FORAGING BEHAVIORS AND PREY DEPLETION BY WINTERING SCOTERS IN BAYNES SOUND, BRITISH COLUMBIA: INFERRING FOOD AVAILABILITY AND HABITAT QUALITY

by

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ABSTRACT

I quantified diet composition and foraging behaviors of Surf Scoters and White-winged Scoters wintering in Baynes Sound, British Columbia. Manila and varnish clams were the predominant prey of both scoter species. Manila clams decreased in density over the winter period, while pronounced declines were not detected for varnish clam density. Estimates of clam consumption by scoters accounted for most of observed declines in combined abundance of Manila and varnish clams. Clam capture success of both scoter species and foraging effort of Surf Scoters were unrelated to variation in clam density, while White-winged Scoter foraging effort was negatively related to clam density. Observed clam densities were apparently high enough to not elicit strong behavioral shifts in foraging scoters. Further, scoters rarely foraged at night, sufficiently meeting energetic requirements during diurnal hours. These combined results suggest that Baynes Sound constituted high-quality winter habitat in which scoters were not constrained by food availability.

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CHAPTER 1

Wintering Surf Scoters and White-Winged Scoters in Baynes Sound: Potential Interactions with the Shellfish Aquaculture Industry

Long-term data indicate that numbers of wintering Surf Scoters (*Melanitta perspicillata*) and White-winged Scoters (*Melanitta fusca*) on the Pacific coast are declining (Goudie et al. 1994). Factors leading to numerical declines of scoters are unknown, including whether limiting factors occur on breeding or wintering grounds. Along the Pacific coast, Baynes Sound, British Columbia supports significant numbers of wintering Surf Scoters (*Melanitta perspicillata*) and White-winged Scoters (*Melanitta fusca*). Baynes Sound is comprised mainly of soft-bottom intertidal habitats (Vermeer and Ydenberg 1989), where the food supplies and predation impacts of wintering scoters have gone largely unstudied.

Soft-bottom habitats used by scoters in Baynes Sound overlap with those used by the shellfish aquaculture industry. The industry modifies these habitats to increase shellfish production, potentially influencing wintering scoters as a result. However, interactions between scoters and the shellfish aquaculture industry have never been studied. Shellfish aquaculture in British Columbia is currently in a phase of expansion, with plans to increase the amount of foreshore area devoted to aquaculture activities. It is thus timely to investigate potential interactions, either detrimental or beneficial, between wintering scoters and the shellfish aquaculture industry.

Infaunal bivalves, such as the Manila clam (*Venerupis philippinarum*), are the primary prey of both scoter species in soft-bottom intertidal habitats, and are commonly grown by the shellfish aquaculture industry (Vermeer and Levings 1977, Vermeer 1981, Bourne 1984). To protect commercial clam stocks from predation by scoters and other predators, the shellfish farmers place semi-permanent, fine-mesh nets on the surface of intertidal flats. Scoters are effectively excluded from foraging underneath the nets, thereby reducing the total amount of habitat available to scoters and other clam predators. Because the most productive clam beds are the first locations to be covered

by anti-predator nets, the habitats from which scoters are excluded may consist mostly of high-quality foraging habitat. In addition to the nets, commercial and recreational clam harvests outside of netted areas may reduce the amount of food available to wintering scoters.

Conversely, some aquaculture activities may have a positive effect on wintering scoters by enhancing their food supply. To increase clam production and harvest loads, the aquaculture industry actively seeds the intertidal zone with hatchery-raised, juvenile clams and then covers seeded sites with anti-predator nets. These actions may have a positive effect on clam abundance for foraging scoters, via clam migration or increased clam spawning. Juvenile seed clams may migrate to non-netted areas through re-suspension in the water column or horizontal migration through the benthos (Martel and Chia 1991), becoming available to foraging scoters in the process. Furthermore, the spawning of seed clams, once fully-mature, may eventually serve as a source of recruitment for clam populations in non-netted areas of Baynes Sound. In this instance, netting may increase the size of recruitment events by providing large populations of non-predated clams that are available for spawning.

The nature of the relationship between scoters and shellfish aquaculture can be more clearly understood by studying the trophic interactions between foraging scoters and their infaunal bivalve prey, which is the topic of this thesis. The degree to which scoters deplete bivalve standing stocks over the winter period, as well as the degree of variation in scoter foraging behaviors, offers important insights into the quality of the foraging habitat and whether clam abundance may be limiting scoter numbers. For example, large over-winter depletions of clams, accompanied by large increases in scoter foraging effort and the occurrence of nocturnal foraging, would suggest that scoters may be limited by winter clam supplies. In this hypothetical scenario, shellfish

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aquaculture activities that reduce the abundance of clams could have a detrimental effect on populations of wintering scoters. Conversely, a lack of over-winter declines in clam abundance, accompanied by foraging efforts unrelated to variation in clam density, would suggest that scoters are not food constrained and current levels of shellfish aquaculture are not detrimentally affecting clam abundance. Therefore, to understand food abundance and habitat quality for wintering scoters, the objectives of this thesis were to investigate (1) the predation impact of scoters on clam abundance, (2) scoter foraging effort in relation to variation in clam abundance, and (3) the propensity of scoters to forage nocturnally.

Thesis overview

Predation is known to be an important process affecting the diversity and abundance of organisms within intertidal marine communities (Paine 1966, 1974). Studies of intertidal predation by sea ducks have documented strong, top-down effects on mussel populations in rocky intertidal communities (Guillemette et al. 1996, Hamilton 2000). However, impacts of these gregarious predators in soft-bottom habitats remain largely unexplored. Within the soft-bottom habitats of Baynes Sound, scoters have a high potential to affect clam abundance because of their large over-winter numbers, their high per-capita consumption rate, and clam populations that are not renewed via growth or recruitment during the winter season. In chapter 2, I investigated the diet composition and effects of predation by wintering scoters on intertidal clam abundance.

Waterfowl have been shown to adjust their foraging behaviors in response to variation in food abundance (Hill and Ellis 1984, McKnight 1998). These changes in foraging behavior, once understood, can be used to assess or predict changes in food availability and habitat quality (Hutto 1990). In Chapter 3, I determined the foraging effort and clam capture success of wintering Surf Scoters and White-winged Scoters,

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relating these foraging behaviors to spatial and temporal variation in clam densities. The strengths of these relationships are used to indicate relative clam abundance and habitat quality for scoters wintering in Baynes Sound.

The ability to feed nocturnally increases the amount of time available for feeding, providing behavioral flexibility in response to environmental change. Studies have shown that some waterfowl species extend their foraging into nocturnal periods when food is scarce or daylight is short (Lane and Hassall 1996, Systad et al. 2000). However, for most sea ducks, nocturnal behavior has not been described. This information gap limits our understanding of sea duck foraging ecology and energy budgets. In Chapter 4, I determined the extent of nocturnal foraging by Surf Scoters and White-winged Scoters. Without a complete understanding of the nocturnal foraging effort of scoters, our diurnal estimates of foraging effort and consumption, the basis of Chapters 2 and 3, would be incomplete. Further, evidence of frequent nocturnal foraging would be consistent with the hypothesis that food restrictions cause scoters to forage beyond preferred daylight periods.

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CHAPTER 2

Sea Ducks are Significant Predators in Soft-bottom Intertidal Habitats: Effects of Predation by Wintering Surf Scoters and White-Winged Scoters on Clam Abundance

Abstract

Recent studies have documented strong, top-down predation effects of sea ducks on mussel populations in rocky intertidal communities. However, the impact of these gregarious predators in soft-bottom communities has been largely unexplored. We evaluated effects of predation by wintering Surf Scoters (*Melanitta perspicillata*) and White-winged Scoters (*M. fusca*) on clam populations in soft-bottom intertidal habitats of the Strait of Georgia, British Columbia. Specifically, we documented spatial and temporal variation in clam density (clams m^{-2}), scoter diet composition, and the consequences of scoter predation on clam abundance. Of the three most numerous clams, Manila (*Venerupis philippinarum*) and varnish clams (*Nuttallia obscurata*) were the primary prey items of both scoter species, while clams of the genus *Macoma* were rarely consumed by scoters. Between scoter arrival in the fall and departure in the spring, Manila clams decreased in density at most sample sites, while varnish clam densities did not change or declined slightly. Estimates of consumption by scoters (no. clams) accounted for most of observed declines in combined abundance of Manila and varnish clams, despite the presence of numerous other vertebrate and invertebrate species known to consume clams. For *Macoma* spp., we detected an over-winter increase in density, presumably due to growth of clams too small to be detected (< 5 mm) during fall sampling, in addition to the lack of predation pressure by scoters. These results illustrate the strong predation potential of scoters in soft-bottom intertidal habitats, as well as their potentially important role in shaping community structure.

Introduction

Numerous studies have demonstrated effects of predators on the abundance, size class distribution, and other attributes of their prey, with subsequent consequences for community structure and function (Paine 1966, 1974, Kvitek et al. 1992, Langlois et al. 2005). Despite having multiple predators, the abundance of an organism may be disproportionately affected by a single predator species (Paine 1966, Estes et al. 1978). The large impact of such predators is a function of both their interaction strength, defined as the direct per capita effect of a predator on the population growth rate of their prey, and their population size (Wootton 1997).

Previous studies have identified invertebrate predators, such as the ochre sea star (*Pisaster ochraceus*), as having large predation effects in marine intertidal areas (Paine 1966, 1974, Virnstein 1977, Navarrete and Castilla 2003). These invertebrate predators are often numerically abundant and widespread throughout their available habitat and can thus exert strong predation pressure (Navarrete and Castilla 2003). Vertebrate predators also can have large predation effects in marine intertidal areas, despite typically being much less abundant than invertebrate predators (Estes et al. 1978). Vertebrate predators tend to have higher feeding rates and increased mobility, allowing them to quickly respond to variation in prey abundance. For example, sea otters (*Enhydra lutris*) have been shown to greatly reduce prey abundance and consequently alter community structure, despite occurring at extremely low densities in comparison to invertebrate predators (Estes and Palmisano 1974, Estes et al. 1978). Although less well studied than other marine predators, a growing body of research has identified avian species as potentially important vertebrate predators in marine intertidal areas (Marsh 1986, Wootton 1992, 1997, Thrush et al. 1994).

One group of avian predators, the sea ducks (tribe: Mergini), have attributes that suggest they could have large predation effects in marine intertidal communities (Stott and Olson 1973). Sea ducks are large-bodied, gregarious predators that often forage in large, dense flocks within intertidal and shallow subtidal zones (Goudie and Ankney 1986). Sea ducks feed almost exclusively by diving for prey, an energetically expensive method of foraging (de Leeuw 1996). In addition to the locomotory cost of diving, sea ducks generally live in cold-water environments, where they incur high energetic costs of thermoregulation (de Vries and van Eerden 1995, de Leeuw 1996). These energetic demands require sea ducks to consume substantial amounts of food, relative to their body size, to maintain a positive energy balance (Goudie and Ankney 1986, Guillemette et al. 1992, Guillemette 1998). The high consumption rates of sea ducks have been the focus of recent studies illustrating their ability to substantially deplete prey in wintering habitats (Guillemette et al. 1996, Larsen and Guillemette 2000, Hamilton 2000). Almost all of these studies, however, have documented the depletion of mussels in rocky intertidal areas, typically by Common Eiders (*Somateria mollissima*).

Large numbers of sea ducks also winter in soft-bottom intertidal areas (Stott and Olson 1973), where their food supplies and predation effects have gone largely unstudied. In the Strait of Georgia, British Columbia, Surf Scoters (*Melanitta perspicillata*) and White-winged Scoters (*M. fusca*) are the most numerous of many sea duck species that winter in soft-bottom habitats, often numbering in the thousands (Vermeer and Ydenberg 1989). In these habitats, clams comprise most of the infaunal biomass and are the predominant prey item of both scoter species, as well as a suite of other vertebrate and invertebrate predators (Vermeer 1981, Bourne 1982, 1984). Within the length range of clams commonly consumed by scoters (10 – 50 mm; Bourne 1984), clam biomass in the Strait of Georgia does not appreciably increase during the winter

residency period of scoters due to low winter growth rates (Nosho and Chew 1972, Williams 1980) and summer-restricted spawning events (Bourne 1982). Accordingly, the non-renewal of winter clam biomass, coupled with the predation potential and large number of scoters, results in a situation in which significant predation effects are expected.

We used fecal samples, clam sampling, and quantification of scoter foraging behaviors to evaluate effects of predation by Surf Scoters and White-winged Scoters on over-winter clam abundance in the Strait of Georgia. Specifically, we (1) determined composition of hard-shelled prey in scoter diets, (2) quantified changes in density of clams during the winter period of scoter residency, and (3) estimated clam consumption by scoters, contrasting consumption estimates with over-winter declines in clam abundance to determine the relative predation effects of scoters.

Methods

Study area

Our study area is located in the Strait of Georgia on the east coast of Vancouver Island, British Columbia and encompasses the marine waters of Baynes Sound (49.5° N, 124.8° W; Figure 2.1). Baynes Sound is a 40 km long coastal channel fringed by a number of small, protected bays. Large expanses of gravel and sand sediments comprise most of the intertidal habitat in Baynes Sound (Dawe et al. 1998). The area produces significant amounts of both wild and cultured bivalves and is an important wintering area for populations of waterfowl and other marine birds (Dawe et al. 1998). Waterbird surveys in Baynes Sound during the winters of 2002-03 and 2003-04 indicated a mean (± SE) population of 6500 ± 250 scoters (Surf Scoters + White-winged

Scoters) and a maximum of ca. 9000 scoters (Canadian Wildlife Service, unpublished data).

Diet estimation

To evaluate scoter diet composition, fecal samples were collected from scoters caught in December of 2001, 2002, and 2003 and in the spring of 2003 and 2004, following the capture procedures described by Lewis et al. (2005). Scoters were captured during morning hours at known foraging sites. Because scoters rarely foraged at night (Lewis et al. 2005), fecal samples originated from food consumed the morning of capture. Fecal samples were collected from clean towels lining the bottoms of portable pet carriers used to hold individual scoters. To process fecal samples, feces from each scoter were first passed through a 250 μm sieve. All fragments of shell retained on the sieve were separated from non-shell objects and sorted into bivalve and non-bivalve groupings. Because shell fragments accounted for over 99% of the gross mass of all fecal samples, and small rocks composed most of the non-shell objects, all non-shell objects were excluded from further analyses. Bivalve groupings were further sorted to species, while non-bivalve groupings were sorted to more coarse taxonomic classifications (e.g. crustacean, gastropod). Shell structure, such as concentric and radial sculpture, and color of exterior and internal shell surface provided the primary diagnostic information needed to identify fecal shell fragments to species. Fecal shell fragments were compared to intact shells of known species to verify classification. For each fecal sample, sorted groupings were placed in separate aluminum petri dishes and dried at 100 °C to constant mass.

Unidentifiable shell fragments were grouped as either unknown (8.0% of all shell fragments) or unknown bivalve (7.5%). These groupings were mainly composed of shell fragments that were too small for identification, but presumably reflect the species

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composition of the identifiable shell fragments. A separate grouping also was created to account for the close similarity in shell structure between Manila clams (*Venerupis philippinarum*) and Pacific littleneck clams (*Protothaca staminea*). When a shell fragment could not be identified to species, but we were certain that it was either Manila or Pacific littleneck, the fragment was placed into a grouping that encompassed both species.

The percent dry mass of all fecal shell fragments was calculated for each prey type. Dry mass percentages do not account for inherent differences between the proportion of shell-to-soft tissue among prey types or across size classes within a prey type. Therefore, percentages are meant to provide a relative index of the importance of each hard-shelled prey item to the diet of scoters, not an exact proportion of dietary intake.

Clam sampling

To determine intertidal clam density, six sample plots were established throughout Baynes Sound in the winter of 2003-04 (Figure 2.1). We sampled these plots on two occasions, timed to coincide with scoter arrival and departure from Baynes Sound: in the fall from 23 September to 17 October 2003, and in the spring from 5 April to 12 April 2004. Each sample plot measured 150 m x 150 m (22 500 m^2) and was contained within an intertidal area bounded by the 1.0 m and 3.5 m tidal heights (based on lowest low tide datum), encompassing the range of the dominant intertidal clam species in Baynes Sound (Gillespie et al. 1999, Gillespie et al. 2001). Because the elevational slope varied among sample plots, the total tidal height encompassed by each plot differed slightly by location.

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Clam sampling was conducted using a two-stage sampling methodology (Gillespie and Kronlund 1999). The entire 150 m x 150 m sampling plot was divided into 300 contiguous strata 0.5 m wide and aligned parallel to shoreline. These strata were then divided into 4 elevational groups, each containing 75 strata (thus each group measured 150 m parallel to shoreline, and 37.5 m perpendicular to shoreline). We then randomly selected 3 strata from each elevational group. Each selected stratum was then divided into 300 units that were 0.5 m x 0.5 m, and of these, 6 units (hereafter termed quadrats) were selected for sampling. Thus, 72 quadrats were sampled per sample plot in both fall and spring. Quadrat locations were selected separately for fall and spring sampling, and no fall quadrat locations were re-sampled in the spring.

Each quadrat was completely excavated to a depth of 15 cm, below which clams were considered inaccessible to foraging scoters (Lovvorn 1989, Richman and Lovvorn 2003). All excavated substrate was passed through a 4 mm sieve. Sieve size was selected to retain the lengths of bivalves consumed by scoters; of whole bivalves found in the esophagi of collected Surf Scoters and White-winged Scoters, as well as similarly sized Canvasbacks (*Aythya valisineria*), Spectacled Eiders (*Somateria fischeri*), and Common Eiders, few if any bivalves smaller than 4 mm were consumed (Bourne 1984, Lovvorn 1989, Nehls and Ketzenberg 2002, Lovvorn et al. 2003). Retained clams were identified to the species level, except for *Macoma balthica, M. expansa, M. inquinata, M. nasuta,* and *M. obliqua,* which were grouped by genus. The shell length of each clam, defined as the greatest linear distance between the anterior and posterior margins of the valve (Gillespie and Kronlund 1999), was measured to the nearest 5 mm length class (beginning with the 5 mm – 9.9 mm size class). All clams were returned to the sample hole and re-buried.

Some of the Baynes Sound intertidal area is used by the shellfish aquaculture industry for production of commercial clams and oysters. In some locations, large nets are placed atop portions of intertidal flats to protect commercial clam stocks from predation. Foraging scoters are effectively excluded from preying on clams underneath these nets. Four of the six sample plots contained nets within their boundaries: Base Flats, Buckley Bay, Deep Bay, and Mud Bay (Figure 2.1). The total amount of net covering each of these sample plots was measured. The Comox Harbor and Fanny Bay sample plots were free of nets. During clam sampling, all quadrats that completely overlapped nets were recorded as net and no substrate was excavated. When quadrats partially overlapped nets, the proportion of the quadrat covered by net was estimated and only the net-free portion of the quadrat was sampled.

To evaluate variation in clam density, we fit a series of candidate general linear models using program SAS (SAS Institute 1999). We constructed separate *a priori* candidate model sets for varnish clam density (*Nuttallia obscurata*), Manila and Pacific littleneck density combined, and *Macoma* spp. density. Manila, Pacific littleneck, and varnish clams were chosen for inclusion in model sets because they were the primary hard-shelled prey items of scoters in Baynes Sound, as determined by fecal sample analyses. A candidate model set also was constructed for the rarely consumed *Macoma* spp. to provide a contrast with the more commonly consumed clam species. Manila and Pacific littleneck clams were considered in combination due to the difficulty of separating the two species in fecal samples and their similar value to foraging scoters (Bourne 1984). This grouping, however, reflects primarily Manila clams, which comprised 33.2% of all clams sampled, while Pacific littlenecks comprised only 1.6%.

