Predation rates, timing, and predator composition for Scoters (*Melanitta* spp.) in marine habitats


Abstract: Studies of declining populations of sea ducks have focused mainly on bottom–up processes with little emphasis on the role of predation. We identified 11 potential predators of White-winged Scoters (*Melanitta fusca* (L., 1758)) and Surf Scoters (*Melanitta perspicillata* (L., 1758)) in North American marine habitats. However, of 596 Scoters marked with VHF transmitters along the Pacific coast, mortalities were recovered in association with just two identifiable categories of predators: in southeast Alaska recoveries occurred mainly near mustelid feeding areas, while those in southern British Columbia and Washington occurred mainly near feeding areas of Bald Eagles (*Haliaeetus leucocephalus* (L., 1766)). Determining whether marked Scoters had been depredated versus scavenged was often not possible, but mortalities occurred more frequently during winter than during wing molt (13.1% versus 0.7% of both species combined, excluding Scoters that died within a postrelease adjustment period). In two sites heavily used by Scoters, diurnal observations revealed no predation attempts and low rates of predator disturbances that altered Scoter behavior (≤0.22/h). These and other results suggest that predation by Bald Eagles occurs mainly at sites and times where densities of Scoters are low, while most predation by mustelids probably occurs when Scoters are energetically compromised.

Résumé : Les études des populations en déclin de canards marins se sont intéressées surtout aux processus ascendants avec peu d’emphase sur le rôle de la prédation. Nous avons identifié 11 prédateurs potentiels de la macreuse brune (*Melanitta fusca* (L., 1758)) et de la macreuse à front blanc (*Melanitta perspicillata* (L., 1758)) dans des habitats marins nord-américains. Cependant, chez les 596 macreuses portées d’émetteur VHF le long de la côte du Pacifique, nous avons noté des mortalités associées à seulement deux catégories identifiables de prédateurs : dans le sud-est de l’Alaska, les émetteurs ont été récupérés principalement près des aires d’alimentation des Mustelidae, alors que ceux du sud de la Colombie-Britannique et du Washington ont été retrouvés surtout près des aires d’alimentation des pygargues à tête blanche (*Haliaeetus leucocephalus* (L., 1766)). Il est souvent impossible de déterminer si les macreuses marquées ont été victimes de prédation ou consommées comme charognes, mais les mortalités ont lieu plus fréquemment pendant l’hiver que durant la mue des ailes (13,1 % par rapport à 0,7 % chez les deux espèces combinées, lorsqu’on exclut les macreuses qui sont mortes durant la période d’ajustement après leur libération). Dans deux sites fortement utilisés par les macreuses, des observations de jour n’indiquent aucune tentative de prédation et révèlent des taux faibles de perturbations par les prédateurs qui viennent modifier le comportement des macreuses (≤0,22/h). Ces résultats et d’autres laissent croire que la prédation par les pygargues à tête blanche se produit à des sites et des moments lorsque la densité des macreuses est basse, alors que la plus grande partie de la prédation par les mustélidés a lieu lorsque les macreuses doivent faire face à des compromis énergétiques.

[Intraduit par la Rédaction]

Introduction

Especially over the last century, anthropogenic impacts have markedly changed the predator landscape for many prey species. Numbers of many predators declined, with some showing subsequent increases after mitigation of limiting factors. For instance, bans on overt disturbances and use of dichlorodiphenyltrichloroethane (DDT) helped recover numbers of Bald Eagles (*Haliaeetus leucocephalus*) (Fig. 1) and Peregrine Falcons (*Falco peregrinus*). These two species commonly depredate marine birds in North America (Knight et al. 1990; Dekker 1995), yet the importance of their popu-
numbers of Bald Eagles (Fig. 1). Waterfowl are flightless
predators and where predation occurs.

Fig. 1. North American Breeding Bird Survey results during 1968–
2007 for Bald Eagles (Haliaeetus leucocephalus) (results not avail-
able for Oregon; Sauer et al. 2008), where 1 mi = 1.61 km.

lation recoveries to concurrent declines in many taxa of ma-
rine birds is unclear. Human impacts have likely modified
predator–prey relationships not only by affecting predator
numbers, but also by altering relative abundances and distri-
butions among a range of their potential prey. For instance,
declines in many stocks of Pacific salmon (genus Onchorhyn-
chus) and Pacific herring (Clupea pallasi) in Valenciennes
in Cuvier and Valenciennes, 1847) that are important foods for Bald Eagles (Nehlsen et al. 1991; Will-
son and Womble 2006) might have increased their predation
on alternative prey species.

