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# REEVALUATING MARINE DIETS OF SURF AND WHITE-WINGED SCOTERS: INTERSPECIFIC DIFFERENCES AND THE IMPORTANCE OF SOFT-BODIED PREY

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*Abstract.* Past studies of the marine diets of Surf Scoters (*Melanitta perspicillata*) and White-winged Scoters (*M. fusca*) have reported that they eat mostly bivalves, but deviations from well-established methods by most studies suggest that the importance of soft-bodied prey has been underestimated for both species. Methods needed to reduce bias in diet estimates include collecting birds that are feeding, immediately preserving gut contents, excluding gizzard contents, averaging food-item percentages across birds versus pooling gut contents for all birds, and using energy or ash-free dry mass versus wet mass values of foods. For Surf Scoters collected in northern Puget Sound, Washington during 2005–2006, adherence to the latter three methods alone resulted in the assessed bivalve component of diet declining by over half and a near doubling of soft-bodied prey (i.e., crustaceans, polychaetes). Diets of Surf Scoters differed among three heavily used bays with distinct benthic habitats, yet 67%–86% of the ash-free dry mass of esophagus contents from each bay was nonbivalve prey. A synthesis of previous and new diet data revealed differences between scoter species: relative to White-winged Scoters, Surf Scoters consume smaller bivalves, a smaller and more variable percentage of mollusk prey (including bivalves and gastropods), and a declining percentage of bivalves as winter progresses. Past diet studies for scoters may provide misleading guidelines to conservation efforts by implying that only standing stocks of bivalves require consideration when prioritizing critical foraging sites.

*Key words:* *bivalves, diet,* Melanitta fusca, Melanitta perspicillata, *Puget Sound, Surf Scoter, White-winged Scoter.*

## Revaluación de las Dietas Marinas de *Melanitta perspicillata* y *M. fusca*: Diferencias Interespecíficas e Importancia de las Presas de Cuerpo Blando

*Resumen.* Los estudios anteriores de la dieta marina de *Melanitta perspicillata* y *M. fusca* mencionan que estas aves comen mayormente bivalvos, pero las desviaciones de los métodos bien establecidos en las que han incurrido la mayoría de los estudios sugiere que la importancia de las presas de cuerpo blando ha sido subestimada para ambas especies. Los métodos necesarios para un muestreo no sesgado de la dieta incluyen coleccionar aves que están forrajeando, preservar inmediatamente el contenido del tubo digestivo, excluir el contenido de la molleja, promediar el porcentaje de los ítems de alimentos entre las aves versus juntar los contenidos del tubo digestivo de todas las aves, y usar los valores de los alimentos de energía o de masa seca libre de cenizas de los alimentos versus su masa húmeda. Para los individuos de la especie *M. perspicillata* coleccionados en el norte de Puget Sound, Washington, durante 2005 y 2006, la aplicación de sólo los últimos tres métodos produjo una disminución de más de la mitad del componente de bivalvos de la dieta y casi una duplicación de las presas de cuerpo blando (i.e., crustáceos, poliquetos). Las dietas de *M. perspicillata* fueron diferentes entre tres bahías con ambientes bentónicos distintos que son usadas intensamente. A pesar de esto, entre el 67% y el 86% de la masa seca libre de cenizas del contenido del esófago de cada bahía no incluyó bivalvos. Una síntesis de los datos previos y nuevos de la dieta reveló diferencias entre las especies de *Melanitta*: en comparación con *M. fusca*, *M. perspicillata* consume bivalvos más pequeños, un porcentaje más pequeño y más variable de moluscos (incluyendo bivalvos y gasterópodos), y presenta una disminución en el porcentaje de bivalvos a medida que avanza el invierno. Al sugerir que sólo las concentraciones de bivalvos deben ser consideradas a la hora de seleccionar sitios críticos de forrajeo, los estudios anteriores de la dieta de estas especies de *Melanitta* podrían brindar lineamientos equivocados a los esfuerzos de conservación.

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## INTRODUCTION

The relative value of habitats to birds usually depends critically on diet (Goss-Custard et al. 2004, Stillman et al. 2005), which in turn affects productivity (Annett and Pierotti 1999) and survival (Oro and Furness 2002). Nondestructive methods of inferring diet are preferable to destructive methods, but are limited by our understanding of relevant physiological processes (Gannes et al. 1997) and are usually more valuable for distinguishing broad dietary patterns than for resolving finer taxonomic distinctions among foods (Kelly 2000).

Most winter and breeding surveys indicate that North American populations of scoters (*Melanitta* spp.) have declined by approximately 60% over the past 30–50 years (Hodges et al. 1996, Dickson and Gilchrist 2002, Nysewander et al. 2005). Scoters spend most of their annual cycle in marine habitats, and thus the quality of marine foods may affect overwinter survival or spring condition (Anteau and Afton 2004). Past studies of marine diets reported that scoters consume mainly bivalves (Bordage and Savard 1995, Brown and Fredrickson 1997, Savard et al. 1998), and efforts to identify and conserve marine habitats for scoters might accordingly focus on bivalve prey (Degraer et al. 1999). However, these studies used methods that likely underestimated the importance of soft-bodied prey.

Deviations from well-established protocols for estimating diet are especially prevalent in scoter studies, and the effects of such deviations have not been evaluated. In particular, most past studies may have biased results toward less digestible foods by collecting birds that have not fed recently (a common result of using decoys), failing to preserve foods within a reasonable amount of time after collection, and including gizzard contents in analyses (Swanson and Bartonek 1970). Also, these studies often pooled gut contents for all individuals into a single sample instead of averaging food-item percentages calculated for each bird (Swanson et al. 1974). Pooling gut contents can bias results toward foods that rarely occur in the diet but that are consumed in large quantities by relatively few birds. Finally, these studies typically measured the wet mass of foods, which may greatly distort relative energy values. For example, compared to bivalves including shells, crustaceans and polychaetes typically have 300% greater ash-free dry mass per unit wet mass (Ricciardi and Bourget 1998).

