

## FORAGING BEHAVIORS OF SURF SCOTERS AND WHITE-WINGED SCOTERS DURING SPAWNING OF PACIFIC HERRING

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**Abstract.** Winter diets of Surf (*Melanitta perspicillata*) and White-winged Scoters (*M. fusca*) are composed primarily of bivalves. During spawning of Pacific herring (*Clupea pallasii*) in early spring, scoters shift their diets to herring eggs. Using radio-telemetry, we contrasted scoter foraging behaviors between winter and herring spawning periods. Scoters increased their dive durations during herring spawning, likely to maximize the amount of roe consumed per dive; in winter, dives were typically terminated upon clam capture. Scoters spent approximately 50% less time foraging (min underwater hr<sup>-1</sup>) and decreased their dive rate (dives hr<sup>-1</sup>) by 70% when feeding on roe. The observed reduction in time spent foraging was presumably caused by the abundance of herring eggs, and thus a reduction in prey search-time. Scoters were able to meet energetic requirements with reduced effort, despite potentially increased demands related to spring fattening. Less time spent foraging may also allow more time for pre-migratory courtship behaviors.

**Key words:** *Clupea pallasii*, herring spawn, *Melanitta fusca*, *Melanitta perspicillata*, sea duck, Surf Scoter, White-winged Scoter.

### Comportamientos de Forrajeo de *Melanitta perspicillata* y *M. fusca* Durante el Desove de *Clupea pallasii*

**Resumen.** Las dietas de invierno de los patos *Melanitta perspicillata* y *M. fusca* están compuestas principalmente por bivalvos. Durante el desove del arenque del Pacífico (*Clupea pallasii*) al inicio de la primavera, estas especies cambian su dieta y se alimentan de huevos de arenque. Utilizando radiotelemetría, contrastamos los comportamientos de forrajeo entre los períodos de invierno y de desove del arenque. Los patos incrementaron la duración de sus inmersiones durante el período de desove,

probablemente para maximizar la cantidad de huevos consumida por inmersión. En el invierno, las inmersiones típicamente terminaron una vez que las aves capturaron almejas. Los patos invirtieron cerca de un 50% menos de tiempo forrajeando (minutos bajo el agua por hora) y disminuyeron su tasa de buceo (inmersiones por hora) en un 70% cuando se alimentaron de huevos. Presumiblemente, la reducción en el tiempo de forrajeo observada fue causada por la abundancia de huevos de arenque, la cual condujo a una reducción en el tiempo de búsqueda de presas. Los patos fueron capaces de suplir sus requerimientos energéticos con un esfuerzo reducido, a pesar de que potencialmente existían mayores exigencias relacionadas con el engordamiento de primavera. Invertir menos tiempo en forrajear también podría permitir dedicar más tiempo a comportamientos de cortejo previos a la migración.

Along the Pacific coast of North America, many nearshore ecosystems receive seasonal pulses of food resources through the spawning of marine fishes. During spawning events, fish move from pelagic to coastal and estuarine environments, where they often aggregate in large numbers and deposit dense masses of eggs. While ephemeral, these spawning events provide a variety of coastal animals, including sea ducks, with a superabundant and predictable food resource in the form of both adult fish and roe deposits (Bishop and Green 2001, Marston et al. 2002, Sigler et al. 2004, Christie and Reimchen 2005).

Pacific herring (*Clupea pallasii*) spawn during late winter and early spring in intertidal and shallow subtidal waters (Haegle and Schweigert 1985). Roe is deposited on rocks and vegetation in large quantities, commonly reaching densities of 10<sup>6</sup> eggs m<sup>-2</sup> or 2–3 kg m<sup>-2</sup> of eggs (Haegle 1993). Herring roe is deposited during a period of 1–2 weeks, and eggs hatch 2–3 weeks later, providing predators with a brief period to utilize this abundant food resource. Sea ducks are known to congregate in large numbers at herring spawning sites to feed on the eggs; aggregations of over 10 000 individuals are common,

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and flocks exceeding 50 000 individuals have been reported (Haegle 1993, Sullivan et al. 2002).