North American populations of Scoters (genus Melanitta
F. Boie, 1822) have declined appreciably over the past 30–
50 years (Dickson and Gilchrist 2002; Nysewander et al.
2005). Two factors suggest that these declines may have re-
sulted at least in part from changes in adult survivorship
during the nonbreeding period. First, population dynamics of
Scoters and other sea ducks (Anatidae: Mergini) are more
sensitive to variation in adult survival than in productivity
and survival of young (Goudie et al. 1994). Second, over
much of their boreal nesting grounds, direct human alteration
of Scoter habitat appears limited in spatial extent (although
effects of climate change may be important; Jorgenson et al.
2001). Conversely, shallow marine habitats used by Scoters
during the nonbreeding period have been altered and dimin-
ished by a range of human activities, several of which are pu-
tative causes for declines in many taxa of marine birds. To
date, studies of Scoters in marine habitats have focused
mainly on the role of food availability in affecting their forag-
ing behavior, movements, and physiological condition (e.g.,
However, because predation risk can also affect these param-
eters (Lima 1985; Rogers 1987), assessments of habitat needs
require understanding which species comprise potential pred-
ators and where predation occurs.

In this study, our objective was to assess predation risk for
Scoters in marine habitats by identifying potential predators
and estimating predation rates, timing, and exposure. We fo-
cused on White-winged Scoters (Melanitta fusca (L., 1758))
and Surf Scoters (Melanitta perspicillata (L., 1758)), the two
species of Scoter that are relatively abundant and widely dis-
tributed along the Pacific coast. We hypothesized that Bald
Eagles are the main predator of Scoters, given the untested
prediction of Savard et al. (1998) and the recent increase in
numbers of Bald Eagles (Fig. 1). Waterfowl are flightless
during wing molt and are believed to select molting sites
based in part on safety from predators (Salomonsen 1968).
Thus, we also hypothesized that predation rates would be
lower during wing molt versus the wintering period. To as-
ess these hypotheses, we coupled (i) fates of marked Scoters
from multiple regions on the Pacific coast, (ii) behavioral ob-
servations of Scoters and their predators, and (iii) a review of
predator diet studies.

Materials and methods

We conducted three types of analyses. First, to identify
spatial and temporal variation in predation rates and the com-
oposition of Scoter predators, we tracked the fate of Scoters
marked with VHF transmitters in sites ranging from Wash-
ington to southeast Alaska. Second, we used focal observa-
tions (Lehner 1996) of Scoters in northern Puget Sound,
Washington, to assess (i) rates of attempted predation on
Scoters and (ii) rates of predator disturbances that altered
Scoter behavior. We contrasted these two factors between
Scoter species, as well as among seasonal and diurnal peri-
ods to identify temporal patterns in predation risk. To iden-
tify spatial patterns in predation risk, we considered
variation in items i and ii above between two study sites in
Washington. We opportunistically recorded predation at-
ttempts on nonfocal individuals, yet systematic monitoring of
Scoter flocks was not feasible because they were often large
and distant from shore. Third, because species accounts for
Scoters provide little information about predators (Brown and
Fredrickson 1997; Savard et al. 1998), we reviewed a range of
sources to identify predators of Scoters within North American
marine habitats.

Fate of marked Scoters

During 2001–2010, we attached VHF transmitters to
White-winged Scoters and Surf Scoters during winter and
the period of wing molt in late summer in three areas: Puget
Sound, Washington; the southern Strait of Georgia, British
Columbia (B.C.); and southeast Alaska (Table 1). All Scoters
were cared for according to accepted standards (National Re-
search Council 2010), and our protocols were approved by
animal care committees at Simon Fraser University and the
Washington Department of Fish and Wildlife (WDFW).
Scoters were captured with decoys and either floating mist
nets in winter or gill nets during wing molt. We used three
types of transmitters: abdominal implants with internal or ex-
ternal antennas, subcutaneous implants with external anten-
as, and external mounts attached with a subcutaneous
anchor. All transmitters were manufactured by Holohil Sys-
tems, Ltd. (Carp, Ontario) or Advanced Telemetry Systems
(Isanti, Minnesota). Iverson et al. (2006) describe methods
used to deploy these transmitters and report that Scoter sur-
vival did not differ among these transmitter types. Protocols
for monitoring marked Scoters varied by area, but we gen-
ernally attempted to locate each individual at least once every
5–10 d throughout the period of observation. Locations were
obtained using antennas that were handheld or mounted on
vehicles or boats (see Kirk et al. 2008); in some sites, anten-
as mounted on fixed-wing aircraft were used infrequently to
locate individuals that had not been observed in the immedi-
ate study area.
Table 1. Locations and periods of observation for White-winged Scoters (*Melanitta fusca*) and Surf Scoters (*Melanitta perspicillata*) marked with VHF transmitters, as well as years of study, number of transmitters deployed for all years combined (nos. deployed), the number of transmitters for which a mortality signal was observed by fate category, and the observed percentage of marked Scoters that were depredated or scavenged.