In this paper we: (1) present new diet data for scoters from Puget Sound, (2) use these new data to evaluate how methodological shortcomings may have altered key findings of past studies of the marine diets of scoters, and (3) review and synthesize results from these past diet studies of scoters. In these analyses, we contrast the diets of Surf (*M. perspicillata*) and White-winged Scoters (*M. fusca*), the two relatively common species of scoter on the Pacific Coast and the subjects of most past diet studies.

## METHODS

### STUDY AREA

We collected scoters in three bays with different benthic habitats in northern Puget Sound, Washington. Penn Cove (48°12′N, 122°42′W) is largely unvegetated, and mussels (*Mytilus trossulus*) are common in the intertidal zone. Intertidal substrates range from coarse sand to cobbles, and subtidal substrates are mainly fine sands. Padilla Bay (48°30′N, 122°30′W), which is mainly intertidal, contains one of the largest contiguous eelgrass (*Zostera* spp.) beds on the Pacific Coast of North America (Bulthuis 1995). Birch Bay (48°54′N, 122°48′W) also has an extensive intertidal zone, with eelgrass becoming increasingly prevalent at lower intertidal to subtidal elevations. Relative to Padilla Bay, however, standing stocks of eelgrass are lower in most areas of Birch Bay. Sediments throughout most of Padilla and Birch Bays are medium- to fine-grained sands (EMA, unpubl. data).

We conducted bimonthly surveys of scoters from shore with a 20–60× spotting scope from 2003–2006. Survey results indicated that numbers of Surf Scoters vary seasonally in all three bays, with typical winter maxima of 6000–10 000 each in Penn Cove and Padilla Bay, and 3000 in Birch Bay (EMA, unpubl. data). Padilla Bay also supports about 8000 Surf Scoters in summer. Only Birch Bay supports substantial numbers of White-winged Scoters, with about 1000 individuals from late fall through early spring.

### SCOTER COLLECTIONS

We collected scoters with shotguns from small boats under the authority of permits from the U.S. Fish and Wildlife Service (MB111993-0) and the Washington Department of Fish and Wildlife (05-608). Scoters were collected in August and December 2005, and in March 2006 (Table 1). Only Padilla Bay had substantial numbers of Surf Scoters during August, although very few were present there during December collections. To avoid partitioning our limited sample size among multiple sex and age classes, we collected only after-hatching-year males; for both species, this was the most common cohort throughout most of the year in these three sites (EMA, unpubl. data). We determined sex by the presence of a penis, and estimated age class by bursal depth (Mather and Esler 1999). We attempted to collect actively feeding individuals but did not require a minimum duration of feeding activity because this duration was not correlated with the quantity of esophageal contents for hundreds of Surf Scoters collected in San Francisco Bay, California (MTW, pers. obs.). All scoters were dissected within 1 hr of collection, and contents of the esophagi (including proventriculi) and gizzards were stored separately in 70% isopropyl alcohol.

### LABORATORY PROCEDURES

For each sample, esophagi and gizzard contents were rinsed separately over a 500-μm sieve. A dissecting scope (10×) was used to sort all food items to the lowest possible taxon (Kozloff 1996).

TABLE 1. After-hatching-year male scoters collected for diet analyses in northern Puget Sound, Washington, during three seasonal periods in 2005–2006.

| Site | 29 August 2005 | 10–14 December 2006 | 12–27 March 2006 |
|---|---|---|---|
| Penn Cove | none | 9 Surf Scoters | 10 Surf Scoters |
| Padilla Bay | 9 Surf Scoters | 3 Surf Scoters | 10 Surf Scoters |
| Birch Bay | none | 9 Surf Scoters and 9 White-winged Scoters | 10 Surf Scoters and 8 White-winged Scoters |

Barnacles (Cirripedia) were reported separately from other crustaceans and excluded from all statistical analyses because they are likely ingested incidentally or function mainly as grit (Cottam 1939, Vermeer and Bourne 1984). For all intact bivalves, we measured shell length (±1 mm) along the longest axis. For each food item, we measured (±0.001 g) wet mass, dry mass, and ash-free dry mass. Ash-free dry mass was estimated by drying representative samples of each taxon to constant mass at 60°C and then measuring loss of mass on ignition at 500°C for 8 hr (Ashkenas et al. 2004).

We determined percent frequency of occurrence and mean percent ash-free dry mass for esophageal foods. In this paper, *mean percent* entails calculating the relative percentage of each food category in each bird, and then averaging the percentages for each category across all birds. *Pooled percent* is the percentage of each food category in the sample of foods combined across all birds. Swanson et al. (1974) named these calculations aggregate percent mass and aggregate mass, respectively. Most individuals had greater numbers of food types in the gizzard than in the esophagus, so we also determined the percent frequency of occurrence for foods from the gizzard. Due to the bias of gizzard contents toward less digestible foods, these results should be used only as an indication of foods that scoters consume, rather than to exclude foods not consumed by scoters. We used the mean percent ash-free dry mass of esophagus contents to evaluate differences in major food categories of Surf Scoters among the three bays, and between Surf and White-winged Scoters collected in Birch Bay.

For Surf Scoters we collected in Puget Sound ($n = 59$ that contained esophagus + gizzard foods), we also analyzed our diet data in multiple ways to evaluate how deviations from acceptable protocols might affect results. In particular, we consider how the relative fractions of gut contents among major categories of foods change depending on how data are summarized (pooled percent versus mean percent), which digestive organs are considered (esophagus versus esophagus + gizzard), and how foods are measured (wet mass versus ash-free dry mass).