While many studies have addressed distributional and dietary responses of sea ducks to herring spawn (Vermeer et al. 1997, Rodway and Cooke 2002, Sullivan et al. 2002, Rodway et al. 2003, Zydelski and Esler 2005), few have addressed potential shifts in foraging behaviors (Rodway and Cooke 2001). Foraging behaviors, such as the amount of time spent foraging or foraging rate, often reflect food availability and quality (Hutto 1990). When food becomes scarce, birds often increase the amount of time spent foraging to maintain sufficient levels of energy intake (Hutto 1990, McKnight 1998, Cope 2003). During the winter months, prior to the spawning of herring, sea ducks feed primarily on marine invertebrates, including mollusks and crustaceans (Stott and Olson 1973, Goudie and Ankney 1986). These invertebrate prey are typically much less abundant per unit area and more cryptic than herring roe. Hence, when feeding on superabundant herring roe, sea ducks may alter their foraging behaviors from those used when feeding on less abundant invertebrate prey.

Surf Scoters (*Melanitta perspicillata*) and White-winged Scoters (*M. fusca*) are the most numerous of many sea duck species that congregate at spawning sites of Pacific herring in the Strait of Georgia, British Columbia (Sullivan et al. 2002). Both scoter species begin their northward migration in mid-April–May (WSB, unpubl. data), shortly after the hatching of herring eggs in March–April. Using radio-telemetry, we documented foraging behaviors of Surf and White-winged Scoters in the Strait of Georgia during both the winter and herring spawn periods. By contrasting foraging behaviors during these two periods, we aim to increase our understanding of the importance of herring roe as a migratory food resource for scoters.

## METHODS

Our study occurred during the winters and springs of 2002–2003 and 2003–2004 and encompassed two core periods for scoters: the winter period and the herring spawn period. During the winter period, foraging behavior data were collected following scoter arrival at their wintering grounds until the commencement of herring spawning in March. Specifically, winter monitoring occurred from 20 December 2002 to 15 March 2003 and from 12 November 2003 to 5 March 2004. Foraging behaviors of scoters during the winter period were monitored exclusively in Baynes Sound, located in the Strait of Georgia, British Columbia. Baynes Sound is a 40 km long coastal channel fringed by a number of small, protected bays composed of gravel and sand sediments (Dawe et al. 1998). Surf and White-winged Scoters are abundant in Baynes Sound during winter: the average number ( $\pm$  SE) of scoters (both species combined) during this study was approximately  $6500 \pm 250$ . The diet of Surf and White-winged Scoters wintering in Baynes Sound is composed almost exclusively of Manila (*Venerupis philippinarum*) and varnish clams (*Nuttallia obscurata*), typically

>25 mm in length (Bourne 1984; Lewis et al., in press).

During the herring spawn period, monitoring of scoter foraging behaviors occurred from the commencement of herring roe deposition in March, at which point almost all scoters abandoned their typical overwinter habitats in Baynes Sound (WSB, unpubl. data), until radio-marked scoters could no longer be located at known herring spawning sites. Specifically, monitoring during the herring spawn period occurred from 17 March 2003 to 10 April 2003 and from 10 March 2004 to 25 March 2004. During this time, we shifted our study to areas near Baynes Sound that experienced herring spawning events. Specific sites included Lambert Channel, Qualicum Beach, Qualicum Bay, and Kye Bay, all of which have a history of being important herring spawning sites (Haegle 1993). Fecal samples from scoters captured during the herring spawn period confirm that their diet is composed entirely of herring roe (Rodway and Cooke 2002; DE, unpubl. data).

Foraging behaviors of scoters were quantified during both winter and herring spawn periods using radio-telemetry. Scoters were captured and fitted with radio-transmitters during December of 2002 and 2003, following procedures described by Lewis et al. (2005). The radio signal of each scoter was lost when the bird dived and resumed when it resurfaced, allowing us to document both the occurrence and duration of dives (Wanless and Harris 1991, Custer et al. 1996). Radio-signals were monitored using hand-held four-element Yagi antennas connected to Advanced Telemetry Systems (ATS; Isanti, Minnesota) R4000 receivers. We used 1 hr observation blocks to record the number of dives and length of each individual dive ( $\pm 1$  sec). Observation blocks of 1 hr duration were chosen based on preliminary sampling of dive activity, because of the high likelihood (>99%) of detecting diving. Foraging behaviors were monitored only during diurnal hours because scoters rarely foraged nocturnally in our study area (Lewis et al. 2005). Observations were spread approximately evenly across daylight hours and tide heights.