<table>
<thead>
<tr>
<th>Period</th>
<th>Years</th>
<th>No. of transmitters displaying mortality signal by fate category</th>
<th>Observed % depredated or scavenged†</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>White-winged Scoters</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Puget Sound, Washington</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Forbes Point Molt (Aug.–Sept.)</td>
<td>2009</td>
<td>8 0 (0) 0 (0) 0 (0)</td>
<td>0.0</td>
</tr>
<tr>
<td>Strait of Georgia, B.C.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fraser Delta Molt (Aug.–Sept.)</td>
<td>2008, 2009</td>
<td>10 0 (0) 0 (0) 0 (0)</td>
<td>0.0</td>
</tr>
<tr>
<td>Southeast Alaska Juneau</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Molt (Aug.–Sept.)</td>
<td>2008, 2009</td>
<td>37 0 (0) 0 (0) 0 (0)</td>
<td>0.0</td>
</tr>
<tr>
<td><strong>Surf Scoters</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Puget Sound, Washington</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Multiple sites Winter (Dec.–Apr.)</td>
<td>2003–2004, 2004–2005, 2005–2006</td>
<td>80 3 (1) 0 (0) 4 (4)</td>
<td>8.8</td>
</tr>
<tr>
<td>Forbes Point, Padilla Bay</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Molt (Aug.–Sept.)</td>
<td>2008, 2009</td>
<td>24 0 (1) 0 (0) 0 (1)</td>
<td>0.0</td>
</tr>
<tr>
<td>Strait of Georgia, B.C.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Malaspina Inlet Winter (Dec.–Mar.)</td>
<td>2004–2005</td>
<td>71 1 (0) 0 (0) 1 (1)</td>
<td>2.8</td>
</tr>
<tr>
<td>Fraser Delta Molt (Aug.–Sept.)</td>
<td>2008, 2009</td>
<td>15 0 (0) 0 (0) 0 (0)</td>
<td>0.0</td>
</tr>
<tr>
<td>Southeast Alaska Juneau</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Winter (Nov.–Mar.)</td>
<td>2008–2009, 2009–2010</td>
<td>88 0 (1) 13 (11) 3 (2)</td>
<td>18.2</td>
</tr>
<tr>
<td>Juneau</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Molt (Aug.–Sept.)</td>
<td>2008, 2009</td>
<td>52 1 (1) 0 (2) 0 (1)</td>
<td>1.9</td>
</tr>
</tbody>
</table>

**Note:** Location coordinates for telemetry studies were as follows: Forbes Point (48.2°N, 122.6°W), Padilla Bay (48.5°N, 122.5°W), Fraser Delta (49.0°N, 123.1°W), Baynes Sound (49.5°N, 124.8°W), Malaspina Inlet (50.0°N, 124.7°W), and Juneau (58.3°N, 134.7°W). Fate categories are based on circumstantial evidence and include transmitter recovered near feeding areas of Bald Eagles (*Haliaeetus leucocephalus*) or a species of Mustelidae (mustelid), or Scoter mortality confirmed or likely but cause unknown (other); smaller numbers of marked Scoters were placed in three additional fate categories (see Results).

Numbers deployed and results are for Scoters that survived a postrelease adjustment period, except for results in parentheses that report mortalities that occurred within this adjustment period (i.e., mortalities that might have resulted from handling effects).

*In Baynes Sound, numbers of transmitters that were abdominally implanted, subcutaneously implanted, and externally mounted with subcutaneous anchors were 107, 10, and 11 for White-winged Scoters, respectively, and 70, 7, and 6 for Surf Scoters, respectively. For Surf Scoters in Puget Sound during winter, all transmitters were abdominally implanted. For Surf Scoters in Malaspina Inlet, we deployed 44 abdominally implanted and 27 subcutaneously implanted transmitters. In all other cases, transmitters were externally mounted with subcutaneous anchors.

†Calculated as the percentage of deployed transmitters in Bald Eagle, mustelid, and other fate categories.

