Effects of off-bottom shellfish aquaculture on winter habitat use by molluscivorous sea ducks

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ABSTRACT

1. Shellfish farming is an expanding segment of marine aquaculture, but environmental effects of this industry are only beginning to be considered.

2. The interaction between off-bottom, suspended oyster farming and wintering sea ducks in coastal British Columbia was studied. Specifically, the habitat use of surf scoters (*Melanitta perspicillata*) and Barrow's goldeneyes (*Bucephala islandica*), the most abundant sea duck species in the study area, was evaluated in relation to natural environmental attributes and shellfish aquaculture.

3. The extent of shellfish farming was the best-supported habitat variable explaining variation in surf scoter densities, and the only habitat attribute from the considered set that was a strong predictor of Barrow's goldeneye densities. In both cases, the findings indicated strong positive relationships between densities of sea ducks and shellfish aquaculture operations. These relationships are presumably the result of large numbers of wild mussels (*Mytilus trossulus*) that settle and grow on aquaculture structures and are preferred prey of these sea ducks.

4. Previous work has shown that aquaculture structures provide good conditions for recruiting and growing mussels, including refuge from invertebrate predators, which in turn provides higher densities of higher quality prey for sea ducks than available in intertidal areas. This offers a rare example in which introduction of an industry leads to positive effects on wildlife populations, which is particularly important given persistent declines in numbers of many sea ducks.
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INTRODUCTION

Marine aquaculture is a rapidly growing industry across the globe, driven by the increasing demand for seafood products and declining wild stocks (Naylor *et al.*, 2000; FAO, 2006). Shellfish farming is an important sector of the industry and, like other forms of aquaculture, is expanding (FAO, 2004, 2006). As such, the environmental consequences of shellfish aquaculture are just beginning to be considered. Concerns related to shellfish aquaculture have centred around the introduction of non-indigenous species, habitat alteration,

changes to community structure or function (Grant *et al.*, 1995; Simenstad and Fresh, 1995; Kaiser *et al.*, 1998; Bartoli *et al.*, 2001; Naylor *et al.*, 2001; Stenton-Dozey *et al.*, 2001; Beadman *et al.*, 2004; Bendell-Young, 2006), and effects on bird and mammal populations (Price and Nickum, 1995; Hilgerloh *et al.*, 2001; Markowitz *et al.*, 2004; Roycroft *et al.*, 2004; Watson-Capps and Mann, 2004).

Shellfish aquaculture typically occurs in shallow, nearshore waters, which also tend to harbour the greatest densities and diversity of marine birds. However, only a relatively small number of studies have evaluated the effects of shellfish

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aquaculture on birds. To date, bird responses to the presence of shellfish aquaculture structures have been shown to vary, with the abundance and density of some species increasing in association with aquaculture and other species decreasing (Hilgerloh *et al.*, 2001; Connolly and Colwell, 2005). Most studies have described the effects of shellfish aquaculture as being neutral (Roycroft *et al.*, 2004; Žydelis *et al.*, 2006) or even beneficial (Caldow *et al.*, 2003; Kirk *et al.*, 2007). The nature of the relationship depends on the bird species involved, the type and intensity of industrial activity, and the habitats affected. Additional studies of interactions between shellfish aquaculture and bird populations are clearly warranted, to fully understand the degree and direction of any effects, and the underlying mechanisms by which effects are manifested.

Sea ducks are a group of birds that are particularly likely to interact with the shellfish aquaculture. These birds are inextricably linked to nearshore intertidal and shallow subtidal habitats, the same areas where most shellfish aquaculture occurs. In addition, both sea ducks and shellfish mariculturists tend to use coastal areas that are highly productive and offer some degree of protection from open ocean wind and waves. Finally, sea duck diets include high proportions of bivalves, making them potential predators of farmed shellfish.

Shellfish aquaculture could negatively affect sea ducks through habitat transformation or exclusion, or by disturbance arising from farming activities and boat traffic. Much of the literature to date has focused on marine waterfowl depredation of cultured bivalve stocks, which in turn sometimes leads to active disturbance or exclusion by shellfish farmers (Vermeer and Morgan, 1989; Thompson and Gillis, 2001; Caldow *et al.*, 2004; Dionne, 2004). Sea ducks may also be attracted to and benefit from shellfish farming in ways that are not in direct conflict with the industry. This could happen if birds consume insignificant amounts of cultured shellfish, forage on non-cultured prey associated with shellfish farms, or forage on prey populations that have been enhanced by aquaculture activities but fall outside of commercially harvested sites. Finally, shellfish aquaculture could be considered neutral, in the event that sea duck fitness, behaviour, and habitat use are not affected. The nature of the interaction between sea ducks and shellfish aquaculture is particularly important to address because of the conservation concerns over persistent declines in many sea duck species.