We used an information-theoretic approach (Burnham and Anderson 2002) to evaluate support for each model within *a priori* candidate model sets. Two explanatory

variables were used to construct identical model sets for each clam species: season (fall or spring) and site (the six sample plots). Candidate model sets consisted of the following: a null model with only an intercept, models with site and season singly, a model with site and season additively, and a model with site, season, and a site by season interaction. We also included two additional models, which were special cases of a site by season interaction, in which site differences were constrained for either the fall or spring season. The fall-constrained model considered all sites to have equal clam density in the fall, while the spring-constrained model considered all sites to have equal clam density in the spring. We refer to these models as fall-constrained and spring-constrained, respectively. Candidate model sets for each clam species consisted of these same seven models. We used Akaike's Information Criterion (AIC) to rank the fit of each model within a candidate set (Burnham and Anderson 2002). ΔAIC values were used to compare the relative explanatory value of the candidate models, with ΔAIC defined as the difference between the AIC value of the best-fitting model and each respective model in the set. AIC weights (w_i), which indicate the relative likelihood of a model given the data and set of candidate models, also were calculated to provide a relative weight of evidence for each model (Burnham and Anderson 2002). All clam densities (clams m^{-2}) are presented as mean ± SE.

Scoter consumption estimate

The total number of clams consumed by scoters, C, at each sample plot for the winter of 2003-04 was estimated by $C = T \times N \times R \times S$, where T is the total time available for foraging (hrs), N is the number of scoters within the sample plot, R is the dive rate (dives hr^{-1}), and S is clam capture success (clams captured dive^{-1}).

During their winter residency period, we estimated the total foraging time available to scoters as $T = 1616.7$ hrs. Scoter residency period, determined from

Baynes Sound waterbird surveys, included all dates from 15 October – 10 March. Spring departure coincides with the commencement of herring spawn, at which point scoters abandoned their typical winter habitats and food sources within Baynes Sound. Only diurnal hours were used to calculate T, as scoters rarely foraged at night (Lewis et al. 2005). Civil twilight was used to define the boundary between diurnal and nocturnal periods.

The number of scoters N per sample plot was estimated by counting all scoters within the boundaries of each sample plot. Offshore corners of each sample plot were marked with buoys to provide visual boundary markers for the observer. Counts were conducted approximately once per week per sample plot for the period of 1 November – 5 March. Sampling effort per sample plot was approximately evenly distributed throughout the core daylight hours of 0800 – 1600. During the winter months within our study site, from mid-October through late-February, the lowest daily low tide occurred exclusively at night. Therefore, diurnal scoter counts were all conducted with a substantially flooded sample plot.

Clam capture success S, defined as the number of clams captured per dive, was monitored once per week at each plot from 1 November – 5 March, unless the plot was unoccupied by scoters during observation attempts. When feeding on bivalves, scoters may bring captured bivalves to the surface for manipulation and ingestion (Ydenberg 1988). As scoters surfaced following a foraging dive, the presence or absence of a clam in the bill was recorded. Only scoters for which the surfacing event was distinctly observed were included in data collection, minimizing potential bias caused by scoters that stayed longer at the surface to manipulate captured bivalves. Sample plots were continually scanned for surfacing scoters, with all observations restricted to the area within each sample plot. Sampling effort per sample plot was approximately evenly

distributed throughout the core daylight hours of 0800 – 1600. Only observations with a minimum of five individuals present in the plot (mean = 29.7 scoters; range: 5 – 120 scoters) and 50 recorded surfacing events were included in analyses. Clam capture success was summarized for each observation period as the proportion of total dives that were successful.

Estimates of clam capture success are dependent on the assumption that captured bivalves are mainly consumed at the surface. Typically, diving ducks bring large bivalves to the surface and swallow small bivalves underwater (de Leeuw and Van Eerden 1992). Although some clams may have been consumed underwater by scoters, length distributions of clams sampled, as well as length of clams for which over-winter declines were detected, indicate that scoters were preying on relatively large clams; thus, our surface observations provide reliable measures of number of clams captured per dive (see discussion).

The dive rate R, defined as the number of dives per hour, was obtained using radio telemetry. Scoters were captured and affixed with radio transmitters during December of 2003, following the procedures described by Lewis et al. (2005). Radio transmitters were deployed on Surf Scoters (18 males, 9 females) and White-winged Scoters (28 males, 20 females). In addition, scoters were captured and affixed with radio transmitters in December 2002 (Surf Scoters: 27 males, 15 females; White-winged Scoters: 21 males, 13 females). Many of these radio-marked scoters returned to Baynes Sound for the winter of 2003-04, allowing us to begin monitoring scoter dive rates prior to that winter's radio transmitter deployment. The radio signal disappeared when the scoter dove and resumed when the scoter resurfaced, allowing us to document the number of dives per unit time (Wanless and Harris 1991, Custer et al. 1996). Dive rates were monitored from 1 November – 5 March, using hand-held 4-element Yagi

antennas connected to Advanced Telemetry Systems (ATS; Isanti, Minnesota) R4000 receivers, and observations were spread approximately evenly across daylight hours for each sample site. Observation blocks of one hour duration were used to determine dive rates.

To assure a spatial and temporal connection between dive rate observations of radio-marked scoters and sample plots, locations of radio-marked scoters were determined on the same day as dive rate observations. Point locations of radio-marked scoters and telemetry accuracy were determined following methods described by Lewis et al. (2005). We used ArcView v.3.2 (ESRI 1999) geographic information system (GIS) software to plot scoter point locations and sample plots on a digital 1:20000 TRIM base-map of the British Columbia coast (British Columbia Ministry of Sustainable Resource Management). A buffer was created around each sample plot, radiating 750 m from the center point of each plot. For each dive behavior observation, inclusion in our foraging effort analyses required the following temporal and spatial criteria: (1) an individual's point location was collected on the same day as that individual's dive behavior observation, and (2) the point location was located within a 750 m sample plot buffer.

Mean values for number of clams consumed by scoters C (Surf Scoters + White-winged Scoters) were calculated for each sample plot, and for all sample plots combined, using a data simulation (Morgan 1984). In each simulation, a value was chosen from raw data for each of three variables: N, R, and S. One thousand simulations were run and the mean was generated from these thousand values. Standard errors for estimates of C were calculated by propagating standard error estimates associated with N, R, and S (Bevington 1969). All model variables used to calculate C are for Surf and White-winged Scoters combined and do not discriminate between sex and age.

Mean values of C were compared to over-winter changes in clam numbers for each sample plot, and for all sample plots combined. Numerical clam changes were estimated by subtracting mean spring estimates of clam numbers from mean fall estimates. Estimates of clam numbers were based on combined density measurements for the clam species consumed by scoters in Baynes Sound: Manila, Pacific littleneck, and varnish clams. All estimates of clam numbers accounted for percent cover of anti-predator nets used by the shellfish aquaculture industry. Standard errors for over-winter change in clam numbers were calculated by propagating the standard errors associated with mean fall and spring clam number estimates (Bevington 1969).

Results

Diet

Bivalves accounted for over 90% of the total dry mass of shell fragments in the feces of both Surf Scoters and White-winged Scoters (Table 2.1). Of the bivalve species, Manila clams and varnish clams dominated the fecal samples for both scoter species, accounting for > 70% of the total dry mass. Varnish clams were the most prominent prey item for White-winged Scoters, accounting for 46% of total dry mass of their fecal samples, while Manila clams accounted for 30%. For Surf Scoters, Manila clams were the most prominent prey item, accounting for 52% of total dry mass of their fecal samples, while varnish clams accounted for 20%. These percentages were likely even greater when considering that the unknown fecal category, composed of shell fragments too small for identification, was likely similar to the species composition of identifiable shell fragments. Also, the Manila/Pacific littleneck category was likely composed of mostly Manila shell fragments.

Clam densities

Manila, varnish, and *Macoma* spp. were the most abundant clams in benthic samples, accounting for > 80% of all clams sampled. Manila clams were most common, accounting for 33.2% of all clams sampled in fall and spring, while *Macoma* spp. and varnish clams accounted for 25.6 and 25.2%, respectively. Other clam species commonly encountered included *Clinocardium nuttallii*, *Cryptomya californica*, *Saxidomus gigantea*, and *Mya arenaria*.

The spring-constrained model best explained variation in Manila/littleneck clam densities (Table 2.2). This model indicated that Manila/littleneck clam densities differed by site in the fall, but that all sites were of a similar density in the spring. The model with site, season, and site*season also received support (ΔAIC = 1.30), although the AIC weight (w_i = 0.33) was approximately half that of the best-fitting model (w_i = 0.62). The top two models thus indicate that only models accounting for both site and seasonal differences received substantial support. As with many studies of benthic invertebrate abundance, there was considerable unexplained variation in the data; however, models incorporating site and seasonal effects fit the data markedly better than the null model (Table 2.2), indicating that these factors explained significant variation in the data. Seasonal differences in the top two models were due to over-winter declines in Manila/littleneck density (Figure 2.2). Declines were heavily concentrated in the 25 – 45 mm length range; in the fall, 70% of Manila clams sampled were 25 – 45 mm while only 57% of Manila clams sampled in the spring were 25 – 45 mm (Figure 2.3).

For varnish clams, the best-fitting model contained only site as an explanatory variable (Table 2.2). The site and season model also received support (ΔAIC = 1.64), but had a small AIC weight (w_i = 0.30) relative to the top model (w_i = 0.69). The explanatory variable of site was included in the top two models, with a combined AIC

weight of 0.99, indicating that only models containing site received support. The explanatory variable of season was only marginally important and thus over-winter declines in varnish clam density were not strongly supported (Figure 2.2). However, models including site and seasonal effects fit better than the null model (Table 2.2) and thus explained some variation in the data. For fall and spring combined, the majority of varnish clams (72%) were 25 – 45 mm in length (Figure 2.3).

For *Macoma* spp., the model containing site and season was the only model that received substantial support (Table 2.2). The explanatory variable of season in the top model results from over-winter increases in *Macoma* spp. densities (Figure 2.2), as opposed to density decreases observed for Manila clams. This result is consistent with our fecal sample analyses, which indicated that *Macoma* spp. are not predated by scoters. Density increases are likely attributable to the over-winter growth of clams that were too small (< 5 mm) to detect during fall sampling, as indicated by the increased frequency of 5 – 15 mm *Macoma* spp. in our spring samples (Figure 2.3).

Scoter consumption

The number of clams (Manila, Pacific littleneck, and varnish clams combined) decreased from fall to spring at all sample plots except for Buckley Bay (Table 2.3). Mean estimates of number of clams consumed by scoters at each sample plot were similar in magnitude to observed over-winter changes in clam numbers (Table 2.3). For all sample plots combined, our mean estimate of scoter consumption accounted for approximately 90% of over-winter decreases in clam abundance. These results suggest that scoter predation is responsible for most of observed over-winter declines in clam abundance.

Discussion

Surf Scoter and White-winged Scoter predation had significant effects on the abundance of infaunal bivalves in Baynes Sound. The scoter diet was dominated by bivalves, which accounted for nearly 90% of all identifiable fecal shell fragments. Of the bivalves, Manila and varnish clams were the primary prey of both scoter species. Our estimates of scoter consumption accounted for most of the observed declines in combined abundance of Manila, Pacific littleneck, and varnish clams, despite the presence of numerous other vertebrate and invertebrate species known to consume clams. These results illustrate the strong predation potential of scoters in soft-bottom intertidal habitats.

Scoter consumption model

Our conclusions regarding the effects of scoter predation are dependent on the accuracy of our scoter consumption model. Clam captures success, one of four variables comprising our consumption model, was estimated by measuring the proportion of scoters that surfaced from dives with a captured clam. When feeding on small bivalves (approximately < 30 mm; J. Lovvorn pers. comm.), however, diving ducks may ingest captured bivalves underwater (De Leeuw and Van Eerden 1992). Consistent underwater ingestion of clams by scoters would cause our surface observations of clam capture success to underestimate the actual number of clams consumed. However, we believe that the majority of consumption by scoters occurred at the water surface. First, the size distribution of clams in our study site was dominated by large clams; 61% of Manila and varnish clams sampled were > 30 mm (74% were > 25 mm). Large bivalves require extended handling times to properly orient the clam for swallowing, as commonly witnessed for scoters (TLL pers. obs.), and are typically handled at the surface to avoid extra costs of diving (Ydenberg 1988, De Leeuw and Van Eerden 1992). Second,

declines in clam abundance were heavily concentrated in the 25 – 45 mm size range (Figure 2.3), while smaller clams did not generally decline in abundance, suggesting that scoters focused their predation on larger clams that likely required surface handling. Finally, De Leeuw and Van Eerden (1992) speculated that diving ducks optimize their intake rate per dive by consuming many small bivalves underwater before surfacing with a large bivalve to be consumed at the surface. Their conclusions were based on experiments in which small bivalves were abundant and all available bivalves, both small and large, were visible to the diving duck, potentially allowing the duck to visually assess available length distributions before choosing the aforementioned dive strategy. When feeding on visually-concealed prey such as clams, however, diving ducks may not be able to accurately or rapidly assess relative availabilities of small and large clams. Accordingly, to adopt such a strategy in our study site would often require scoters to bypass large clams, which are more abundant, in pursuit of small clams that occur at much lower densities, a potentially risky strategy if small clams are not found and/or a large clam is not subsequently relocated prior to dive termination.

As a whole, we recognize that our consumption model is simple, as it was intended only to provide a rough index of the magnitude of scoter consumption. Many finer details were not considered in this exercise, such as differences between scoter species and seasonal variation in foraging behaviors. Nonetheless, a consistent pattern emerges across multiple sample plots, with mean scoter consumption estimates closely matching in magnitude the observed declines of clam numbers. Hence, we conclude that scoters are largely responsible for the observed over-winter decline in clam abundance.

Other sources of clam mortality

A number of potential clam predators other than scoters occur in Baynes Sound during winter, the most common of which are the red rock crab (*Cancer productus*), the moon snail (*Polinices lewisii*), and other diving duck species. Although these predators undoubtedly contribute to winter clam depletions, biological and numerical considerations likely restrict their overall predation effects. Invertebrate predators of clams, although often abundant, have metabolic rates and consumption requirements much lower than those of vertebrate predators such as birds. Red rock crabs can be major clam predators; their intake rates, however, are greatly reduced during winter because of low water temperatures (Walne and Deane 1972). Moon snails are rarely observed in the mid to high intertidal zone, where the majority of Manila and varnish clams are found, and have winter feeding rates of < 0.02 clams per day in the Strait of Georgia (Peitso et al. 1994). Other diving duck species are numerous in Baynes Sound, the most common of which include Barrow's Goldeneye (*Bucephala islandica*), Common Goldeneye (*Bucephala clangula*), Bufflehead (*Bucephala albeola*), Harlequin Ducks (*Histrionicus histrionicus*), and Greater Scaup (*Aythya marila*). None occur in numbers or densities nearly as high as scoters. Surf and White-winged Scoters account for > 60% of all diving ducks that potentially feed on clams within Baynes Sound. The next most common diving duck, Greater Scaup, are known to feed on clams and other benthic invertebrates (Kessel et al. 2002), but account for only 12% of potential clam foraging ducks present in Baynes Sound. Barrow's Goldeneye often have a diet composed mainly of bivalves, primarily mussels (Eadie et al. 2000), but account for less than 1% of potential clam foraging ducks. The other common diving ducks typically have more diverse diets, not relying as heavily on bivalves as scoters (Gauthier 1993, Robertson and Goudie 1999, Eadie et al. 1995).

Winter weather conditions are another potential mechanism leading to numerical declines of clams. Winter clam mortality may occur as a result of freezing, primarily when low air temperatures coincide with exposure of clam habitat at low tides. Freezing of clams is known to cause irreparable gill and tissue damage (Bower 1992). In the Strait of Georgia, Manila clams are susceptible to winter mortality by freezing during prolonged or severe cold spells (Bourne 1982). Large-scale winter die-offs are marked by the presence of abundant empty shells or recently dead clams scattered over the beach (Bower 1992). Although some clams within our study site undoubtedly died as a result of adverse weather conditions, large-scale die-offs were not likely experienced during the winter of 2003-04. At no point did we observe unusual numbers of dead clams or shells on any beaches near our sample plots, despite frequent monitoring (≥ 1 visit per week) for the entire duration of winter.

Manila and pacific littleneck clams

Manila/littleneck clam densities differed by site in the fall, prior to the arrival of large numbers of scoters to Baynes Sound. By spring, however, inter-site differences were reduced and Manila/littleneck clam densities were of a similar magnitude across sites, perhaps due to the effects of scoter predation. This large-scale homogenization could be a result of scoters depleting Manila/littleneck clams to some minimal density, and subsequently moving to a new foraging site that offered higher Manila/littleneck clam densities. Many of our sample plots, however, were > 10 km apart, and scoter movements of this magnitude were rare (Esler, unpublished radio-telemetry data). Instead, scoters used distinct over-winter foraging areas of a size that did not typically encompass multiple and/or distantly located sample plots. The over-winter homogenization of Manila/littleneck clam densities across our six sample plots is more likely attributable to differential scoter numbers within our sample plots. Winter sea duck

distribution and flock size is often closely related to the density of prey (Guillemette et al. 1992, Guillemette and Himmelman 1996). Plots of higher clam density presumably attracted more scoters, and these areas experienced greater rates of predation than sites with lower clam density and fewer scoters. The persistence of this pattern for the duration of winter would eventually lead towards our observed equalization of Manila/littleneck clam densities across sites.

Varnish clams

Despite being one of only two predominant prey items found in scoter fecal samples, varnish clams did not markedly decrease in density, in contrast to Manila clams. Manila clams had overall higher densities than varnish clams, increasing their probability of detection and predation by foraging scoters, and might thus be expected to experience more pronounced over-winter declines. Differential predation by scoters, however, may not fully account for the more pronounced declines of Manila clams; the unique biology of varnish clams, along with our clam sampling protocol, may also partially explain differences between the two clam species.

In addition to deposit feeding, varnish clams may utilize pedal-sweep feeding (Gillespie et al. 1999), which involves collection of sub-surface organic detritus on the pedal cilia and subsequent ciliary movement of detritus to the oral region (Reid et al. 1992). This access to sub-surface food sources, together with their longer siphons and deeper pallial sinuses, greatly increases the burial depth capacity of varnish clams. Our clam sampling was performed to a depth of 15 cm. This sampling regime captured all Manila clams present in a sample quadrat, as their obligatory filter feeding and short siphon length restricts their burial depth to the upper 10 cm (Bourne 1982). Our sampling, however, did not document all varnish clams present, as we often observed varnish clams residing deeper than 15 cm. Although clams buried at these depths are

considered unavailable to foraging scoters (Lovvorn 1989, Richman and Lovvorn 2003), varnish clams can likely migrate vertically between upper and lower sediments. The burial depth of many soft-bottom bivalves is negatively related to food intake rate and often varies seasonally (Edelaar 2000). Accordingly, many bivalves migrate to shallow sediments during spring or early summer, thereby providing the increased food necessary to regain body weight lost during winter and produce gametes for summer-restricted spawning events (Zwarts 1991, Zwarts and Wanink 1993). During our initial clam sampling in fall, some varnish clams may have already migrated to deeper burial depths for the duration of winter, as has been reported for other clam species in northern temperate locations (Zwarts and Wanink 1993). By the time we re-sampled clam densities in April, some varnish clams too deep to detect in the fall (> 15 cm) may have migrated to sediment depths shallow enough to be detected. This hypothesized vertical migration would partially mask our ability to detect predation of varnish clams and may partially explain the much larger over-winter declines documented for Manila clams.