Visual observations of radio-marked scoters during the winter period confirmed the loss of radio-signals during dives and that radio-marked scoters were foraging exclusively by diving. During the herring spawn period, when many species of birds consume displaced herring roe at the surface (Haegle 1993), we performed focal observations on unmarked scoters to determine whether scoters were engaging in surface feeding behaviors that might not result in radio-signal loss. During 4 hr 40 min of observations on 213 individuals, no scoters were observed feeding on roe at the surface, indicating that scoters were feeding on herring roe exclusively by diving.

## STATISTICAL ANALYSES

We evaluated variation in foraging behaviors of scoters in relation to the following explanatory variables: sex, age (first-year versus adult), species (Surf versus White-winged Scoter), and season (winter versus herring spawn). We specifically addressed three distinct foraging behaviors: dive dura-

tion (sec), dive rate (dives  $\text{hr}^{-1}$ ), and time spent foraging (min underwater  $\text{hr}^{-1}$ ). Our primary interest was changes in scoter foraging behaviors during the herring spawn period and we present winter data mainly to provide a basis for assessing the relative magnitude of change (in-depth analyses of factors affecting foraging behaviors of scoters during the winter period can be found in Lewis [2005] and Lewis et al. [2005]). Therefore, we first tested for effects of age, sex, and species on variation in foraging behaviors using only data from the herring spawn period. We then tested for differences in foraging behaviors across seasons (winter versus herring spawn), accounting for any significant effects of sex, age, or species detected in previous analyses. ANOVAs were used to infer statistical significance of the various explanatory variables. To account for repeated measures on radio-marked individuals, we calculated mean values of each foraging behavior per scoter, based on all observations per individual per season, and used only these mean values in all ANOVAs.

We also tested for temporal changes in foraging behaviors during the herring spawn period, which could result from temporally declining amounts of herring roe due to predation and hatching. We used general linear mixed models to account for repeated measures on radio-marked individuals and to include subject as a random effect (Littell et al. 2000). We used spawning date as an explanatory variable, defined as number of days since commencement of herring roe deposition. Because herring spawning commenced on different dates in 2003 and 2004, spawning date allowed us to standardize our observation dates across years. We tested for effects of spawning date on each of the three foraging behaviors: dive duration, dive rate, and time spent foraging. All analyses were performed using SAS version 8.0 (SAS Institute 1999) and significance levels were set at  $\alpha = 0.05$ .

## RESULTS

For the winter period, we collected 280 hr of foraging behavior data for 29 Surf Scoters and 321 hr of data for 46 White-winged Scoters. For the herring spawn period, we collected 43 hr of foraging behavior data for 20 Surf Scoters and 48 hr of data for 25 White-winged Scoters. Overall, we found no effect of sex or age, but a slight effect of species on scoter foraging behaviors during herring spawning. For dive duration, there was no effect of sex ( $F_{1,41} = 0.3$ ,  $P = 0.60$ ) or age ( $F_{1,41} = 0.0$ ,  $P = 0.89$ ), but there was a significant species effect ( $F_{1,41} = 5.6$ ,  $P = 0.02$ ). Dives of White-winged Scoters during the herring spawn period averaged 5 sec longer than those of Surf Scoters (Fig. 1). For dive rate, there was no effect of sex ( $F_{1,42} = 0.3$ ,  $P = 0.59$ ), age ( $F_{1,42} = 0.7$ ,  $P = 0.39$ ), or species ( $F_{1,42} = 0.4$ ,  $P = 0.56$ ). Similarly, for amount of time spent foraging during herring spawning, there was no effect of sex ( $F_{1,42} = 0.0$ ,  $P = 0.97$ ), age ( $F_{1,42} = 0.0$ ,  $P = 0.85$ ), or species ( $F_{1,42} = 0.1$ ,  $P = 0.71$ ).

