

## Use of fecal analysis to determine seasonal changes in the diet of wintering Harlequin Ducks at a herring spawning site

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**ABSTRACT.** Few data are available on seasonal changes in winter diet of Harlequin Ducks (*Histrionicus histrionicus*), especially in relation to their use of Pacific herring (*Clupea pallasii*) spawn. We used fecal analyses to determine seasonal changes in Harlequin Duck winter diet at a site where Pacific herring spawn. We measured frequency of occurrence and relative abundance by volume of prey remains in 202 fecal samples collected during four date periods in 1998 and 1999. These two measures were highly correlated. We identified snails, crabs, limpets, and chitons as the principal animal prey, and ranked relative importance of most prey types in similar order as previous studies using stomach analyses. Crabs parts constituted the majority of prey remains during molt, and we concluded that crabs were dominant in the diet during molt because crabs generally have greater organic content and less hard-part remains per unit of body mass than other hard-shelled prey consumed at that time. Snail remains were highest in frequency of occurrence during winter. Herring eggs were not detected in feces until a week after herring spawned, but abrupt changes in other prey types indicated that herring eggs were the principal prey throughout the spawn period. Polychaetes increased in importance in winter and spring, and rated third in frequency of occurrence in spring. We recommend using fecal analyses to determine frequency of occurrence of prey in the diet of other sea-ducks that are known to feed on hard-shelled molluscs and crustaceans. Measures of relative abundance of prey remains can be useful if conversion factors relating hard-part remains to whole-body biomass are available.

**SINOPSIS.** Uso de análisis fecal en detectar cambios estacionales en la dieta de *Histrionicus histrionicus* invernando en un área de desove de *Clupea pallasii*

Existen pocos datos sobre los cambios estacionales en la dieta de *Histrionicus histrionicus*, en especial en relación al uso de huevos de *Clupea pallasii*. Usamos análisis fecales para detectar cambios estacionales en la dieta invernal de *Histrionicus histrionicus* donde *Clupea pallasii* desova. Medimos la frecuencia en ocurrir y la abundancia relativa por volumen de presas en 202 muestras fecales tomadas en cuatro períodos en 1998 y 1999. Estas dos medidas correlacionaron altamente. Identificamos gasterópodos, decápodos, cirrípedos y polioplacóforos como los principales alimentos animales, y colocamos la mayoría de los tipos de presas en rangos de importancia relativa en un orden similar al de estudios previos que usaron análisis estomacales. Las piezas de decápodos fueron la mayoría de los residuos de presa durante la muda, y concluimos que estos dominaban en la dieta durante la muda porque generalmente tienen mayor contenido orgánico y menos remanentes de partes duras por unidad de masa corporal que otras presas de cubierta dura comida en ese tiempo. Los residuos de gasterópodos ocurrieron más frecuentemente durante el invierno. No se detectaron los huevos de *Clupea pallasii* en las heces fecales hasta una semana posterior al desove de esta especie, pero los cambios abruptos en otros tipos de presas indican que los huevos de esta especie fueron la presa principal a través del período de desove. Los poliquetos fueron importantes en invierno y primavera, siendo terceros en frecuencia de consumo en primavera. Recomendamos el uso de análisis fecales para determinar la frecuencia de ocurrencia de presas en la dieta de otros anátidos marinos que se sabe se alimentan en moluscos y crustáceos de cubierta dura. Las medidas de abundancia relativa de residuos de presa pueden ser útiles si se dispone de los factores de conversión relacionando remanentes duros a la biomasa total de las presas.

*Key words:* diet, fecal analysis, Harlequin Duck, *Histrionicus histrionicus*, herring spawn, seasonal change

Harlequin Ducks (*Histrionicus histrionicus*) are sea-ducks (Mergini) inhabiting nearshore marine waters of the north Pacific and north Atlantic (Robertson and Goudie 1999). Populations are considered endangered in eastern

North America and, along with populations of other sea-duck species, are of special concern in western North America (Goudie et al. 1994). Burgeoning human activity, shoreline development, rapid expansion of aquaculture industries in the nearshore habitat used for foraging, and potential impacts of invasive species such as the green crab (*Carcinus maenas*) present management challenges and make it important to un-

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derstand habitat use and diet requirements. Seasonal changes in diet are important to investigate because of differences in nutritional requirements during annual events such as molt, migration, and reproduction (Hohman et al. 1992).