Vertical migrations of varnish clams may also partly explain our inability to detect a reduction in clam density at our Buckley Bay sample plot. For the scoter-predated clam species of Manila, Pacific littleneck, and varnish clams combined, Buckley Bay was the only sample plot for which an over-winter density reduction was not detected, despite the confirmed predation by scoters within the sample plot. The Buckley Bay sample plot had the highest varnish clam density and lowest Manila clam density of any sample plot, with varnish clam density being approximately 3.5 times greater than Manila clam density. Accordingly, the hypothesized vertical migration of varnish clams may have had a larger effect on our ability to detect clam declines at our Buckley Bay sample plot relative to the other sample plots.

Macoma spp. clams

Macoma spp. clams, although comprising 25.6% of all clams sampled, were rarely consumed by scoters in Baynes Sound. We predicted that *Macoma* spp. densities would not decrease over the winter, due to the lack of predation pressure from scoters. As predicted, we did not detect over-winter decreases of *Macoma* spp. density, but rather over-winter increases. The lack of scoter predation pressure is likely attributable to the smaller size of *Macoma* spp., as 67% of all sampled *Macoma* spp. were < 15 mm in length, while only 16% of Manila clams and 5% of varnish clams were < 15 mm. Bourne (1984), in an analysis of scoter stomach contents, found that only 11% of consumed clams in Baynes Sound were < 10 mm.

Inspection of *Macoma* spp. abundance by length revealed a spring increase in clam abundance for the 5 – 10 and 10 – 15 mm length classes, while length classes > 15 mm experienced little over-winter change. This suggests that *Macoma* spp. clams grew during the period between fall and spring clam sampling, as clams too small to detect in the fall (< 5 mm) grew into sizes large enough to detect by spring. Although clam growth is minimal during winter months in Baynes Sound (Bourne 1982), the period between our fall and spring clam sampling encompassed six months and small amounts of growth may occur during this period. Any growth over the six month period would be most noticeable in the smallest size classes because small biomass increases in these size classes causes proportionally larger changes in shell size than for larger clams. For *Macoma* spp. > 15 mm, the absence of pronounced declines in abundance is consistent with our predicted lack of scoter predation pressure for *Macoma* spp. clams.

Sea duck predation and community effects

This study corroborates a growing body of literature indicating the important effects of sea duck predation on intertidal populations and communities (Guillemette et

al. 1996, Larsen and Guillemette 2000, Hamilton 2000). Their large body size, high metabolic rates, and gregarious nature leads to high rates of predation, and potentially important effects on prey abundance. To date, studies documenting effects of sea duck predation have mainly focused on mussel prey. These studies have documented the ability of sea ducks to significantly reduce the abundance of mussels in intertidal communities. The large predation effects of sea ducks on mussels may lead to subsequent changes in community structure, as mussels are dominant competitors for space, and their depredation creates open habitat for competing species (Paine 1966, 1974). Lacroix (2001) documented complete local extirpation of some mussel beds by Surf Scoters in coastal British Columbia, with much of the extirpation occurring high in the intertidal zone. This upper zone had been previously viewed as a predation refuge for mussels along the Pacific coast, as the classic keystone predator, *Pisaster ochraceus*, is typically restricted to the lower intertidal zones. The predation of mussels by Surf Scoters may thus cause cascading community effects in the upper intertidal similar to those documented for *Pisaster ochraceus* predation in the lower intertidal zone (Paine 1966, 1974). The presence of sea ducks as a top predator may also affect community dynamics by limiting the abundance of competing predators. Hamilton (2000) found that exclusion of Common Eiders led to an increase in the abundance of dogwhelks (*Nucella lapillus*), as whelks were released from interspecific competition for available mussel prey.

The effects of sea duck predation on infaunal bivalve numbers in soft-bottom habitats had not been previously documented. By selectively preying on Manila and varnish clams, which compose the majority of infaunal biomass, scoters potentially assume a particularly important role in structuring these communities. Schneider (1978) documented the selective removal of numerically dominant prey by migratory shorebirds

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in a soft-bottom mudflat. Shorebird predation reduced variation in the relative abundance of prey, which stabilized the prey community by limiting the continued expansion of the numerically dominant species. Within our study site during the fall, Manila, varnish, and *Macoma* spp. clams composed 39%, 27%, and 23%, respectively, of all clams sampled. Following a winter of selective scoter predation, overall variation in the relative abundance of these three clam species was considerably reduced: Manila, varnish, and *Macoma* spp. clams composed 28%, 23%, and 29%, respectively, of all clams sampled in the spring. In addition to changes in relative abundance, scoter predation may alter community structure via competition-dependent pathways. For example, predation by scoters on the abundant Manila and varnish clams may promote species persistence and community diversity by creating space for competitively subordinate species. Soft-bottom communities, however, are typically defined by weaker spatial competition than rocky intertidal communities, and predation is believed to be of more importance than competition in limiting infaunal invertebrate densities (Virnstein 1977, Peterson 1979). Scoter predation may therefore provide a major numerical control of the abundant varnish and Manila clams, while having a less pronounced cascading community impact than might be expected in rocky intertidal habitats characterized by stronger spatial competition (Kvitek et al. 1992).

In conclusion, our study has shown the ability of scoters to deplete their winter food sources and assume a significant predation role in soft-bottom intertidal areas. Despite the presence of many other predator species, scoter predation on clams appeared responsible for most of the over-winter declines in clam abundance. Future research is needed to determine if the seasonal predation impacts we observed affect long-term clam densities and community structure. Recruitment and growth of most Baynes Sound clam species occurs during the summer months, and this re-population

may be more than adequate to renew clam numbers following winter decreases. Nonetheless, the strong predation potential of scoters requires the presence of wintering areas with robust bivalve populations. Previous studies in the Dutch Wadden Sea have linked significant over-winter mortality of Common Eiders to shortages of bivalve food supplies (Camphuysen et al. 2002). In areas used by wintering scoters, availability of bivalve stocks should be considered when reviewing activities, such as foreshore development or commercial bivalve harvesting, which may significantly reduce bivalve numbers.

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Table 2.1. Percentage dry weight (g) of fecal shell fragments collected from Surf Scoters (n = 71) and White-winged Scoters (n = 162) in coastal British Columbia during the winters of 2002, 2003, and 2004.

Prey group Species	% mass of fecal shell fragments	
	Surf Scoter	White-winged Scoter
Bivalves	90.1	91.1
Manila clam (*Venerupis philippinarum*)	51.9	29.7
Varnish clam (*Nuttallia obscurata*)	19.8	46.0
Pacific Littleneck clam (*Protothaca staminea*)	0.8	1.3
Manila / Pacific littleneck	9.5	5.6
Macoma spp.	0.4	0.9
Heart cockle (*Clinocardium nuttallii*)	0	0.2
Bay mussel (*Mytilus trossulus*)	0.4	0
Unknown bivalve	7.4	7.5
Gastropods	0	0.6
Crustaceans	0.1	0.7
Unknown	9.7	7.5

Table 2.2. General linear models evaluating variation in density (clams m^{-2}) of Manila/Pacific Littleneck, Varnish, and *Macoma* spp. clams during winter in coastal British Columbia, 2003-04. For all models, the number of parameters (k) includes +1k for an intercept and +1k for variance estimate. Candidate models are listed in order of ΔAIC.

Response variable	Model	Number of parameters	ΔAIC	AIC weight (w_i)	R^2
Manila/Pacific littleneck density	spring-constrained	8	0	0.62	0.10
	site + season + site*season	13	1.30	0.33	0.11
	site + season	8	5.00	0.05	0.09
	site	7	20.10	0	0.07
	season	3	43.05	0	0.02
	fall-constrained	8	45.02	0	0.03
	null	2	45.85	0	0.00
Varnish density	site	7	0	0.69	0.10
	site + season	8	1.64	0.30	0.10
	site + season + site*season	13	11.05	0	0.10
	spring-constrained	8	37.35	0	0.05
	fall-constrained	8	38.38	0	0.05
	null	2	61.35	0	0.00
	season	3	67.76	0	0.00
Macoma spp. density	site + season	8	0	0.82	0.14
	site + season + site*season	13	3.74	0.13	0.15
	site	7	5.26	0.06	0.13
	fall-constrained	8	32.89	0	0.10
	spring-constrained	3	58.25	0	0.06
	season	8	83.90	0	0.01
	null	8	89.00	0	0.00

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Table 2.3. Over-winter numerical clam change (± SE) and scoter consumption estimates (mean ± SE) for all sample plots combined and for each individual sample plot during winter in coastal British Columbia, 2003-04. Over-winter clam change is calculated from the mean fall numerical total minus mean spring numerical total for Manila, littleneck, and varnish clams combined. Scoter consumption estimates are means of 1,000 iterations of our scoter consumption model.

Sample plot	Over-winter clam change (no. clams)	Scoter consumption estimate (no. clams)
All plots combined	$-4 \times 10^6 \pm 1 \times 10^6$	$3.67 \times 10^6 \pm 0.12 \times 10^6$
Base Flats	$-9 \times 10^5 \pm 3 \times 10^5$	$5.2 \times 10^5 \pm 0.31 \times 10^5$
Buckley Bay	$+1 \times 10^5 \pm 6 \times 10^5$	$3.7 \times 10^5 \pm 0.29 \times 10^5$
Comox Harbor	$-1.4 \times 10^6 \pm 0.86 \times 10^6$	$1.1 \times 10^6 \pm 0.12 \times 10^6$
Deep Bay	$-4 \times 10^5 \pm 7 \times 10^5$	$3.2 \times 10^5 \pm 0.29 \times 10^5$
Fanny Bay	$-9 \times 10^5 \pm 5 \times 10^5$	$9.1 \times 10^5 \pm 1.2 \times 10^5$
Mud Bay	$-3 \times 10^5 \pm 9 \times 10^5$	$5.0 \times 10^5 \pm 0.5 \times 10^5$
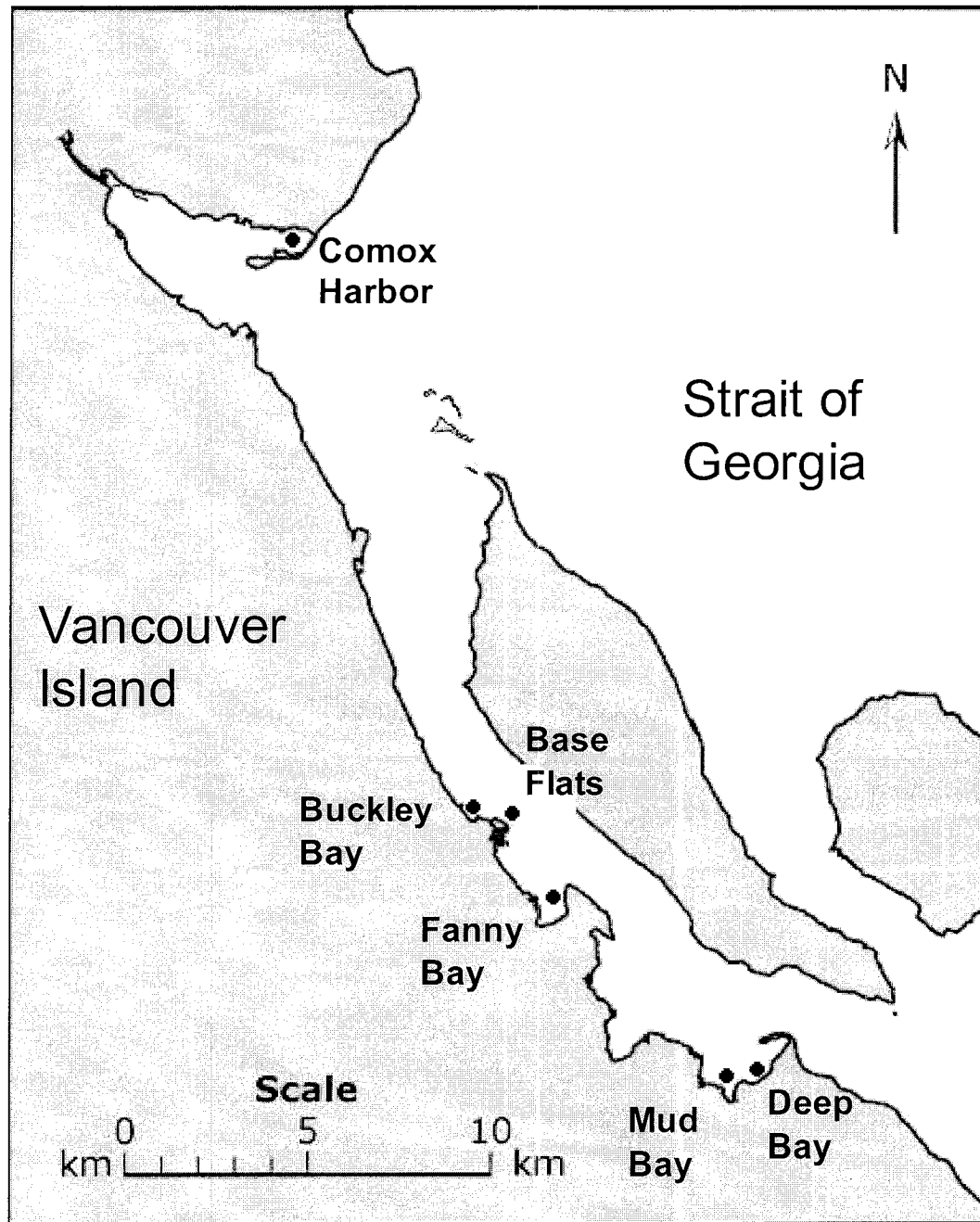
Figure 2.1.Map of Baynes Sound, located in the Strait of Georgia, British Columbia, showing the six sample plots.
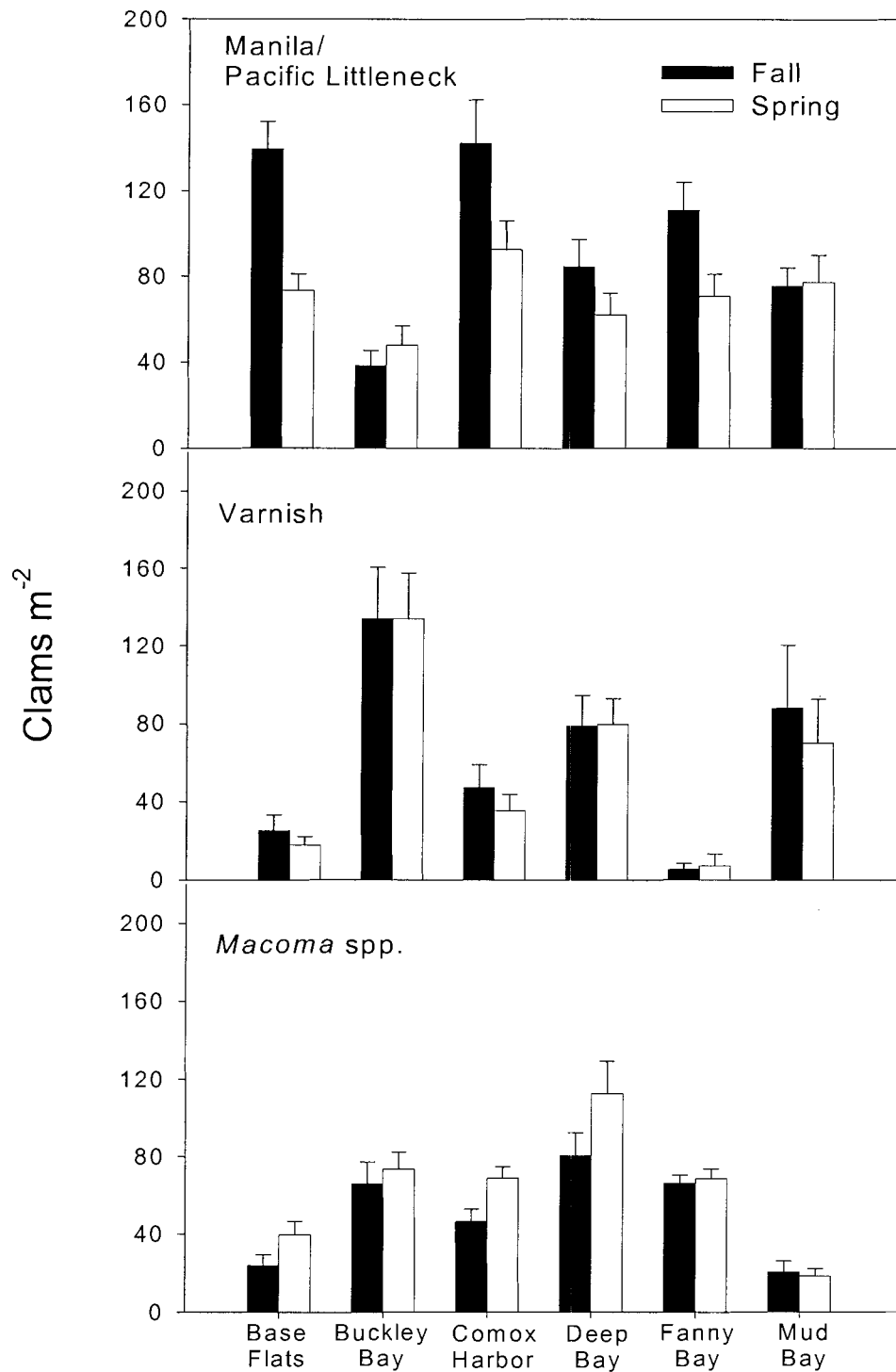
Figure 2.2. Clams m^{-2} (mean ± SE) of Manila/Pacific Littleneck, Varnish, and *Macoma* spp. clams at six sample plots in Baynes Sound, British Columbia, during fall (23 September-17 October 2003) and spring (5 April-12 April 2004). All values of clams m^{-2} are based on sampling performed with a 4 mm sieve.
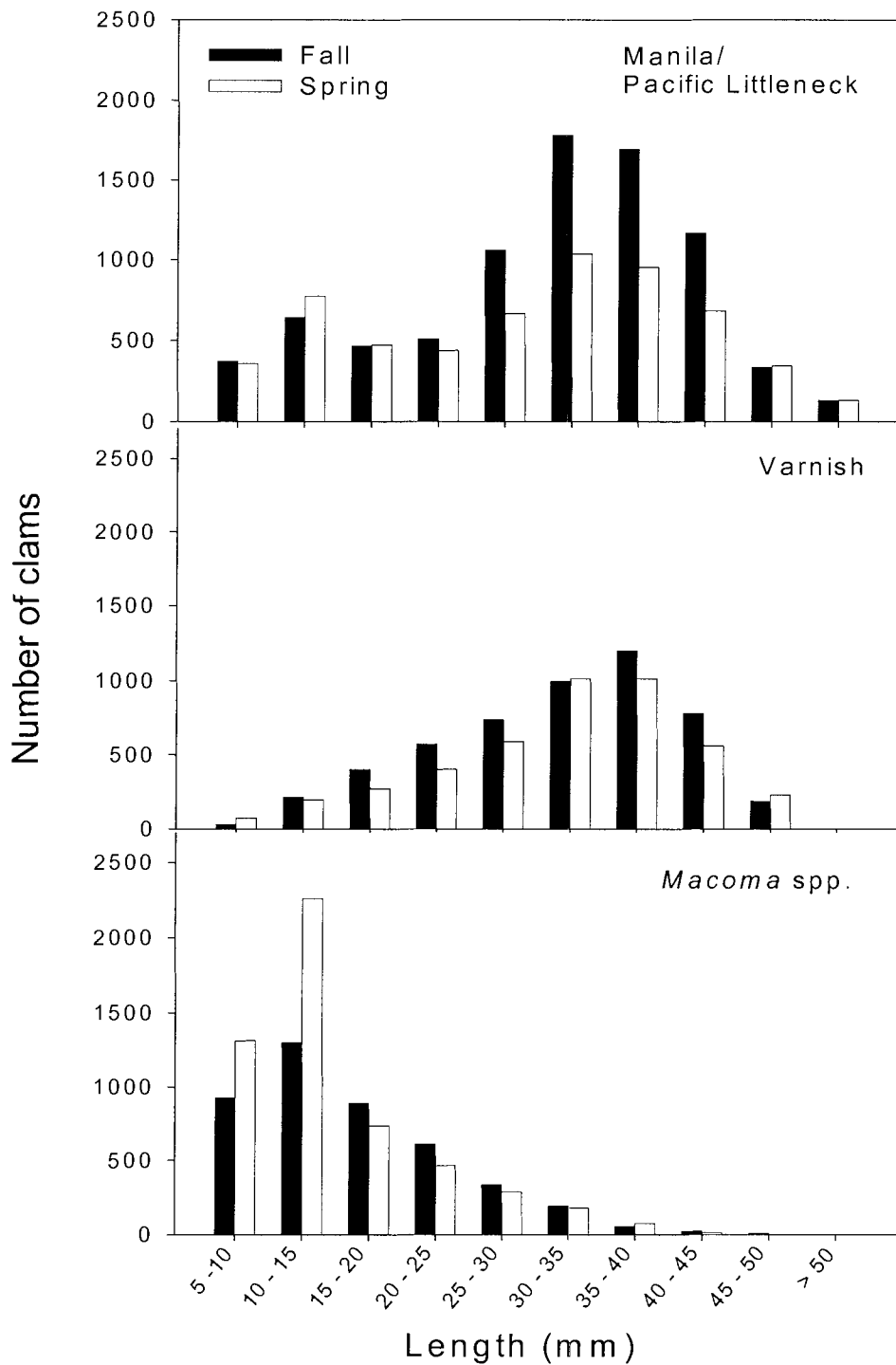
Figure 2.3. Length frequency distribution, summarized into 5 mm length classes, of Manila/Pacific Littleneck, Varnish, and *Macoma* spp. clams in Baynes Sound, British Columbia. Number of clams are for all six sample plots combined during fall (23 September-17 October 2003; n = 332 quadrats) and spring (5 April-12 April 2004; n = 326 quadrats). Clam numbers are based on sampling performed with a 4 mm sieve.