Because we detected a slight effect of species on foraging behaviors during herring spawning, we

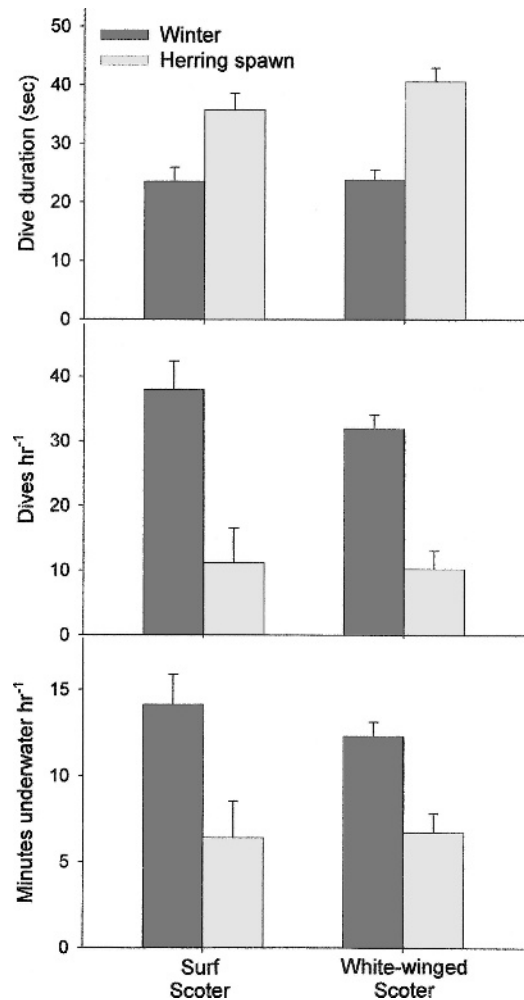


FIGURE 1. Radio-marked Surf Scoters and White-winged Scoters increased their dive duration (sec) and decreased their dive rate (dives  $\text{hr}^{-1}$ ) and time spent foraging (min underwater  $\text{hr}^{-1}$ ) during the herring spawn period, when their diets were composed exclusively of superabundant herring roe, versus during winter, when their diets were composed primarily of clams. All values are means  $\pm$  95% CI.

analyzed seasonal effects separately by species. During the herring spawn period, when scoters were feeding exclusively on herring roe, the duration of dives (sec) for both Surf Scoters ( $F_{1,47} = 43.7$ ,  $P < 0.001$ ) and White-winged Scoters ( $F_{1,69} = 127.6$ ,  $P < 0.001$ ) was significantly longer than during the winter period, when they were eating primarily clams (Fig. 1). Surf Scoters increased their dive duration by 52% and White-winged Scoters by 70%. Both Surf Scoters ( $F_{1,47} = 60.1$ ,  $P < 0.001$ ) and White-winged Scoters ( $F_{1,70} = 150.9$ ,  $P < 0.001$ ) had significantly lower dive rates (dives  $\text{hr}^{-1}$ ) during the herring spawn period (Fig. 1), reducing their dive rates by approx-

imately 70%. Finally, during the herring spawn period both Surf Scoters ( $F_{1,47} = 32.3$ ,  $P < 0.001$ ) and White-winged Scoters ( $F_{1,70} = 63.0$ ,  $P < 0.001$ ) spent less time foraging, measured as min underwater  $\text{hr}^{-1}$ , than during the winter period (Fig. 1). Expressed as a percentage, both scoter species spent 11% of their time underwater during the herring spawn period, versus winter averages of 23% for Surf Scoters and 21% for White-winged Scoters.

As with seasonal effects, we analyzed effects of spawning date separately by species. Spawning date was defined as the number of days since commencement of herring roe deposition. For White-winged Scoters, there was no significant effect of spawning date on dive duration ( $F_{1,20} = 4.0$ ,  $P = 0.06$ ), dive rate ( $F_{1,21} = 0.1$ ,  $P = 0.77$ ), or time spent foraging ( $F_{1,21} = 0.0$ ,  $P = 0.98$ ), indicating that White-winged Scoters did not temporally alter their foraging behaviors during the 2–3 week herring roe incubation period. However, for Surf Scoters, spawning date had a significant effect on dive duration ( $F_{1,17} = 4.5$ ,  $P = 0.05$ ), dive rate ( $F_{1,21} = 6.4$ ,  $P = 0.02$ ), and time spent foraging ( $F_{1,21} = 4.2$ ,  $P = 0.05$ ). Over the 2–3 week period of herring roe incubation, parameter estimates ( $\pm$  SE) indicated that Surf Scoters gradually decreased their dive duration ( $-0.35 \pm 0.17$  sec  $\text{day}^{-1}$ ), while increasing their dive rate ( $0.50 \pm 0.20$  dives  $\text{hr}^{-1} \text{day}^{-1}$ ) and time spent foraging ( $0.21 \pm 0.10$  min  $\text{hr}^{-1} \text{day}^{-1}$ ). For each foraging behavior, however, the temporal changes during the herring roe incubation period did not result in values at the end of incubation that approached winter values. Twenty-three days after spawn deposition, which was the latest spawning date for which foraging behavior data was available, we estimated that Surf Scoters dived for 30.0 sec, made 19.2 dives  $\text{hr}^{-1}$ , and spent 9.7 min underwater  $\text{hr}^{-1}$ , compared to winter averages of 23.5 sec dives, 37.9 dives  $\text{hr}^{-1}$ , and 14.1 min underwater  $\text{hr}^{-1}$ .