All transmitters included mortality switches that doubled the pulse rate if the transmitter remained motionless for >12 h. For each transmitter that displayed a mortality signal, we documented circumstantial evidence of the marked individual’s fate and placed it into one of the following five fate categories: (1) transmitter recovered near an obvious feeding area of a predator (with subcategories for each identifiable type of predator); (2) Scoter killed by hunter; (3) Scoter mortality confirmed or likely but cause unknown; (4) transmitter may have been dislodged with possible survival of Scoter; or (5) Scoter mortality could not be confirmed. When a possible cause of mortality was unclear, transmitters were included in category 3 if they were abdominal implants, or if they were subcutaneously implanted or externally mounted and were recovered in or reliably biangled to upland sites (mortality likely because Scoters use upland habitats only during breeding) or to intertidal sites with Scoter remains. Category 4 included externally mounted and subcutaneously implanted transmitters that were recovered in the intertidal zone without Scoter remains; we assumed that abdominal implants could not be dislodged within the relatively short observation periods. Category 5 included externally mounted and subcutaneously implanted transmitters that we could not recover or reliably locate.
Scoter remains were often inadequate for forensic analyses, and thus we do not report the fraction of Scoters that were likely depredated versus those that died of other causes and were then scavenged. However, we consider only those Scoters that survived a postrelease adjustment period. Specifically, as in Iverson et al. (2006), we assumed that recovery from handling effects and acclimation to transmitters would be complete after 14 d for implanted transmitters and after 7 d for external transmitters. Beyond these adjustment periods even the relatively invasive abdominally implanted transmitters likely had minimal impacts on Scoter survival (Mulcahy and Esler 1999). Mortalities of Scoters that occurred after these adjustment periods are more likely due to natural causes, rather than to handling effects that might have reduced survivorship. As a summary measure, we report the percentage of all marked Scoters that appeared to have been depredated or scavenged (i.e., those in categories 1 and 3 above). We did not statistically analyze the fates of marked Scoters because our ability to confirm mortalities and assess probable causes of death varied among sites and seasonal periods because of differences in local conditions and logistical support. Thus, we qualitatively compared species, seasonal periods, and sites with respect to differences in apparent predators and rates of predation or scavenging.

Focal observations of Scoters

Field methods

We conducted 5 min focal observations of Scoters from shore with a 20×–60× spotting scope in Penn Cove (48.2°N, 122.7°W) and Birch Bay (48.9°N, 122.8°W), two bays heavily used by Scoters in Puget Sound, Washington (Anderson and Lovvorn 2011). We conducted observations in 2003–2005 during three seasonal periods (November, late January–February, April 2004 only) and three diurnal periods (before 1000, 1000–1400, after 1400). Within each year, observation time was partitioned about equally among all combinations of site × season × diurnal period (about 250 h total observation time). In April, observations spanned the diurnal period in which Scoters fed in each site (during nocturnal periods in this region, Scoters use habitats farther from shore where feeding is rare; Lewis et al. 2005). In November and January–February when day length was shorter than in April, Scoters arrived before and departed after the diurnal period in which light conditions made observations possible. Thus, in November and January–February, our observations could not completely span the period in which Scoters fed in each site and were simply begun 30 min before sunrise and concluded 30 min after sunset. As in Anderson and Lovvorn (2011), we randomly sampled focal Scoters and grouped focal individuals into two categories: (1) after-hatch-year males and (2) females + hatch-year males.

During each focal observation, we recorded predation attempts and predator disturbances by category of predator. Predation attempts were defined as rapid and direct movement of a predator toward Scoters. Predator disturbances were defined as sudden escape responses by Scoters including flying, diving, or rapid swimming that were initiated by activity of a potential predator (but without a clear predation attempt). We included a disturbance category for which the source could not be identified—these may have included disturbances by predators that we could not see, but did not appear to include human disturbances that were recorded separately and are not reported here.

Statistical analyses

We set significance levels at α = 0.05, report means ± SE, and conducted all statistical analyses using JMP version 8.0.2 (SAS Institute Inc. 2009). We used ANCOVA to contrast Scoter species and cohorts (after-hatch-year males, females + hatch-year males) in terms of hourly rates of predation attempts and predator disturbances by predator type. Site, year, season, and diurnal period were included as additional factors in these analyses.

Review of Scoter predators

We used three methods to identify predators of Scoters within North American marine habitats. First, we compiled published reports of predation on Scoters by searching Google Scholar and BioOne Abstracts and Indexes for citations that included anywhere in their text one or a combination of the following terms: Scoter, Melanitta, predation, predator, and diet. Second, we located additional published reports by reviewing diet analyses for a range of plausible marine predators of Scoters. Finally, we included our own observations conducted during these and related field efforts, and queried collaborators for unpublished observations of predation on Scoters in marine habitats. For all sources, we distinguished between predation on live Scoters versus observations of Scoter remains in gut contents or near feeding areas for which Scoters may have been scavenged.

