marine predators predictably aggregate should reduce the risk of some impacts, such as overexploitation, by-catch, and contaminant exposure. However, to understand functional dependencies on foraging sites, we also need complementary data comparing foods in terms of their contributions to the physiological condition of predators.

During late winter and spring, many species of predators aggregate at spawning sites of the Pacific herring *Clupea pallasii*, which might be critical foraging areas (Høines & Bergstad 1999, Willson & Womble 2006). Although spawning adults and deposited eggs are seasonally preferred foods for many marine preda-

metry and aerial counts (Lok 2008). We used data collected by the Alaska Department of Fish and Game to determine the timing and locations of spawning events in SE Alaska (Davidson et al. 2005, 2006, Pritchett et al. 2007).

We contrasted scoter body mass among capture and collection periods. We then used fatty acid and stable isotope analyses of scoter tissues and foods to evaluate the influence of spawn consumption on body mass. Combined use of these 2 biomarker approaches adds

where $N_{\text{max-spawn}}$ is the maximum number of scoters observed during spawn availability and $N_{\text{pre-spawn}}$ is the average number observed during the 2 surveys prior to spawn availability. Surf scoters are 2 to 4 times more numerous than white-winged scoters in Puget Sound

whole blood of carnivorous gulls (Hobson & Clark 1992).

Plasma metabolite analyses. We analyzed concentrations of triglycerides in scoter blood plasma using spectrophotometric assays (Beckman DU-64 Spectrophotometer) and a Sigma Serum Triglyceride Determination Kit (Sigma TR0100). We report true triglyceride values, which we obtained by subtracting free glycerol from the total bound and unbound glycerol.

Data analyses. We conducted statistical analyses using JMP 5.0.1 (SAS 2002), set all significance levels at $\alpha = 0.05$, and report all means ($\pm$ SE). For each scoter species, we evaluated the relationship between each of the 2 measures of numerical response and characteristics of spawning events using multiple linear regression with backward selection (variables retained

Fig. 4. *Melanitta perspicillata*. Size-corrected body mass (least-squares means ± SE) of surf scoters from SE Vancouver Island, BC in 2002 to 2004 and SE Alaska in 2005 to 2006. Collections in SE Alaska during each year occurred at increasingly northern sites (Table 1). Conventions as in Fig. 3

the period of spawn availability in 2004 (Fig. 3; $F_{7,160}$ = 16.72, p < 0.001 for males; $F_{6,103}$ = 8.89, p < 0.001 for females). For surf scoters in BC, body mass of males declined from December to February in one study year (2002/2003); otherwise, there was no clear change in body mass of either sex through winter and early spring migration when spawn was available (Fig. 4). Mean body mass of surf scoters increased and reached highest values during migration in SE Alaska, in areas both with and without availability of spawn (Fig. 4; $F_{13,272}$ = 31.46, p < 0.001 for males; $F_{12,102}$ = 11.23, p < 0.001 for females).

Scores from the first principal component (PC1) of the 12 fatty acids examined (Table 2) distinguished spawn from bivalve samples (Fig. 5a; $F_{1,7}$ = 175.71, p < 0.001). Mean values among locations of $\delta^{15}N$ were greater for spawn than for classes of non-predatory ($F_{1,26}$ = 272.56, p < 0.001) and predatory invertebrates ($F_{1,12}$ = 34.19, p < 0.001), although values overlapped for spawn and predatory invertebrates (Fig. 5b). Thus, PC1 of the 12 fatty acids and $\delta^{15}N$ of scoter tissues should be positively correlated with spawn consumption, because predatory invertebrates comprise a minor component of scoter diets (Anderson et al. 2008) and provided that fatty acid and stable isotope signatures do not vary greatly among scoters before spawn consumption (see 'Discussion').