CHAPTER 3

Foraging Behaviors of Surf Scoters and White-Winged Scoters in Relation to Intertidal Clam Density: are Scoters Food Constrained During Winter?

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Abstract

Birds are known to modify their foraging behaviors in relation to food availability. Once understood, these relationships can be used to draw inferences about relative food availability and habitat quality. We measured foraging behaviors of Surf Scoters (Melanitta perspicillata) and White-winged Scoters (Melanitta fusca) feeding on clams during winter in the Strait of Georgia, British Columbia to evaluate the relative quality of the foraging landscape for wintering scoters. Because clam biomass does not appreciably increase during winter through growth or recruitment, scoters are faced with a depleting and potentially exhaustible food supply. Along with this temporal variation, clam densities vary widely by site. Therefore, we considered the influence of variation in clam density on scoter foraging behaviors, along with other factors known to affect foraging by other sea duck species, such as season, sex, age, and environmental attributes. We found that clam capture success and foraging effort of Surf Scoters were not related to variation in clam density. White-winged Scoter foraging effort was negatively related to clam density, while their clam capture success was unrelated. Foraging behaviors were generally more strongly related to other factors, especially seasonal and age effects. These results suggest that (1) observed variation in clam density was relatively insignificant for foraging scoters and (2) our study site constituted high quality winter habitat in which scoters were not constrained by food availability.

Introduction

Acquisition of energy and nutrition has direct effects on the reproductive potential and survival of animals (Lemon 1991). Because of these fitness consequences, animals typically select food sources and employ foraging behaviors that optimize energy intake (Pyke 1984, Stephens and Krebs 1986). When faced with variation in food availability, animals tend to modify their foraging behaviors. For example, when food becomes scarce, individuals often increase their overall foraging effort to maintain sufficient levels of energy intake (Hutto 1990, McKnight 1998, Cope 2003). Hence, foraging behaviors often reflect food availability as perceived by the foraging animal, and an understanding of this relationship can be used to evaluate general habitat quality (Hutto 1990).

Waterfowl, like other birds, have been shown to adjust their foraging behaviors in response to variation in food abundance or quality (Hassall et al. 2001, Cope 2003). Previous studies have documented an increased foraging effort by waterfowl, measured as the amount of time spent foraging, in response to decreasing food availability (Hill and Ellis 1984, Percival and Evans 1997). Similarly, waterfowl may adjust specific foraging behaviors, independent of the amount of time spent foraging, to contend with variation in food supplies. When faced with declining food availability, dabbling duck species increased their surface feeding rate or swam faster while feeding to maintain adequate levels of food intake (McKnight 1998). For diving ducks, changes in foraging behaviors are often manifested through changes in dive behaviors. During a foraging dive, variation in prey availability directly alters the amount of time spent searching and travelling by diving ducks (Draulans 1982, Tome 1988). In areas with high prey availability, dive duration is often shorter due to the greater likelihood of prey encounter (Draulans 1982).

Surf Scoters (*Melanitta perspicillata*) and White-winged Scoters (*Melanitta fusca*) forage exclusively by diving for prey (Brown and Fredrickson 1997, Savard et al 1998). During winter, diets of both scoter species are composed predominantly of bivalves (Vermeer and Levings 1977, Vermeer 1981). Successful predation of bivalves is largely influenced by bivalve density (Richman and Lovvorn 2003), as most bivalve species are sessile and unable to actively escape predation. At low bivalve densities, scoters are predicted to increase their foraging effort to compensate for the lower likelihood of encountering and capturing a bivalve during a foraging dive. At some minimal bivalve density, scoters likely choose to leave the foraging site rather than incur the energetic costs of further increases in foraging effort (Lovvorn and Gillingham 1996). Conversely, as bivalve densities increase, scoters are predicted to decrease their foraging effort due to a higher likelihood of bivalve capture. Foraging effort can continue to decrease until search time is completely minimized, at which point foraging effort remains constant regardless of further increases in bivalve density. An understanding of variation in foraging effort and bivalve capture of scoters will therefore provide a strong indication of bivalve availability and general habitat quality.

Our study occurred in the Strait of Georgia, British Columbia, in areas composed of soft-bottom intertidal flats. Within the Strait of Georgia, wintering scoters are potentially exposed to large amounts of variation in the density of intertidal clams, their primary prey in soft-bottom habitats (Vermeer 1981, Bourne 1984). Temporal variation arises via the predation and mortality of clam populations that are not renewed by growth or recruitment during the winter (Nosho and Chew 1972, Williams 1980, Bourne 1982), thus providing wintering scoters with a depleting and potentially exhaustible food supply. Similarly, scoters are exposed to spatial variation in clam density, resulting from soft-bottom intertidal flats that differ widely in basic abiotic characteristics (Bourne 1982).

Therefore, to assess food availability and general habitat quality from the perspective of foraging scoters, we monitored foraging effort and clam capture success of wintering Surf Scoters and White-winged Scoters in relation to spatial and temporal variation in clam density.

Methods

Study area

Our study area is located in the Strait of Georgia on the east coast of Vancouver Island, British Columbia and encompasses the marine waters of Baynes Sound (49.5° N, 124.8° W). Baynes Sound is a 40 km long coastal channel fringed by a number of small, protected bays. Large expanses of gravel and sand sediments comprise most of the intertidal habitat (Dawe et al. 1998). The area produces significant amounts of both wild and cultured bivalves and is an important wintering area for populations of waterfowl and other marine birds (Dawe et al. 1998). Waterbird surveys in Baynes Sound during the winters of 2002-03 and 2003-04 indicated a mean (± SE) population of 6500 ± 250 scoters (Surf Scoters + White-winged Scoters) and a maximum of ca. 9000 scoters (Canadian Wildlife Service, unpublished data).

Clam sampling

We based all data collection around six sample plots established throughout Baynes Sound in the winter of 2003-04. To determine intertidal clam density, we sampled these plots on two occasions, timed to coincide with scoter arrival to and departure from Baynes Sound: in the fall from 23 September – 17 October 2003, and in the spring from 5 – 12 April 2004. Each sample plot measured 150 m x 150 m (22 500 m^2) and was contained within an intertidal area bounded by the 1.0 m and 3.5 m tidal heights, encompassing the range of the dominant intertidal clam species in Baynes

Sound (Gillespie et al. 1999, Gillespie et al. 2001). Because the elevational slope varied among sample plots, the total tidal height encompassed by each plot differed slightly by location.

Clam sampling was conducted using a two-stage sampling methodology (Gillespie and Kronlund 1999). The entire 150 m x 150 m sampling plot was divided into 300 contiguous strata 0.5 m wide and aligned parallel to shoreline. These strata were then divided into 4 elevational groups, each containing 75 strata (thus each group measured 150 m parallel to shoreline, and 37.5 m perpendicular to shoreline). We then randomly selected 3 strata from each elevational group. Each selected stratum was then divided into 300 units that were 0.5 m x 0.5 m, and of these, 6 units (hereafter termed quadrats) were selected for sampling. Thus, 72 quadrats were sampled per sample plot in both fall and spring. Quadrat locations were selected separately for fall and spring sampling, and no fall quadrat locations were re-sampled in the spring.

Each quadrat was completely excavated to a depth of 15 cm, below which clams were considered inaccessible to foraging scoters (Lovvorn 1989, Richman and Lovvorn 2003). All excavated substrate was passed through a 4 mm sieve. Sieve size was selected to retain the lengths of bivalves consumed by scoters; of entire bivalves found in the esophagi of collected Surf Scoters and White-winged Scoters, as well as similarly sized Canvasbacks (*Aythya valisineria*), Spectacled Eiders (*Somateria fischeri*), and Common Eiders, few if any bivalves smaller than 4 mm were consumed (Bourne 1984, Lovvorn 1989, Nehls and Ketzenberg 2002, Lovvorn et al. 2003). Retained clams were identified to the species level, except for *Macoma balthica, M. expansa, M. inquinata, M. nasuta,* and *M. obliqua,* which were grouped by genus. The shell length of each clam, defined as the greatest linear distance between the anterior and posterior margins of the valve (Gillespie and Kronlund 1999), was measured to the nearest 5 mm length class

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(beginning with the 5 mm – 9.9 mm size class). All clams were returned to the sample hole and re-buried.

Some of the Baynes Sound intertidal area is used by the shellfish aquaculture industry for production of commercial clams and oysters. In some locations, large nets are placed atop portions of intertidal flats to protect commercial clam stocks from predation. Foraging scoters are effectively excluded from predating clams underneath these nets. Four of the six sample plots contained nets within their boundaries, and the total amount of net covering each of these sample plots was measured. During clam sampling, all quadrats that completely overlapped nets were recorded as net and no substrate was excavated. When quadrats partially overlapped nets, the proportion of the quadrat covered by net was estimated and only the net-free portion of the quadrat was sampled.

Foraging effort

To estimate foraging effort, dive behaviors of scoters were monitored via radio telemetry during the winter of 2003-04. Scoters were captured and affixed with radio transmitters during December of 2002 and 2003, following the procedures described by Lewis et al. (2005). Radio transmitter batteries lasted 18 months and some radio-marked scoters returned to Baynes Sound for consecutive winters, allowing us to monitor radio-marked scoters captured in December 2002 during winter 2003-04. The total number of radio-marked scoters present in Baynes Sound during winter 2003-4 was 42 Surf Scoters (28 males, 14 females) and 56 White-winged Scoters (34 males, 22 females). The radio signal disappeared when the scoter dove and resumed when the scoter resurfaced, allowing us to document both the occurrence and duration of dives (Wanless and Harris 1991, Custer et al. 1996). Radio-signals were detected using hand-held 4-element Yagi antennas connected to Advanced Telemetry Systems (ATS;

Isanti, Minnesota) R4000 receivers. Foraging effort was monitored from 12 November –

16 March, concluding in March due to the start of herring spawn, at which point scoters

abandoned their typical winter habitats and food sources within Baynes Sound.

Foraging effort was monitored only during diurnal hours due to the rarity of nocturnal

foraging by scoters within our study site (Lewis et al. 2005) and observations were

spread approximately evenly across daylight hours for each sample site. One hour

observation blocks were used to record the number of dives and length of each

individual dive (± 1 sec). Based on preliminary sampling of dive activity, observation

blocks of one hour duration were chosen because of their high likelihood (> 99%) to

detect diving. We used a maximum of one randomly selected foraging effort observation

per individual per day in analyses.

To assure a spatial and temporal connection between foraging effort

observations of radio-marked scoters and clam density of sample plots, we determined

locations of radio-marked scoters via biangulation. Biangulated scoter locations and

telemetry accuracy were determined following methods described by Lewis et al. (2005).

We used ArcView v.3.2 (ESRI 1999) geographic information system (GIS) software to

plot scoter point locations and sample plots on a digital 1:20000 TRIM base-map of the

British Columbia coast (British Columbia Ministry of Sustainable Resource

Management). A buffer was created around each sample plot, radiating 750 m from the

center point of each sample plot. For each foraging effort observation, inclusion in our

data analyses required the following temporal and spatial criteria: (1) an individual's

point location was collected on the same day as that individual's foraging effort

observation, and (2) the point location was located within a 750 m sample plot buffer.

Clam capture success

Clam capture success, defined as the number of clams captured per dive, was monitored at all six sample plots during the winter of 2003-04. When feeding on bivalves, scoters often bring captured bivalves to the surface for manipulation and ingestion (Ydenberg 1988). As scoters surfaced from dives, the presence or absence of a clam in the bill was recorded for each observed surfacing event, as well as scoter species and sex. Sample plots were continually scanned for surfacing scoters and all observations were restricted to the area bound by the sample plot. Only scoters for which the surfacing event was distinctly observed were included in data collection, minimizing potential bias caused by scoters that stayed longer at the surface to manipulate captured bivalves. Unmarked scoters were used for these observations, thereby preventing the observer from distinguishing between individuals. Observations were performed once per week at each plot from 1 November – 5 March, unless the plot was unoccupied by scoters during observation attempts. Sampling effort per sample plot was approximately evenly distributed throughout the core daylight hours of 0800 – 1600. Only observations with a minimum of five individuals present in the plot (mean = 29.7 scoters; range: 5 – 120 scoters) and 30 recorded surfacing events were included in analyses. Clam capture success was summarized for each observation period per scoter species as the proportion of total dives that were successful. Thus, observation periods served as our unit of measurement for data analyses.

Accurate estimates of clam capture success are dependent on the assumption that captured bivalves are mainly consumed at the surface. Typically, diving ducks bring large bivalves to the surface and swallow small bivalves underwater (de Leeuw and van Eerden 1992). Although some clams were certainly consumed underwater by scoters, length distribution of total clams sampled, as well as length of clams for which over-

winter declines were detected, indicates that our surface observations provide reliable measures of number of clams captured per dive (Lewis 2005, chapter 2).

Statistical analyses

We examined factors affecting foraging effort and clam capture success of Surf Scoters and White-winged Scoters. Our primary interest was the relationship between foraging effort/clam capture success and clam density. Clam density was measured twice per sample plot, once in the fall and once in the spring. Thus, to obtain a clam density estimate for the specific date and location of each foraging effort/clam capture success observation, daily clam density values for each sample plot were estimated from linear regression equations based on the fall and spring clam density measures (Table 3.1). Measures of clam density were a composite density of Manila (*Venerupis philippinarum*), varnish (*Nuttallia obscurata*), and pacific littleneck clams (*Protothaca staminea*), which constitute the majority (> 80%) of the scoter diet within our study site (Lewis 2005, chapter 2).

To evaluate variation in foraging effort, we considered three response variables for each scoter species: (1) dive duration, (2) number of dives per hour, and (3) minutes underwater per hour. Values of dive duration are averaged for all dives that occurred within each one hour observation period. In total, 137 and 168 one hour observations were used in our analyses of foraging effort for Surf Scoters and White-winged Scoters, respectively. For each response variable, we fit a series of candidate general linear mixed models (Littell et al. 2000) using PROC MIXED of program SAS (SAS Institute 1999), with separate and identical models sets for Surf Scoters and White-winged Scoters. We considered the following explanatory variables to examine variation in foraging effort: clam density, tidal height, time of day, wind speed, scoter age, scoter sex, and date. We used quadratic date (DATE), with all values of date adjusted relative

to 1 November 2003 = 1, to account for well established patterns of foraging effort that vary non-linearly over the course of winter for sea ducks (Guillemette 1998, Fischer and Griffin 2000, Systad et al. 2000). To restrict the size of our candidate model set, while still accounting for individual and environmental effects known to affect waterfowl foraging effort (Brodsky and Weatherhead 1985, Goudie 1999, Systad et al. 2000), certain explanatory variables were always considered in combination. Scoter age, defined as hatch year (< 1 yr) or adult (> 1 yr), and scoter sex were always considered in combination and are together referred to as individual effects (INDIV). Time of day, wind speed (estimated from Beaufort sea state), and tidal height were also always considered in combination and are together referred to as environmental effects (ENVIR). Daylight was not included as an environmental effect variable due to its high correlation (r^2 = 0.98) with date; no other explanatory variables were strongly correlated. Using DATE, INDIV, ENVIR, and clam density (CLAM) as units for model construction, we constructed separate and identical a priori candidate model sets for Surf Scoters and White-winged Scoters that consisted of the following 16 models: all single variable models, all additive combination models, and a null model with only an intercept. Models with interaction terms were not used in order to restrict the number of candidate models and because there were no strong a priori biological explanations for putative interactions.

We used an information theoretic approach to guide model selection (Burnham and Anderson 2002). Akaike's Information Criterion (AIC_c), adjusted for small sample size, was calculated for each model in the candidate set. ΔAIC_c and AIC_c weights (w_i) were used to infer the relative support of each model (Burnham and Anderson 2002). To determine the relative importance of each explanatory variable within a candidate model set, w_i were summed for all candidate models containing the explanatory variable under consideration, providing a parameter likelihood value. Parameters that are well

supported will have parameter likelihood values close to one. Also, model averaged parameter estimates and unconditional SE were calculated for each explanatory variable (Burnham and Anderson 2002).

General linear mixed models were used in our analyses of foraging effort to account for repeated measures on radio-marked individuals and to include subject as a random effect (Littell et al. 2000). Mixed models structure the correlation of residuals both within and among individuals by incorporating covariance parameters in the models. The best-fitting covariance structure for each response variable, as applied to the global model, was chosen using AIC model selection criteria (Littell et al. 2000). For both scoter species, compound symmetry was selected as the best-fitting covariance structure and was included in all foraging effort models.

To evaluate variation in clam capture success, we fit a candidate set of generalized linear models using PROC GENMOD of program SAS (SAS Institute 1999), with separate and identical models sets for Surf Scoters and White-winged Scoters. A total of 57 and 70 observation periods were used for Surf Scoters and White-winged Scoters, representing 5972 and 8381 surfacing events, respectively. We used generalized linear models based on logistic regressions to account for the binary measurement of clam capture success (successful or unsuccessful). To construct a priori candidate model sets, we included explanatory variables that could explain the probability of clam capture by scoters, which differed from the explanatory variables considered for foraging effort. Specifically, we examined the following explanatory variables: clam density (CLAM), tide, and sex. Because scoters in Baynes Sound foraged predominantly in the intertidal zone by diving, tide was included to account for differences in water depth and the amount of submerged intertidal habitat. Sex was measured as the proportion of surfacing events per observation that were male. Age

was not included because only hatch year Surf Scoter males can be differentiated by plumage (Iverson et al. 2003) and their observations accounted for < 0.5% of total observations. Candidate model sets consisted of all single explanatory variable models, all additive combination models, and a null model with only an intercept, for a total of 8 models. Models with interaction terms were not used because there were no strong *a priori* biological explanations for putative interactions.