### SYNTHESIS OF PAST DIET STUDIES

We compiled results of marine diet studies in North America for Surf and White-winged Scoters. Across studies for each species, we calculated means for the percentage of gut contents comprised by major categories of foods. All past studies used wet mass or wet volume estimates of foods, which we combined because these measures are typically assumed to yield similar results. We did not summarize percent frequency of occurrence because this value was rarely available for major categories of foods. Results reported in a single paper, yet conducted at distinct times or locations, were treated as separate data points. We excluded one study in which diets were reported only anecdotally (Cleaver and Franett 1946) and one study in which the authors suggested that results were biased due to collection of scoters that had not recently fed (Guillemette et al. 1994). When a food type was not listed, we assumed it was not present in gut contents. We focused on gut contents consumed as food as opposed to incidentally consumed grit by removing barnacles and sediment from all diet estimates in past studies and recalculating wet mass or volume percentages for remaining gut contents. Authors specifically claimed that barnacles likely function as grit in the few studies in which the percentage of barnacles in esophagus + gizzard contents ranged from 9% to 40% (one study for Surf Scoters, four studies for White-winged Scoters; Vermeer 1981, Vermeer and Bourne 1984); barnacles comprised ≤3% of esophagus + gizzard contents in the remaining studies.

Across past studies and our new study, we also contrasted for Surf and White-winged Scoters the mean and maximum shell lengths of bivalves consumed, as well as seasonal changes in the percentage wet mass of bivalves in esophagi + gizzards. For the latter analysis, we considered only studies that were repeated in multiple seasons in the same area (i.e., within approximately 5 km), although seasonal sampling did not always occur in the same year.

### STATISTICAL ANALYSES

We conducted statistical analyses using JMP 5.0.1 (SAS Institute 2007), and all significance levels were set at $\alpha = 0.05$. All percentage data were arcsine–square root transformed before statistical tests (Sheskin 2007), but all means ± SE reported here are for back-transformed data. We used MANOVA to contrast diets expressed as percentages of major categories of foods in three separate analyses: (1) among our three collection sites in Puget Sound for Surf Scoters, (2) between Surf and White-winged Scoters we collected in Birch Bay, and (3) between Surf and White-winged Scoters for diet data compiled from past studies. Arcsine–square root transformations of data in all three analyses reduced but did not eliminate deviations from the assumptions of multivariate normality and equality of covariances (Box's $M$ test, all $P < 0.001$). However, MANOVA is generally robust to such deviations (Sheskin 2007). We included season as an additional factor in the diet analysis for the sample of Surf Scoters pooled across our three Puget Sound sites but did not analyze seasonal changes in diet within each Puget Sound site due to limited sample sizes. For each MANOVA analysis, we conducted post hoc tests on least-squares means of food categories using the Tukey HSD method of adjusting for multiple comparisons. All remaining analyses were of comparisons between two means, for which we used one-way ANOVA. We did not statistically compare the multiple methods used to calculate diets for the single sample of Surf Scoters we collected in Puget Sound because separate analyses were not based on independent samples, and because the pooled percent method of summarizing data provides no measures of variation.

## RESULTS

No individuals contained esophageal foods among Surf Scoters collected during August in Padilla Bay or among White-winged Scoters collected during March in Birch Bay (Table 2). The mean percent ash-free dry mass of scoter esophagus contents comprised by major food categories (bivalvia, gastropoda, crustacea, polychaeta, and echinodermata) in Puget Sound differed for Surf Scoters by location ($F_{10,40} = 2.7$, $P = 0.01$; Table 2) and season ($F_{5,19} = 5.8$, $P = 0.002$). Across locations, the only significant difference (Tukey HSD test, $P < 0.05$) in the mean percent ash-free dry mass of Surf Scoter esophagus contents was that the percentage of crustaceans was greater in Padilla Bay (56% ± 18%) relative to Penn Cove (8% ± 8%) and Birch Bay (2% ± 2%). Although the mean percent of polychaetes appeared greater in Birch Bay (55% ± 16%) and Penn Cove (46% ± 14%) than in Padilla Bay (3% ± 3%), the difference was not significant. Across seasons, the only significant difference (Tukey HSD test, $P < 0.05$) in the mean percent ash-free dry mass of Surf Scoter esophagus contents was that polychaetes declined from December (72% ± 12%) to March (13% ± 9%). The mean percent ash-free dry mass of esophagus contents differed for Surf and White-winged Scoters within Birch Bay ($F_{5,5} = 62.9$, $P < 0.001$), but the only significant difference in post hoc tests (Tukey HSD test, $P < 0.05$) was that the percentage of bivalves was greater for White-winged Scoters (98% ± 2%) than for Surf Scoters (14% ± 8%).

For Surf Scoters that we collected in Puget Sound, the assessed percentages of major categories of foods consumed were altered both by using the mean percent method of analyzing diet and by excluding gizzard contents (Fig. 1). Converting food measures from wet mass to ash-free dry mass had comparatively little effect on percentages of food categories. Following all three changes in protocol, the percentage of bivalves declined (55% to 23% ± 7%), while there were increases in gastropods (9% to 14% ± 6%), crustaceans (8% to 17% ± 7%), and polychaetes (23% to 39% ± 9%).

In our Puget Sound collections, Surf Scoters generally consumed smaller bivalves than did White-winged Scoters (Fig. 2A). The single exception to this pattern was the larger *Solen sicarius* bivalves found during the March collections in the esophagus + gizzard contents of two and three Surf Scoters in Padilla Bay and Birch Bay, respectively (25% of all Surf Scoters collected in these two bays in March). In this study and others, both the mean ($F_{1,8} = 12.6$, $P = 0.01$) and maximum ($F_{1,13} = 11.7$, $P = 0.01$) lengths of bivalves in esophagus + gizzard contents were smaller for Surf than for White-winged Scoters (excluding *S. sicarius* in this study; Fig. 2B).

Our synthesis of past studies indicated that average wet mass percentages of major food categories differed between Surf and White-winged Scoters (Table 3). Though diets were particularly variable among studies for Surf Scoters, post hoc analyses indicate that differences between scoter species result mainly from greater consumption by White-winged Scoters of gastropods (Tukey HSD test, $P < 0.05$) and of mollusks in general (i.e., gastropods and bivalves combined; $F_{1,34} = 4.7$, $P = 0.04$; Fig. 2C). In this study and others, the relative change in wet mass percentage of bivalves in esophagus + gizzard contents from fall or winter to subsequent seasons of the year differed between scoter species: the percentage typically increased slightly for White-winged Scoters (17% ± 18%) but declined for Surf Scoters (–34% ± 12%; $F_{1,12} = 5.5$, $P = 0.04$; Fig. 3).