For male and female white-winged scoters in BC, PC1 of 12 fatty acids in their adipose and $\delta^{15}N$ of their blood cells were both positively related to body mass (Table 3, Fig. 6). For male surf scoters in BC, body mass was positively related to PC1 in 2003 (but not in 2004) and weakly related to $\delta^{15}N$ based on the relatively large sample of scoters from all periods in 2004 (Table 3, Fig. 7). For the 3 periods of spawn availability in BC during 2004, $\delta^{15}N$ and body mass for male surf scoters
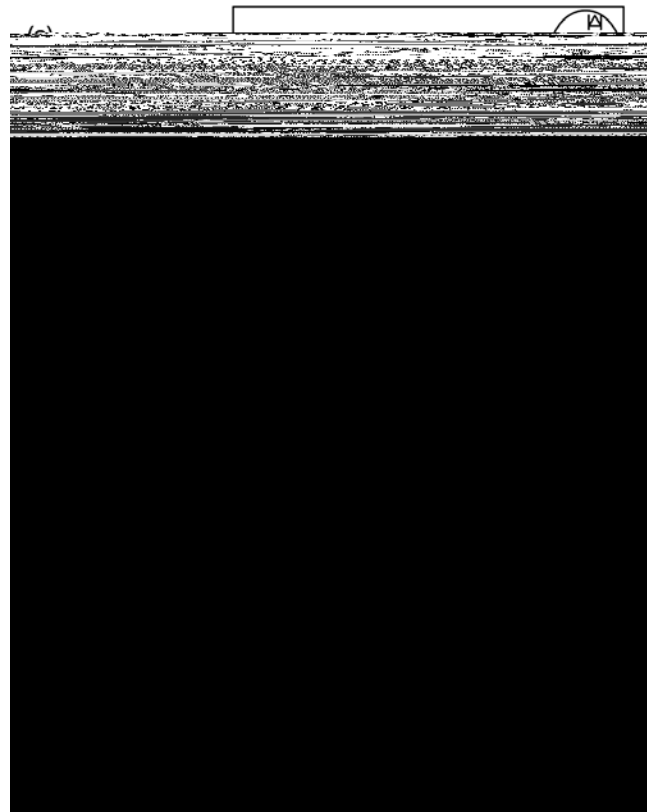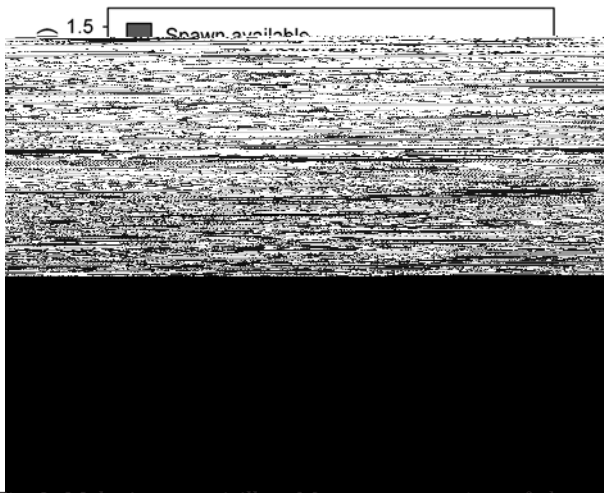
Fig. 9. *Melanitta perspicillata*. Mean concentrations of plasma triglycerides (±SE) for surf scoters collected in SE Alaska during spring migration in 2005 and 2006 (numbers in bars are sample sizes). Means associated with different letters differed significantly (Tukey's HSD test, p < 0.05), and collections during each year occurred at increasingly northern sites (Table 1)

for differences in local abundances of these species, surf scoters still showed a 4-fold greater numerical response than white-winged scoters to the biomass of spawning herring. Telemetry studies near our capture sites on Vancouver Island, BC, indicated that surf scoters also traveled longer mean distances to spawning areas (17 km) than did white-winged scoters (10 km; Lok et al. 2008).

The numerical response of white-winged scoters to spawning events in Puget Sound decreased slightly with later dates of spawn initiation. This pattern suggests that spawn does not increase in importance for white-winged scoters during migration. Conversely, the increasing numerical response of surf scoters to spawning events later in spring is likely due to aggregations of migrants from farther south (Lok et al. 2008). We observed < 3000 surf scoters at each spawning area in Washington from mid-January to mid-April. However, far greater aggregations occur at spawning events later during spring migration (late April to May), particularly for those in SE Alaska, where numbers of surf scoters may exceed 75 000 at a single spawning area (Lok 2008). Such aggregations, together with the large number of herring spawning areas along the Pacific coast, suggest that a substantial fraction of surf scoters consume spawn each year.