Detecting seasonal changes requires large sample sizes, making lethal methods of diet analysis unattractive. Although absolute measures of diet composition are sometimes difficult to obtain without sacrificing some individuals to procure stomach samples, such methods need careful justification, and are inappropriate for small or endangered populations. Also, public acceptance increasingly requires stringent rationale for sacrificing animals for scientific knowledge.

Fecal analysis provides a non-intrusive method that is commonly used to investigate diet of mammal and many bird species (Tigar and Osborne 2000). Such analysis can accurately determine frequency of occurrence of prey types and diet diversity if there are identifiable, undigested remains of all prey types. Accurate measures of diet composition are less feasible because of differences in digestibility and hardpart remains of various prey, although correction factors can sometimes be applied (Owen 1975; Tigar and Osborne 2000). Fecal analysis is an accepted method for diet studies of herbivorous waterfowl and can provide quantitative measures of diet composition of these species because throughput times of vegetative matter are relatively consistent across the taxa consumed (Owen 1975; Krapu and Reinecke 1992). This is not so for animal prey, and the method has rarely been used for carnivorous or omnivorous species (Wakelin 1993; Veltman et al. 1995; Rodway 1998).

Previous studies using stomach analyses indicate that winter prey of Harlequin Ducks are mainly intertidal and subtidal crustaceans and mollusks (Cottam 1939; Vermeer 1983; Goudie and Ankney 1986; Gaines and Fitzner 1987; Fischer and Griffin 2000). Fish eggs can be important when they are available (Munro and Clemens 1931; Vermeer 1983; Dzinbal and Jarvis 1984; Haegele and Schweigert 1989). All major prey except fish eggs have identifiable hard parts that are voided in the feces. Fecal analysis thus may be an effective method for diet studies in most cases.

Winter diet varies seasonally in the Aleutian

Islands, Alaska (Fischer and Griffin 2000), but there is little information on how the diet may vary in other areas (Vermeer 1983), and no information on variation during molt or at sites where Pacific herring (*Clupea pallasii*) spawn. Herring eggs are an ephemerally superabundant prey available to waterbirds for three to four weeks in late winter-early spring at spawning sites in the northeastern Pacific (Haegele 1993). Harlequin Ducks are known to aggregate at herring spawning sites and have been observed feeding on herring eggs (Munro and Clemens 1931; Bayer 1980; Haegele and Schweigert 1989; Haegele 1993; Vermeer et al. 1997).

Our objective was to determine seasonal changes in Harlequin Duck winter diet at a site where Pacific herring spawn. Concern for the birds, public interest in the Harlequin Duck in the study area, and the large sample size required to detect seasonal changes, precluded collecting specimens for stomach analyses. We investigated diet using fecal analysis, discuss the limitations of the method, and compare our results with those of previous studies that used stomach analyses.

## METHODS

The study was conducted on Hornby Island (49°33'N 124°40'W) in the Strait of Georgia, British Columbia, during the winters of 1998 and 1999. The area is a molting and wintering site for several hundred Harlequin Ducks and an important spawning site for Pacific herring. We compared diet during four date periods: molt (August–September), winter (November–February), herring spawn (three-week interval after herring spawn was first deposited in the study area, which occurred on 11 March in 1998 and 5 March in 1999), and spring (April). Timing of spawning was determined by visual inspection; shoreline waters turn milky when spawn is released.

During molt, feces were collected on seven different occasions from birds that had been captured in drive traps for banding purposes. Individuals often defecated when being handled and feces could be collected from known, banded individuals in those cases. Only one sample was collected from each bird. In winter, spawn, and spring, feces were scraped from tidal rocks where Harlequin Ducks hauled out. Collections were made opportunistically throughout these

date periods. Feces were only collected from roosts where Harlequin Ducks had been observed immediately prior to collection and where no other species had been roosting at that time. Care was taken not to contaminate the sample when scraping it off the substrate.