## DISCUSSION

We found significant changes in foraging behaviors of scoters during Pacific herring spawning, when their diet is composed exclusively of herring roe, compared to winter, when they consume primarily clams. When feeding on superabundant herring roe, Surf and White-winged Scoters reduced their average time spent foraging by 54% and 47%, respectively, relative to the winter period. Furthermore, time spent foraging increased slightly over the winter period from November to February (Lewis 2005), indicating that the reduced foraging effort during March spawning events was not merely a continuation of a temporal trend, but rather a distinct behavioral shift.

The extremely high quantity of herring roe presumably explains most of the observed reduction in foraging effort of scoters. When feeding on herring roe, scoters likely encountered abundant roe immediately upon reaching the benthos or associated vegetation, significantly reducing or even eliminating searching time for prey (Draulans 1982, Tome 1988, Richman and Lovvorn 2003). Decreased searching time would allow a greater proportion of each dive to

be used for roe consumption, thereby increasing the amount of food consumed per dive. In contrast, clam biomass is much lower per unit area and clams are cryptically buried in the substrate. Foraging for clams requires periods of searching and excavating in the benthos and many dives are terminated without successful clam capture (Lewis et al., in press). As a result, scoters likely consume less food per dive when feeding on clams and thus spend more time foraging to reach necessary energetic requirements or satiation.

In addition to higher availability, the energy content, size, digestibility, and gut retention time of herring roe may further contribute to observed reductions in time spent foraging. Herring roe has higher energy density than clams and most other invertebrate prey items (Juanes and Hartwick 1990, Bishop and Green 2001), thereby increasing the energetic gain per amount of food consumed. The small size of herring roe may also be advantageous by reducing time spent handling prey. Large clams, such as those commonly consumed in our study area (Bourne 1984; Lewis et al., in press), often require extended handling times to properly orient the clam for swallowing (Ydenberg 1988). Furthermore, when feeding on small prey items of high density such as herring roe, diving ducks have been observed using suction feeding, which considerably reduces handling time and increases profitability in comparison to nonsuction feeding on larger prey items (de Leeuw and van Eerden 1992). Finally, the amount of time and energy needed to process and digest herring roe may be considerably lower than for clams, which have long gut retention times relative to soft-bodied prey and require shell crushing in the gizzard (Richman and Lovvorn 2003, van Gills et al. 2003).

Scoters modified their overall dive strategy when feeding on herring roe, decreasing their dive rates by approximately 70% and increasing their dive durations by approximately 60%. As with time spent foraging, decreased dive rates during herring spawning are presumably due to the great abundance of herring roe, thereby requiring fewer dives to obtain sufficient amounts of food. Additionally, because dive descent is energetically expensive (de Leeuw 1996, Lovvorn and Gillingham 1996) and herring roe is only consumed underwater (TLL, pers. obs.), scoters may have minimized the costs of dive descent and maximized the amount of roe consumed per dive by making fewer dives of longer duration. In contrast, when feeding on large clams, dives are typically terminated upon capture of a single clam and clams are ingested at the surface to avoid extra costs of diving associated with extended clam handling times (Ydenberg 1988, de Leeuw and van Eerden 1992; Lewis et al., in press). As a result, dive durations were on average much shorter during the winter period of clam consumption.