## DISCUSSION

All past diet studies for Surf and White-winged Scoters deviated from protocols needed to reduce bias in diet estimates (Swanson and Bartonek 1970, Swanson et al. 1974). Acceptable methods include: (1) collecting birds that are feeding to reduce bias due to differences among foods in passage rates (Guillemette et al. 1994), (2) immediately preserving gut contents to avoid postmortem digestion, (3) excluding gizzard contents from analyses, (4) summarizing data using the mean percent versus pooled percent method, and (5) using energy or ash-free dry mass versus wet mass values of foods. Gut contents were chemically preserved in the field in about half of past diet studies for Surf and White-winged Scoters, yet few studies adhered to the remaining acceptable protocols (Table 4). For Surf Scoters we collected in northern Puget Sound, our results indicate that deviations from protocols 3–5 above can more than double estimates of the diet fraction comprised of bivalves. Our diet estimates do not incorporate costs of processing ingested shell matter and thus may still overestimate the value of bivalves relative to soft-bodied prey. Diet estimates for scoters we collected in Puget Sound should be viewed with caution due to the limited number of scoters at each site that contained foods in the esophagus, particularly for White-winged Scoters in Birch Bay. However, our synthesis of previous and new diet data revealed differences between the two species: relative to White-winged Scoters, Surf Scoters consume smaller bivalves, and their diets consist of

TABLE 2. Foods of Surf and White-winged Scoters collected in three bays in northern Puget Sound, Washington, in 2005–2006. Percent frequency of occurrence (%FO, for esophagus and gizzard contents separately) and mean percent ash-free dry mass (%AFDM) for foods comprising ≥1% AFDM of esophagus contents; a dash indicates that foods were not observed in the sample, and t (trace) indicates that foods were present but comprised <1% AFDM of esophagus contents. Results are for all birds combined across collection seasons, but numbers of birds that contained food in each season are given in parentheses (A = August, D = December, M = March).

| | Surf Scoter Penn Cove | | | Surf Scoter Padilla Bay | | | Surf Scoter Birch Bay | | | White-winged Scoter Birch Bay | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Esophagus (6D,7M) | | Gizzard (9D,10M) | Esophagus (1D,5M) | | Gizzard (8A,3D,10M) | Esophagus (5D,3M) | | Gizzard (9D,10M) | Esophagus (3D) | | Gizzard (9D,8M) |
| | %FO | %AFDM | %FO | %FO | %AFDM | %FO | %FO | %AFDM | %FO | %FO | %AFDM | %FO |
| Bivalvia | 46 | 33 | 84 | 17 | 17 | 52 | 88 | 14 | 100 | 100 | 98 | 100 |
| Nuculidae | — | — | — | — | — | — | 13 | 8 | 11 | — | — | 6 |
| *Acila castrensis* | — | — | — | — | — | — | — | — | 11 | — | — | — |
| *Nucula tenuis* | — | — | — | — | — | — | — | — | 5 | — | — | — |
| Unidentified Nuculidae | — | — | — | — | — | — | 13 | 8 | — | — | — | 6 |
| Nuculanidae | — | — | — | — | — | — | — | — | 5 | — | — | — |
| Mytilidae (*Mytilus trossulus*) | — | — | 16 | — | — | — | — | — | — | — | — | — |
| Thyasiridae | 39 | 19 | 5 | — | — | — | 13 | t | 5 | — | — | — |
| Montacutidae (*Mysella tumida*) | — | — | — | — | — | — | 13 | t | 5 | — | — | — |
| Cardiidae | — | — | — | — | — | — | 13 | t | 21 | — | — | — |
| *Clinocardium* sp. | — | — | — | — | — | — | — | — | 11 | — | — | — |
| Unidentified Cardiidae | — | — | — | — | — | — | — | — | 11 | — | — | — |
| Solenidae (*Solen sicarius*) | — | — | — | 17 | 17 | 10 | — | — | 16 | — | — | — |
| Tellinidae | — | — | — | — | — | — | 25 | 1 | 32 | — | — | 18 |
| *Tellina* sp. | — | — | — | — | — | — | 25 | 1 | — | — | — | — |
| *Macoma* sp. | — | — | — | — | — | — | 13 | t | 5 | — | — | 6 |
| Unidentified Tellinidae | — | — | — | — | — | — | — | — | 26 | — | — | 12 |
| Psammobiidae (*Nuttallia obscurata*) | — | — | — | — | — | — | 25 | 2 | 53 | 67 | 65 | 82 |
| Veneridae | — | — | 16 | — | — | 19 | 38 | 3 | 53 | 33 | 32 | 59 |
| *Tapes philippinarum* | — | — | — | — | — | — | 13 | 3 | 37 | 33 | 32 | 53 |
| Unidentified Veneridae | — | — | 16 | — | — | 19 | 25 | 1 | 16 | — | — | 6 |
| Myidae | — | — | — | — | — | — | — | — | — | 33 | 2 | — |
| Unidentified Bivalvia | 15 | 14 | 68 | — | — | 29 | 13 | t | 11 | — | — | 53 |
| Gastropoda | 31 | 13 | 79 | 50 | 22 | 67 | 38 | 5 | 37 | — | — | 12 |
| Trochidae | — | — | — | 17 | 1 | 33 | 13 | t | 11 | — | — | — |
| Lacunidae | — | — | — | — | — | 24 | — | — | — | — | — | — |
| Littorinidae | — | — | 5 | — | — | 5 | — | — | — | — | — | — |
| Muricidae | — | — | — | — | — | — | 13 | t | 5 | — | — | — |
| Columbellidae | 8 | 8 | 37 | 17 | 5 | 14 | 13 | 1 | 5 | — | — | 6 |
| Nassariidae | — | — | 11 | — | — | — | 13 | 1 | 5 | — | — | 6 |
| Pyramidellidae | 23 | 6 | 21 | 17 | t | 33 | 13 | t | 16 | — | — | — |
| *Turbonilla* sp. | — | — | — | — | — | — | — | — | 16 | — | — | — |
| *Odostomia* sp. | 23 | 6 | 21 | 17 | t | 33 | — | — | — | — | — | — |
| Unidentified Pyramidellidae | — | — | — | — | — | — | 13 | t | — | — | — | — |
| Unidentified Opisthobranchia | — | — | — | — | — | 5 | — | — | — | — | — | — |
| Unidentified Gastropoda | — | — | 47 | 17 | 17 | 24 | 13 | 3 | 21 | — | — | 6 |
| Crustacea (excluding Cirripedia) | 15 | 8 | 5 | 67 | 56 | 86 | 25 | 2 | 32 | 33 | 2 | 6 |
| Idoteidae | — | — | — | 33 | 28 | 24 | — | — | — | — | — | — |
| Caridea | 8 | t | — | — | — | — | — | — | 11 | — | — | — |
| Paguridae | — | — | — | 17 | t | — | — | — | — | — | — | — |
| Cancridae | — | — | — | 17 | 12 | 10 | — | — | — | — | — | — |
| Grapsidae | — | — | — | — | — | — | — | — | — | 33 | 2 | — |
| Pinnotheridae | 8 | 8 | 5 | 33 | 16 | 24 | 25 | 2 | 32 | — | — | — |
| *Scleroplax granulata* | — | — | — | — | — | — | 13 | t | 5 | — | — | — |
| *Pinnixa* sp. | 8 | 8 | — | 33 | 16 | 10 | 25 | 2 | 32 | — | — | — |
| Unidentified Pinnotheridae | — | — | 5 | — | — | 14 | — | — | — | — | — | — |
| Unidentified Brachyura | — | — | — | — | — | 48 | — | — | — | — | — | 6 |
| Cirripedia | — | — | 5 | — | — | — | — | — | — | — | — | — |
| Polychaeta | 46 | 46 | 74 | 17 | 3 | 14 | 75 | 55 | 42 | — | — | 6 |
| Echinodermata (Ophiuroidea) | — | — | 16 | 17 | 2 | 5 | 38 | 23 | 16 | — | — | — |
| Unidentified animal prey | — | — | — | — | — | — | 13 | t | — | — | — | — |