Collected feces were dried or frozen until they could be analyzed. Feces were mixed and carefully rinsed with water to separate prey fragments, which were then examined under a stereoscopic microscope. Prey remains were identified with reference to mollusk and crustacean shell specimens collected at Hornby Island where Harlequin Ducks were feeding, and to Griffith (1967), Ricketts et al. (1968), Kozloff (1983), and Elner et al. (1985). Identification was made to the lowest taxonomic level possible based on unique indicator fragments. More general prey categories, to which all types of prey fragments could be dependably assigned, were used for quantitative analyses (see Table 2). Percent occurrence for each prey category was defined as the percentage of fecal samples in which that particular prey type occurred.

A modified points index (Hyslop 1980; Williams 1981) was developed to estimate relative proportions of different prey types in each fecal sample. Relative abundance by volume was visually estimated and scored: 1 (<1%), 2 (1–10%), 3 (10–50%), 4 (50–90%), or 5 (>90%). Proportion of grit in the sample was scored relative to the volume of total remains, and animal and plant remains were scored relative to total remains minus grit. Fragments of unknown type were rare, formed a tiny proportion of the total, and were ignored.

Likelihood ratio ( $G$ ) tests were used to analyze differences in frequency of occurrence. Differences in relative abundance scores were analyzed using Kruskal-Wallis tests followed by Mann-Whitney  $U$ -tests for pairwise comparisons and Bonferroni adjustments for the number of pairwise comparisons. Number of prey types per sample was compared among seasons with ANOVA and Tukey post-hoc tests. Tolerance for Type I error was set at 5%. Means  $\pm$  SD are given.

## RESULTS

Species of snails were the most easily identified prey in Harlequin Duck feces (Table 1). Entire shells of small individuals (1–5 mm)

Table 1. Prey types identified from remains found in Harlequin Duck feces ( $n = 202$ ) at Hornby Island, British Columbia, 1998–1999. The number of fecal samples in which a prey type was identified is given in parentheses.

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Bryozoan (2)
Polychaete
<i>Nereis</i> spp. (22)
Polynoidae (5)
Chiton
<i>Mopalia</i> spp. (13)
<i>Tonicella lineata</i> (39)
Snail
<i>Amphissa columbiana</i> (14)
<i>Bittium attenuatum</i> (22)
<i>Calliostoma ligatum</i> (9)
<i>Cypraeolina pyriformis</i> (4)
<i>Eulima rutila</i> (1)
<i>Lacuna variagata</i> (13)
<i>Lirularia lirulata</i> (9)
<i>Littorina scutulata</i> (61)
<i>L. sitkana</i> (15)
<i>Margarites helicinus</i> (1)
<i>Mitrella gausapata</i> (2)
<i>Nassarius mendicus</i> (3)
<i>Nucella emarginata</i> (4)
Limpet
<i>Notoacmaea scutum</i> (12)
<i>N. persona</i> (8)
<i>Collisella pelta</i> (19)
Mussel
<i>Mytilus edulis</i> (26)
Urchin
<i>Strongylocentrotus</i> spp. (12)
Barnacle
<i>Balanus</i> spp. (49)
Isopod (3)
Amphipod (26)
Crab
<i>Cancer</i> spp. (7)
<i>Haplogaster mertensii</i> (1)
<i>Hemigrapsus nudus</i> (31)
<i>Lophopanopeus bellus</i> (4)
<i>Pagurus</i> spp. (21)
Fish
<i>Clupea pallasii</i> (eggs) (43)
Algae
<i>Corallina</i> spp. (3)
<i>Fucus</i> spp. (3)
<i>Ulva</i> spp. (14)
Eelgrass
Zosteraceae (2)

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Table 2. Percent occurrence of prey remains in Harlequin Duck feces during four seasons at Hornby Island, British Columbia, 1998–1999. "Spawn" was defined as a three-week period after herring spawn was first deposited in early March.