Consistent with the global trend, shellfish aquaculture has expanded rapidly in coastal British Columbia, Canada since the 1980s and is expected to continue to grow (Salmon and Kingzett, 2002; BC Shellfish Growers Association, 2006). The most common forms of shellfish farming in British Columbia include culturing of Manila clams (*Venerupis philippinarum*), Pacific oysters (*Crassostrea gigas*) and mussels (*Mytilus edulis* and *M. galloprovincialis*). Oysters and mussels are typically grown suspended in the water column on longlines or in trays, and clam culturing takes place in the intertidal zone. British Columbia's coastal waters are also important as wintering and staging grounds for a number of sea duck species (Vermeer and Butler, 1989). A study conducted in Baynes Sound, the most important area for intertidal clam aquaculture in British Columbia, addressed soft-bottom habitat use by sea ducks (Žydelis *et al.*, 2006). However, the relationship between off-bottom, longline shellfish aquaculture, which constitutes the
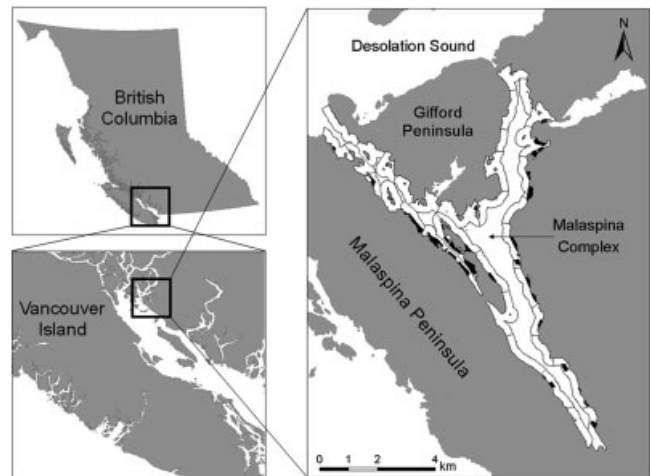

Figure 1. Geographical location of the Malaspina Complex and Desolation Sound with index maps of the Strait of Georgia and British Columbia, Canada. Filled, black polygons indicate locations of shellfish aquaculture plots, and continuous open polygons represent survey polygons used in this study.

vast majority of shellfish aquaculture outside of Baynes Sound, and habitat use by sea ducks has never been considered. Therefore, the relationships between off-bottom longline shellfish aquaculture and habitat use by wintering sea ducks in Desolation Sound, British Columbia (Figure 1) was investigated. Positive associations between densities of sea ducks and shellfish aquaculture operations would suggest beneficial effects and the converse would be true for negative correlations. Because the species of birds and type of shellfish aquaculture evaluated here also occur in many areas of coastal North America, these findings have application well beyond this specific study area.

METHODS

Study area

This study was conducted in the Malaspina Complex, which is a coastal basin in British Columbia, Canada, consisting of Malaspina, Okeover, Lancelot, and Theodosia Inlets (50°02′N, 124°44′W, Figure 1). The total aquatic area of the complex is about 26 km². Steep rocky shores dominate the coastline, with a few soft sediment beaches and estuaries. Several small streams drain into the complex, but the hydrographic regime is primarily determined by currents, driven by tides with spring tidal range of about 4 m (Ministry of Sustainable Resource Management, 2004). The Malaspina Complex is part of the Desolation Sound designated Important Bird Area (IBA Canada, 2007) in part owing to its high densities of wintering surf scoters and Barrow's goldeneyes (*Bucephala islandica*). Scoters and goldeneyes forage almost exclusively on mussels in rocky habitats such as those available in the study area (Vermeer and Ydenberg, 1989).

The first licence for commercial shellfish farming in the Malaspina Complex was issued in 1966, and since the 1970s the complex, along with Baynes Sound and Cortes Island, has been one of the most productive shellfish aquaculture areas in

British Columbia. At the time of this study, there were 40 beach and off-bottom shellfish farming tenures covering nearly 200 ha in the Malaspina Complex (Ministry of Sustainable Resource Management, 2004). Oyster culturing on longlines suspended in the water column under floating barrels, rafts, and buoys was the dominant form of aquaculture in the Malaspina Complex. Some farmers also grew mussels and clams, although this is a small, but increasing, fraction of the aquaculture crop in the complex (Ministry of Sustainable Resource Management, 2004).