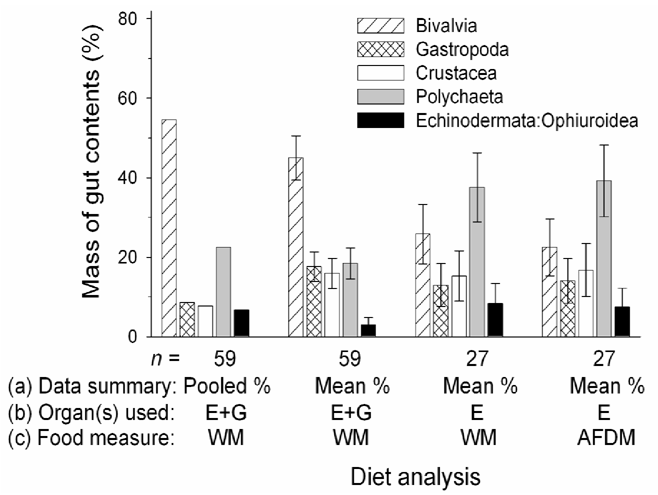

FIGURE 1. Contrast of results from four diet analyses for a single sample of Surf Scoters collected in Puget Sound, Washington, in 2005–2006 (scoters from all three bays combined). Values are means (± SE), except in the first analysis, for which error bars are lacking since foods were pooled into a single sample for all birds. Analyses differed based on: (a) how data were summarized (pooled %, mean %), (b) the organ(s) from which foods were considered (E = esophagus, G = gizzard), and (c) how foods were measured (WM = wet mass, AFDM = ash-free dry mass). The number of Surf Scoters (*n*) is lower for the last two analyses since birds containing foods in the esophagus are a subset of those containing foods in the esophagus + gizzard.

smaller and more variable percentages of mollusks (including bivalves and gastropods).

## DISTINCTIONS IN FORAGING STRATEGIES BETWEEN SURF AND WHITE-WINGED SCOTERS

To a much greater extent than White-winged Scoters, Surf Scoters aggregate in late winter and spring to consume spawn of Pacific Herring (*Clupea pallasi*; Bishop and Green 2001, Sullivan et al. 2002). Our study suggests that during this time of year, important foods for Surf Scoters may also include epifauna in eelgrass habitats (particularly crustaceans) and *S. sicarius* bivalves. Greater consumption of crustaceans by Surf Scoters in Padilla Bay versus our two other sites is likely related to the more extensive eelgrass habitat in Padilla Bay. Eelgrass typically supports a substantial biomass of epifaunal invertebrates, and seasonal changes in this biomass can be dramatic (Hemminga and Duarte 2000, Nakaoka et al. 2001). Further study is needed to evaluate the importance of eelgrass epifauna to the many thousands of Surf Scoters that stage in Padilla Bay in spring and summer. Surf Scoters may consume more *S. sicarius* as winter progresses if the slender morphology of these bivalves enables ingestion of larger sizes while preferred lengths of other bivalves decline (see below). Foraging costs of obtaining *S. sicarius*, which is mainly found in subtidal habitats (Kozloff 1996), will decline in spring as