Prey	Season (number of samples)				
	Molt (25)	Winter (33)	Spawn (61)	Spring (83)	Total (202)
Bryozoan	0.0	3.0	1.6	0.0	1.0
Polychaete	0.0	21.2	0.0	43.4	21.3
Chiton	0.0	72.7	11.5	37.3	30.7
Snail	72.0	97.0	54.1	65.1	67.8
Limpet	68.0	75.8	8.2	28.9	35.1
Mussel	8.0	12.1	11.5	15.7	12.9
Urchin	0.0	12.1	1.6	8.4	5.9
Barnacle	4.0	18.2	31.1	27.7	24.3
Isopod	4.0	0.0	1.6	1.2	1.5
Amphipod	0.0	12.1	6.6	21.7	12.9
Crab	96.0	78.8	13.1	43.4	46.5
Fish	4.0	3.0	0.0	0.0	1.0
Herring eggs	0.0	0.0	31.1	28.9	21.3
Algae	4.0	75.8	98.4	92.8	80.7
Grit	12.0	54.5	73.8	90.4	69.8

were frequently present and readily identified. With practice, fragments of larger shells could also be identified to species. Numerous operculi were present in many samples, indicating that the snails were an important food source and that their shells were not merely the temporary abodes of hermit crabs. *Littorina scutulata* was the most frequently identified species (Table 1). Except for minute (1–2 mm) individuals, limpet shells were always fragmented and only larger fragments could be identified to species. Jaws of nereid and polynoid polychaetes, fragments of mussel, barnacle, and urchin shells, and small plate fragments of the distinctively patterned chiton *Tonicella lineata* were unmistakable. Crabs could be identified to species when claws or peripods were present, but often only comminuted shell remained. Undigested herring eggs and portions of egg membranes were easily recognized when present.

Snails and crabs were the most frequently occurring animal prey in fecal samples (Table 2). Limpets, chitons, barnacles, polychaetes, and herring eggs each occurred in more than 20% of samples. Significant seasonal differences in frequency of occurrence were found for polychaetes, chitons, snails, limpets, barnacles, amphipods, crabs, herring eggs, algae, and grit (Ta-

ble 2;  $G$  tests,  $P < 0.05$ ). Algae was recorded in more than 80% of feces and was uncommon only during molt. Percent occurrence of snails remained high in all seasons, and was highest in the winter when they occurred in almost all samples. Percent occurrence of crabs was highest during molt and lowest during spawn. Chitons, polychaetes, and amphipods were important only in winter and spring. Algae, snails, barnacles, and herring eggs were the most frequent remains recorded during the spawn period. Grit occurred in most samples with increasing frequency through the winter.

Among the major prey types, percent occurrence was greater for crabs than snails ( $G_1 = 5.9$ ,  $P = 0.015$ ) and limpets ( $G_1 = 7.3$ ,  $P = 0.007$ ) during molt (Table 2). During winter, percent occurrence was higher for snails than crabs ( $G_1 = 5.7$ ,  $P = 0.017$ ), limpets ( $G_1 = 7.1$ ,  $P = 0.008$ ), and chitons ( $G_1 = 8.5$ ,  $P = 0.004$ ), and higher for chitons than polychaetes ( $G_1 = 18.5$ ,  $P < 0.001$ ). During the spawning period, percent occurrence was higher for algae than all other prey types ( $P < 0.001$ ), higher for snails than spawn and barnacles ( $G_1 = 6.6$ ,  $P = 0.010$  for both comparisons), and higher for spawn than crabs ( $G_1 = 5.9$ ,  $P = 0.015$ ). In spring, percent occurrence was higher for algae than all other prey types ( $P < 0.001$ ), higher for snails than all other types except algae ( $P < 0.005$ ), and not significantly different among crabs, polychaetes, chitons, limpets, spawn, and barnacles ( $P > 0.05$ ).