Oyster farmers typically acquire juvenile oyster seed approximately 2.5 cm long, and grow them on ropes, PVC tubes, or in trays suspended vertically from longlines or rafts. Usually it takes about two years for oysters to reach marketable size (10–15 cm) in off-bottom culture (Salmon and Kingzett, 2002). Oysters are harvested by retrieving ropes, tubes or trays with a hoist and winch. Sea ducks do not eat oysters but there are a number of indirect mechanisms by which sea ducks could be affected by oyster aquaculture operations. First, extensive shellfish farming structures could prevent sea ducks from accessing their natural intertidal and shallow subtidal foraging habitats. Also, birds could be disturbed by boat traffic or other activities as farmers service aquaculture tenures. Alternatively, sea ducks might benefit from the presence of aquaculture structures that serve as substrate for fouling organisms including wild mussels (*Mytilus trossulus*), which in turn may offer abundant food resources. Kirk et al. (2007) documented extensive recruitment of wild mussels on aquaculture structures in the Malaspina Complex, and suggested that these mussels constitute both abundant and profitable prey for sea ducks.

Bird surveys

Bird surveys were conducted two or three times per month from early October 2004 through April 2005. Birds were surveyed during daylight hours between 8:00 and 17:00, as these sea ducks typically do not forage at night and use different areas for night-roosting (Lewis et al., 2005). Surveys were conducted from an inflatable boat equipped with an outboard motor cruising at no more than $10 \, km \, h^{-1}$ approximately 100 m from the shore. Birds in the study area were habituated to boat traffic to some degree as all shellfish farmers work from boats, and appropriate distances to birds were maintained during the surveys to reduce the probability of flushing. The survey team included one driver/observer, one observer, and one data recorder. The study area was subdivided into 34 survey polygons based on distinct geological features or area use designations (e.g. aquaculture lease or marine protected area), and included all water to 250 m from shore. Mean shoreline length of a survey polygon was $2356 \pm 172 \, m$ ($\pm$ SE), and area averaged $0.45 \pm 0.02 \, km^2$ ($\pm$ SE). Survey polygons were considered as sampling units in all further analyses. All birds were counted on both sides of the boat within each survey polygon. At each sighting of an individual bird or flock, a GPS waypoint was marked and a compass bearing and estimated distance to the bird or flock were noted. This allowed bird location data to be directly overlaid onto GIS maps of the study area polygons and habitats.

Analyses of bird and aquaculture interactions were focused on the two most abundant sea duck species in the study area: surf scoters and Barrow's goldeneyes. Analyses were limited to the core wintering period (12 surveys between late October and late February); early autumn surveys, when bird numbers were still low, and late wintering season counts, when many ducks abandoned the study area, possibly to forage at herring spawning sites were not included (Lewis et al., 2007a).

Environmental data

Relevant habitat features of each survey polygon were described from attribute data collected in the field or gleaned from existing sources, including extent of shellfish aquaculture, intertidal width, presence of reefs, intertidal mussel density, and percent of rocky shore (Table 1). These factors were known or assumed to be potentially important in determining sea duck distribution based on previous literature. Intertidal area was identified as the most important environmental parameter influencing scoter densities in Baynes Sound (Žydelis et al., 2006). Reefs serve as substrate for various epifauna, including mussels, which are an important part of the diet of surf scoter and Barrow's goldeneye (Vermeer and Ydenberg, 1989; Lacroix, 2001), and the presence of reefs has been shown to influence distribution of harlequin duck (*Histrionicus histrionicus*), (Esler et al., 2000a). Mussel densities in intertidal habitat were also measured as these represent the natural sea duck food resources available in the area. Food abundance and distribution has been shown to be a strong determinant of habitat use for many sea duck species

Table 1. Response and explanatory variables used to evaluate habitat use by wintering surf scoters and Barrow's goldeneyes in the Malaspina Complex, British Columbia, 2004–2005

