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

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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 596 macreuses porteuses 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.

[Traduit 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-

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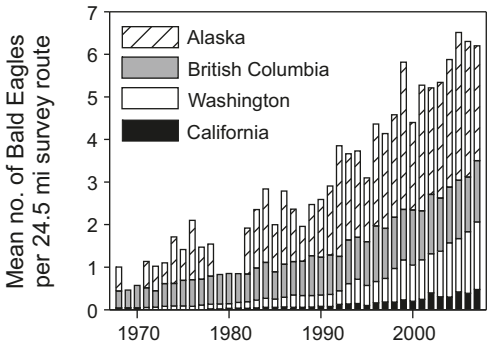
Fig. 1. North American Breeding Bird Survey results during 1968–2007 for Bald Eagles (*Haliaeetus leucocephalus*) (results not available for Oregon; Sauer et al. 2008), where 1 mi = 1.61 km.



lation recoveries to concurrent declines in many taxa of marine birds is unclear. Human impacts have likely modified predator–prey relationships not only by affecting predator numbers, but also by altering relative abundances and distributions among a range of their potential prey. For instance, declines in many stocks of Pacific salmon (genus *Oncorhynchus* Suckley, 1861) and Pacific herring (*Clupea pallasii* Valenciennes in Cuvier and Valenciennes, 1847) that are important foods for Bald Eagles (Nehlsen et al. 1991; Willson 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 resulted 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 diminished by a range of human activities, several of which are putative 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 foraging behavior, movements, and physiological condition (e.g., Lewis et al. 2005; Kirk et al. 2008; Anderson et al. 2009). However, because predation risk can also affect these parameters (Lima 1985; Rogers 1987), assessments of habitat needs require understanding which species comprise potential predators 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 focused 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 distributed 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 assess these hypotheses, we coupled (*i*) fates of marked Scoters from multiple regions on the Pacific coast, (*ii*) behavioral observations 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 composition of Scoter predators, we tracked the fate of Scoters marked with VHF transmitters in sites ranging from Washington to southeast Alaska. Second, we used focal observations (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 periods to identify temporal patterns in predation risk. To identify spatial patterns in predation risk, we considered variation in items *i* and *ii* above between two study sites in Washington. We opportunistically recorded predation attempts 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 Research 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 external antennas, subcutaneous implants with external antennas, and external mounts attached with a subcutaneous anchor. All transmitters were manufactured by Holohil Systems, Ltd. (Carp, Ontario) or Advanced Telemetry Systems (Isanti, Minnesota). Iverson et al. (2006) describe methods used to deploy these transmitters and report that Scoter survival did not differ among these transmitter types. Protocols for monitoring marked Scoters varied by area, but we generally 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, antennas mounted on fixed-wing aircraft were used infrequently to locate individuals that had not been observed in the immediate study area.

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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.

				No. of transmitters displaying mortality signal by fate category			
	Period	Years	Nos. deployed*	Bald Eagle	Mustelid	Other	Observed % depredated or scavenged†
White-winged Scoters							
Puget Sound, Washington							
Forbes Point	Molt (Aug.–Sept.)	2009	8	0 (0)	0 (0)	0 (0)	0.0
Strait of Georgia, B.C.							
Baynes Sound	Winter (Dec.–Apr.)	2001–2002, 2002–2003, 2003–2004	128	2 (0)	1 (1)	14 (9)	13.3
Fraser Delta	Molt (Aug.–Sept.)	2008, 2009	10	0 (0)	0 (0)	0 (0)	0.0
Southeast Alaska							
Juneau	Molt (Aug.–Sept.)	2008, 2009	37	0 (0)	0 (0)	0 (0)	0.0
Surf Scoters							
Puget Sound, Washington							
Multiple sites	Winter (Dec.–Apr.)	2003–2004, 2004–2005, 2005–2006	80	3 (1)	0 (0)	4 (4)	8.8
Forbes Point, Padilla Bay	Molt (Aug.–Sept.)	2008, 2009	24	0 (1)	0 (0)	0 (1)	0.0
Strait of Georgia, B.C.							
Baynes Sound	Winter (Dec.–Apr.)	2001–2002, 2002–2003, 2003–2004	83	4 (6)	0 (0)	13 (9)	20.5
Malaspina Inlet	Winter (Dec.–Mar.)	2004–2005	71	1 (0)	0 (0)	1 (1)	2.8
Fraser Delta	Molt (Aug.–Sept.)	2008, 2009	15	0 (0)	0 (0)	0 (0)	0.0
Southeast Alaska							
Juneau	Winter (Nov.–Mar.)	2008–2009, 2009–2010	88	0 (1)	13 (11)	3 (2)	18.2
Juneau	Molt (Aug.–Sept.)	2008, 2009	52	1 (1)	0 (2)	0 (1)	1.9

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 biangulated 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.

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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 $\alpha = 0.05$, 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

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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.

		No. of disturbances/h by		
	n	Bald Eagle	Pinniped	Unidentified
Penn Cove				
White-winged Scoters	360	0±0 (0)	0±0 (0)	0.19±0.10 (10)
Surf Scoters	1168	0.01±0.01 (1)	0.01±0.01 (1)	0.10±0.06 (6)
Birch Bay				
White-winged Scoters	783	0.03±0.02 (2)	0±0 (0)	0.22±0.06 (13)
Surf Scoters	650	0.06±0.03 (3)	0±0 (0)	0.09±0.06 (3)

Note: Values are means ± SE. The total number of 5 min observations during which a predator disturbance was observed is reported in parentheses.