Results

Fate of marked Scoters

We deployed 183 and 413 VHF transmitters for White-winged Scoters and Surf Scoters, respectively (these deployments and all results unless stated otherwise include only individuals that survived a postrelease adjustment period; Table 1). The fraction of marked Scoters of both species that were depredated or scavenged was greater during winter (13.1%) than during wing molt (0.7%). This seasonal difference was proportionally greater than the difference in duration of observations in winter (4–5 months) versus wing molt (2 months). Among sites in which Scoters were marked over multiple years, a possible annual effect on the rate of scavenging or predation was evident only in Baynes Sound, B.C. In that site, total numbers that were depredated or scavenged for White-winged Scoters and Surf Scoters, respectively, were 1 and 4 in 2001–2002, 7 and 6 in 2002–2003, and 8 and 7 in 2003–2004.

Transmitters and remains of marked Scoters were recovered near feeding areas of two identifiable categories of predators: Bald Eagles and mustelid species. Recoveries near mustelid feeding areas occurred mainly in our southeast Alaska sites (14.8% of Surf Scoters marked in Alaska during winter), while those near Bald Eagle feeding areas occurred mainly south of Alaska (1.6% and 3.4% of White-winged Scoters and Surf Scoters, respectively, marked in B.C. and Washington during winter). However, the fraction of all observed mortality signals for which a probable cause of death could not be identified (other) or for which mortality could
not be confirmed was greater in B.C. sites (9.8%) than in all other sites combined (3.7%). Of cases in which species of mustelid could be identified, remains of two wintering Surf Scoters in southeast Alaska were associated with river otters (*Lontra canadensis*) and remains of nine wintering Surf Scoters in southeast Alaska and two wintering White-winged Scoters in Baynes Sound, B.C., were associated with American mink (*Neovison vison*). As indicated by appreciable quantities of blood observed with recovered transmitters, at least one mink and two unknown mustelid species preyed on live Surf Scoters during winter in southeast Alaska. Remains of other marked Scoters were insufficient to distinguish whether they had been depredated or scavenged.

Smaller numbers of transmitters for which mortality signals were observed occurred in three additional fate categories. Numbers of Scoters harvested by hunters during winter included one Surf Scoter in Puget Sound and one Surf Scoter in Juneau. Numbers of Scoters that may have shed transmitters included three White-winged Scoters and four Surf Scoters in Baynes Sound, two Surf Scoters in Malaspina Inlet, and five Surf Scoters in Juneau during winter. Mortality could not be confirmed for one White-winged Scoter in Baynes Sound and four Surf Scoters in Juneau during winter.

In Baynes Sound, the single site in which both Scoter species were marked during winter, the fraction of individuals that were depredated or scavenged was nearly 50% greater for Surf Scoters compared with White-winged Scoters. However, results from the four sites in which Surf Scoters were marked during winter suggest that rates of predation vary by area. Of all marked Scoters that were likely depredated or scavenged, mortality signals of nearly half (51 out of 111) were observed within the postrelease adjustment period. The rate of apparent transmitter dislodgement was greater during winter (3.1%) compared with wing molt (0.0%), and was slightly greater for Surf Scoters (2.7%) compared with White-winged Scoters (1.6%; Table 1). The fraction of marked Scoters for which mortality could not be confirmed was low for each Scoter species (<1.0% in each location).

### Focal observations of Scoters

In Penn Cove and Birch Bay in Puget Sound during 2003–2005, we did not observe any predation attempts on White-winged Scoters or Surf Scoters in 2961 five minute observations or in opportunistic observations of nonfocal individuals during this and related fieldwork in these sites. However, during concurrent work in other sites, we observed for each Scoter species a small number (<5) of predation attempts by Bald Eagles. These attempts included only one successful predation event: on 2 March 2004 in Semiahmoo Bay, B.C. (49.0°N, 122.8°W), a Bald Eagle depredated a male Surf Scoter that we had released about 5 min earlier from banding operations. This Bald Eagle appeared to be hunting from an offshore structure and carried the Surf Scoter inland.

During focal observations we observed disturbances of Scoter behavior by Bald Eagles and, on a single occasion, by an unidentified pinniped species, yet the source of most disturbances could not be identified (Table 2). Mean hourly rates of disturbance by Bald Eagles and by unidentified sources did not differ significantly between Scoter species or sites (Bald Eagles: $P = 0.498$ for species and $P = 0.097$ for site; unidentified sources: $P = 0.141$ for species and $P = 0.932$ for site; for each source of disturbance: df = 5, 2948 and $P > 0.410$ for effects of species × site, year, and cohort). For focal observations combined across species and sites, Bald Eagle and unidentified disturbances did not vary among seasonal or diurnal periods (Bald Eagles: $P = 0.538$ for season and $P = 0.865$ for diurnal period; unidentified sources: $P = 0.468$ for season and $P = 0.686$ for diurnal period; for each source of disturbance: df = 4, 2956).