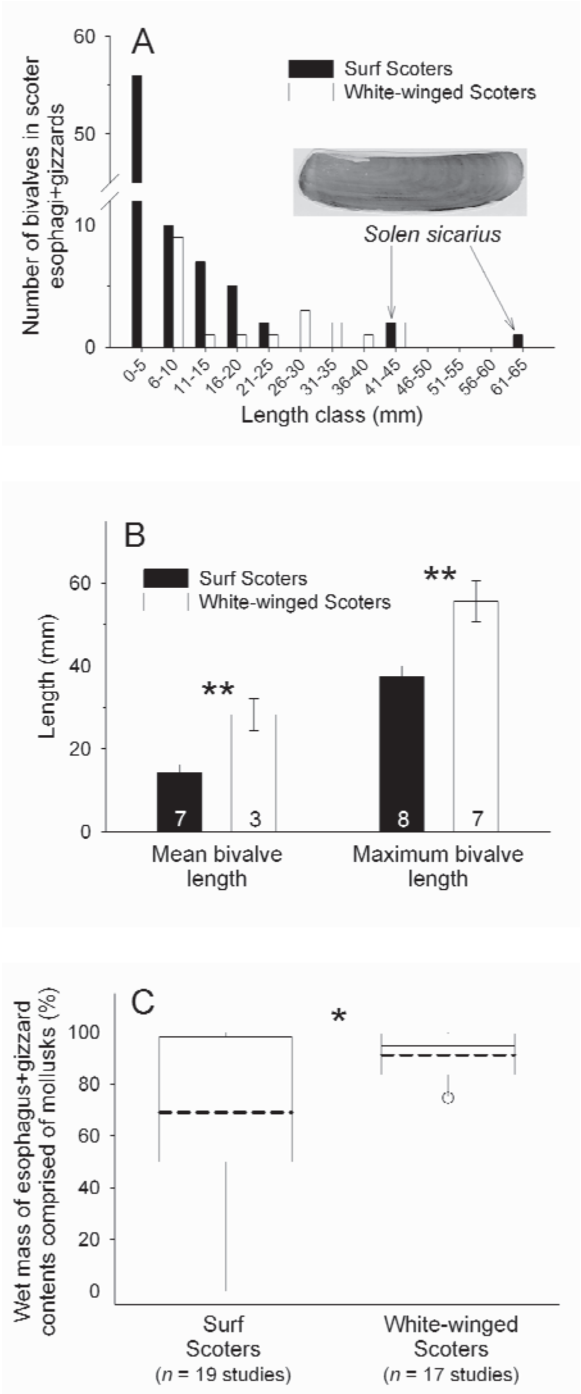

FIGURE 2. (A) Lengths of whole bivalves (*n* = 104) consumed by scoters collected in Puget Sound, Washington, in 2005–2006. (B) Averages (± SE) across this and past studies (number of studies within each bar) for the mean and maximum lengths of bivalves in esophagus + gizzard contents for Surf and White-winged Scoters. (C) Average percent of diet across this and past studies comprised of hard-bodied prey (mollusks) for Surf and White-winged Scoters. In (C), medians and means are represented by solid and dashed lines, respectively; boxes indicate the 25th and 75th percentiles, and whiskers the 10th and 90th percentiles (the circle is an outlier). $^{*}P < 0.05$, $^{**}P < 0.01$.

TABLE 3. Mean percentages of foods (least-squares means ± SE) and their ranges (in parentheses) across past studies of the gut contents (esophagus + gizzard in all but one study) of Surf and White-winged Scoters in marine habitats, including both wet mass and volume data. Diets differed overall between scoter species (one-way MANOVA, $F_{6,29} = 5.6$, $P < 0.001$), yet in post hoc tests, only the percentage of gastropods differed between scoter species (Tukey HSD test, $P < 0.05$).

| | Past diet studies for scoters[a] | |
|---|---|---|
| Taxon | Surf Scoters (*n* = 19 studies) | White-winged Scoters (*n* = 17 studies) |
| Bivalvia | 66 ± 8 (0–100) | 77 ± 4 (34–100) |
| Gastropoda | 3 ± 1 (0–15) | 14 ± 3 (0–40) |
| Crustacea | 3 ± 1 (0–26) | 6 ± 2 (0–24) |
| Polychaeta | 4 ± 3 (0–44) | <1 ± <1 (0–1) |
| Echinodermata | <1 ± <1 (0–4) | <1 ± <1 (0–3) |
| Herring spawn | 16 ± 8 (0–100) | 0 ± 0 (0–0) |

[a] Cottam (1939), Yocum and Keller (1961), McGilvrey (1967), Grosz and Yocum (1972), Stott and Olson (1973), Vermeer and Levings (1977), Hirsch (1980), Vermeer (1981), Sanger and Jones (1982), Bourne (1984), Vermeer and Bourne (1984), Reed et al. (1996), Mahaffy et al. (1997), Bishop and Green (2001), Lacroix (2001). Several references include more than one study.