Although not measured by our study, water depth can influence dive duration and time spent foraging by affecting the distances of descent and ascent during a dive. Relative to mean low water, the main species of clams consumed by scoters in Baynes Sound are found from 3 m to 1 m depth (Gillespie et

al. 2001), while the bulk of Pacific herring roe is found from 3 m to -5 m depth (Rooper et al. 1999). Consequently, our estimates of dive duration and time spent foraging during the herring spawn period may have been partially influenced by water depth. Free-diving Common Eiders (*Somateria mollissima*) typically travel 1.2 m s<sup>-1</sup> during descent and even faster during ascent (J. Heath, Simon Fraser University, pers. comm.). Assuming a similar dive velocity for similarly sized scoters, the 0–6 m greater depth of herring spawn would add 0–10 sec of transit time to a dive. Accordingly, the 12 sec (Surf Scoters) and 17 sec (White-winged Scoters) increases in average dive duration during herring spawning are likely attributable to both increased transit time and increased feeding time per dive. However, water depth does not influence our central conclusion that scoters reduced their time spent foraging during herring spawning. Had we accounted for differential transit times associated with water depth, our estimates of time spent foraging during the herring spawn period would have been even lower relative to winter due to the slightly greater depth of herring roe.

During the 2–3 week period of herring egg incubation, Surf Scoters gradually increased their foraging effort. This observation can be generally attributed to two nonexclusive hypotheses: (1) herring roe was temporally depleted to a degree that would affect Surf Scoter foraging effort through predation or hatching, or (2) Surf Scoters were gradually entering a state of hyperphagia, in which individuals increased their food intake to provide energy reserves for future use (Odum 1960). Had herring roe been depleted, concurrent temporal changes in foraging behaviors would also have been expected for White-winged Scoters, but none were observed. Consequently, Surf Scoters may have entered a state of hyperphagia, as has been observed for other birds prior to migration and breeding, including sea ducks (Guillemette 2001). Differences between scoter species may be attributable to species-specific strategies for energy accumulation and body mass regulation prior to migration and reproduction.

In addition to utilizing ephemerally abundant prey items that are predictably available, such as herring roe, sea ducks are also known to opportunistically forage on sudden, unpredictable aggregations of ephemerally abundant prey. Lacroix et al. (2005) documented a flock of approximately 5000 Surf Scoters, as well as smaller numbers of other sea duck species, feeding on large aggregations of polychaetes (*Ophryotrocha* sp.) in our study area of Baynes Sound, British Columbia. These polychaetes had not previously been documented as a food source of scoters and aggregations of sea ducks were not observed at the same site the following year (TLL, pers. obs.). Similarly, Frengen and Thingstad (2002) observed large flocks of sea ducks opportunistically foraging on mass aggregations of spawning sandeels (*Ammodytes* spp.) at sites not typically used as foraging grounds. The energetic advantages associated with reduced foraging effort, as demonstrated by our study, may explain the propensity of sea ducks

to congregate and forage on such mass aggregations, despite their spatial and temporal unpredictability.

The significantly reduced foraging effort of scoters, along with previously documented distributional and dietary responses of scoters and other sea ducks (Haegle 1993, Vermeer et al. 1997, Rodway and Cooke 2002, Sullivan et al. 2002, Žydelis and Esler 2005), highlights the importance of herring spawning events as an annual food resource for these species. Despite the decrease in foraging effort, the average mass of Surf and White-winged Scoters captured near spawning events in the Strait of Georgia did not decline (E. Anderson, University of Wyoming, unpubl. data). Accordingly, herring roe may be an important premigratory food resource for sea ducks by providing them the energetic flexibility to regulate time budgets and body reserves in preparation for ensuing migration. Furthermore, for sea duck species that form pairs prior to spring migration, the relaxation of foraging time demands during herring spawn may allow more time for important social behaviors such as courtship and pair formation (Rodway and Cooke 2001, Rodway et al. 2003).