Variable	Description	Units	Average $\pm$ SE	Range (min–max)
Cumulative densities of surf scoters	Densities of summed number of surf scoters counted during 12 surveys	Number of birds per km²	1666 ± 330	17–9898
Cumulative densities of Barrow's goldeneyes	Densities of summed number of Barrow's goldeneyes counted during 12 surveys	Number of birds per km²	662 ± 118	50–3511
Extent of shellfish aquaculture	Percentage of survey polygon surface area occupied by structures of shellfish aquaculture	%	6.4 ± 1.6	0–31.5
Intertidal width	Average distance between the shoreline and chart datum measured every 100 m along the shoreline	m	31.5 ± 7.6	9.6–268.7
Presence of reefs	Presence or absence of reefs	Yes		21
		No		13
Density of intertidal mussels	Number of mussels per square metre of intertidal area	mussels m⁻²	74.8 ± 40.3	0–1250
Percentage of rocky shore		%	71.3 ± 5.0	0–100

(Stott and Olson, 1973; Guillemette et al., 1993; Lovvorn and Gillingham, 1996). The extent of rocky shore was considered as an indicator of substrate type in the adjacent nearshore area, which also has been shown to be important (Stott and Olson, 1973; Bustnes and Lønne, 1997; Esler et al., 2000a, b). Finally, this study was designed to evaluate the effect of shellfish aquaculture on sea duck distribution and abundance; therefore, the area of aquaculture coverage was included as an environmental attribute in the analysis.

Intertidal width was measured as the distance between the shoreline and chart datum (0.0 m isobath) digitized from nautical charts at a scale of 1:10 000. Using ArcView 3.2 (ESRI, 1999), points were generated every 100 m along the shoreline using the extension 'Add Points Evenly Along a Line' (Lead, 2003), and the shortest distance to the 0.0 depth isobath measured using the 'Nearest Feature' extension. Using all of these distances, the average intertidal width for each survey polygon was calculated.

Presence or absence of reefs within survey polygons were recorded based on rocks emerging above chart datum but separated by water from the shore, as represented in nautical charts at a scale of 1:10 000.

Mussel densities in intertidal habitats were estimated throughout the study site, as described by Kirk et al. (2007). Using the Random Point Generator extension in ArcView 3.2 (ESRI, 1999; Jenness, 2005), two points were selected randomly in each survey polygon as start points for transects (for a total of 68 transects). Each 100 m transect ran parallel to shore and fell within the mid-tidal range (between 1.5 and 4.5 m above chart datum) to reflect mussel habitat. At each transect, height above chart datum was determined by measuring the distance to a known height of water (determined by comparing the time to available tide predictions) and measuring the angle to the water using a clinometer. Basic trigonometry was used to calculate the height above chart datum. Along each transect, ten quadrats (1×1 m) were placed at 10 m intervals and percentage cover of mussels was estimated. Within each large quadrat where mussels occurred, a subsample quadrat (0.1×0.1 m) was tossed haphazardly and mussels were counted and measured to 5 mm size classes. An average intertidal mussel density was calculated for each survey polygon by pooling all size classes together, as all measured mussels fell within the size range potentially taken by Barrow's goldeneyes and surf scoters (Kirk et al., 2007).

The Province of British Columbia has mapped the physical character (geomorphology) of the study area according to the Physical Shoreline Mapping System for British Columbia (Howes et al., 1994) and maintains this information in the BC bio-physical shore zone geodatabase (Ogborne et al., 2001). The classification identifies over 20 unique shoreline types based on their morphology (form), width, exposure and material type (rock, unconsolidated, man-made, organic). This shoreline type classification was used to estimate the percentage of rocky shoreline within each polygon by sampling the shore zone geodatabase every 100 m along the shoreline to determine coastal type. The geodatabase contained 12 shoreline types in the study area, four of which represented rocky shore: Rock Cliff; Rock with Gravel Beach; Rock with Sand Beach; Rock, Sand and Gravel Beach. These categories were summed together and the percentage of rocky shoreline per polygon was estimated relative to all shoreline points sampled within a survey polygon.

Out of 34 survey polygons, 18 contained structures associated with shellfish aquaculture. The extent of shellfish aquaculture in each polygon was calculated as the percentage of polygon area occupied by shellfish aquaculture structures. The boundaries of shellfish aquaculture sites were delineated using a GPS unit mounted on a boat, with waypoints collected as each site was circumnavigated, these points were then used to generate shellfish aquaculture polygons and calculate their areas in ArcView 3.2 (ESRI, 1999).