Most spawning events in Puget Sound occurred between January and March, a period before spring migration, when scoters move to spawning sites that are relatively close to their winter foraging areas (mostly < 30 km; Lok et al. 2008). For spawning events later in spring migration, when surf scoters are more

mobile (Lok 2008), their numerical response may increase with spawning duration because of continuing arrival of migrants from more southerly wintering grounds. The extent of spawn along shorelines did not affect the numerical response of scoters, possibly because scoter foraging profitability may be influenced by spawn density more than extent — spawn density was unrelated to shoreline extent of spawn and often varied within a spawning area (K. C. Stick unpubl. data).

Effects of spawn consumption on scoter condition

Based on correlations between body mass and biomarkers of diet, both scoter species gained mass while consuming spawn during late winter and early spring in BC. Male white-winged scoters gained mass during this period even at non-spawn sites, suggesting that spawn is not a uniquely important food to them. In contrast, surf scoters may depend strongly on spawn in years when body reserves have declined over winter — in 2003, but not 2004, body mass in males declined between December and February, and subsequent mass gains were correlated with biomarkers of spawn consumption. However, this correlation weakened throughout the period of spawn availability, until there was no correlation during late spring migration in BC and SE Alaska. This decreased correlation probably did not result from decreased spawn consumption because both feeding behaviour and fecal contents suggest that the birds were mainly eating spawn (D. Esler unpubl. data). Rather, the decreased correlation of body mass with spawn biomarkers likely reflected the greater diversity of migration histories among the much higher numbers of surf scoters attracted to spawning sites.

For surf scoters, continued influx to spawning sites from many distant wintering areas should increasingly obscure relationships between body mass and spawn consumption. Body mass will differ among birds within a site during migration, owing to varying quality of feeding opportunities encountered earlier in migration and the extent of reserve-depleting movements (Arzel et al. 2006, Newton 2006). Also, tissue fatty acids and stable isotopes typically vary among birds from different foraging areas and regions (Hobson 1999, Iverson et al. 2007, Wang et al. 2007). Increased variation in diet biomarkers among individual surf scoters in late winter and spring could also be related to increases in the diversity of food items they consume as winter progresses (Anderson et al. 2008). For white-winged scoters, the lower numerical response to spawn and greater seasonal stability in diet reduce these complications.

For white-winged scoters captured during the later period at the non-spawn site, values of δ^{15}N in their blood cells indicate that they probably had not eaten appreciable amounts of spawn at other areas in BC or Washington. (The δ^{15}N of blood cells integrates diet over a period of several weeks to months; Hobson 1999.) Thus, for male white-winged scoters, similar increase in body mass at both the non-spawn site (5.8%) and spawn sites (5.2%) indicates that their mass gains did not depend on spawn consumption. For female white-winged scoters, body mass increased at spawn sites but not at the non-spawn site, suggesting that spawn was important to mass gains. For surf scoters, δ^{15}N of blood cells and their greater numerical response to spawn suggest that captures at both spawn and non-spawn sites included birds from other wintering areas that may have consumed spawn before their arrival. Thus, comparisons of body mass at spawn versus non-spawn sites are not appropriate for assessing whether reserves of surf scoters increased independently of spawn consumption. Also, results from the non-spawn site should be viewed with caution given that this site had limited sample sizes, was from a single wintering area, and did not provide data on body mass changes throughout spring migration.

For surf scoters, mean body mass and plasma triglyceride levels increased during late spring migration in SE Alaska. Given the similarity of mass gains at sites with spawn in 2005 and sites lacking spawn in 2006 (Fig. 4), these increases probably did not result from differences in spawn availability among our capture and collection sites. During each year of our sampling, the biomass of spawning herring was about 30 000 t near our capture sites in BC, <1100 t in Behm Canal near Ketchikan, <350 t in Berner's Bay near Juneau, and 0 t in Chilkoot Inlet near Haines (Davidson et al.

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