### Review of Scoter predators

We identified reports of two species preying on live White-winged Scoters and five species preying on live Surf Scoters in North American marine habitats, with observations of prey remains and feeding behavior suggesting that several additional species constitute likely predators (Table 3). Bald Eagles and orcas (*Orcinus Orca*) were the most commonly reported predators of all three Scoter species, and many additional reports included observations of Scoter remains near Bald Eagle feeding sites. Predators of Surf Scoters also included Steller sea lions (*Eumetopias jubatus*), sea otters (*Enhydra lutris*), and American mink.

### Discussion

#### Composition of Scoter predators

Although a range of species prey on Scoters in marine habitats, overall rates of predation in sites we considered ap-

---

**Table 2.** Number of 5 min focal observations ($n$) of White-winged Scoters (*Melanitta fusca*) and Surf Scoters (*Melanitta perspicillata*) and hourly rate of predator disturbances by category for two sites in northern Puget Sound, Washington, during 2003–2004 and 2004–2005 combined.  

<table>
<thead>
<tr>
<th>Area</th>
<th>Species</th>
<th>n</th>
<th>Bald Eagle</th>
<th>Pinniped</th>
<th>Unidentified</th>
</tr>
</thead>
<tbody>
<tr>
<td>Penn Cove</td>
<td>White-winged Scoters</td>
<td>360</td>
<td>0±0 (0)</td>
<td>0±0 (0)</td>
<td>0.19±0.10 (10)</td>
</tr>
<tr>
<td></td>
<td>Surf Scoters</td>
<td>1168</td>
<td>0.01±0.01 (1)</td>
<td>0.01±0.01 (1)</td>
<td>0.10±0.06 (6)</td>
</tr>
<tr>
<td>Birch Bay</td>
<td>White-winged Scoters</td>
<td>783</td>
<td>0.03±0.02 (2)</td>
<td>0±0 (0)</td>
<td>0.22±0.06 (13)</td>
</tr>
<tr>
<td></td>
<td>Surf Scoters</td>
<td>650</td>
<td>0.06±0.03 (3)</td>
<td>0±0 (0)</td>
<td>0.09±0.06 (3)</td>
</tr>
</tbody>
</table>

**Note:** Values are means ± SE. The total number of 5 min observations during which a predator disturbance was observed is reported in parentheses.
Table 3. Predators of Scoters in marine habitats, including animals observed feeding on (predation) or pursuing (chase) live Scoters, or with Scoter remains found in gut contents or near feeding areas (prey remains).

<table>
<thead>
<tr>
<th>Predator</th>
<th>White-winged Scoter (Melanitta fusca)</th>
<th>Surf Scoter (Melanitta perspicillata)</th>
<th>Unidentified Scoter (or Black Scoter, Melanitta nigra (L., 1758))</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bald Eagle, <em>Haliaeetus leucocephalus</em> (L., 1766)</td>
<td>Predation<em>a,b,c,d,e,f,g</em></td>
<td>Predation<em>a,g</em></td>
<td>Predation<em>c (Black Scoter), prey remains</em></td>
</tr>
<tr>
<td>Gyrfalcon, <em>Falco rusticolus</em></td>
<td>Prey remains*</td>
<td>Prey remains*</td>
<td>Possible*</td>
</tr>
<tr>
<td>Peregrine Falcon, <em>Falco peregrinus Tunstall</em>, 1771</td>
<td>Prey remains*</td>
<td>Prey remains*</td>
<td>Possible*</td>
</tr>
<tr>
<td>Snowy Owl, <em>Bubo scandiacus</em> (L., 1758)</td>
<td>Prey remains*</td>
<td>Prey remains*</td>
<td>Chase* (Black Scoter)</td>
</tr>
<tr>
<td>Common Raven, <em>Corvus corax</em> L., 1758</td>
<td>Predation<em>a,o</em></td>
<td>Predation<em>a,p</em></td>
<td>Predation*a (Black Scoter)</td>
</tr>
<tr>
<td>Orca, <em>Orcinus orca</em> (L., 1758)</td>
<td>Predation<em>a,o</em></td>
<td>Predation<em>a,p</em></td>
<td>Predation*a (Black Scoter)</td>
</tr>
<tr>
<td>Steller sea lion, <em>Eumetopias jubatus</em> (Schreber, 1776)</td>
<td>Prey remains*</td>
<td>Prey remains*</td>
<td></td>
</tr>
<tr>
<td>Harbor seal, <em>Phoca vitulina</em> L., 1758</td>
<td></td>
<td></td>
<td>Possible*</td>
</tr>
<tr>
<td>Sea otter, <em>Enhydra lutris</em> (L., 1758)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>River otter, <em>Lontra canadensis</em> (Schreber, 1777)</td>
<td>Prey remains*</td>
<td>Prey remains*</td>
<td></td>
</tr>
<tr>
<td>American mink, <em>Neovison vison</em> (Schreber, 1777)</td>
<td>Prey remains*</td>
<td>Predation*</td>
<td></td>
</tr>
</tbody>
</table>

Note: Three additional species are included as potential predators of Scoters (possible) because they have been observed feeding in marine habitats on live sea ducks that have distributions and feeding behavior similar to those of Scoters. Citations are provided for published accounts (letter footnotes) and personal communications (* and † footnotes).