Data analyses

For each survey polygon, the numbers of surf scoters and Barrow's goldeneyes observed during all surveys were summed, on the assumption that these figures represented relative use of each polygon through the winter. Kirk et al. (2008) found that wintering surf scoter distribution patterns in the Malaspina Complex varied considerably through the season; individual surf scoters displayed extensive movements, had large home ranges, and little fidelity to specific foraging sites. Therefore, in order to capture an overall measure of use of each survey polygon, the cumulative numbers of birds were used as an index and corrected for differences in survey polygon size by expressing the cumulative numbers as densities (number of birds per km²). These densities were used as response variables in the analyses.

Multiple regression models were run using SAS V8 (SAS Institute, 1999) for surf scoters and Barrow's goldeneyes separately to relate bird densities to all possible predictor environmental variable combinations, resulting in a candidate set of 31 models for each species. It was not possible to apply a priori constraints to the combinations of variables, as each represented biologically plausible hypotheses. Null models were also included for both sea duck species, which included only the mean and associated variation of the response variable. Support for the null model would suggest that factors other than those included in the candidate model set determine variability of the response variable.

An information-theoretic approach for model selection, using Akaike Information Criteria corrected for small samples (AIC_c), was used to rank models according to their degree of parsimony (Burnham and Anderson, 2002). The ΔAIC_c for each model, which is the difference between the AIC_c value of the best-supported model and each respective model in the set, was used to assess the explanatory value of each model, and AIC weights were calculated to compare the relative likelihood of each model in the candidate set (Burnham and Anderson, 2002). To draw inferences about the importance of environmental variables in explaining variation in bird densities, parameter likelihoods, which are summed AIC weights of all models that included a given parameter, were calculated. Also, model-averaged parameter estimates and unconditional standard errors were calculated, accounting for model uncertainty based on AIC weights (Burnham and Anderson, 2002). Attributes with 95% CI ($1.96 \times$ the unconditional SE) overlapping 0 were considered to have low explanatory value. In addition, calculated R^2 values were used to indicate the proportion of variation in the response variable that was explained by each model.

RESULTS

Surf scoter

Numbers of surf scoters in the study area ranged from 1168 to 3308 per survey and averaged 2100 ± 201 ($\pm$ SE) during the surveys used for analyses. Densities of cumulative surf scoter numbers averaged 1666 ± 330 ($\pm$ SE) birds km^{-2} per polygon. The most parsimonious model based on ΔAIC_c included the environmental variables characterizing shellfish aquaculture area and intertidal width (Table 2). Model ranking according to ΔAIC_c, and also model R^2 values, indicated that models that included the area of aquaculture were well supported by the data and all ranked above the null model (Table 2). Intertidal width also received relatively good support from the data and was the only variable in addition to aquaculture area that ranked above the null model when modelled as a single explanatory variable. Other environmental variables had low explanatory value, and almost all models without the Aquaculture variable ranked below the null model. The parameter likelihood for the Aquaculture variable equalled 1, after accounting for rounding error, and the model-averaged parameter estimate was positive with 95% CI considerably above 0 (Table 3). Intertidal width also received a high summed model weight (0.88) and the 95% CI of averaged parameter estimate was positive and above 0 (Table 3). Other explanatory variables (Rocky Shore, Reef Presence, and Mussel Density) had negligible predictive value,

as indicated by low parameter likelihoods and averaged parameter estimates with 95% CI widely overlapping 0. These results clearly indicate that densities of surf scoters were strongly and positively associated with percentage aquaculture coverage and intertidal width.

Barrow's goldeneye

Numbers of Barrow's goldeneyes varied between 262 and 1596 per survey, and averaged 859 ± 130 ($\pm$ SE) birds. Densities of summed Barrow's goldeneye numbers per coastal polygon averaged 662 ± 118 ($\pm$ SE) birds km^{-2}. The most parsimonious model based on ΔAIC_c included only the Aquaculture variable, which also appeared in all models ranked above the null model (Table 4). Further, all models including aquaculture area explained considerable variation in the response ($R^2 > 0.65$), whereas models without aquaculture area explained very little variation ($R^2 < 0.05$). AIC weights of models that included Aquaculture summed to 1, after accounting for rounding error (Table 3). Finally, the model-averaged parameter estimate of this variable was positive with a small unconditional SE. Other environmental variables were poor predictors in our models, with small summed AIC weights, and small averaged parameter estimates with unconditional SE widely overlapping 0 (Table 3).

