

Effects of predation by sea ducks on clam abundance in soft-bottom intertidal habitats

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INTRODUCTION

Numerous studies of marine communities have demonstrated effects of predators on the abundance, size distribution, and other attributes of their prey, with subsequent consequences for community structure and function (Paine 1966, 1974, Virnstein 1977, Kvitek et al. 1992, Langlois et al. 2005). In rocky intertidal habitats, which are often characterized by intense competition for space, predators may have a marked, indirect effect on the abundance of certain species by directly limiting the abundance of their strongest competitors (Paine 1966, 1974). In soft-bottom marine habitats, however, infaunal animals are not generally lim-

ited by interspecific competition for space, and the abundance of infaunal animals is often directly affected by their major predators (Virnstein 1977, Peterson 1979, 1982, Wilson 1989, Estes & Peterson 2000).

Previous studies have identified invertebrate predators, such as crabs and polychaetes, as having considerable predation effects in soft-bottom intertidal areas (Virnstein 1977, Commito 1982, Hines et al. 1990, Eggleston et al. 1992). These invertebrate predators are often numerically abundant and widespread throughout their available habitat and can thus exert strong predation pressure on infaunal animals. Vertebrate predators can also have significant predation effects in soft-bottom habitats, although they are typi-

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cally far less abundant than invertebrate predators

between the anterior and posterior margins of the valve (Gillespie & Kronlund 1999), was measured to the nearest 5 mm length class (beginning with the 5 to 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 on top of portions of intertidal flats to protect commercial clam stocks from predation by sea ducks and other large predators. Foraging scoters are effectively excluded from preying on clams underneath these nets. Four of the 6 sample plots contained nets within their boundaries: Base Flats, Buckley Bay, Deep Bay, and Mud Bay (Fig. 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 general linear models using the program SAS (SAS Institute 1999). We constructed separate *a priori* model sets for varnish clam *Nuttallia obscurata* density, Manila and Pacific littleneck density combined, and *Macoma* spp. density. Varnish, Manila, and Pacific littleneck 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 set of *a priori* general linear models was also 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 2 species in fecal samples and their similar value to foraging scoters (Bourne 1984). This grouping, however, reflects primarily Manila clams, which numerically comprised 33.2% of all clams sampled, while Pacific littlenecks comprised only 1.6%.

We used an information-theoretic approach (Burnham & Anderson 2002) to evaluate support for each general linear model within a model set. Two explanatory variables were used to construct identical model sets for each clam species: season (fall or spring) and site (the 6 sample plots). 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 2 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. Model sets for each clam species consisted of these same 7 models. We used Akaike's information criterion (AIC) to rank the fit of each model within a model set (Burnham & Anderson 2002). Δ AIC values were used to compare the relative explanatory value of the models, with Δ AIC 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 models, were also calculated to provide a relative weight of evidence for each model (Burnham & Anderson 2002). Because Δ AIC and

throughout the core daylight hours of 08:00 to 16:00 h. 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 was monitored once per week at each plot from 1 November to 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 or by differences in handling times of bivalve species. Sample plots were continually

To assess the general aptitude of our scoter consumption estimates, we converted consumption estimates to energetic values and compared them with independent estimates of energy consumption. The amount of energy consumed over the winter period by scoters in our sample plots was independently estimated as follows: energy consumed = (field metabolic rate/energy assimilation rate) number of bird days (Larsen & Guillemette 2000). Field metabolic rate (FMR) was calculated using allometric estimates for seabirds (Nagy 1987), where $\log \text{FMR} (\text{kJ d}^{-1}) = 0.904 + 0.704 \log \text{body mass (g)}$.

We estimated scoter body mass as 1250 g, based on body masses of surf and white-winged scoters captured in our study area during winter 2003/2004. Number of bird days was estimated from the average number of scoters in all sample plots per day multiplied by the number of days (147 d; 15 October to 10 March). Because no energy assimilation data are available for Manila and varnish clams, we used an energy assimilation rate of 0.75, approximated from other studies of bivalve digestion by diving ducks (Larsen & Guillemette 2000, Richman & Lovvorn 2003). Similarly, because no energy density estimates are available for Manila and varnish clams, we converted our scoter consumption estimate, measured as number of clams, into energy using an allometric relationship ($\text{energy} = 0.194 [\text{length}/10]^{3.18}$), with energy measured in kJ and length in mm, derived for Pacific littleneck clams (Juanes & Hartwick 1990).