For clam capture success, we again used an information theoretic approach to guide model selection (Burham and Anderson 2002). To account for the over-dispersion of variance, possibly caused by repeated measurement of individual scoters during clam capture success observations, we based our data inference on $QAIC_c$ and $QAIC_c$ weights (Burnham and Anderson 2002). All $QAIC_c$ and $QAIC_c$ weights were based on estimates of $ĉ$ calculated from the global model. Model averaged estimates of clam capture success were back transformed from the logit scale to estimates of probability. All other data inference methods follow those described for our foraging effort variables.

Results

On November 1, the first day we monitored scoter foraging behaviors, clam densities within our sample plots ranged between $112 - 178$ clams m^{-2} (Table 3.1). Clam density decreased over the winter at five of six sample plots, with density decreases ranging from 8 - 42% per sample plot. At one sample plot, we estimated a clam density increase of 4%. For the duration of winter 2003-04, total variation in clam density, both spatial and temporal, ranged between $82 - 180$ clams m^{-2} (Table 3.1).

Surf Scoter foraging effort

Surf Scoter dive duration averaged $20 - 27$ sec (Table 3.2), with a maximum recorded dive of 69 sec. The best-supported model for dive duration of Surf Scoters

included the INDIV, ENVIR, and DATE variables, and received nearly twice as much support as any other model based on ΔAIC_c and w_i (Table 3.3). Of the explanatory variables, only ENVIR was included in all four models with $\Delta AIC_c \leq 2$, and consequently had the largest parameter likelihood value, approaching 1.0 (Table 3.4). Model averaged parameter estimates indicated that, of the ENVIR parameters, tide level and wind speed had strong, positive associations with dive duration, while time of day had only minor effects (Table 3.4). As tide level increases, scoters have to travel a greater distance to reach the benthos during a dive, presumably explaining the effect of tide. DATE and INDIV received moderate support (Table 3.4). Dive duration was negatively related to DATE, although duration varied by less than 3 sec across the range of dates (Figure 3.1). With regards to INDIV, hatch year Surf Scoters had longer dives than adult Surf Scoters, while sexes were similar (Table 3.4). Of the explanatory variables, CLAM received the least support and had the lowest parameter likelihood value (Table 3.4). The model averaged parameter estimate for CLAM indicated that dive duration remained relatively constant across all clam densities documented within our study site (Figure 3.2).

Surf Scoters completed approximately 30 – 33 dives per hour (Table 3.2). There was a high degree of uncertainty regarding support for models evaluating variation in dives per hour of Surf Scoters, with no model receiving markedly higher support (Table 3.3). All of the best-supported models, however, contained DATE as an explanatory variable. The parameter likelihood value for DATE was 0.99, indicating that only models with DATE as an explanatory variable received substantial support (Table 3.4). Model averaged parameter estimates for DATE indicated that dives per hour slightly decreased in early winter, from approximately 12 November to 1 January, and then increased during the latter half of winter, from approximately 1 January to 15 March (Figure 3.1).

The explanatory variable of INDIV was moderately supported, with adults having higher dive rates than hatch year individuals (Table 3.4). ENVIR and CLAM were not well supported and offered little power for explaining variation in dives per hour. The model averaged parameter estimate for CLAM indicated that Surf Scoters did not vary their dive rate in response to the range of clam densities documented within our study site (Figure 3.2).

Averaged over the entire winter, Surf Scoters spent between 11 – 14 minutes underwater per hour, or between 18 to 23% of their time (Table 3.2). For total minutes underwater per hour, the best-fitting model contained only DATE as an explanatory variable (Table 3.3). The model containing DATE and INDIV received moderate support, although its AIC weight was half that of the top model (Table 3.3). DATE was the only well supported explanatory variable, and the only explanatory variable with a parameter likelihood > 0.33 (Table 3.4). Based on model averaged parameter estimates for DATE, minutes underwater per hour decreased from approximately 12 November to 1 January, and then increased from approximately 1 January to 15 March (Figure 3.1). The amount of time spent underwater is a function of both the number of dives and the duration of each dive. As indicated by our analyses of dives per hour and dive duration, Surf Scoters are adjusting their amount of time spent underwater in relation to date by adjusting their dive rate. Minutes underwater per hour and dives per hour had very similar relationships to date, while dive duration changed very little in relation to date (Figure 3.1). CLAM had a model averaged parameter estimate of essentially zero, indicating no change in minutes underwater per hour across the range of clam densities in our study site (Figure 3.2).

White-winged Scoter foraging effort

White-winged Scoter dive duration averaged 19 – 24 sec (Table 3.2), with a maximum recorded dive of 72 sec. Dive duration of White-winged Scoters was best explained by the model containing ENVIR and DATE as explanatory variables (Table 3.3). ENVIR had a parameter likelihood of 1.00, indicating that only models containing ENVIR received support (Table 3.4). As with Surf Scoters, tide had a strong, positive effect on dive duration of White-winged Scoters. Wind speed also had a positive association, though less pronounced than tide effects, while time of day had only minor effects (Table 3.4). DATE also received considerable support, as it occurred in the best-fitting model and had a relatively large parameter likelihood value (Table 3.4). Dive duration of White-winged Scoters was negatively related to DATE and the model averaged parameter estimate indicated that dive duration gradually decreased from approximately November to February (Figure 3.1). CLAM and INDIV received little support, and the model averaged parameter estimate for CLAM indicated no change in dive duration over the range of clam densities (Figure 3.2).

White-winged Scoters averaged 34 – 37 dives per hour (Table 3.2). Variation in dives per hour of White-winged Scoters was best explained by the model containing CLAM, INDIV, and DATE (Table 3.3). All three explanatory variables in the best-fitting model had large parameter likelihood values and were important for explaining variation in dives per hour (Table 3.4). DATE had a parameter likelihood of 0.99 and had a strong relationship with dives per hour. Based on model averaged estimates of DATE, White-winged Scoters steadily increased the number of dives per hour from approximately 1 January until their mid-March departure from our study site (Figure 3.1). INDIV was well supported and indicated that adults had higher dive rates than hatch year individuals (Table 3.4). CLAM was also well supported, but less so than the explanatory variables

of DATE and INDIV. Dives per hour was negatively related to CLAM, as White-winged Scoters dove less at higher clam densities (Figure 3.2). ENVIR was not well supported and offered little power for explaining variation in dives per hour.

Averaged over the winter period, White-winged Scoters spent approximately 11 – 14 minutes underwater per hour, or 18-23% of their time (Table 3.2). For minutes underwater per hour, two models were well-supported, each of which contained CLAM and INDIV as explanatory variables (Table 3.3). INDIV had the largest parameter likelihood value, as adults spent more time underwater than hatch year individuals (Table 3.4). Minutes spent underwater per hour was negatively related to CLAM. Based on model averaged estimates, White-winged Scoters foraging at the highest observed clam density of 180 clams m^{-2} dove for approximately 4 min less per hour than individuals at the lowest clam density of 82 clams m^{-2} (Figure 3.2). White-winged Scoters adjusted their minutes spent underwater per hour in relation to clam density via adjustment of number of dives per hour, as opposed to dive duration. DATE was not well supported and minutes spent underwater varied relatively little in relation to date (Figure 3.1). Similarly, ENVIR variables received almost no support.

Surf Scoter clam capture success

The best-supported model for describing variation in clam capture success of Surf Scoters was our null model, which fit an intercept only (Table 3.5). Six of eight models had ΔQAICc ≤4, indicating that the best-fitting model did not receive substantial support over lower-ranking models (Table 3.5). All of the explanatory variables had low parameter likelihood values, offering little power for explaining variation in clam capture success (Table 3.6). Based on model averaged parameter estimates, clam capture success changed less than 1% over the range of clam densities documented within our study site (Figure 3.3).

White-winged Scoter clam capture success

The best-supported model for describing variation in clam capture success of White-winged Scoters contained CLAM as an explanatory variable. However, seven of eight models had $\Delta QAIC_c \leq 4$, including the null model, indicating a high degree of model uncertainty and general lack of explanatory power for any of the models (Table 3.5). Of the explanatory variables, only CLAM received marginal support (Table 3.6). Based on model averaged parameter estimates, clam capture success at the highest clam density was approximately 4% lower than at the lowest clam density (Figure 3.3). This result is opposite our prediction of higher clam capture success at higher clam densities. A difference of only 4% at the extreme clam density values of our study site, however, is very small, essentially indicating no relation between clam density and clam capture probability. Further, non-transformed, unconditional 95% confidence intervals for CLAM were larger in magnitude than the actual parameter estimate.

Discussion

Inferring food availability and habitat quality

Baynes Sound clam stocks, which are not renewed via growth or recruitment during winter (Williams 1980, Bourne 1982), and declined in density at five of six samples sites, remained sufficiently abundant such that scoter foraging behaviors were largely unaffected. Neither foraging effort nor clam capture success of Surf Scoters was related to clam density. While foraging effort of White-winged Scoters was negatively related to clam density, their clam capture success was unrelated. Any significant food shortage would be expected to cause noticeable decreases in clam capture success, which is a direct measurement of the ability of scoters to obtain food. Our results suggest that over-winter variation in clam density was relatively insignificant for foraging scoters. Furthermore, we conclude that Baynes Sound constituted high quality foraging

habitat for wintering scoters, based on the lack of strong behavioral responses to clam density variation and the relatively low overall foraging effort of scoters (see below).

For obligate divers such as scoters, time spent underwater is a good, composite measure of foraging effort. Averaged over the entire winter, both scoter species spent approximately 18-23% of their time underwater in our study site. Goudie (1999) reported values of between 30-35% of time spent underwater for Surf Scoters and White-winged Scoters during winter in the Queen Charlotte Islands, British Columbia. Even during March in our study area, when clam densities during the winter residency period of scoters are at their lowest and pre-migratory hyperphagia may have started, Surf Scoters and White-winged Scoters spent an average of 23% and 28% of time underwater, respectively. In the event of food limitations, scoters would be expected to increase their foraging effort towards maximal values to compensate for the decreased probability of food encounter and capture. The values reported by Goudie (1999) indicate that both scoter species are capable of increasing their overall foraging effort well beyond the values we observed, further suggesting that clam availability was relatively high for scoters in Baynes Sound. Furthermore, scoters in Baynes Sound did not switch winter prey sources or undertake large-scale movements to new foraging sites (Esler, unpublished data), as has been documented for other marine birds experiencing food limitations (Guillemette et al. 1996, Lovvorn and Gillingham 1996, Suryan et al. 2000).

Relating foraging behaviors to clam density

For diving ducks feeding on benthic prey, the rate of prey intake often follows a type II functional response (Lovvorn and Gillingham 1996, Richman and Lovvorn 2003). In the type II functional response, intake rate increases with increasing prey density up to an asymptote, after which intake rate becomes limited by handling time and cannot

increase further. Accordingly, our observed lack of correlation between clam density and clam capture success of both scoter species, as well as foraging effort of Surf Scoters, could result from clam density values in the asymptote range of a type II functional response curve (Poulton et al. 2002). Clam densities, however, were more likely in the gradient section of the functional response curve, as indicated by clam capture success values that consistently ranged from 30 - 50%. This inability of scoters to consistently capture clams suggests that scoters were not limited strictly by handling time, but rather a combination of both search and handling times. Furthermore, Richman and Lovvorn (2003) documented increasing intake rates of captive White-winged Scoters for clam densities up to at least 1600 clams m^{-2} for small clams, and up to 400 clams m^{-2} for larger clams. The average clam densities of our sample plots did not exceed 180 clams m^{-2}, and only two individual quadrats from our sample plots, of more than 700 quadrats sampled, had clam densities > 1000 clams m^{-2}.

Assuming clam densities were in the gradient section of a type II functional response curve, the general lack of correlation between clam density and scoter foraging behaviors suggests that the range of clam density variation in Baynes Sound (82 - 180 clams m^{-2}) was relatively insignificant from the perspective of scoters. For Surf Scoters, this range of clam density variation was not large enough to elicit pronounced shifts in either foraging effort or clam capture success. For White-winged Scoters, this range of clam density variation was only large enough to affect their foraging effort. At the highest clam densities, White-winged Scoters spent approximately 16.8% of their time underwater, versus 23.6% at the lowest densities. While we expected changes in foraging effort to be accompanied by changes in clam capture success, the < 7% range of variation in time spent underwater for White-winged Scoters may have been too small to detect parallel changes in clam capture success. As well, White-winged Scoter dive

duration was not related to clam density, indicating that they were not increasing the length of their dives at low clam densities to maintain a heightened clam capture success.

Correlating clam density to foraging behavior is dependent on the spatial scale at which these factors are examined. All of our measures of clam density are at the scale of our sample plots, which measure 22,500 m^2 in area. This scale was chosen to provide a reasonable probability of locating radio-marked scoters or foraging flocks within a sample plot, thereby providing a spatial link between clam density and scoter foraging behaviors. Within an individual sample plot, clams were patchily located, and clam densities measured at the scale of our quadrats (0.25 m^2) occasionally detected variation of > 500 clams m^{-2}. While we do not know the scale at which scoters assess clam density, they can likely recognize and choose foraging patches at a scale smaller than our sample plots (Lovvorn and Gillingham 1996, Richman and Lovvorn 2003). When a foraging patch becomes energetically unprofitable, scoters likely move to a new patch that offers greater profitability (Lovvorn and Gillingham 1996). Accordingly, scoters may have moved amongst clam patches within the scale of a sample plot, potentially decreasing our ability to detect correlations between clam density and scoter foraging behaviors. Nonetheless, we accounted for larger-scale (i.e. > 500 m) scoter movements by establishing distinct spatial links between our measures of clam density and our observations of scoter foraging behavior. Furthermore, our sample plots were of a fine enough scale to detect significant temporal and spatial variation in clam density (Lewis 2005, Chapter 2), and any significant plot-wide clam depletion would be expected to noticeably affect the average foraging behaviors of associated scoters.

Species, age, and season effects

In relation to clam density, scoter species differed in that foraging effort of White-winged Scoters was negatively related to clam density while foraging effort of Surf Scoters was not. Foraging effort should reflect an individual's daily energetic intake and expenditure. Goudie and Ankney (1986) found that of four sea duck species, the smaller sea duck species spent more time feeding and consumed prey of higher energy density to compensate for their greater energetic demands per unit body mass. The smaller sea duck species, however, consumed predominantly small prey items, such as amphipods and isopods, while the larger sea duck species consumed prey of substantially larger biomass, such as mussels and urchins. When consuming foods of a similar size and energetic value, individuals of larger species must consume more biomass per day than smaller species (Goudie and Ankney 1986). White-winged Scoters (males 1500 g, females 1200 g) are larger than Surf Scoters (males 1000 g, females 900 g) and the diets of both scoter species in Baynes Sound are quite similar, being largely composed of only two clam species: Manila and varnish clams (Lewis, Chapter 2). Although White-winged Scoters consume slightly larger clams on average, size class preferences are not pronounced and both scoter species typically consume clams in the 10 – 50 mm range (Bourne 1984). Based on such similar diets, larger-bodied White-winged Scoters are predicted to consume more food and exert greater foraging effort. Accordingly, the greater energetic and time demands of White-winged Scoters may make them more sensitive to variation in clam density, resulting in the slightly negative correlation between their foraging effort and clam density.

Of the two clam species that were primary prey of scoters, White-winged Scoters consumed disproportionately more varnish clams than did Surf Scoters (Lewis 2005). The energy density of varnish clams is unknown and cannot be energetically compared

to Manila clams. Averaged over all our sample plots, however, varnish clams were less abundant (60 clams m^{-2}) than were Manila clams (76 clams m^{-2}). Furthermore, varnish clams typically reside at greater burial depths than do Manila clams (Gillespie et al. 1999, Byers 2005). The lower density and deeper burial depth of varnish clams may result in higher energy expenditure per unit search and handling time for White-winged Scoters (Byers 2005), as suggested by an overall lower clam capture success for White-winged Scoters (40%) than for Surf Scoters (45%). Hence, White-winged Scoters greater reliance on varnish clams may also partially explain the negative correlation between White-winged Scoter foraging effort and clam density.

In addition to species differences, age related differences also were evident in several dive behavior analyses. For Surf Scoters, adults had shorter dive durations and higher dive rates than hatch year individuals. The overall amount of time spent underwater, however, did not appreciably differ between the two age groups, indicating that both age groups were exerting approximately equal foraging efforts. For White-winged Scoters, adults spent more time underwater than did hatch year individuals. This was an unexpected result, as hatch year birds are often less adept foragers, due to their inexperience, and typically exert greater foraging efforts and lower foraging efficiencies (Heise and Moore 2003). Adult White-winged Scoters, however, typically weigh more than juveniles and may thus have to spend more time foraging to sustain their greater body mass. Also, hatch year white-winged scoters do not breed during the subsequent summer (Kehoe et al. 1989), and may have had less need to acquire fat stores prior to migration and reproduction via increased foraging efforts.

With respect to date, the amount of time spent underwater by Surf Scoters decreased by 4% from mid-November to mid-winter, and then increased by 10% to mid-March. This pattern is opposite that observed for Surf Scoters wintering at the Queen

Charlotte Islands (53°N), in which time spent feeding increased from October to January (Goudie 1999). Previous studies with other sea duck species at northern latitudes have typically documented increased amounts of time spent feeding during mid-winter (Guillemette 1998, Fischer and Griffin 2000, Systad et al. 2000). Many sea duck species are not thought to forage nocturnally (Nilsson 1970, McNeil et al. 1992, Rizzolo et al. 2005), and are thus daylight constrained during the shortest days of winter. To compensate for this decreased amount of feeding time during mid-winter, many sea duck species increase the proportion of daylight hours spent feeding. During the shortest days of winter at 70°N, Common Eiders (*Somateria mollissima*) and Long-tailed Ducks (*Clangula hyemalis*) spent at least twice as much time underwater per hour than during spring (Systad et al. 2000). Similarly, Harlequin Ducks wintering at 52°N (*Histrionicus histrionicus*) spent a greater proportion of time underwater during mid-winter than during early or late winter (Fischer and Griffin 2000). Surf Scoters in Baynes Sound, at latitude 49°N, rarely engaged in nocturnal foraging (Lewis et al. 2005). The observed minimization of foraging effort during mid-winter suggests that Surf Scoters in Baynes Sound were not constrained by daylight, sufficiently meeting their energetic requirements during the short days of mid-winter.

Due to their negative correlation between foraging effort and clam density, seasonal patterns of foraging effort by White-winged Scoters may have differed from those observed for Surf Scoters. White-winged Scoters decreased their dive duration and increased their dive rate as winter progressed, resulting in an approximately equal amount of time spent underwater in relation to date. As opposed to Surf Scoters, White-winged Scoters may have been restricted in their ability to decrease time spent underwater during mid-winter, when daylight is shortest, due to mild clam density constraints. The reasons for seasonal shifts in dive duration and dive rate, however,

remain perplexing. Perhaps, shorter, more frequent dives are used by scoters to search for profitable feeding patches, while longer, less frequent dives are used to capture clams from feeding patches of known profitability; as profitable feeding patches progressively became rarer over the winter period, White-winged Scoters utilized short, frequent dives on a more recurrent basis.