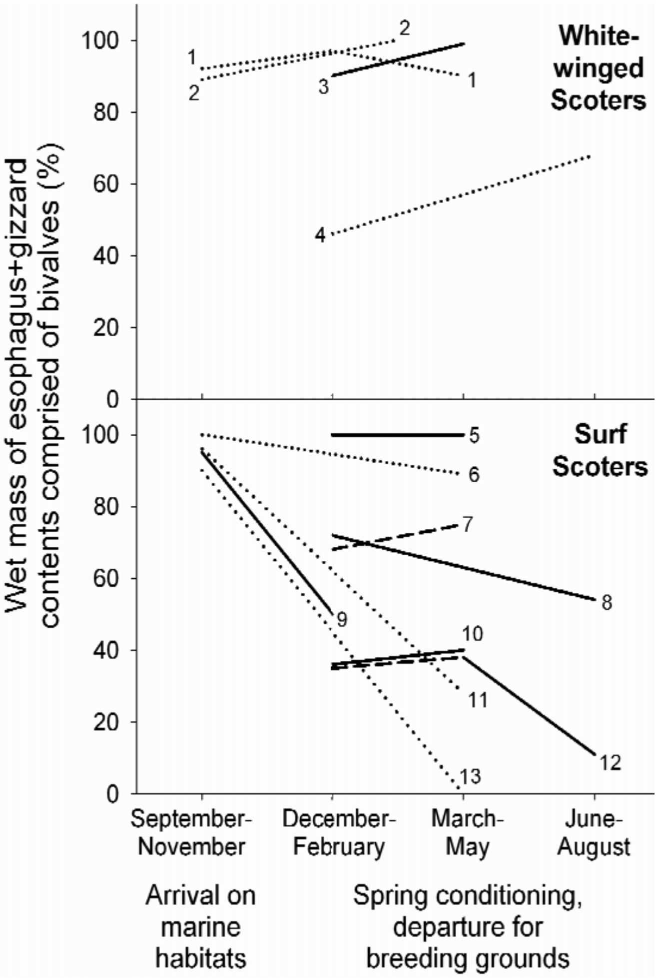

FIGURE 3. Seasonal trends in percent of esophagus + gizzard contents comprised of bivalves for scoters collected in Puget Sound, Washington, in 2005–2006 and in past studies. The dotted lines refer to trends in which seasonal samples were not collected in the same year. The two dashed lines for Surf Scoters represent seasonal trends for two of our Puget Sound sites that also show decline when multiple birds that consumed mainly *Solen sicarius* bivalves are omitted. Each line is numbered to clarify its source: [1,2,4]Vermeer and Bourne (1984), [3,7,10,12]this study, [5]Lacroix (2001), [6,11,13]Vermeer (1981), [8]Vermeer and Levings (1977), [9]Mahaffy et al. (1997). Only percent frequency of occurrence was available for Mahaffy et al. (1997).

Puget Sound experiences lower diurnal tides (scoters in this region feed mainly during daylight; Lewis et al. 2005).

Consumption of mollusks and alternative foods such as polychaetes and herring spawn is more variable across past studies for Surf Scoters than for White-winged Scoters. Differences among study protocols and habitats where collections were made probably affect results, yet this variability likely also results from greater diversity and seasonal changes in diet for Surf Scoters. In some cases, Surf Scoters display clear specialization on bivalves, particularly mussels (Vermeer 1981, Lacroix 2001). However, while specialization on bivalves appears seasonally stable for White-winged Scoters, diet patterns often change for Surf Scoters when they forage for prey at greater depths (*S. sicarius* bivalves) and for foods with seasonal availabilities that are either predictable (herring spawn, eelgrass epifauna) or unpredictable (commercial grain, reproducing polychaetes; Henny et al. 1991, Lacroix et al. 2005). Our diet estimates within Birch Bay indicate that Surf Scoters consume more nonbivalve prey than do White-winged Scoters. To determine reasons for these divergent foraging strategies between scoter species, future studies must integrate diet with seasonal movements, nutritional condition, and habitat-specific food availability.

For Surf Scoters, a seasonal decline in bivalve consumption accompanied by increased diet diversity may be influenced by at least three factors that are not mutually exclusive. First, the availability of preferred sizes of bivalves may decline over winter. Seasonal increases for Surf Scoters in the lengths of bivalves consumed (Lacroix 2001), consumption of smaller bivalves than those consumed by White-winged Scoters, and seasonal depletions of bivalves by scoters and other sea ducks (Hamilton 2000, Lewis et al. 2007a, Kirk et al. 2007) suggest that bivalves may become limiting. Second, seasonal declines in bivalve consumption may be related to increased availability of other foods that are suitable or even preferred. The value of foods will depend largely on the tradeoff between nutritional properties of prey (e.g., size, nutrient and energy content, assimilation efficiency) and factors that affect foraging effort (e.g., density, patch structure, burial depth, and mobility of prey). Consumption of seasonally abundant herring spawn greatly reduces foraging effort when

TABLE 4. Protocols used in past studies to estimate the diets of Surf and White-winged Scoters. Proportions are the number of past studies that used the acceptable protocol. See Table 3 for references to studies included in this analysis.

| Acceptable protocols | Surf Scoter studies[a] | White-winged Scoter studies[a] |
|---|---|---|
| Collected actively feeding birds | 7 of 24[b] | 0 of 19[b] |
| Chemically preserved gut contents in the field | 13 of 24 | 9 of 19[c] |
| Excluded gizzard contents from analyses | 1 of 24 | 0 of 19 |
| Summarized data using mean percent mass or volume | 0 of 24 | 0 of 19 |
| Converted gut contents to ash-free dry mass or energy values | 0 of 24 | 0 of 19 |

[a] When relevant information was not reported in a past study, we assumed that the study deviated from the acceptable protocol.

[b] The number of studies considered for each scoter species is greater than indicated in Table 3 because not all studies provided wet mass or volume data.

[c] Discrepancies among reported methods suggest that up to six of these nine studies may not have chemically preserved gut contents in the field (Vermeer and Levings [1977], Bourne [1984], Vermeer and Bourne [1984]).

demands of spring conditioning may be high (Lewis et al. 2007b). Whether motile epifauna and subtidal foods require greater foraging effort than intertidal bivalves likely depends on the relative density and patch structure of each of these food categories. Finally, Surf Scoters are smaller than White-winged Scoters (Vermeer and Bourne 1984) and thus have higher energy demands per unit body mass. If foraging time becomes limiting as winter progresses, energy demands may prevent Surf Scoters to a greater extent than White-winged Scoters from forgoing foods that are ordinarily less profitable than bivalves (Goudie and Ankney 1986).

Lack of evidence for seasonal declines in bivalve consumption for the Surf Scoters we collected in Puget Sound may indicate that this pattern does not occur in all locations or years. However, the lack of declines was at least partly due to increased consumption of *S. sicarius* bivalves in Padilla and Birch Bays during March, and unusually low consumption of mussels in Penn Cove during December (see below). Whether seasonal trends in bivalve consumption are reliable for past studies in which sampling periods did not occur in a single year depends on the degree to which prey availability is similar among years. In the three such studies for Surf Scoters (Vermeer 1981), seasonal declines in bivalve consumption are likely reliable because diet in each study consisted mainly of either mussels in early winter or herring spawn in late winter. Surf Scoters deplete acceptable sizes of mussels as winter progresses (Lacroix 2001, Kirk et al. 2007) and aggregate to consume predictable pulses of herring spawn in late winter and spring (Vermeer 1981). Sampling in different years may be less important for White-winged Scoters since consumption of bivalves in most studies appears to remain high and change little among seasons. However, more studies are needed to support this pattern for White-winged Scoters. More studies are also needed to clarify whether similar trends in seasonal bivalve consumption for both scoter species occur outside Puget Sound and the Strait of Georgia, British Columbia, the only region for which seasonal diets are available.