RESULTS

Diet

Bivalves accounted for >90% of the total dry mass of shell fragments in the feces of both surf scoters *Melanitta perspicillata* and white-winged scoters *M. fusca* (Table 1). Of the bivalve species, Manila clams *Venerupis philippinarum* and varnish clams *Nuttallia obscurata* 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, in fact, likely even greater since species composition within the unknown fecal category, composed of shell fragments too small for identification, was presumably similar to that of identifiable shell fragments. Also, the Manila/Pacific littleneck category was probably composed of mostly Manila shell fragments.

Table 1. *Melanitta perspicillata*, *M. fusca*. 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 and species	% weight of fecal shell fragments	
	Surf scoter	White-winged scoter
Bivalves	90.1	91.1
Manila clam <i>Venerupis philippinarum</i>	51.9	29.7
Varnish clam <i>Nuttallia obscurata</i>	19.8	46.0
Pacific littleneck clam <i>Protothaca staminea</i>	0.8	1.3
Manila/Pacific littleneck <i>Macoma</i> spp.	9.5	5.6
Heart cockle <i>Clinocardium nuttallii</i>	0.4	0.9
Bay mussel <i>Mytilus trossulus</i>	0	0.2
Unknown bivalve	0.4	0
Gastropods	7.4	7.5
Crustaceans	0	0.6
Unknown	0.1	0.7
	9.7	7.5

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 and had an $R^2 = 0.10$ (Table 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 ($\Delta\text{AIC} = 1.30$), although the AIC weight ($w_i = 0.33$) was approximately half that of the best-fitting model ($w_i = 0.62$). The top 2 models thus indicate that only models accounting for both site and seasonal differences received substantial support. Furthermore, the null model received no support ($w_i = 0.00$), indicating that the explanatory variables used in our models explained a significant amount of variance in the data. Seasonal differences in the top 2 models were due to over-winter declines in Manila/Pacific littleneck density (Fig. 2). Declines were heavily concentrated in the 25 to 45 mm length range; in the fall, 70% of Manila clams sampled were 25 to 45 mm, while

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, is known to feed on clams and other benthic invertebrates (Kessel et al. 2002), but accounts for only 12% of the potential clam-foraging ducks present in Baynes Sound. Barrow's goldeneye often has a diet composed mainly of bivalves, primarily mussels (Eadie et al. 2000), but accounts for <1% of the potential clam-foraging ducks. The other common diving ducks typically have more diverse diets, not relying as heavily on bivalves as scoters (Gauthier 1993, Eadie et al. 1995, Robertson & Goudie 1999).

Winter weather conditions are another potential mechanism leading to numerical declines of clams. Winter clam mortality may occur as a result of freez-

burial depth of many soft-bottom bivalves varies with both season and predation risk (Zwarts 1991, Zwarts & Wanink 1993, Peterson & Skilleter 1994, Skilleter & Peterson 1994). During our initial clam sampling in fall, some varnish clams may have already migrated to deeper burial depths for the duration of winter, possibly in response to predation risk of recently arriving scoters. Winter migrations to deeper sediment depths have been reported for other clam species in northern temperate locations (Zwarts & Wanink 1993). By the time we re-sampled clam densities in April, following

competing predators. Hamilton (2000) found that exclusion of common eiders led to an increase in the abundance of dogwhelks *Nucella lapillus*, as whelks were likely released from interspecific competition for available mussel prey.

The effects of sea duck predation on infaunal bivalve abundance in soft-bottom habitats had not been documented prior to the present study. By selectively preying on the most abundant infaunal animals, such as Manila and varnish clams in our study area of Baynes Sound, scoters potentially assume a particularly important role in structuring these communities. For example, Schneider (1978) documented the selective removal of numerically dominant prey by migratory shorebirds in a soft-bottom mudflat. This selective predation by shorebirds resulted in reduced variation in the relative abundance of prey by decreasing the abundance of the most common 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 3 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 that found in rocky intertidal communities, and predation is believed to be of more importance than competition in limiting infaunal invertebrate densities (Virnstein 1977, Peterson 1982, 1991). 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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