Conclusions

Our results suggest that wintering Surf Scoters and White-winged Scoters are not constrained by availability of prey in Baynes Sound. The recent invasion of the exotic varnish clam, within the last 10 - 15 years, has likely increased clam densities significantly above historic levels (Gillespie et al. 1999, 2001), enhancing overall habitat quality for wintering scoters. Similarly, recent activities of the shellfish aquaculture industry in Baynes Sound may have further increased clam abundance, mainly via the spread and spawning of aquaculture-planted Manila clams. For these reasons, Baynes Sound likely provides important, high-quality habitat for wintering scoters, as witnessed by the large numbers of scoters (mean population of ca. 6500 scoters) currently wintering in the area and the strong distributional relationship between scoters and clams (Lacroix et al., unpublished data, Zydelis et al. unpublished data). More studies across a range of prey densities and prey types would further establish the foraging variability and limitations of Surf Scoters and White-winged Scoters, as well as provide researchers with a foundation for site-by-site comparisons.

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Table 3.1. Linear regression equations describing changes in clam density (clams m^{-2}) over winter for each of six sample plots in coastal British Columbia, 2003-2004. Regression equations are based on clam density measurements determined from fall and spring clam sampling for Manila (*Venerupis philippinarum*), varnish (*Nuttallia obscurata*), and pacific littleneck clams (*Protothaca staminea*) combined. Date is scaled so that 1 November 2003 = 1.

Sample plot	Regression equation
1	Clam density = 155.38 – 0.49*date
2	Clam density = 173.30 + 0.06*date
3	Clam density = 178.29 – 0.39*date
4	Clam density = 158.32 – 0.13*date
5	Clam density = 112.35 – 0.27*date
6	Clam density = 159.78 – 0.10*date

Table 3.2. Mean ± SE for three variables defining foraging effort of radio-marked Surf Scoters and White-winged Scoters wintering in coastal British Columbia, 2003-2004. Data are summarized for the period from 12 November 2003 – 16 March 2004.

Foraging effort variable	Surf Scoter		White-winged Scoter	
	Male (N = 13)	Female (N = 6)	Male (N = 19)	Female (N = 11)
Dive duration (sec)	20.49 ± 0.14	26.94 ± 0.30	24.14 ± 0.14	18.84 ± 0.17
Dives hr^{-1}	32.61 ± 1.55	30.89 ± 2.09	34.47 ± 1.27	37.11 ± 2.78
Minutes underwater hr^{-1}	11.04 ± 0.57	13.81 ± 1.25	13.82 ± 0.41	11.64 ± 0.73

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Table 3.3. General linear mixed models evaluating variation in foraging effort of radio-marked Surf Scoters and White-winged Scoters during winter in coastal British Columbia, 2003-2004. For all models, the number of parameters (k) includes +1k for an intercept and +1k for variance estimate. Covariance structures for repeated measures include +1k for all models except the null model. The models best-supported by our data (ΔAICc ≤2) and the null model are presented, listed in order of ΔAICc.

Species	Foraging effort variable	Model[a]	k	ΔAICc	w_i
Surf Scoter	Dive duration (sec)	INDIV + ENVIR + DATE	10	0.00	0.30
		INDIV + ENVIR	8	1.26	0.16
		ENVIR + DATE	8	1.37	0.15
		CLAM + INDIV + ENVIR + DATE	11	2.00	0.11
		Null	2	93.57	0.00
	Dives hr^{-1}	INDIV + DATE	7	0.00	0.26
		DATE	5	0.33	0.22
		CLAM + INDIV + DATE	8	1.49	0.12
		INDIV + ENVIR + DATE	10	1.50	0.12
		ENVIR + DATE	8	1.67	0.11
		Null	2	31.80	0.00
	Minutes underwater hr^{-1}	DATE	5	0.00	0.38
		INDIV + DATE	7	1.41	0.19
		Null	2	56.42	0.00
White-winged Scoter	Dive duration (sec)	ENVIR + DATE	8	0.00	0.49
		Null	2	80.40	0.00

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Table 3.3 continued

Species	Foraging effort variable	Model[a]	k	ΔAIC_c	w_i
White-winged Scoter	Dives per hour	CLAM + INDIV + DATE	8	0.00	0.59
		Null	2	28.02	0.00
	Minutes underwater hr^{-1}	CLAM + INDIV + DATE	8	0.00	0.47
		CLAM + INDIV	6	0.60	0.35
		Null	2	16.41	0.00

[a] Explanatory variable abbreviations: CLAM = clam density; DATE = quadratic date; INDIV = age, sex; ENVIR = tidal height, time of day, wind speed.

Table 3.4. Parameter likelihoods and weighted parameter estimates ± unconditional SE from general linear mixed models evaluating variance in foraging effort of radio-marked Surf Scoters and White-winged Scoters during winter in coastal British Columbia, 2003-2004. Explanatory variables with the greatest relative support have parameter likelihoods close to 1.0. Explanatory variable abbreviations are defined in Table 3.3. Parameter estimates for DATE are scaled so that 1 November 2003 = 1.

		Surf Scoter		White-winged Scoter	
Foraging effort variable	Explanatory variable	Parameter likelihood	Parameter estimate ± SE	Parameter likelihood	Parameter estimate ± SE
Dive duration (sec)	Intercept		28.000 ± 8.888		22.997 ± 6.283
	CLAM	0.30	0.010 ± 0.016	0.28	0.000 ± 0.008
	ENVIR	0.99		1.00	
	Tide		1.729 ± 0.748		1.856 ± 0.631
	Time of day		-0.306 ± 0.227		-0.213 ± 0.184
	Wind		0.220 ± 0.0850		0.150 ± 0.079
	INDIV	0.69		0.22	
	Age^a		-8.045 ± 4.028		0.225 ± 0.559
	Sex^b		0.940 ± 2.137		-0.569 ± 0.614
	DATE	0.62		0.84	
	Date		-0.081 ±0.048		-0.111 ± 0.059
	$Date^2$		0.000 ± 0.000		0.000 ± 0.000
Dives hr^{-1}	Intercept		22.290 ± 14.754		34.639 ± 15.632
	CLAM	0.29	-0.016 ± 0.028	0.75	-0.103 ± 0.055
	ENVIR	0.32		0.18	
	Tide		-0.150 ± 0.587		-0.107 ± 0.353
	Time of day		0.337 ± 0.278		0.143 ± 0.159

Table 3.4 continued

Foraging effort variable	Explanatory variable	Surf Scoter		White-winged Scoter	
		Parameter likelihood	Parameter estimate ± SE	Parameter likelihood	Parameter estimate ± SE
Dives hr^{-1}	Wind		0.033 ± 0.067		-0.027 ± 0.048
	INDIV	0.55		0.85	
	Age[a]		9.404 ± 5.863		12.213 ± 4.593
	Sex[b]		1.771 ± 2.865		2.040 ± 2.608
	DATE	0.99		0.99	
	Date		-0.199 ± 0.135		-0.157 ± 0.211
	Date^2		0.002 ± 0.001		0.002 ± 0.001
Minutes underwater hr^{-1}	Intercept		11.781 ± 5.577		17.590 ± 4.116
	CLAM	0.25	-0.000 ± 0.010	0.89	-0.041 ± 0.017
	ENVIR	0.24		0.05	
	Tide		0.243 ± 0.258		0.021 ± 0.036
	Time of day		0.053 ± 0.066		0.006 ± 0.011
	Wind		0.026 ± 0.028		-0.000 ± 0.004
	INDIV	0.33		0.94	
	Age[a]		1.136 ± 1.333		3.842 ± 1.441
	Sex[b]		1.154 ± 1.062		-1.538 ± 0.931
	DATE	0.98		0.58	
	Date		-0.146 ± 0.056		-0.067 ± 0.047
	Date^2		0.001 ± 0.000		0.000 ± 0.000

a Age is a categorical variable (hatch-year or adult) with hatch-year as the reference value.
b Sex is a categorical variable (female or male) with male as the reference value.

Table 3.5. Generalized linear models based on logistic regressions evaluating variation in clam capture probability of Surf Scoters and White-winged Scoters during winter in coastal British Columbia, 2003-2004. For all models, the number of parameters (k) includes +1k for an intercept, +1k for a variance estimate, and +1k for a variance inflation factor. The models best-fit by our data ($\Delta QAIC_c \leq 2$) and the null model are presented, listed in order of $\Delta QAIC_c$.

Species	Model [a]	k	$\Delta QAIC_c$	w_i
Surf Scoter	Null	3	0.00	0.37
	Sex	4	1.42	0.18
White-winged Scoter	CLAM	4	0.00	0.34
	Null	3	1.16	0.19
	CLAM + Tide	5	1.83	0.14

a Explanatory variable abbreviations: CLAM = clam density

Table 3.6. Parameter likelihoods from generalized linear models, based on logistic regressions, evaluating variance in clam capture probability of Surf Scoters and White-winged Scoters during winter in coastal British Columbia, 2003-2004. Explanatory variables with the greatest relative support have parameter likelihoods close to 1.0.

	Surf Scoter	White-winged Scoter
Explanatory variable [a]	Parameter likelihood	
CLAM[a]	0.24	0.64
Sex	0.33	0.25
Tide	0.27	0.29

a Explanatory variable abbreviations: CLAM = clam density
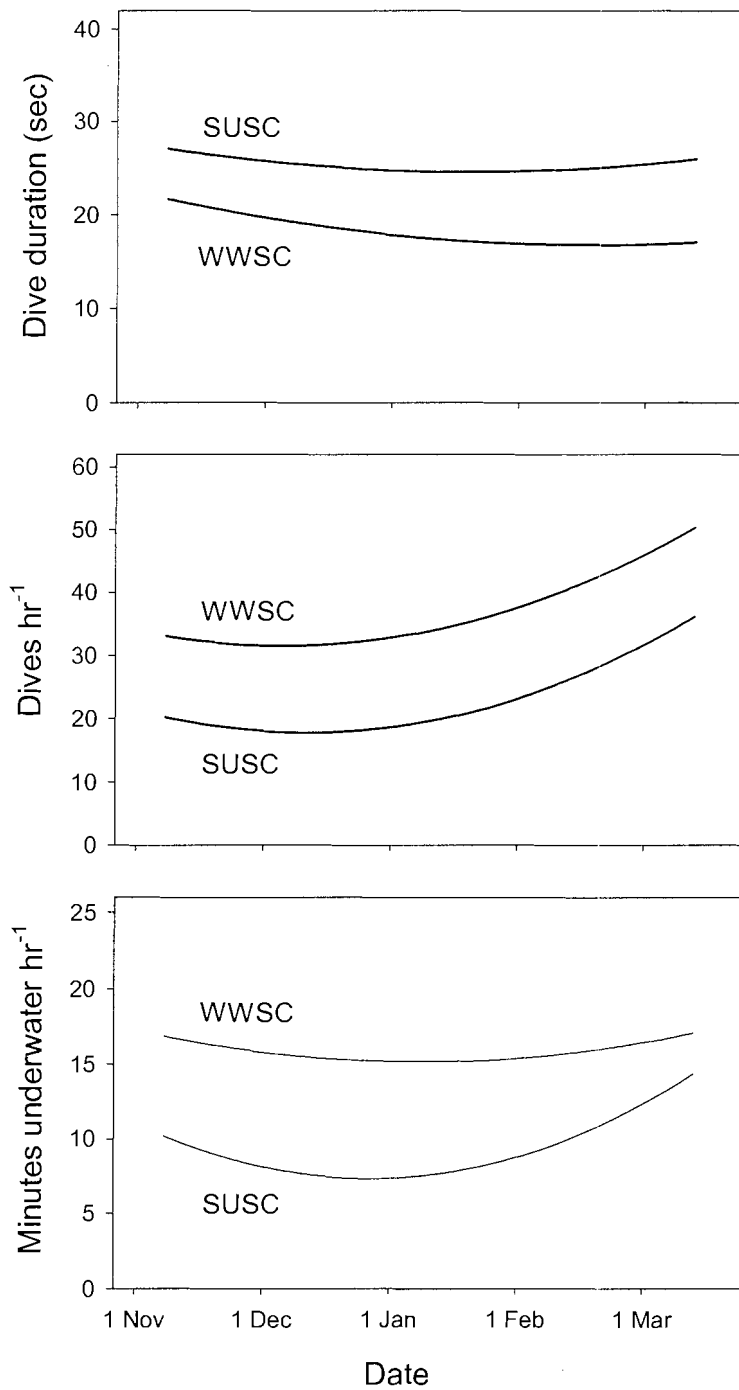
Figure 3.1. Model-averaged estimates of foraging effort (dive duration, dives per hour, and minutes underwater per hour) by date for radio-marked Surf Scoters and White-winged Scoters wintering in coastal British Columbia, 2003-2004. Model averaged estimates are restricted to the range of dates for which foraging effort was sampled.
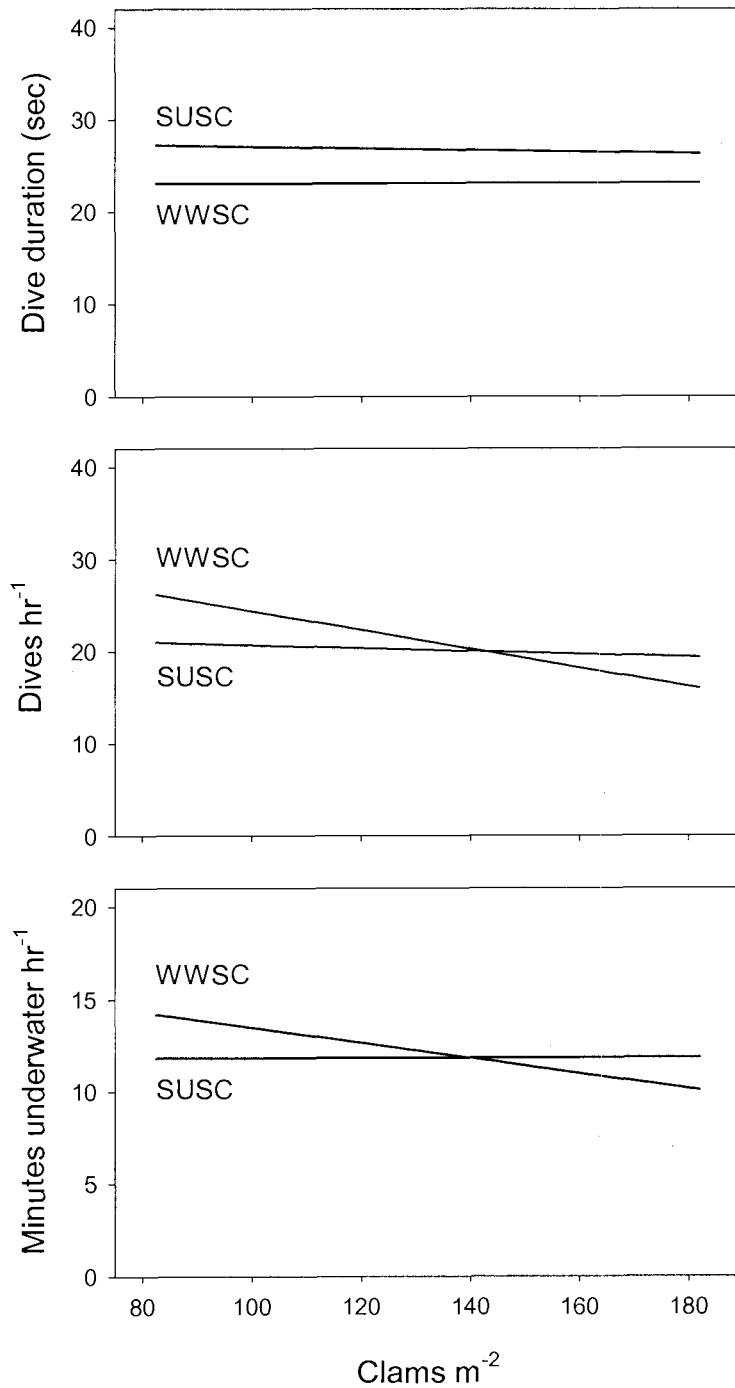
Figure 3.2. Model-averaged estimates of foraging effort (dive duration, dives per hour, and minutes underwater per hour) by clam density for Surf Scoters and White-winged Scoters wintering in coastal British Columbia, 2003-2004. Model averaged estimates are restricted to the range of clam densities observed within our sample plots.
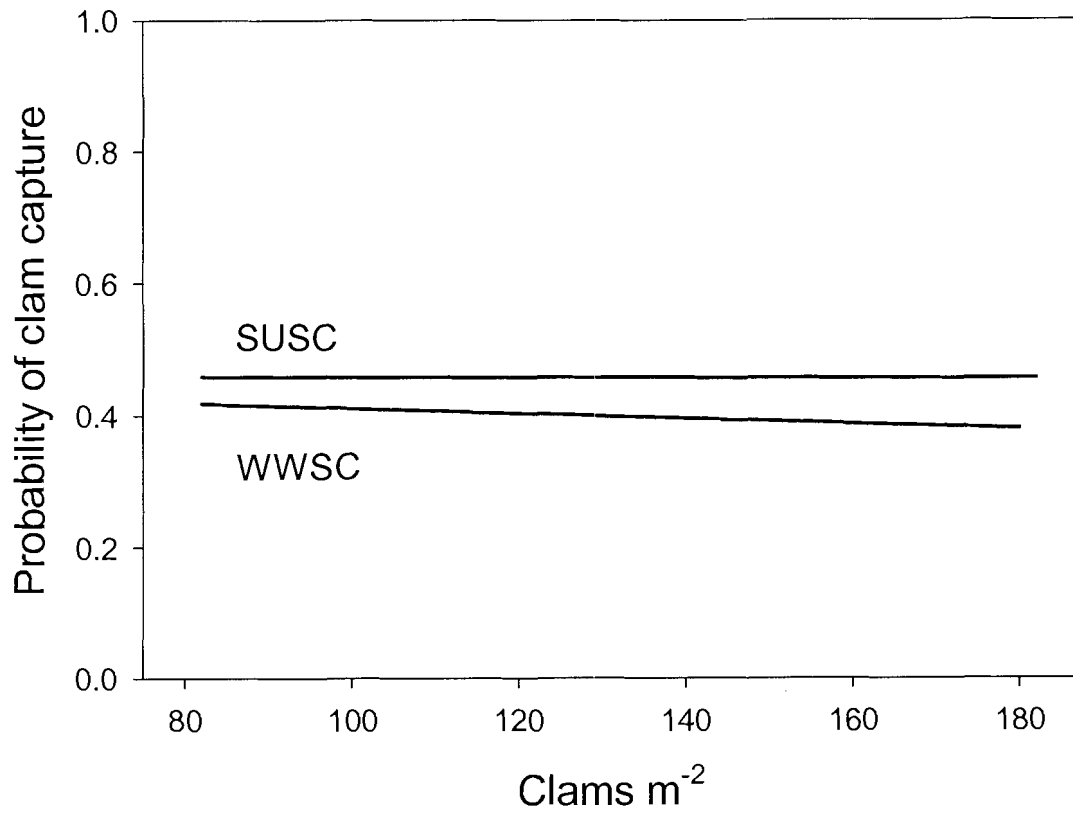
Figure 3.3. Model-averaged estimate of clam capture probability by clam density for Surf Scoters and White-winged Scoters wintering in coastal British Columbia, 2003-2004. Model averaged estimates are restricted to the range of clam density values experienced within our sample plots.

