--	--	1995	22263	360215
1981	--	--			

Table 7a: Biomass estimates for toothed whales in Hecate Strait.

Species	Range	Abundance estimate	Sex ratio (f/m)	Weight (kg) female	Weight (kg) male	Ave. Wt.	Occur. (mo./12)	Biomass (t/yr)	Ration (kg/day)	Q/B ratio
Sperm whale	10 – 150	50	0	na	27400	27400	0.50	685		
Killer whale (transient)	200 – 240	220	0.64	1974	2587	2195	0.20	97	73	12.1
Killer whale (resident)	200 – 225	210	0.64	1974	2587	2195	0.90	415	85	14.1
Dall's porpoise	300 – 3000	1000	0.5	61	63	62	0.80	50	2.7	16
Harbour porpoise	1000 – 4000	2500	0.5	33	29	31	1.00	78	1.6	18.4
Pacific white-sided	2000 – 4000	3000	0.5	73	85	79	0.58	137	3.3	15.2

Table 7b: Annual population estimates for northern resident killer whales from 1975 to 2002 (J. Ford, personal communication).

Year	Count	Biomass (t)	Year	Count	Biomass (t)
1975	132	290	1989	187	410
1976	131	288	1990	194	426
1977	134	294	1991	201	441
1978	137	301	1992	199	437
1979	140	307	1993	197	432
1980	147	323	1994	202	443
1981	150	329	1995	205	450
1982	151	331	1996	211	463
1983	155	340	1997	219	481
1984	156	342	1998	216	474
1985	163	358	1999	217	476
1986	171	375	2000	208	456
1987	177	388	2001	202	443
1988	184	404	2002*	206	452

*Provisional pending the completion of data analysis.

Table 8a: Diet composition estimates for toothed whales (excluding killer whales) in Hecate Strait.

Prey species	Misc. Fish	Ragfish	Large squid	Small squid	Herring	Sandlance	Pollock	Rockfish	Sablefish	Salmon	Gadids	Eelpout	Eulachon	Smelt	Capelin	Shrimp	Misc. demersals
Sperm whale	0.10	0.15	0.60	0.05				0.10									
Dall's porpoise				0.10	0.30	0.10	0.30					0.10	0.10				
Harbour porpoise				0.30	0.30	0.10	0.10					0.05	0.05				0.10
Pacific white-sided dolphin				0.05	0.40	0.20	0.02	0.10	0.02	0.10	0.05			0.02	0.02	0.02	

Table 8b: Diet composition estimates for killer whales in Hecate Strait.

Prey species	Harbour seals	Steller sea lions	Harbour porpoise	Dall's porpoise	Minke whale	Grey whale	Chinook salmon	Transient salmon	Other salmon	Pacific halibut	Rockfish	Hexagrammids	Small squid	Other demersals
Transient	0.58	0.10	0.15	0.10	0.05	0.02								
Resident							0.45	0.10	0.05	0.10	0.10	0.10	0.05	0.05

Table 9: Minimum number of Steller sea lions, harbour seals and killer whales removed annually from Hecate Strait, 1950 – 1975.

Year	Steller sea lions	Harbour seals	Killer whales (resident)	Killer whales (transient)
1950	2110	1897		
1951	231	2259		
1952	252	2727		
1953	311	2599		
1954	180	3429		
1955	275	2924		
1956	339	2407		
1957	521	2756		
1958	1103	2637		
1959	3444	2394		
1960	2053	2169		
1961	812	1891		
1962	1390	1743		
1963	1013	3898		
1964	967	6356		
1965	548	2685	1	
1966	227	1970		
1967	70	153	1	
1968	15	254	7	
1969		11	6	
1970		5		3
1971		8		
1972				
1973				
1974				
1975				2
Totals	15861	47172	15	5

Table 10: Annual abundance estimates for Steller sea lions in British Columbia, 1982 – 2002.

	1913	1916	1938	1956	1961	1971	1973	1977	1982	1987	1992	1994	1998	2002
BC abundance[1]	18105	18250	20023	15667	7590	5808	5397	6558	6295	7206	8846	9290	11891	15402
April-September	14484	14600	16018	12534	6072	4646	4318	5246	5036	5765	7077	7432	9513	12322
October-March	16295	16425	18021	14100	6831	5227	4857	5902	5666	6485	7961	8361	10702	13862
Study area abundance	15389	15513	17020	13317	6452	4937	4587	5574	5351	6125	7519	7897	10107	13092
Biomass (t)	3032	3056	3353	2623	1271	973	904	1098	1054	1207	1481	1556	1991	2579

1. Shaded abundance modified from Bigg (1985); unshaded from Olesiuk (unpublished data). See text for details.

Table 11a: Seasonal diet composition for Steller sea lions in Southeast Alaska (Winship and Trites 2003).