Mean relative abundance scores for prey remains were highly correlated with percent occurrence ( $r = 0.94$ ,  $P < 0.001$ ), and seasonal differences in relative abundance scores matched differences in percent occurrence. Mean relative abundance scores were  $4.0 \pm 1.4$ ,  $1.8 \pm 1.7$ , and  $1.6 \pm 1.2$  for crabs, limpets, and snails, respectively, during molt;  $2.8 \pm 1.3$ ,  $2.3 \pm 1.7$ ,  $2.0 \pm 1.7$ ,  $1.8 \pm 1.2$ , and  $1.5 \pm 0.9$  for snails, algae, chitons, crabs, and limpets, respectively, during winter;  $4.4 \pm 1.1$  for algae during spawn;  $3.1 \pm 1.6$ ,  $1.5 \pm 1.3$ , and  $1.1 \pm 1.4$  for algae, snails, and crab, respectively, during spring; and  $< 1.0$  for all other prey types in each season. Pairwise comparisons between main prey types within each season showed the same significant differences in relative abundance scores (Kruskal-Wallis tests, followed Mann-Whitney pairwise comparisons, all  $P <$

0.05) as we found for comparisons of percent occurrence above.

Number of prey types per sample ranged from one to nine, and was lower during molt ( $2.6 \pm 0.7$ ) and spawn ( $2.7 \pm 1.5$ ) than during winter ( $4.8 \pm 1.3$ ) and spring ( $4.2 \pm 1.8$ ;  $F_{3,198} = 21.6$ ,  $P < 0.001$ ; Tukey pairwise comparisons, all  $P < 0.001$ ). Numbers of species in the diet were greater than these estimates because multiple species were subsumed within most prey type categories.

Herring eggs were not detected in feces until about a week after spawning first occurred (Fig. 1). Herring eggs formed the greatest proportion of fecal remains during the second 10-d interval after spawning, when they occurred in 67% of samples, declined thereafter, and were still present, and last recorded, 32 d after spawning. Algae made up most of the remains during the first 10 d of spawn and decreased afterwards. Remains of all other prey types made up a small proportion of the fecal samples during the first 20 d after spawn, and then increased in abundance.

#### DISCUSSION

Most prey identified in Harlequin Duck feces have been found in stomach samples in previous studies. Types not formerly reported in the diet include Polynoidae, snails *Amphissa columbiana*, *Bittium attenuatum*, *Cypraeolina pyriformis*, and *Eulima rutila*, crabs *Haplogaster mertensii* and *Lophopanopeus bellus*, coralline algae, and eelgrass. Eelgrass, along with *Fucus* and a variety of unidentified algae, were detected in fecal samples only during spawn and likely were incidentally ingested by birds feeding on herring eggs, which are mainly deposited on eelgrass and *Fucus* (Haegele and Schweigert 1985). *Eulima rutila* and *Cypraeolina pyriformis* are tiny and also may have been taken incidentally, although more frequent snail species were often as small. *Eulima* spp. are often commensal or parasitic on echinoderms, polychaetes, or other animals, and *Cypraeolina pyriformis* may occur on the backs of larger shells (Griffith 1967).

Algae has not been reported (Kurichi and Yamada 1984; Goudie and Ankney 1986; Gaines and Fitzner 1987; Patten et al. 1998) or has been found with low frequency and considered an incidental item in the diet (Cottam 1939; Palmer 1976; Fischer and Griffin 2000; Rob-