## EFFECTS OF PROTOCOL ON DIET ESTIMATES

Differences in diet composition between scoter species must be interpreted with caution because most past studies deviated from multiple acceptable protocols. However, this synthesis should reliably describe broad dietary patterns, including, for example, the greater likelihood for Surf Scoters versus White-winged Scoters to consume smaller bivalves and higher percentages of nonmollusk prey including herring spawn. Further, results of this synthesis are valuable in explaining why the current paradigm is that scoters consume mainly bivalves; our analyses indicate that this paradigm is likely inaccurate, particularly for Surf Scoters.

With the exception of the pooled percent method of analyzing diet, the deviations from acceptable protocols that we have discussed bias results against soft-bodied prey (Swanson and Bartonek 1970, Swanson et al. 1974). Although the pooled percent method can bias results against a food independent of its relative digestibility, use of this method in all past studies for scoters is unlikely to have biased results toward soft-bodied prey. Most importantly, all of these studies deviated from acceptable protocols before applying the pooled percent method to summarize gut contents; for Surf Scoters we collected in Puget Sound, inclusion of gizzard contents alone biased diet estimates heavily against soft-bodied prey. Based on frequency-of-occurrence results provided by many past studies, bias of diet estimates toward soft-bodied prey and away from bivalves is further unlikely, given that bivalves are not a rare food item for scoters (Swanson et al. 1974).

Surf Scoters in northern Puget Sound consumed slightly lower fractions of bivalves and higher fractions of polychaetes when similar methods are used to compare our data to results of past studies (i.e., first analysis in Fig. 1 versus Table 3). These differences likely resulted in part from our collection of mainly actively feeding birds (for which any soft-bodied prey was digested for less time than in birds that had not fed recently), and our preservation of gut contents soon after collections. Further, diets of Surf Scoters can vary by benthic habitat, and we may have selected bays in which soft-bodied prey is particularly important: the ash-free dry mass of Surf Scoter esophageal contents consisted of about 50% crustaceans in Padilla Bay and about 50% polychaetes in Penn Cove and Birch Bay. At least in early winter of many years, Surf Scoters in Penn Cove likely acquire a greater fraction of foods from extensive mussel beds than our results indicate (based on foraging observations and limited analyses of hunter-killed birds). Surf Scoter numbers were much lower in Penn Cove in 2005–2006 than in most winters (maxima of 1500 versus 6000–10 000), although the relationships between numbers of scoters, food availability, and diet are unclear.

Excluding gizzard contents probably changed our diet estimates for Surf Scoters partly because of a sampling effect. Specifically, birds with esophagus contents comprise only a subset of those containing either esophagus or gizzard contents. However, a priori, we expect birds containing foods only in the gizzard (i.e., those that have fed less recently) to contain smaller fractions of soft-bodied prey. Thus, an increase in the fraction of soft-bodied prey due to exclusion of such birds is both predictable and a more accurate representation of diet. Expressing diet in terms of wet mass versus ash-free dry mass had little effect for our Puget Sound data (i.e., third versus final analysis in Fig. 1). It is likely that this effect was small because most individual birds contained either mainly mollusk or mainly soft-bodied prey, and thus, average diets varied little when the mean percent method was used. As differences in ash-free dry mass or energy content increase among foods consumed by individual birds, use of these alternatives to wet mass values is increasingly necessary to avoid bias in diet estimates.

### CONSERVATION IMPLICATIONS

Past diet studies for scoters may provide misleading guidelines to conservation efforts by implying that only standing stocks of bivalves require consideration when prioritizing critical foraging sites. Eelgrass habitats, which are declining worldwide and often lack protections, support a much greater biomass of soft-bodied prey than occurs in unvegetated habitats that may be rich in bivalves (Short and Wyllie-Echeverria 1996, Hemminga and Duarte 2000). Our results suggest that past diet studies conducted over eelgrass beds likely underestimated the value of soft-bodied foods to scoters (Vermeer and Levings 1977, Hirsch 1980, Bourne 1984, Vermeer and Bourne 1984). These studies therefore inappropriately provide little justification for protecting eelgrass habitats such as Padilla Bay that lack both spawning herring and a high biomass of bivalves (EMA, unpubl. data).

Adherence to acceptable protocols for diet studies has likely increased in recent years for many species of waterfowl (Strand et al. 2008), but adequate descriptions of methods often are not provided and biased methods persist, sometimes due to logistical constraints. Studies that used biased methods can provide some useful information. However, conservation efforts should carefully evaluate diet assumptions, which for many species of waterfowl are often based on less recent studies that deviated from acceptable protocols and did not consider seasonal and area effects.

Populations have declined for 10 of the 15 species of North American sea ducks, yet available data for most sea duck species are not adequate to identify the causes of these declines (Sea Duck Joint Venture Management Board 2001). If population limitations exist for scoters in marine ecosystems, habitats that support critical foods should be identified and considered for protection. Areas that support foods of predictably high value such as herring spawn may be designated marine reserves or marine protected areas (Boersma et al. 2007). Marine management zones (e.g., time-area closures for hunting or shellfish harvest) may be more appropriate if locations of critical foods for scoters vary among years or seasons. As do many other marine birds, Surf Scoters appear to use a complex of habitats with varying food values, and thus effective conservation efforts may require a combination of marine reserves, protected areas, and management zones (Lovvorn and Baldwin 1996, Shepherd and Lank 2004).

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