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#### LITERATURE CITED

- BISHOP, M. A., AND S. P. GREEN. 2001. Predation of Pacific herring (*Clupea pallasii*) spawn by birds in Prince William Sound, Alaska. Fisheries Oceanography 10, Supplement 1:149–158.
- BOURNE, N. 1984. Clam predation by scoter ducks in the Strait of Georgia, British Columbia, Canada. Canadian Technical Report of Fisheries and Aquatic Science 1331.
- CHRISTIE, K. S., AND T. E. REIMCHEN. 2005. Post-reproductive salmon, *Oncorhynchus* spp., as a major nutrient source for large aggregations of gulls, *Larus* spp. Canadian Field-Naturalist 119:202–207.
- COPE, D. R. 2003. Variation in daily and seasonal foraging routines of non-breeding Barnacle Geese (*Branta leucopsis*): working harder does not overcome environmental constraints. Journal of Zoology 260:65–71.
- CUSTER, C. M., T. W. CUSTER, AND D. W. SPARKS. 1996. Radio telemetry documents 24-hour feeding activity of wintering Lesser Scaup. Wilson Bulletin 108:556–566.

- DAWE, N. K., R. BUECHERT, AND D. E. C. TRETHERWEY. 1998. Bird use of Baynes Sound–Comox Harbour, Vancouver Island, British Columbia, 1980–1981. Technical Report Series No. 286, Canadian Wildlife Service, Pacific and Yukon Region, British Columbia, Canada.
- DE LEEUW, J. J. 1996. Diving costs as a component of daily energy budgets of aquatic birds and mammals: generalizing the inclusion of dive-recovery costs demonstrated in Tufted Ducks. *Canadian Journal of Zoology* 74:2131–2142.
- DE LEEUW, J. J., AND M. R. VAN EERDEN. 1992. Size selection in diving Tufted Ducks *Aythya fuligula* explained by differential handling of small and large mussels *Dreissena polymorpha*. *Ardea* 80:353–362.
- DRAULANS, D. 1982. Foraging and size selection of mussels by the Tufted Duck, *Aythya fuligula*. *Journal of Animal Ecology* 51:943–956.
- FRENGEN, O., AND P. G. THINGSTAD. 2002. Mass occurrences of sandeels (*Ammodytes* spp.) causing aggregations of diving ducks. *Fauna Norvegica Series B* 22:32–36.
- GILLESPIE, G. E., B. RUSCH, S. J. GORMICAN, R. MARSHALL, AND D. MUNROE. 2001. Further investigations of the fisheries potential of the exotic varnish clam (*Nuttallia obscurata*) in British Columbia. Canadian Stock Assessment Secretariat Research Document 2001/143.
- GOUDIE, R. I., AND C. D. ANKNEY. 1986. Body size, activity budgets, and diets of sea ducks wintering in Newfoundland. *Ecology* 67:1475–1482.
- GUILLEMETTE, M. 2001. Foraging before spring migration and before breeding in Common Eiders: does hyperphagia occur? *Condor* 103:633–638.
- HAEGLE, C. W. 1993. Seabird predation of Pacific herring, *Clupea pallasii*, spawn in British Columbia. *Canadian Field-Naturalist* 107:73–82.
- HAEGLE, C. W., AND J. F. SCHWEIGERT. 1985. Distribution and characteristics of herring spawning grounds and description of spawning behaviour. *Canadian Journal of Fisheries and Aquatic Sciences* 42, Supplement 1:39–55.
- HUTTO, R. T. 1990. Measuring the availability of resources. *Studies in Avian Biology* 13:20–28.
- JUANES, F., AND E. B. HARTWICK. 1990. Prey size selection in Dungeness crabs: the effect of claw damage. *Ecology* 71:744–758.
- LACROIX, D. L., S. BOYD, D. ESLER, M. KIRK, T. LEWIS, AND S. LIPOVSKY. 2005. Surf Scoters *Melanitta perspicillata* aggregate in association with ephemerally abundant polychaetes. *Marine Ornithology* 33:61–63.
- LEWIS, T. L. 2005. Foraging behaviors and prey depletion by wintering scoters in Baynes Sound, British Columbia: inferring food availability and habitat quality. M.Sc. thesis, Simon Fraser University, Burnaby, British Columbia, Canada.
- LEWIS, T. L., D. ESLER, AND W. S. BOYD. In press. Effects of predation by sea ducks on clam abundance in soft-bottom intertidal habitats. *Marine Ecology Progress Series*.