Prey species	Salmon	Flatfish	Gadids	Forage fish	Cephalopod	Other
Winter (Dec - Feb)	0.01	0.08	0.49	0.14	0.08	0.2
Spring (Mar - May)	0.01	0.08	0.53	0.21	0.05	0.13
Summer (Jun - Aug)	0.27	0.06	0.27	0.22	0.01	0.16
Autumn (Sep - Nov)	0.03	0.06	0.62	0.13	0.07	0.09
mean annual	0.08	0.07	0.48	0.17	0.05	0.14

Cephalopods = squid and octopus; flatfish = Pleuronectidae; forage fish = herring, sandlance, eulachon and capelin; gadids = walleye pollock, Pacific cod and others; Others = rockfish, sculpins, prickelbacks, skates, lamprey, sharks and other demersal fish.

Table 11b: Summer diet composition for Steller sea lions in and around Hecate Strait (Trites unpubl. data).

Prey species	Salmon	Flatfish	Gadids	Rockfish	Forage fish	Cephalopod	Other
Steller sea lion (summer)	0.09	0.12	0.06	0.22	0.42	0.01	0.07

Table 11c: Seasonal diet composition for Steller sea lions on the Southern British Columbia shelf (Trites and Heise 1996).

Prey species	Salmon	Flatfish	Pollock	Cod	Rockfish	Herring	Sandlance	Skates	Smelts	Hake	Octopus	Small squid	Other
Steller sea lion (summer)	0.17	0.11	0.12	0.12	0.11	0.16	0.08	0.03	0.01	0.01	0.02	0.01	0.05
Steller sea lion (winter)	0.11	0.08	0.22	0.22	0.05	0.13	0.04	0.05	0.02	0	0.04	0.02	0.02

Table 11d: Estimated diet composition for Steller sea lions in the Hecate Strait study area.

Prey species	Transient salmon	Other salmon	Flatfish	Gadids	Rockfish	Herring	Sandlance	Other forage fish	Cephalopods	Other demersals
Steller sea lion (summer)	0.20	--	0.10	0.20	0.15	0.15	0.08	0.04	0.03	0.05
Steller sea lion (winter)	--	0.10	0.10	0.45	0.10	0.10	0.05	0.02	0.06	0.02

Flatfish = Pleuronectidae; Gadids = walleye pollock, Pacific cod and others; Other forage fish = smelt, eulachon and capelin; Cephalopods = squid and octopus; Other demersals = sculpins, prickelbacks, skates, lamprey, sharks and others.

Table 12: Population estimates for Harbour seals in Hecate Strait from 1950 to 2002 (Olesiuk pers. comm.).

Year	Abundance	Biomass (t)	Year	Abundance	Biomass (t)
1950	19722	1223	1977	6094	378
1951	19991	1239	1978	6795	421
1952	19855	1231	1979	7577	470
1953	19504	1209	1980	8448	524
1954	18766	1163	1981	9419	584
1955	17721	1099	1982	10503	651
1956	17088	1059	1983	11710	726
1957	16492	1023	1984	13057	810
1958	15684	972	1985	14558	903
1959	14964	928	1986	16231	1006
1960	14403	893	1987	18096	1122
1961	14039	870	1988	20171	1251
1962	13858	859	1989	22477	1394
1963	12661	785	1990	25028	1552
1964	8873	550	1991	27826	1725
1965	5065	314	1992	30835	1912
1966	3203	199	1993	33938	2104
1967	2419	150	1994	36871	2286
1968	2508	155	1995	39201	2430
1969	2673	166	1996	40555	2514
1970	2998	186	1997	41054	2545
1971	3367	209	1998	41173	2553
1972	3783	235	1999	41195	2554
1973	3943	244	2000	41199	2554
1974	4396	273	2001	41200	2554
1975	4902	304	2002	41200	2554
1976	5466	339			

Table 13: Diet composition estimates for harbour seals in Hecate Strait.

Species	Salmon	Herring	Gadids	Flatfish	Sandlance	Cephalopods	Smelts	Hake	Other
Summer[1]	0.02	0.15	0.08		0.02	0.02	0.02	0.65	
Winter[1]	0.02	0.60	0.09			0.02	0.01	0.20	
Summer[2]	0.10	0.10	0.10	0.18	0.40	0.05	0.02		0.05
Winter[2]	0.05	0.25	0.35	0.14	0.10	0.05	0.01		0.05

1. from Trites and Heise (1996)
2. modified for this report.