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 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).

	White-winged Scoter (*Melanitta fusca*)	Surf Scoter (*Melanitta perspicillata*)	Unidentified Scoter (or Black Scoter, *Melanitta nigra* (L., 1758))
Bald Eagle, *Haliaeetus leucocephalus* (L., 1766)	Predation,[a,b,*] prey remains[c,d,e,f,g]	Predation,[a,g] prey remains[d,e,f,g,h]	Predation[a] (Black Scoter), prey remains[i]
Gyrfalcon, *Falco rusticolus*			Possible[j]
Peregrine Falcon, *Falco peregrinus* Tunstall, 1771			Possible[k]
Snowy Owl, *Bubo scandiacus* (L., 1758)	Prey remains[l]	Prey remains[l]	
Common Raven, *Corvus corax* L., 1758			Chase[m] (Black Scoter)
Orca, *Orcinus orca* (L., 1758)	Predation,[n,o] prey remains[p]	Predation[o,p]	Predation[o] (Black Scoter)
Steller sea lion, *Eumetopias jubatus* (Schreber, 1776)		Predation[†]	
Harbor seal, *Phoca vitulina* L., 1758			Possible[q,r]
Sea otter, *Enhydra lutris* (L., 1758)		Predation[s]	
River otter, *Lontra canadensis* (Schreber, 1777)		Prey remains[g]	
American mink, *Neovison vison* (Schreber, 1777)	Prey remains[g]	Predation[g]	

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).
[h]Retfalvi (1970).
[i]Vermeer and Morgan (1989).
[j]Nielsen and Cade (1990).
[k]Dekker (1995).
[l]Campbell and MacColl (1978).
[m]Maguire (2000).
[n]Odlum (1948).
[o]Matkin et al. (2007).
[p]Ford et al. (1998).
[q]MacKenzie (2000).
[r]Tallman and Sullivan (2004).
[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).

peared low by predators other than Bald Eagles and mustelid species (including mainly American mink), the only predators identified in our study of 596 marked Scoters. However, this conclusion about predator composition for Scoters requires several qualifications. First, individuals within a predator species may display strong specialization on a specific prey type, even for prey that may be atypical for the species. For instance, some individual river and sea otters appear to prey heavily on marine birds (Stenson et al. 1984; Riedman and Estes 1988). Second, White-winged Scoters are >50% larger than Surf Scoters, meaning that White-winged Scoters are probably a less manageable prey type for many of the avian and mustelid predators that we identified. Indeed, Bald Eagles may not be able to lift some White-winged Scoters off the water (B. Troutman, WDFW, personal communication). Third, direct observations needed to clearly distinguish predation from scavenging are under-represented for species that feed nocturnally (Snowy Owl (*Bubo scandiacus*), American

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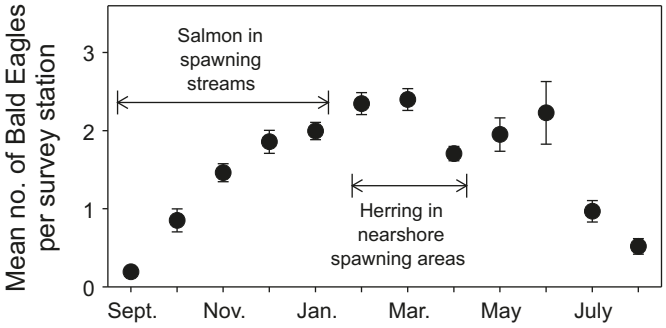
Fig. 2. Monthly counts (mean ± SE) of Bald Eagles per survey station (n = 281) for the B.C. Coastal Waterbird Survey during 1999–2009 (Bird Studies Canada 2010). Arrows indicate the main periods when Pacific salmon (genus *Oncorhynchus*) and Pacific herring (*Clupea pallasii*) are available to Bald Eagles,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



mink) and for species that prey on marine birds from underwater (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 appears to be challenging for these species (M. Ben-David, University of Wyoming, personal communication). Thus, we conjecture that remains of marked Scoters found near mustelid feeding areas included mainly Scoters that were compromised by weather or handling effects. Of all mortalities of Surf Scoters associated with mustelids during winter in Juneau, Alaska, most (16 out of 24) were of hatch-year birds that may have had difficulty meeting their energetic requirements 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 definitively distinguish predation from scavenging, they suggest at least three tentative results for further inquiry. First, consistent with our hypothesis, predation rates appear lower during wing molt than winter, although rates varied among wintering sites. Second, predation rates in some wintering sites may have contributed to declines in Scoter populations because 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 result is that in Baynes Sound, B.C., a high fraction of mortalities 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 identification of predators and we were able to allocate relatively greater effort to retrieving transmitters that displayed mortality signals (burial in mustelid burrows greatly attenuated VHF signals). Moreover, variation in rates of Bald Eagle predation by region were probably not due to differences in Bald Eagle densities, which are greater in Alaska than in sites farther south (Fig. 1). Densities of mustelids by region were not available.

Predation risk for Scoters has received little attention probably 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 declines (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 protecting 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 priorities include assessments of whether predation risk influences Scoter habitat needs and whether specific human impacts have increased predation risk. For instance, even where predation rates are low, individual birds reduce predation risk by varying their movements and rates of foraging and vigilance (Rogers 1987; Ydenberg et al. 2007). Flexibility in regulating 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 species such as American mink and river otters that may be limited 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 Ruxton 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 species may have changed over recent decades with increasing

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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 piscivorours 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).

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