- LEWIS, T. L., D. ESLER, W. S. BOYD, AND R. ZYDELIS. 2005. Nocturnal foraging behaviors of wintering Surf Scoters and White-winged Scoters. *Condor* 107:637–647.
- LITTELL, R. C., G. A. MILLIKEN, W. W. STROUP, AND R. D. WOLFINGER. 2000. SAS System for mixed models. 4th ed. SAS Institute, Inc., Cary, NC.
- LOVVORN, J. R., AND M. P. GILLINGHAM. 1996. Food dispersion and foraging energetics: a mechanistic synthesis for field studies of avian benthivores. *Ecology* 77:435–451.
- MARSTON, B. H., M. F. WILSON, AND S. M. GENDE. 2002. Predator aggregations during eulachon *Thaleichthys pacificus* spawning runs. *Marine Ecology Progress Series* 231:229–236.
- MCKNIGHT, S. K. 1998. Effects of food abundance and environmental parameters on foraging behaviour of Gadwalls and American Coots in winter. *Canadian Journal of Zoology* 76:1993–1998.
- ODUM, E. P. 1960. Premigratory hyperphagia in birds. *American Journal of Clinical Nutrition* 8:621–629.
- RICHMAN, S. E., AND J. R. LOVVORN. 2003. Effects of clam species dominance on nutrient and energy acquisition by Spectacled Eiders in the Bering Sea. *Marine Ecology Progress Series* 261:283–297.
- RODWAY, M. S., AND F. COOKE. 2001. Effect of food availability on arrival and departure decisions of Harlequin Ducks at diurnal feeding grounds. *Condor* 103:870–874.
- RODWAY, M. S., AND F. COOKE. 2002. Use of fecal analysis to determine seasonal changes in the diet of wintering Harlequin Ducks at a herring spawning site. *Journal of Field Ornithology* 73:363–371.
- RODWAY, M. S., H. M. REGEHR, J. ASHLEY, P. V. CLARKSON, R. I. GOUDIE, D. E. HAY, C. M. SMITH, AND K. G. WRIGHT. 2003. Aggregative response of Harlequin Ducks to herring spawning in the Strait of Georgia, British Columbia. *Canadian Journal of Zoology* 81:504–514.
- ROOPER, C. N., L. J. HALDORSON, AND T. J. QUINN II. 1999. Habitat factors controlling Pacific herring (*Clupea pallasii*) egg loss in Prince William Sound, Alaska. *Canadian Journal of Fisheries and Aquatic Sciences* 56:1133–1142.
- SAS INSTITUTE. 1999. SAS/STAT software, version 8.0. SAS Institute, Inc., Cary, NC.
- SIGLER, M. F., J. N. WOMBLE, AND J. J. VOLLENWEIDER. 2004. Availability to Steller sea lions (*Eumetopias jubatus*) of a seasonal prey resource: a prespawning aggregation of eulachon (*Thaleichthys pacificus*). *Canadian Journal of Fisheries and Aquatic Science* 61:1475–1484.
- STOTT, R. S., AND D. P. OLSON. 1973. Food-habitat relationship of sea ducks on the New Hampshire coastline. *Ecology* 54:996–1007.
- SULLIVAN, T. M., R. W. BUTLER, AND W. S. BOYD. 2002. Seasonal distribution of waterbirds in relation to spawning Pacific herring, *Clupea pallasii*, in the Strait of Georgia, British Columbia. *Canadian Field-Naturalist* 116:366–370.

- TOME, M. W. 1988. Optimal foraging: food patch depletion by Ruddy Ducks. *Oecologia* 76:27–36.
- VAN GILLS, J. A., T. PIERSMA, A. DEKINGA, AND M. W. DIETZ. 2003. Cost-benefit analysis of mollusc-eating in a shorebird II: optimizing gizzard size in the face of seasonal demands. *Journal of Experimental Biology* 206:3369–3380.
- VERMEER, K., M. BENTLEY, K. H. MORGAN, AND G. E. J. SMITH. 1997. Association of feeding flocks of Brant and sea ducks with herring spawn at Skidegate Inlet. Canadian Wildlife Service Occasional Paper 93:102–107.
- WANLESS, S., AND M. P. HARRIS. 1991. Diving patterns of full-grown and juvenile Rock Shags. *Condor* 93:44–48.
- YDENBERG, R. C. 1988. Foraging by diving birds. *Proceedings of the International Ornithological Congress* 19:1832–1842.
- ŽYDELIS, R., AND D. ESLER. 2005. Responses of wintering Steller's Eiders to herring spawn. *Waterbirds* 28:344–350.