*a* Brooks (1922).
*b* Bayer (1987).
*c* Todd et al. (1982).
*d* Knight et al. (1990).
*e* Watson (2002).
*f* Erlandson et al. (2007).
*g* This study (see Results).
*i* Vermeer and Morgan (1989).
*k* Dekker (1995).
*l* Campbell and MacColl (1978).
*m* Maguire (2000).
*n* Odlum (1948).
*o* Matkin et al. (2007).
*p* Ford et al. (1998).
*s* Riedman and Estes (1988).

*Predation occurred in southern Puget Sound, Washington, on 1 May 2004 (B. Troutman, WDFW, personal communication).
* Predation occurred in Resurrection Bay, Alaska, in late November 1998 (M. Ben-David, University of Wyoming, personal communication).
cause sea ducks exhibit may have contributed to declines in Scoter populations be-

Fig. 2. Monthly counts (mean ± SE) of Bald Eagles per survey sta-
tion (n = 281) for the B.C. Coastal Waterbird Survey during 1999–
2009 (Bird Studies Canada 2010). Arrows indicate the main periods
when Pacific salmon (genus Oncorhynchus) and Pacific herring
(Clupea pallasi) are available to Bald Eagles, although these im-
portant foods have declined markedly in recent decades.

mink) and for species that prey on marine birds from under-
water (mustelids, pinnipeds, cetaceans, fish). Last, results of
our telemetry studies and many past diet studies of predators
focus on prey remains, which can reflect either predation or
scavenging.

Past results suggest that river otters and mink are unlikely
to eat dead Scoters (Stenson et al. 1984; Larivière 1999), yet
preying on large sea ducks that remain distant from shore ap-
pears to be challenging for these species (M. Ben-David,
University of Wyoming, personal communication). Thus, we
conjecture that remains of marked Scoters found near mus-
telid feeding areas included mainly Scoters that were compro-
bised by weather or handling effects. Of all mortalities of
Surf Scoters associated with mustelids during winter in Ju-
neau, Alaska, most (16 out of 24) were of hatch-year birds
that may have had difficulty meeting their energetic require-
ments and nearly half (11 out of 24) were observed in the
postrelease adjustment period. Hatch-year Surf Scoters are
more likely to winter south of Alaska (Iverson et al. 2004),
perhaps because their lack of feeding experience and smaller
body size impose greater constraints on meeting the energy
demands of extreme climates.

Rates, timing, and location of predation

While recognizing that our telemetry studies cannot definit-
ively distinguish predation from scavenging, they suggest at
least three tentative results for further inquiry. First, consist-
tent with our hypothesis, predation rates appear lower during
wing molt than winter, although rates varied among winter-
ing sites. Second, predation rates in some wintering sites
may have contributed to declines in Scoter populations be-
cause sea ducks exhibit K-selected life-history traits. Goudie
et al. (1994) used a simple population projection model to
show that even annual adult mortality of 3%–5% may not be
sustainable. Ultimately, formal survival analyses are needed
to assess factors constraining recovery of Scoter populations.
Third, while mustelids appear to be the dominant predator of
Scoters in our southeast Alaska site, Bald Eagles may be a
more frequent predator south of Alaska. A caveat to this re-
sult is that in Baynes Sound, B.C., a high fraction of mortal-
ities in our marked birds could not be assigned a probable
cause of death and some of these may have been depredated
by mustelids. In our Alaska sites, snow facilitated identifica-
tion of predators and we were able to allocate relatively
greater effort to retrieving transmitters that displayed mortal-
ity signals (burial in mustelid burrows greatly attenuated
VHF signals). Moreover, variation in rates of Bald Eagle pre-
dation by region were probably not due to differences in Bald
Eagle densities, which are greater in Alaska than in sites far-
ther south (Fig. 1). Densities of mustelids by region were not
available.