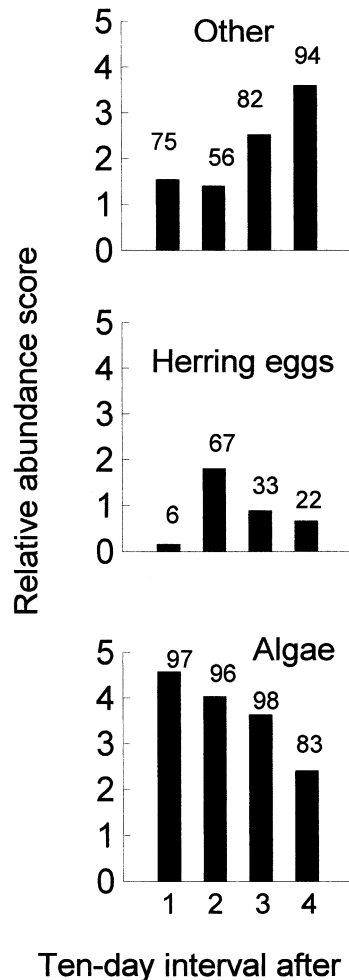


Fig. 1. Changes in relative abundance of algae, herring eggs, and all other animal prey type remains found in Harlequin Duck feces over 10-d intervals after herring first spawned on Hornby Island, British Columbia, 1998–1999. Percent occurrence of each prey category per 10-d period is given above each bar.

ertson and Goudie 1999) in most previous studies of Harlequin Ducks. The high percent occurrence and relative abundance of algae throughout the winter and spring in this study suggest that it may have provided some nutrition and was not solely incidental. Polychaetes also have been a minor and infrequent prey type in previous studies (Cottam 1939; Gudmundsson 1971; Goudie and Ankney 1986; Patten et al. 1998; Fischer and Griffin 2000). They occurred in 43% of the samples taken in spring in this study and were the third most

frequent prey type at that time. Barnacles rarely have been reported in diet studies of Harlequin Ducks (Cottam 1939; Vermeer 1983). They occurred in 24% of samples in this study, most frequently during herring spawn and spring.

Previous diet studies using stomach analyses conducted in the Strait of Georgia (Vermeer 1983) and Puget Sound, Washington (Gaines and Fitzner 1987) also identified snails, limpets, crabs, and chitons as the dominant winter prey, and ranked most prey types in similar order to our study. Most differences among the three studies seem to reflect real differences in the diet. Algae and amphipods were more frequent in this study than in Vermeer's, and were not mentioned in Gaines and Fitzner (1987). Polychaetes were also frequent in this study and not mentioned in either of the other two. Shrimp were the only prey type reported in the other two studies and not identified in this study. Soft-bodied crustaceans, including shrimp, are quickly broken down beyond recognition in a bird's stomach (Cottam 1939), and thus may not be easily detected in fecal samples. However, shrimp may not have occurred in the diet during this study, because amphipods and isopods are also soft-bodied and were identified by exoskeleton remains.

Herring eggs were visible in feces, but not until the second week after spawning and generally in small quantities. We suspect that herring eggs were the principal prey of most if not all Harlequin Ducks for the first three weeks after spawning occurred. This conclusion is based on the concomitant decrease in other types of animal prey and the increase in the proportion of algal remains, direct observations of birds feeding on eggs, and observed changes in foraging behavior from predominantly diving to dabbling (M. Rodway, unpubl. data). If true, this suggests that digestion of herring eggs is complete for the first week of egg development and is less complete as eggs age or weather. Egg mortality and desiccation can be high in the intertidal zone (Grosse and Hay 1988) where Harlequin Ducks feed, and the increase in undigested egg remains we found in fecal samples may relate to the increase in dead or desiccated eggs over the spawn period. An unlikely, alternative explanation is that birds switch to feeding predominantly on algae when herring spawn. Fecal analysis thus failed accurately to quantify the use and relative impor-

tance of herring eggs in the diet, although abrupt changes in percent occurrence and relative abundance of other prey types at that time were indicative of a shift to feeding on herring spawn.

Crabs generally have greater organic content and less hard-part remains per unit of body mass than hard-shelled univalves and bivalves (Guillemette et al. 1992). Thus, we can be confident that the high relative abundance of crab remains during molt indicates absolute dominance in the diet at that time. Specialized diet during molt has been reported for Greylag Geese (*Anser anser*; Fox et al. 1998), but not for other waterfowl species (Hohman et al. 1992; Combs and Fredrickson 1996; Thompson and Drobney 1997). Whether Harlequin Ducks were selecting crabs specifically during molt, or whether crabs were the preferred food generally and changes in their relative abundance in the diet through the winter were due to depletion or decreased availability relative to other prey is unknown. Number of different prey types in fecal samples decreased when herring eggs were available and increased again when their availability declined. Similarly, greater numbers of prey types during winter than molt could indicate decreased availability of crabs during winter.