CHAPTER 4

Nocturnal Foraging Behaviors of Wintering Surf Scoters and White-Winged Scoters

Abstract

We studied the nocturnal foraging behavior of Surf Scoters (*Melanitta perspicillata*) and White-winged Scoters (*Melanitta fusca*) during winter in coastal British Columbia. Using radio telemetry, we collected nocturnal and diurnal data documenting the frequency of foraging dives and the location of scoters in relation to their intertidal foraging grounds. We found that dive foraging rarely occurred during nocturnal periods for either species. Only 2% of nocturnal observation blocks for both scoter species contained diving, compared with 98% of diurnal observation blocks. This corresponded to an average of only 0.1 min spent underwater per half-hour observation block during the night and over 7 min during the day. Both species of scoters were located farther offshore and in deeper waters during nocturnal hours, indicating that they were not using intertidal foraging areas at night. Our results suggest that Surf Scoters and White-winged Scoters face daylight-imposed limits on the amount of available foraging time. These potential day length restrictions should be considered when reviewing human activities that potentially alter the amount of available foraging time or food supplies in winter habitats.

Introduction

Understanding the foraging strategies that animals employ when balancing energy budgets can lead to a clearer understanding of potential constraints to populations, as well a species' behavioral scope when responding to environmental change (Pyke 1984). The allocation of time to foraging varies among taxa and individuals, and can have important implications for meeting energy requirements (Bautista et al. 1998). When faced with food or energetic shortfalls, the ability to adjust foraging time allows animals to maintain the necessary rate of energy acquisition. For obligate diurnal foragers, day length imposes strict limits on available foraging time. However, having the flexibility to forage both diurnally and nocturnally greatly increases the amount of potential foraging time.

Studies have shown that some waterfowl regularly forage at night (Owen 1990, McNeil et al. 1992), while others extend foraging into nocturnal periods when food is scarce or day length is short (Lane and Hassall 1996, Systad and Bustnes 2001). Most sea duck species (tribe Mergini) are thought to be diurnal foragers (Nilsson 1970, Guillemette et al. 1992, McNeil et al. 1992), although few data exist to adequately address this assumption. This information gap limits thorough understanding of sea duck foraging ecology and energy management strategies.

Many sea duck species winter at northern temperate to subarctic latitudes, where day length is short and ambient temperatures are low during mid-winter. This combination of winter conditions, which reduces diurnal foraging time and increases energy demands, may require that sea ducks forage at night to obtain necessary energy requirements. Previous studies have shown that some sea duck species compensate for short winter days by increasing the proportion of daylight hours spent feeding (Guillemette 1998, Fischer and Griffin 2000, Systad et al. 2000) or by extending their

feeding into low-light crepuscular periods (Nilsson 1970, Systad et al. 2000). However, recent data from high latitudes have demonstrated nocturnal feeding by some sea duck species during the shortest days of winter (Systad and Bustnes 2001). These nocturnal foraging sea ducks fed in shallow waters and employed non-dive feeding behaviors, such as surface-feeding and up-ending (Systad and Bustnes 2001). Owing to the high energetic cost of diving (de Leeuw 1996), the utilization of shallow water habitats and surface-feeding techniques may minimize energetic foraging costs that may be higher during nocturnal hours.

Surf Scoters (*Melanitta fusca*) and White-winged Scoters (*Melanitta perspicillata*) are believed to feed only diurnally (McNeil et al. 1992), although no studies have attempted to directly measure their nocturnal foraging during winter. Both scoter species feed primarily on bivalves during winter (Bourne 1984, Vermeer and Bourne 1984). Bivalves are sessile and often concealed beneath the substrate, potentially minimizing the need for visually-directed predation. Indeed, some non-sea duck species of diving ducks (tribe Aythyini) commonly prey upon bivalves at night (Nilsson 1970, Pedroli 1982, Custer et al. 1996). Therefore, scoters could potentially utilize nocturnal foraging, especially under conditions of shortened day length, decreased food availability, or diurnal anthropogenic disturbances.

To determine the extent to which Surf Scoters and White-winged Scoters forage nocturnally, we monitored their nocturnal activities in Baynes Sound, British Columbia, Canada during the winters of 2002-03 and 2003-04. The paucity of information about nocturnal foraging by sea ducks is largely due to the difficulty of locating and observing them at night. To overcome these difficulties, we used radio telemetry to remotely monitor the location and diving behavior of scoters during the nocturnal period. Our objective was to gain an understanding of nocturnal foraging behaviors of scoters by

determining (1) the frequency of foraging dives at night and (2) the location of scoters at night in relation to their intertidal foraging grounds. While documentation of diving provides a definitive quantification of nocturnal foraging, the location data also provide information regarding the potential use of non-dive foraging behaviors in shallow water habitats. These nocturnal data were compared with similarly collected diurnal data to provide an understanding of scoter foraging activity over a 24 hour period.

Methods

Study area

Our study area is located in the Strait of Georgia on the east coast of Vancouver Island, British Columbia and encompasses the marine waters of Baynes Sound (49.5° N, 124.8° W). Baynes Sound is a 40 km long coastal channel fringed by a number of small, protected bays. Large expanses of gravel and sand sediments compose a majority of the intertidal habitat in Baynes Sound (Dawe et al. 1998). The area produces significant amounts of both wild and cultured bivalves, and is internationally recognized as an important wintering area for populations of waterfowl and other marine birds (Dawe et al. 1998). Of the diving duck species, Surf Scoters and White-winged Scoters are most numerous, accounting for 41% of all diving ducks in Baynes Sound (Dawe et al. 1998). Waterbird surveys in Baynes Sound for the winters of 2002-03 and 2003-04 estimated a mean (± SE) population of ca. 6500 ± 250 scoters (Surf Scoters + White-winged Scoters) and a maximum of ca. 9000 scoters (Canadian Wildlife Service [CWS], unpublished data). Surf Scoters and White-winged Scoters within Baynes Sound feed almost exclusively on infaunal bivalves (clams) in small sediment, intertidal areas (CWS, unpublished data).

Scoter captures

Surf and White-winged Scoters were captured during December 2002 and 2003 using modified floating mist nets (Kaiser et al. 1995). Mist nets were deployed pre-dawn and positioned in foraging areas used by scoters. Captured scoters were removed from mist nets, placed into holding kennels, and transferred to shore for radio transmitter implantation. Radio transmitters with external antennae were surgically implanted in the abdominal cavities of Surf Scoters (2002: 27 males, 15 females; 2003: 18 males, 9 females) and White-winged Scoters (2002: 21 males, 13 females; 2003: 28 males, 20 females). Abdominally implanted transmitters have been successfully used in other sea duck species without evidence of either undue short-term (Mulcahy and Esler 1999) or long-term (Esler et al. 2000) consequences. The transmitters (Holohil Systems, Ltd., Carp, Ontario) were cylindrical, weighed 17.5 g, transmitted at 45 pulses per minute, and contained mortality switches that doubled the pulse rate if the transmitter remained motionless for ≥12 hr. Surgeries to implant radio transmitters were performed by experienced veterinarians following procedures developed for other sea duck species (Mulcahy and Esler 1999). Scoters were held for at least one hour post-surgery and subsequently released at their capture sites.

Radio telemetry

We monitored the diving behavior and locations of radio-marked scoters during the winters of 2002-03 (20 December -15 March) and 2003-04 (1 November -1 March). Diving behavior data were gathered only during the winter of 2002-03. Collection of location data in 2003 began in November 2003, prior to that winter's transmitter deployment, due to the return of radio-marked scoters from the previous winter. We concluded monitoring each winter at the start of herring spawn, at which point scoters abandoned their typical winter habitats and food sources within Baynes Sound.

Dive behaviors of radio-marked scoters were monitored with hand-held 4-element Yagi antennas connected to Advanced Telemetry Systems (ATS; Isanti, Minnesota) R4000 receivers. The radio-signal disappeared when the bird dove and resumed when the bird resurfaced, allowing the observer to document both the occurrence and duration of foraging dives (Wanless and Harris 1991, Custer et al. 1996). To determine an appropriate observation duration, radio-signals were monitored diurnally for $\geq$1 hr. Of all diurnal non-diving periods lasting $\geq$5 min (n = 1320), only 4.5% were $\geq$30 min. Therefore, a 30 min observation time was used for monitoring, given the high likelihood of detecting dive foraging if it were to occur. The number of dives and length of each individual dive ($\pm$ 1 sec) were recorded during each 30 min observation block. Telemetry observations were conducted diurnally and nocturnally at multiple sites throughout Baynes Sound that offered both unobstructed water views and heightened elevation. Nautical twilight was used to define the boundary between night and day, as it assured almost complete darkness for nocturnally-defined time periods. Start times of telemetry observation bouts were set so that a broad range of tide levels were frequently and evenly sampled within both diurnal and nocturnal periods. Furthermore, sampling bouts within nocturnal and diurnal observation periods were evenly spread across winter dates and the 24 hour cycle. Daytime visual observations of radio-marked scoters were used to confirm the loss of radio-signal during a dive. These observations also confirmed that scoters foraged exclusively by diving during the day, not engaging in surface feeding behaviors that might not result in radio-signal loss.

Point locations of radio-marked scoters were determined using biangulation with vehicles outfitted with two 4-element Yagi antennas mounted on extending masts (White and Garrott 1990). Yagi antennas were connected to ATS R4000 receivers and equipped with null/peak combiners. Compass bearings for each radio-marked individual

of interest were collected simultaneously by two different observers at known telemetry locations, eliminating location error associated with animal movement (Schmutz and White 1990). Diurnal point locations were collected ≥1 time per week for each radio-marked individual within the study area. Nocturnal locations were collected less frequently, with approximately one point location obtained monthly per individual within the study area. Telemetry accuracy tests of point locations indicated that signal bearings collected by observers had a standard deviation of ± 4.2° from the true bearing. Using this standard deviation, the mean (± SE) 90% error polygon for all nocturnal and diurnal bearings was estimated to be 3.0 ha ± 0.2 (Lee et al. 1985, White and Garrott 1990), a sufficient accuracy for our point location analyses.

We estimated point location coordinates and distances between the observer and point locations using Location of a Signal (LOAS v. 3.0) triangulation software (Ecological Software Systems, Ltd., Sacramento, California). Location data were filtered to assure we were using the most accurate information, excluding locations that met the following criteria: locations with non-intersecting bearings, locations without bearing separation between 20° and 160°, locations estimated to be on land, and locations with observer to location distances ≥4 km. Locations ≥4 km from the observer were unreliable due to weak radio-signal reception. Only one location per individual during a single diurnal or nocturnal observation session was used in the analyses. If more than one location per individual was obtained during an observation session, a single location was randomly selected for inclusion in analyses.

We used ArcView v.3.2 (ESRI 1999) geographic information system (GIS) software and associated supplementary extensions to retrieve geographic characteristics of points representing scoter locations. To determine the minimum distance between each point location and shore, we plotted point locations on a digital

1:20 000 TRIM base-map of the British Columbia coast (British Columbia Ministry of Sustainable Resource Management). The TRIM base-map shoreline within our study area was divided into 10 m segments using the Polyline-Chopper script (Gee 2004) developed for ArcView v.3.2. The distance was then estimated using the Nearest Features v.3.7a extension (Jenness 2004), which measured the distance between the point location and the center of the nearest 10 m shoreline segment. Water depth at point locations was determined by intersecting the point locations with a digitized 1:40 000 Baynes Sound nautical bathymetry chart (Fisheries and Oceans Canada, no. 3527) using the Geoprocessing extension built into ArcView v.3.2. Depth zones were defined as either intertidal or subtidal, with subtidal waters being broken into 10 m depth zones (i.e., 1-10 m, 11-20 m, etc.). Intertidal zone includes all locations where depth ≤ 0 m at the lowest low tide. For statistical analyses, intertidal locations were scored as 0 m depth and the mid-point of each subtidal 10 m depth zone was used for all other depths.

Statistical analyses

We estimated the frequency of dive foraging for diurnal and nocturnal periods as the proportion of 30 min observation blocks containing ≥ 1 dive. The amount of time spent foraging was determined by summing the total amount of time spent underwater per 30 min observation block. Time spent foraging and frequencies of dive foraging were compared between diurnal and nocturnal periods.

We used an information-theoretic approach to data analysis (Burnham and Anderson 2002). We examined three response variables: (1) total time underwater per 30 min (2) water depth at scoter locations, and (3) distance to shore. For each response variable, we fit a series of candidate general linear mixed models (Littell et al. 2000) using PROC MIXED of program SAS (SAS Institute 1999). The candidate model set for each response variable incorporated the same explanatory variables: species (Surf

Scoter, White-winged Scoter), sex, and night/day (defined nominally as either night or day). Without any background knowledge of scoter nocturnal behavior or species/sex differences, all additive model combinations of the explanatory variables and all single explanatory variable models were regarded as biologically plausible. A null model was also included in each candidate model set to assess model fit (Burnham and Anderson 2002). Models with interaction terms were not used in order to restrict the number of candidate models and because there were no strong biological explanations for putative interactions. Thus, identical candidate model sets for each response variable consisted of all single explanatory variable models, all additive combination models, and a null model. We used Akaike's Information Criterion (AIC) to rank the fit of each model within a candidate set (Burnham and Anderson 2002). For each of our analyses, the large sample size (n) relative to the total number of parameters (k) did not require the use of small-sample-size AIC corrections. ΔAIC were used to compare the relative explanatory value of the candidate models, with ΔAIC defined as the difference between the AIC value of the best-fitting model and each respective model in the set. Thus, ΔAIC = 0 for the model of best fit. All models with a ΔAIC $\leq$ 2 were considered to have substantial support and received consideration in making data inferences (Burnham and Anderson 2002). AIC weights (w_i), which indicate the relative likelihood of a model given the data and set of candidate models, also were calculated to provide a relative weight of evidence for each model (Burnham and Anderson 2002). To determine the relative importance of each explanatory variable within a candidate model set, AIC weights were summed for all candidate models containing the explanatory variable under consideration, providing a parameter likelihood value. Also, weighted parameter estimates and unconditional SE were calculated for the explanatory variables in each analysis, based on AIC weights for all candidate models, to account for model uncertainty (Burnham and Anderson 2002).

General linear mixed models were used to account for repeated measures on individuals and to include subject as a random effect (Littell et al. 2000). Mixed models structure the correlation of residuals both within and among individuals by incorporating covariance parameters in the models. The covariance structures we considered for each response variable included the spatial power law, both with and without a random between-subject effect, to model decreasing correlation with increasing time between repeated observations and compound symmetry to model constant correlation among repeated observations. The best-fitting covariance structure for each response variable was chosen using AIC model selection criteria (Littell et al. 2000). For the response variables of distance to shore and water depth, compound symmetry was selected as the best fitting covariance structure. For total time underwater per 30 min, the spatial power law structure with a random between-subject effect was chosen as the best fitting covariance structure. The selected covariance structure for each response variable was included in all fixed effects candidate model combinations.

Results

Dive foraging

Of 587 diurnal 30 min observation blocks for both Surf Scoters and White-winged Scoters combined, 98% of observation blocks contained radio-signal loss indicative of diving. In contrast, only 2% of 138 nocturnal observation blocks contained diving. Results were similar for both species, as Surf Scoters dove in 97% of diurnal observations ($n = 271$) and 3% of nocturnal observations ($n = 61$), and White-winged Scoters dove during 98% of diurnal observations ($n = 316$) and 1% of nocturnal observations ($n = 77$).

Both scoter species spent more time diving during the day than at night (Table 4.1). Results indicated that the model containing only night/day as an explanatory variable best explained variation in minutes diving per 30 min (Table 4.2). Two additional model combinations also received substantial support (ΔAIC $\leq$ 2), each of which included night/day (Table 4.2). All models without night/day received no empirical support from the data (ΔAIC > 265, w_i = 0). Further, only night/day had a large parameter likelihood value and 95% confidence intervals (weighted parameter estimate ± 1.96*SE) that did not overlap zero (Table 4.3). Hence, species and sex offered little value for explaining variation in the amount of time spent diving.

Water depth

In general, both scoter species were located within intertidal areas during diurnal hours and in subtidal areas during nocturnal hours (Figure 4.1). The model that best explained variation in water depth at scoter locations contained only night/day as an explanatory variable (Table 4.2). The model containing night/day and species, as well as the global model, also received substantial support (ΔAIC $\leq$ 2), although their AIC weights were low (w_i = 0.23) relative to the top model (w_i = 0.41). Model combinations not including night/day as an explanatory variable received no empirical support, as indicated by their large ΔAIC values (ΔAIC > 289) and low AIC weights (w_i = 0). Parameter likelihoods and parameter estimates further emphasized the importance of night/day as an explanatory variable (Table 4.3). Night/day had a parameter likelihood = 1.00, indicating that only models containing night/day were well supported. Parameter likelihood values for species and sex were much lower than night/day and their parameter estimates had relatively large unconditional SE (Table 4.3).

Distance from shore

Both scoter species were located closer to shore during day than at night (Table 4.1). The best-fitting candidate model included night/day and species as explanatory variables (Table 4.2). The next best-fitting model, with a ΔAIC ≤ 2, was the global model containing night/day, species, and sex as explanatory variables. All models without night/day received no support, as indicated by their large ΔAIC values (> 468) and low AIC weights (w_i = 0). Night/day had a parameter likelihood = 1.00 and the unconditional SE was small relative to the weighted parameter estimate, indicating that night/day had strong explanatory value for variation in distance to shore (Table 4.3). The species parameter also was well supported, with a parameter likelihood = 0.87, and the parameter estimate indicating that Surf Scoters tended to be closer to shore than White-winged Scoters (Table 4.3). The sex parameter was not well supported, as indicated by a small parameter likelihood value and a unconditional SE that is larger in magnitude than the actual parameter estimate.

Discussion

We found dramatic differences in foraging behaviors of Surf Scoters and White-winged Scoters between diurnal and nocturnal periods. Our results indicated that Surf Scoters and White-winged Scoters rarely forage at night. Only 2% of nocturnal observation blocks contained radio-signal loss indicative of diving, compared to 98% of diurnal observation blocks. This corresponded to an average of only 7 sec of diving per 30 min during nocturnal periods, compared to over 7 min during daylight hours. Information theoretic analyses of model sets indicated that amount of time spent diving was almost wholly explained by day or night period, with little effect associated with species or sex.

Both species of scoters were located farther offshore and in deeper waters during nocturnal hours, generally removed from the intertidal foraging areas used during the day. The concomitant relationship between distance from shore and water depth was expected, given that these variable are highly positively correlated. Mean distances to shore for Surf Scoters and White-winged Scoters were 231 m and 254 m during the day, respectively, compared to 704 m and 911 m during the night. Likewise, 70% of diurnal locations of both scoter species were within the intertidal area, compared with only 5% of nocturnal locations. Other sea duck species have been documented utilizing non-dive foraging behaviors during nocturnal hours, such as surface-feeding or up-ending during low tides (Systad and Bustnes 2001). For sea duck species that prey upon infaunal or epifaunal invertebrates, such non-dive foraging behaviors would require shallow water to access prey items from the surface. These non-dive feeding behaviors, which were never diurnally witnessed for scoters, do not result in a lost radio-signal and would thus not be detected by our radio telemetry observations. The deep-water, offshore location of scoters during nocturnal hours, however, precludes the potential use of non-dive feeding behaviors. This result further indicates that the observed differences between day and night foraging behaviors reflect true differences in foraging effort.

Of the three individual scoters detected foraging at night, one was detected on 17 January and two were detected on 22 January. The duration of daylight on these days was approximately 10 hr, which is only 35 min longer than the shortest day of the year. The rare occurrence of nocturnal diving during the shortest days of winter suggests that these scoters may have been compensating for the short duration of daylight. No further nocturnal diving was detected, despite continued monitoring until mid-March. During the shortest days of winter, some sea duck species extend their diurnal feeding into low-light crepuscular periods to cope with reduced daylight (Systad et al. 2000). With regards to

sunrise and sunset, the scoter on the 17 January was diving 2 hr before sunrise and the two scoters on the 22 January were diving approximately 4 hr after sunset. None of these nocturnal foraging bouts were adjacent to daylight periods, indicating that these scoters were not merely extending their diurnal diving into periods adjacent to sunrise and sunset, but rather were actively choosing to engage in nocturnal foraging.