Predation risk for Scoters has received little attention prob-
ably because predation occurs mainly at times and places that
are not readily observable. While mink predation of Scoters
is likely nocturnal (Larivière 1999), we hypothesize that
Bald Eagle predation occurs mainly where Scoter numbers
are low. Bald Eagles pose a risk of predation to Scoters, as
indicated by the escape responses that we observed Scoters
display whenever Bald Eagles flew over the study site. The
low frequency of such responses appeared to result from
there being few Bald Eagles present during our observations,
suggesting that Bald Eagle predation of Scoters may be less
profitable in sites such as Penn Cove and Birch Bay that are
heavily used by Scoters. Indeed, most predation attempts by
Bald Eagles that we observed or that were reported by others
occurred in sites where Scoter numbers were low. In Penn
Cove and Birch Bay, other spatial and temporal patterns in
predation risk for Scoters and in predator disturbances of
Scoters were not apparent.

Predation risk in an altered seascape

Populations have declined for 10 out of the 15 species of
North American sea ducks, yet available data for most sea
duck species are not adequate to identify causes of these de-
clines (Sea Duck Joint Venture 2008). Studies of Scoters in
marine habitats have focused mainly on bottom-up processes
(e.g., Kirk et al. 2008; Anderson and Lovvorn 2011). As
such, management recommendations have emphasized pro-
tecting habitats that provide putatively important seasonal
foods. However, even heavily used foods such as herring
spawn do not entirely explain patterns in Scoter habitat use
and body reserves (Anderson et al. 2009). Thus, research pri-
orities include assessments of whether predation risk influen-
ces Scoter habitat needs and whether specific human impacts
have increased predation risk. For instance, even where pre-
dation rates are low, individual birds reduce predation risk
by varying their movements and rates of foraging and vigi-
lance (Rogers 1987; Ydenberg et al. 2007). Flexibility in regu-
lating these behaviors may have declined where greater
foraging effort is needed to counter declines in physiological
condition, as can result from increased contaminant exposure
or disturbances from recreational activities (Takekawa et al.
2002; Béchet et al. 2004). Human impacts that reduce Scoter
energy balance may also increase rates of predation by spe-
cies such as American mink and river otters that may be lim-
ited to preying on Scoters that are in a weakened state. Also,
flocking is common by Scoters and may reduce predation
risk through early detection or risk dilution (Krause and Rux-
ton 2002), yet this strategy may be diminished if typical
flock sizes have declined concurrently with declines in Scoter
populations.

Bald Eagles and mustelid species appear to be principal
predators of Scoters, and the risk of predation by these spe-
cies may have changed over recent decades with increasing
human impacts to marine ecosystems. Pacific herring and Pacific salmon are important foods for Bald Eagles, and together form a prey base that spans the majority of the seasonal period when Bald Eagles are particularly abundant in coastal ecosystems (Fig. 2). However, Pacific herring and Pacific salmon have declined at the same time that numbers of Bald Eagles have increased (Fig. 1); declines in these traditional foods are especially pronounced south of Alaska where Bald Eagles may be the most common predator of Scoters (Nehlsen et al. 1991; Willson and Womble 2006). In Washington, <50% of stocks of Pacific herring and Pacific salmon are considered healthy (Stick 2005; Stinson et al. 2007). Declines in fish that are important prey for Bald Eagles, American mink, and many other marine predators may have shifted some predation risk to already diminished numbers of marine birds. Such a shift is perhaps most likely of predators such as Bald Eagles for which marine birds were probably a traditional dietary item (Erlandson et al. 2007). It is less certain whether predation of marine birds has increased by other mainly piscivorous predators for which predation of marine birds has been documented less often, such as mustelid species and harbor seals (Phoca vitulina) (Stenson et al. 1984; Tallman and Sullivan 2004).

Acknowledgements

Field assistance was provided by J. Barrett, B. Bartzen, T. Bowman, J. Brown, S. Coulter, D. Cushing, A. DuBour, L. Heisler, S. Iverson, M. Kirk, L. Koloski, D. Lacroix, P. Levshue, T. Lewis, R. Lis, R. MacDonald, M. McAdie, A. Mclean, A. Pagano, L. Parker, A. Patterson, K. Pontius, J. Ray, J. Reed, J. Reynolds, V. Richard, J. Whissel, and many others. With much volunteer support, Bird Studies Canada supplied B.C. Coastal Waterbirds Survey data. This study was funded by the NOAA National Estuarine Research Reserve System (fellowship to E.M.A.), the Sea Duck Joint Venture, the USFWS Western Washington Fish and Wildlife Office, the SeaDoc Society, Ducks Unlimited Canada, the Natural Sciences and Engineering Research Council of Canada, the Province of British Columbia through the Ministry of Advanced Education (funding for C.S.V.), the Department of Biology at Simon Fraser University, the USGS Alaska Science Center, and the Washington Brant Foundation. Logistic support was provided by the Centre for Wildlife Ecology, the Canadian Wildlife Service, Auke Bay Laboratories, the Ted Stevens Marine Research Institute, the USFWS Juneau Office, and the USDA Forest Service Juneau Ranger District.

References