Table 2. General linear multiple regression models used to evaluate habitat features related to variation in surf scoter densities in the Malaspina Complex, British Columbia, during winter 2004–2005

Models	ΔAIC_c[a]	AIC_w	R^2
Aquaculture + Intertidal	0.00	0.35	0.56
Aquaculture + Intertidal + Reefs	1.45	0.17	0.57
Aquaculture + Intertidal + Rocky Shore	2.20	0.12	0.56
Aquaculture + Intertidal + Mussel Density	2.66	0.09	0.56
Aquaculture + Intertidal + Rocky Shore + Reefs	3.50	0.06	0.59
Aquaculture + Rocky Shore	3.90	0.05	0.50
Aquaculture + Intertidal + Reefs + Mussel Density	4.16	0.04	0.58
Aquaculture + Intertidal + Rocky Shore + Mussel Density	5.11	0.03	0.57
Aquaculture + Rocky Shore + Reefs	5.72	0.02	0.52
Aquaculture	5.79	0.02	0.43
Aquaculture + Intertidal + Rocky Shore + Reefs + Mussel Density	6.52	0.01	0.59
Aquaculture + Rocky Shore + Mussel Density	6.60	0.01	0.50
Aquaculture + Mussel Density	8.11	0.01	0.44
Aquaculture + Reefs	8.23	0.01	0.44
Aquaculture + Rocky Shore + Reefs + Mussel Density	8.55	0.00	0.52
Aquaculture + Reefs + Mussel Density	10.66	0.00	0.44
Intertidal	21.62	0.00	0.10
NULL	22.73	0.00	
Intertidal + Mussel Density	22.99	0.00	0.13
Mussel Density	23.78	0.00	0.04
Intertidal + Reefs	23.96	0.00	0.10
Intertidal + Rocky Shore	24.19	0.00	0.10
Rocky Shore	24.24	0.00	0.03
Reefs	25.14	0.00	0.00
Intertidal + Reefs + Mussel Density	25.29	0.00	0.14
Rocky Shore + Mussel Density	25.65	0.00	0.06
Intertidal + Rocky Shore + Mussel Density	25.72	0.00	0.13
Reefs + Mussel Density	26.30	0.00	0.04
Intertidal + Rocky Shore + Reefs	26.72	0.00	0.10
Rocky Shore + Reefs	26.75	0.00	0.03
Rocky Shore + Reefs + Mussel Density	28.21	0.00	0.06
Intertidal + Rocky Shore + Reefs + Mussel Density	28.25	0.00	0.14

[a] Models were ranked according to ΔAIC_c values, which indicate the relative support for each model, given the data.

Table 3. Summed AIC weights, model-weighted parameter estimates, and unconditional standard errors (SE_u) of weighted parameter estimates calculated from all candidate models of variation in surf scoter and Barrow's goldeneye densities in the Malaspina Complex, British Columbia, winter 2004–2005

Parameter	Surf scoter			Barrow's goldeneye		
	Summed AIC weights	Weighted parameter estimate	SE_u	Summed AIC weights	Weighted parameter estimate	SE_u
Intercept	1	459.25	677.75	1	218.50	145.50
Aquaculture	1	144.75	25.97	1	62.38	7.88
Intertidal Width	0.88	13.21	5.22	0.22	0.14	0.39
Rocky Shore	0.31	−3.19	3.80	0.22	−0.23	0.61
Reefs	0.32	170.27	195.14	0.44	90.64	81.35
Mussel Density	0.20	−0.07	0.22	0.24	0.05	18.31

Table 4. General linear multiple regression models used to evaluate habitat features related to variation in Barrow's goldeneye densities in the Malaspina Complex, British Columbia, during winter 2004–2005