The low rate of nocturnal foraging by scoters can be broadly explained by two exclusive hypotheses: (1) scoters are unable to forage nocturnally or (2) scoters choose not to forage nocturnally. An inability to forage nocturnally would result from a complete dependence upon visual cues for location of prey. The fact that we observed nocturnal foraging, albeit rarely, suggests that scoters possess this ability. Other diving ducks are known to forage on infaunal bivalves at night (Klima 1966, Nilsson 1970, Custer et al. 1996), presumably using tactile cues, suggesting that it would be possible for scoters. Therefore, it appears that scoters are choosing not to forage nocturnally. Non-profitable nocturnal foraging, nocturnal predation risk, and visual constraints, acting solely or in combination, could potentially force scoters to avoid nocturnal foraging. Also, acquisition of sufficient energy quantities during daylight hours may pre-empt the need for nocturnal foraging. Below, we consider potential reasons scoters at our study site rarely foraged at night.

Scoters in Baynes Sound feed primarily on clams, which are abundant throughout much of the intertidal zone (Bourne 1984, Vermeer and Bourne 1984). Clams within Baynes Sound may be so abundant and energetically profitable that the daily energetic requirements of scoters can be sufficiently met during daylight hours, making nocturnal foraging unnecessary. Other wintering areas with different prey items and abundances could alter a scoter's decision to forage nocturnally.

At the latitude of our study area (49° N), the amount of daylight within our study site ranges between 9 and 10 hr during the shortest days of winter. Nocturnal hours thus predominate the 24 hour cycle during winter, a potentially significant amount of time from which to abstain from foraging. Along the Pacific coast, Surf Scoters and White-winged Scoters winter as far north as coastal Alaska (60° N), experiencing less than 7 hr of daylight during mid-winter (Brown and Fredrickson 1997, Savard et al. 1998). Nocturnal foraging studies of other sea duck species have been conducted at high northern latitudes. Systad and Bustnes (2001) documented nocturnal foraging and increased crepuscular foraging by Steller's Eiders (*Polysticta stelleri*) during the shortest days of winter at the northern extent of their wintering range (70° N). However, Rizzolo et al. (2005) found that Harlequin Ducks (*Histrionicus histrionicus*) wintering at 60° N did not forage at night. Although scoters within our study site rarely engaged in nocturnal foraging, this foraging strategy may be necessary at more northerly latitudes to compensate for the shortened day length. Scoters residing at the southern extent of their winter range, including the coastal waters of California and Baja California, clearly have greater time-budget flexibility and may not need to forage nocturnally as a result of day length constraints.

Some non-sea duck species of diving ducks (tribe Aythyini) commonly feed both diurnally and nocturnally on infaunal invertebrates, presumably locating prey using tactile methods (Klima 1966, Nilsson 1970, Custer et al. 1996). The regularity of this behavior indicates that these diving duck species can profitably dive-forage at night without reliance upon visual cues. Additionally, some sea duck species are known to dive to depths greater than 40 m (Lovvorn et al. 2003, Guillemette et al. 1993), presumably foraging in very low light levels or complete darkness at such depths. Within our study area, scoters foraging during the day were diving almost exclusively in the intertidal zone

(Esler, unpublished data), typically in water depths less than 5 m. Winter water clarity in our study area is high (> 5 m) due to the reduced plankton load, and the benthos are well lit during daylight hours at shallow water depths (T. Lewis, personal observation), likely providing scoters full visual acuity. During night, however, the loss of visual cues and greater dependence upon tactile cues may make nocturnal foraging energetically less profitable and thus avoided by most scoters. Potential visual cues for scoters foraging on clams may include the location of clam siphon holes or the recognition of successful bivalve capture by other foraging scoters, indicating profitable feeding patches. Indeed, scoters almost always feed in groups (Beauchamp 1992, Savard et al. 1998) and underwater group feeding dynamics, such as recognition of successful prey capture by conspecifics or group-digging, seems highly plausible.

The offshore location of scoters at night may be a predator avoidance tactic. Predation risk near shore at night, from nocturnally active predators such as mink (*Mustela vison*) or river otters (*Lutra canadensis*), may offset any energetic advantages gained from foraging nocturnally. During the day, scoters can visually assess predation risk from common predators such as Bald Eagles (*Haliaeetus leucocephalus*), providing sufficient warning to reduce predation risks. Without the aid of visual predator recognition, scoters may be susceptible to near shore predation pressures and thus move to safer, offshore waters at night.

Future studies are needed across a range of latitudes, habitats, and food availabilities to fully understand the nocturnal behaviors of scoters. Further, a histological examination of the eyes of sea ducks, including rod and cone counts, could provide an indication of the ability of sea ducks to feed in darkness. The overall rarity of nocturnal foraging in our study site, however, strongly suggests that the amount of foraging time available to Surf Scoters and White-winged Scoters may be daylight

limited, a potentially important restriction considering the northern winter ranges of both species. This restriction may limit the ability of scoters to increase time spent foraging in response to potential food or energetic shortfalls. Daylight restrictions could be especially limiting during the shortest days of winter and at high northerly wintering latitudes. Anthropogenic disturbances, such as hunting, have been known to force some waterfowl species to adjust their daily activity patterns and increase nocturnal foraging in response to the loss of diurnal foraging time (Raveling et al. 1972, McNiel et al. 1992). Although lightly hunted along the Pacific Coast during winter, similar disturbances from industrial, nautical, or other anthropogenic activities could restrict daytime foraging opportunities for scoters. Decreases in available food supplies could exert similar foraging-time pressures, forcing individuals to spend more time searching for food while consuming less food per unit effort (Percival and Evans 1997, Tuckwell and Nol 1997). The potential nocturnal foraging limitations of scoters should be considered when reviewing anthropogenic activities that may alter the amount of available feeding time or food supplies.

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Table 4.1. Mean ± SE for minutes diving per half-hour and distance to shore (m) of Surf Scoters and White-winged Scoters wintering in coastal British Columbia, 2002-2004. Data are summarized for day and night periods, and scoter species. Numbers in parentheses indicate sample sizes.

	Surf Scoter		White-winged Scoter	
	Minutes diving per half-hour	Distance to shore (meters)	Minutes diving per half-hour	Distance to shore (meters)
Day	7.2 ± 0.3 (271)	231.1 ± 8.4 (481)	6.9 ± 0.2 (316)	254.4 ± 9.6 (649)
Night	0.1 ± 0.1 (61)	703.8 ± 44.0 (46)	0.2 ± 0.1 (77)	911.6 ± 54.1 (58)

Table 4.2. General linear mixed models evaluating variation in foraging effort and location of radio-marked Surf Scoters and White-winged Scoters during winter in coastal British Columbia, 2002-2004. Night/day is a categorical variable with two levels (night and day). For all models, the number of parameters (k) includes +1k for an intercept and +1k for variance estimate. Covariance structures for repeated measures and random between-subject effect include +2k for all models of minutes diving per half-hour and +1k for all models of water depth and distance to shore. Only models with $w_i > 0.01$ and the null model are presented. Candidate models are listed in order of ΔAIC.

Response variable	Model	Number of parameters (k)	Log-likelihood	ΔAIC	AIC weight (w_i)
Minutes diving per half-hour	night/day	5	-1907.26	0.00	0.46
	night/day + species	6	-1906.88	1.26	0.25
	night/day + sex	6	-1907.11	1.74	0.19
	night/day + species +sex	7	-1906.74	3.03	0.10
	null	2	-2095.10	369.7	0.00
Water depth (m)	night/day	4	-4627.61	0.00	0.41
	night/day + species	5	-4627.17	1.14	0.23
	night/day + sex	5	-4627.19	1.19	0.23
	night/day + species + sex	6	-4626.74	2.31	0.13
	null	2	-4784.30	309.4	0.00
Distance to shore (m)	night/day + species	5	-8277.47	0.00	0.63
	night/day + species +sex	6	-8277.45	1.96	0.24
	night/day	4	-8280.34	6.39	0.10
	night/day + sex	5	-8280.31	16.97	0.03
	null	2	-8536.70	512.4	0.00

Table 4.3. Parameter likelihoods and weighted parameter estimates ± unconditional SE from general linear mixed models evaluating variance in foraging effort and location of radio-marked Surf Scoters and White-winged Scoters during winter in coastal British Columbia, 2002-2004. Explanatory variables are listed in order of parameter likelihood values. Parameter likelihoods are the summed AIC weights (w_i) for all candidate models containing the explanatory variable under consideration.

Response variable	Explanatory variable	Parameter likelihood	Parameter estimate ± SE
Minutes diving per half-hour	Intercept		0.11 ± 0.40
	Night/day[a]	1.00	6.77 ± 0.37
	Species[c]	0.35	0.14 ± 0.18
	Sex[b]	0.29	-0.07 ± 0.15
Water depth (m)	Intercept		26.07 ± 1.25
	Night/day[a]	1.00	-21.39 ± 1.18
	Species[c]	0.36	0.34 ± 0.42
	Sex[b]	0.36	0.34 ± 0.43
Minimum distance to shore (m)	Intercept		854.01 ± 27.15
	Night/day[a]	1.00	-584.07 ± 20.65
	Species[c]	0.87	-47.54 ± 20.65
	Sex[b]	0.27	1.49 ± 6.29

[a] Night/day is a categorical variable (day or night) with night as the reference value.
[b] Sex is a categorical variable (male or female) with male as the reference value.
[c] Species is a categorical variable (Surf Scoter or White-winged Scoter) with White-winged Scoter as the reference value.

DAY   NIGHT

Surf Scoter

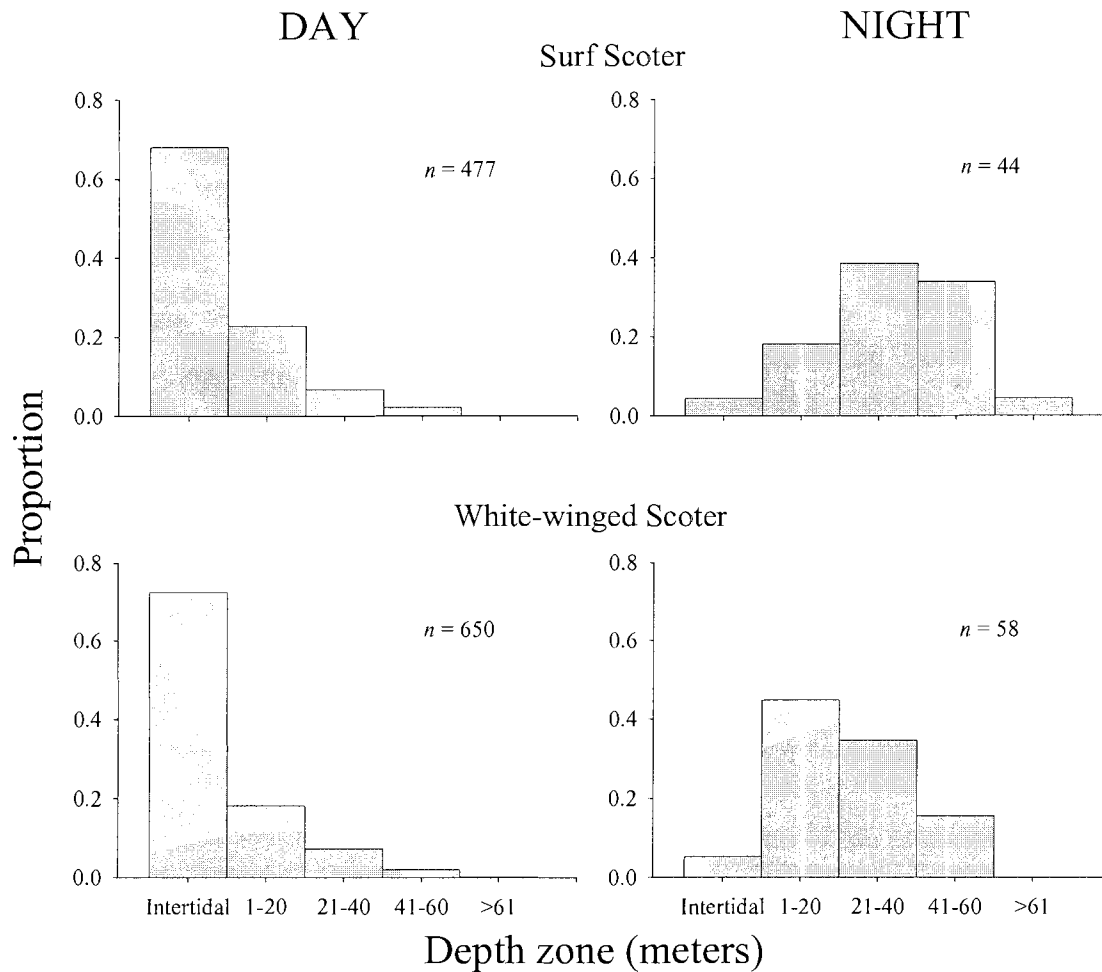White-winged Scoter

Depth zone (meters)

Figure 4.1. Proportion of telemetry point locations by water depth zone for wintering Surf Scoters and White-winged Scoters during day and night periods in coastal British Columbia, 2002-2004. Intertidal zone includes all locations where depth ≤0 m at the lowest low tide. All other locations are grouped into 20 m depth zones.

CHAPTER 5

General Summary: Assessing Shellfish Aquaculture and Over-Winter Food Abundance for Scoters

This study was initiated to understand interactions between the shellfish aquaculture industry and wintering Surf Scoters (*Melanitta perspicillata*) and White-winged Scoters (*Melanitta fusca*) in Baynes Sound, British Columbia. Predation effects and foraging behaviors can be indicative of food availability and habitat quality, thus providing a measure of the value of Baynes Sound for wintering scoters, in light of shellfish aquaculture activity. Specifically, I investigated (1) the effect of scoter predation on clam abundance, (2) the foraging behaviors of scoters in response to spatial and temporal variation in clam density, and (3) the propensity of scoters to forage nocturnally.

Manila and varnish clams, the main prey items of scoters in Baynes Sound, decreased in density over the winter period. Scoter consumption accounted for approximately 90% of these density decreases, despite the presence of other species known to predate clams. This study corroborates other research indicating the important effects of sea duck predation on intertidal prey populations and communities (Guillemette et al. 1996, Larsen and Guillemette 2000, Hamilton 2000, Lacroix 2001). The strong predation potential of sea ducks can generally be attributed to their large wintering densities, gregarious nature, and high per-capita consumption rates (Goudie and Ankney 1986). Within Baynes Sound, Surf Scoters and White-winged Scoters are the most numerous marine birds, with winter numbers averaging approximately 6500 for both scoter species combined. In other sites with large populations of wintering sea ducks, strong predation effects on prey numbers would also be expected, given the strength of our results and those of previous studies.

Birds respond rapidly and predictably to changes in food availability (Hutto 1990). Therefore, avian foraging behaviors can be used to infer food availability and habitat quality from the perspective of the forager (Pienkowski 1983, Hutto 1990). To assess

the habitat quality of Baynes Sound for scoters, we measured their foraging effort and clam capture success in response to variation in clam densities. Clam capture success of both scoter species and foraging effort of Surf Scoters was not correlated to clam density, while White-winged Scoter foraging effort was slightly, negatively correlated to clam density. We interpret our results to indicate that over-winter variation in clam density, including both spatial and temporal variation, is relatively insignificant for foraging scoters.

Previous studies of sea ducks wintering at northern latitudes have reported maximum foraging efforts during mid-winter (Guillemette 1998, Fischer et al. 2000, Systad et al. 2000). This seasonal trend is likely a result of daylight constraints; because sea ducks are not believed to forage nocturnally (Nilsson 1970, McNeil et al. 1992), they increase their foraging effort during mid-winter to compensate for the shortened days. No previous studies, however, have definitively documented the presence or absence of nocturnal foraging by scoters. I found that Surf Scoters and White-winged Scoters in Baynes Sound rarely engaged in nocturnal foraging, as only 2% of nocturnal telemetry observation bouts detected diving, compared with 98% of diurnal bouts. Despite the lack of nocturnal foraging, both scoter species decreased their foraging effort during mid-winter and were apparently not constrained by the length of day.

Taken as a whole, these results provide an informed assessment of food availability and general habitat quality for scoters wintering in Baynes Sound. Scoters predated an estimated 3.7 million clams from sample plots during the winter of 2003-2004. Despite this large removal of clams, Manila and varnish clam densities were reduced by only 27% and 13%, respectively. While these reductions are not insignificant, they are not large enough to suggest that scoters are near exhausting their winter food supplies. This is the first known study to quantify predation effects of sea

ducks on benthic prey in soft-bottom habitats, so direct comparisons cannot be made with other sea duck studies. However, similar studies on shorebirds have documented benthic prey depletions in excess of 50% of standing stocks (Evans et al. 1979, Szekely and Bamberger 1992, Zharikov and Skilleter 2003). Prey depletions of this magnitude by shorebirds have resulted in decreased intake rates and emigration to new foraging sites (Zwarts et al. 1996, Zharikov and Skilleter 2003). By contrast, our over-winter clam depletions in Baynes Sound were well below 50% of standing stock, and scoter foraging effort and clam capture success remained largely unrelated to variation in clam density (80 – 182 clams m^{-2}). In relation to season, Surf Scoters possessed sufficient energetic flexibility to decrease their foraging effort during the shortest days of winter, despite their lack of nocturnal foraging. Furthermore, overall measures of foraging effort were well below those reported by Goudie (1999) for Surf Scoters and White-winged Scoters wintering in the Queen Charlotte Islands, British Columbia, indicating that scoters in Baynes Sound were not expending maximal foraging effort. From these combined results, I conclude that clam stocks during the winter of 2003-2004 were not limiting for wintering scoters, and that clam depletions were not of a sufficient magnitude to markedly influence scoter foraging effort.

Shellfish aquaculture practices, such as anti-predator netting and commercial clam harvesting, reduce the amount of foraging area and number of clams available to scoters. My conclusion that scoters are not food limited during winter suggests that current levels of shellfish aquaculture in Baynes Sound are not adversely affecting clam availability for scoters. Scoters were able to locate and consume enough clams to meet their energetic requirements, irrespective of anti-predator netting and clam harvesting. This conclusion, however, only applies to current levels of shellfish aquaculture in Baynes Sound and to current numbers of scoters. Approximately 76 ha (5%) of the

Baynes Sound intertidal area is covered by anti-predator netting (based on June 2001 air photos; Ministry of Sustainable Resource Management 2002). Increased levels of anti-predator netting in habitats currently utilized by foraging scoters could have adverse effects. Furthermore, my results are derived from only one winter in Baynes Sound, and extrapolation to future years or alternate sites requires caution. For instance, clams are susceptible to large die-offs in the event of prolonged cold spells or disease (Bower 1992). Had such an event occurred during our study, we may have concluded that scoters were food-limited, and that shellfish aquaculture posed a threat to scoter viability under those circumstances.

In addition, this study could not address the potentially positive effects of shellfish aquaculture for wintering scoters. To increase the density of clams for harvest, the aquaculture industry actively seeds the intertidal area with juvenile clams. Although mostly covered by anti-predator nets, these seed clams may eventually contribute to wild, non-netted clam populations via spawning or migration (Martel and Chia 1991), thereby increasing food availability for scoters. Future research that quantifies these potentially positive contributions would lead to a more complete assessment of interactions between scoters and shellfish aquaculture. Such research could ultimately be used to predict sustainable levels of shellfish aquaculture in Baynes Sound that balance positive aquaculture contributions (i.e. migration and spawning of seed clams) with negative contributions (i.e. habitat loss via anti-predator nets).

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