Throughout the winter, Harlequin Ducks depend on access to productive inter-tidal habitats for foraging. The importance in the diet of crabs during molt and herring eggs in the spring pre-migration period indicates specific needs for access to habitats with high crab productivity and to sites where herring spawn. Displacement of birds or degradation of habitat quality by continually increasing human activity requires monitoring and mitigation. Spatial and temporal contraction of herring spawning (Hay and McCarter 1999) is also a concern because it may be limiting access to herring eggs for birds that winter distant from extant spawning locations. Potential impacts of the northward-spreading green crab (McDonald et al. 2001) on native species used by Harlequin Ducks warrant investigation.

We did not collect birds in this study and were unable to determine the relationships between diet measures obtained from fecal samples and those from stomach samples. Comparisons with studies conducted in similar geographical areas suggest that our fecal analyses

provided similar quantitative estimates of diet as stomach analyses. Percent occurrence measures from fecal analyses were likely accurate for all taxa that have dependably identifiable hard parts, even if the proportion is small, such as for polychaetes. We undoubtedly underestimated percent occurrence in the diet for herring eggs that have no hard part remains. However, differential digestion and mastication can also reduce the accuracy of quantitative measures from stomach analyses (Hyslop 1980; Williams 1981), and analyses of stomach samples may also underestimate the importance of herring eggs.

We recommend using fecal analyses to determine percent occurrence of prey in the diet of other sea-ducks such as eiders (*Somateria* spp.), scoters (*Melanitta* spp.), and goldeneye (*Bucephala* spp.) that are known to feed on hard-shelled molluscs and crustaceans (Cottam 1939). The method also may be useful for diet investigations of piscivorous species, but experimental work using captive birds is required to determine how otoliths and other identifiable fish remains pass through the digestive tract (Duffy and Jackson 1986). Fecal analysis has been successfully used to determine freshwater invertebrate prey of breeding Harlequin Ducks and other river specialists (Wakelin 1993; Veltman et al. 1995; Rodway 1998), and could be used for other species feeding on such prey. Collecting fecal samples from other sea-ducks would likely require capturing the birds because they rarely roost on shoreline rocks like Harlequin Ducks. Capturing birds has the advantage that samples can be obtained from known individuals, making sex and age comparisons possible.

We also measured relative abundance of prey remains in feces. This measure cannot be used to estimate diet composition without experimental work to calibrate fecal remains to whole body biomass of prey because of differences among prey types in the ratio of hard to soft parts. We were able to use our relative abundance scores to conclude that crabs were the most important prey type during molt only because we had information from other studies on the ratio of hard to soft parts in crabs and hard-shelled molluscs. Additional data calibrating the ratio of hard to soft parts in the variety of prey used by diving waterfowl would allow conversions of relative abundance of prey re-

mains in feces into estimates of diet composition that could be compared among locations and species.

Appropriate methods for diet studies will depend on objectives and the kind of diet information required. Non-lethal methods can likely provide most information required for management purposes. Observations to identify foraging habitats and handled prey, stable isotope analysis (SIA; Hobson et al. 1994), and stomach pumping are possible alternate or complementary methods to fecal analysis for diet studies of diving waterfowl. Fecal analysis has advantages of being inexpensive compared to SIA and of providing more detailed data on prey types than either SIA or behavioral observations. The shortcomings of fecal analysis are that it cannot provide quantitative estimates of diet composition unless conversion factors are available, and it cannot measure percent occurrence for prey types that have no identifiable parts that are voided in the feces. Stomach pumping has been a successful method for seabird species (Duffy and Jackson 1986), but to date has not been proven effective, and warrants more experimentation, for waterfowl.

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