Models	ΔAIC_c[a]	AIC_w	R^2
Aquaculture	0.00	0.25	0.66
Aquaculture + Reefs	0.45	0.20	0.68
Aquaculture + Mussel Density	2.05	0.09	0.67
Aquaculture + Intertidal	2.50	0.07	0.66
Aquaculture + Rocky Shore	2.51	0.07	0.66
Aquaculture + Rocky Shore + Reefs	2.77	0.06	0.69
Aquaculture + Intertidal + Reefs	2.79	0.06	0.69
Aquaculture + Reefs + Mussel Density	2.94	0.06	0.69
Aquaculture + Rocky Shore + Mussel Density	4.66	0.02	0.67
Aquaculture + Intertidal + Mussel Density	4.69	0.02	0.67
Aquaculture + Intertidal + Rocky Shore	5.24	0.02	0.66
Aquaculture + Rocky Shore + Reefs + Mussel Density	5.37	0.02	0.69
Aquaculture + Intertidal + Reefs + Mussel Density	5.45	0.02	0.69
Aquaculture + Intertidal + Rocky Shore + Reefs	5.61	0.02	0.69
Aquaculture + Intertidal + Rocky Shore + Mussel Density	7.60	0.01	0.67
Aquaculture + Intertidal + Rocky Shore + Reefs + Mussel Density	8.44	0.00	0.69
NULL	34.60	0.00	
Rocky Shore	36.70	0.00	0.01
Mussel Density	36.71	0.00	0.01
Reefs	36.71	0.00	0.01
Intertidal	37.00	0.00	0.00
Reefs + Mussel Density	38.86	0.00	0.02
Rocky Shore + Mussel Density	38.89	0.00	0.02
Rocky Shore + Reefs	39.09	0.00	0.01
Intertidal + Rocky Shore	39.21	0.00	0.01
Intertidal + Mussel Density	39.27	0.00	0.01
Intertidal + Reefs	39.29	0.00	0.01
Rocky Shore + Reefs + Mussel Density	41.37	0.00	0.03
Intertidal + Rocky Shore + Mussel Density	41.59	0.00	0.02
Intertidal + Reefs + Mussel Density	41.62	0.00	0.02
Intertidal + Rocky Shore + Reefs	41.76	0.00	0.02
Intertidal + Rocky Shore + Reefs + Mussel Density	44.24	0.00	0.03

[a] Models were ranked according to ΔAIC_c values, which indicate the relative support for each model, given the data.

DISCUSSION

The results of this study indicate that both sea duck species, surf scoter and Barrow's goldeneye, were strongly attracted to shellfish aquaculture operations. This represents a case in which introduction of an industry led to positive effects on wildlife populations. This also contributes to the growing body of literature addressing environmental consequences of shellfish aquaculture, particularly the effects on birds, which have rarely been evaluated.

The strong positive relationship observed between shellfish aquaculture and sea duck densities is almost certainly explained by the introduction of novel structures that become heavily fouled with mussels, the primary food of both Barrow's goldeneyes and surf scoters in wintering areas

with rocky shorelines (Vermeer, 1981, 1982; Vermeer and Ydenberg, 1989). Introduced structures are known to support different epibiotic communities from adjacent natural intertidal areas (Glasby and Connell, 1999; Connell, 2001), and subsequently these habitats are differentially preferred by foraging predators. In the case of shellfish aquaculture, Kirk et al. (2007) found that mussel densities on aquaculture structures in the Malaspina complex were much greater than in intertidal areas (9000 and 80 mussels m^{-2} respectively). Also, mussels on aquaculture structures had a number of morphological properties that made them a more profitable prey than intertidal mussels, such as weaker byssal attachment, and more fragile and thinner shells (Bustnes, 1998; Richman and Lovvorn, 2003, 2004; Kirk et al., 2007). The higher density and quality of mussels on aquaculture structures, relative to

intertidal mussels, suggest that feeding on aquaculture plots is an advantageous foraging decision (Pyke *et al.*, 1977). Differences in availability and morphology of mussels may result from either differential settlement on structures and intertidal areas, from differential predation between habitats, or both. One of the main mussel predators, the intertidal sea star *Pisaster ochre*, is effectively excluded from off-bottom aquaculture structures, and these predators are known to have strong effects on mussel availability and morphology (Paine, 1974; Navarrete and Menge, 1996).

The interactions between sea ducks and shellfish aquaculture in the Malaspina Complex were very different from those found in Baynes Sound, the most intensive shellfish farming area in British Columbia. Surf scoter and Barrow's goldeneye distributions were primarily driven by shellfish aquaculture in the Malaspina Complex, while in Baynes Sound surf and white-winged scoter habitat use was almost exclusively explained by natural environmental attributes and few effects of shellfish aquaculture, either positive or negative, were detected (Žydelis *et al.*, 2006). The primary differences between these two sites are the dominant habitat types and shellfish farming practices: off-bottom culturing of oysters on longlines suspended in the water column takes place in the Malaspina Complex, and clams are farmed over broad and soft-sediment intertidal flats in Baynes Sound. The composition of sea duck species also differed between these sites: surf scoters were abundant in both areas, but white-winged scoters were numerous only in Baynes Sound, and Barrow's goldeneyes only in the Malaspina Complex. These habitat preference patterns agree with existing knowledge about winter ecology of these species. Surf scoters are known to occur over both soft bottom and rocky coastal habitats, where they forage on either infaunal and epifaunal bivalves (Vermeer and Ydenberg, 1989; Lewis *et al.*, 2007b). White-winged scoters prefer soft-bottom habitats and are clam specialists (Vermeer and Ydenberg, 1989), whereas Barrow's goldeneyes prefer rocky shorelines and primarily feed on mussels (Vermeer, 1982; Vermeer and Ydenberg, 1989).

The extent of intertidal area, which was identified as an important predictor of surf scoter distribution in the Malaspina Complex, also was an important environmental factor determining surf scoter distribution in Baynes Sound (Žydelis *et al.*, 2006) and has been shown to be important for other sea ducks (including Barrow's goldeneye) in other studies (Esler *et al.*, 2000a, b; Hamilton, 2000). Although habitats in the Malaspina Complex and Baynes Sound are very different (steep rocky shores versus broad intertidal soft-sediment flats, respectively), the intertidal zone is known to be the most important foraging habitat for surf scoters, who dig for clams in soft bottoms and take mussels from hard substrates (Lacroix, 2001; Lewis *et al.*, 2007b).

Connolly and Colwell (2005) observed that many species of shorebirds and wading birds were more abundant on intertidal oyster farming plots than on control sites in Humboldt Bay, California. Similarly, intertidal mussel cultivation had positive effect on shorebird numbers in Wales (Caldow *et al.*, 2003). In these cases, shorebirds and wading birds responded positively to increased diversity and biomass of both cultured bivalves and other benthic fauna (Caldow *et al.*, 2003; Connolly and Colwell, 2005). This mechanism of bird attraction is somewhat similar to that found in the present study, where off-bottom structures of oyster aquaculture created a new habitat for associated fauna — blue mussels, which subsequently resulted in increased abundances of sea ducks.

A great deal of attention has been focused on sea duck predation on mussel farms, with the goal of developing ways to deter birds from foraging on aquaculture products, particularly cultivated mussels. Scoters, long-tailed ducks (*Clangula hyemalis*), and greater scaup (*Aythya marila*) were estimated to reduce harvestable yields of mussels by 20% on Prince Edward Island (Thompson and Gillis, 2001). Common eider (*Somateria mollissima*) predation on cultivated mussels was identified as a serious and increasing problem in Scotland (Ross and Furness, 2000; Ross *et al.*, 2001). A variety of measures were identified to mitigate duck predation. Many of them involved active deterring of birds, such as chasing by boat, firing blank shots, propane cannons, underwater playback systems and use of powerful laser lights (Ross and Furness, 2000; Ross *et al.*, 2001; Thompson and Gillis, 2001). There are also passive deterrents such as protective netting or socking, which restrict bird's access to cultured mussels (Ross and Furness, 2000; Dionne *et al.*, 2006). In contrast to these studies, birds did not deplete cultured bivalves in Malaspina Complex and there are no records indicating that sea ducks feed on natural or cultured oysters.

Sea duck predation on epifauna, chiefly wild mussels, fouling aquaculture structures was not negatively perceived by shellfish farmers in Malaspina Complex, who on the contrary, appreciated birds cleaning their equipment of unwanted ballast. Kirk *et al.* (2007) found that densities of wild mussel on shellfish farming structures were reduced by 97% during the winter, the decrease almost certainly attributable to sea duck predation. Such mutually beneficial interactions between the shellfish farmers and sea ducks are welcome, as positive interactions between industrial development and wildlife populations are all too rare. Careful consideration will be necessary to maintain this positive interaction. The mussel culture industry in British Columbia is increasing (Salmon and Kingzett, 2002), which in turn could lead to conflict if sea ducks start consuming significant amounts of cultured mussels. Currently, farmers are effectively preventing loss of mussel stock with the use of nets and trays.

Findings of this study could offer ideas for future management of sea duck populations and sustainable development of human activities in the coastal zone. Building off-bottom structures could be considered analogous to creation of artificial reefs, aiming to mitigate loss or degradation of natural coastal areas. Introduction of such novel habitats could also be attempted to distract diving ducks from mussel farming sites, minimizing effects of duck predation of cultured stocks. The conclusion that off-bottom shellfish aquaculture structures provide positive wildlife benefits is specific to molluscivorous sea ducks, and additional research is encouraged to consider interactions of the industry with other components of the ecosystems in which they occur.

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