

## SIZE-SELECTIVE PREDATION OF BLUE MUSSELS (*MYTILUS EDULIS*) BY COMMON EIDERS (*SOMATERIA MOLLISSIMA*) UNDER CONTROLLED FIELD CONDITIONS

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**ABSTRACT.**—We studied size-selective predation by Common Eiders (*Somateria mollissima*) feeding on blue mussels (*Mytilus edulis*). Selection varied with location, season, and prey availability, and for the most part ducks preferred smaller mussels than those that would have been the most energetically profitable on a per prey basis. We tested predictions from two related hypotheses concerning optimal prey selection: (1) the shell-mass minimization hypothesis, which states that predators select food that minimizes shell ingestion, as opposed to maximizing energy intake per prey item; and (2) the risk-averse foraging hypothesis, which, assuming large prey are not preferred (because of high shell content, low energy value, or some other reason), states that predators feed on smaller prey when the risk of mistakenly taking large prey increases. We found support for both hypotheses, although the risk-averse foraging hypothesis should be tested further due to conflicting results and small sample sizes. During most of the year, Common Eiders selected relatively small mussels that minimized shell ingestion, even though larger available prey would have provided higher net energy gain per prey item. In winter, differences among length classes in shell ingestion became small, and birds switched to feeding on larger prey that provided more energy per unit work and probably were more profitable. During times when small and mid-sized prey were preferred, ducks foraging where large mussels were abundant usually selected smaller length classes of prey than did those feeding where large mussels were less common. Birds avoided the risk of inadvertently ingesting large prey by selecting smaller mussels. Our results provide insight into the mechanisms of prey selection by Common Eiders and may also help explain some of the discrepancies reported in previous studies of prey-size selection in this species. Received 31 October 1997, accepted 26 August 1998.

MANY OPTIMAL DIET MODELS assume that animals sample a variety of prey types or sizes such that energy intake is maximized relative to costs associated with feeding (Stephens and Krebs 1986). However, the performance of such models under complex natural situations is questionable (Ball 1994), and it is seldom possible to determine how animals perceive costs, benefits, and risks associated with foraging choices. The ability of individuals to assess their environment and distinguish among prey may influence how they perceive these factors, and in turn, may determine the degree to which they are selective and the prey that they choose (e.g. Elner and Hughes 1978, Hughes 1979).

It might be inferred, from the observation

that prey are not always selected according to model predictions, that animals feed “suboptimally” (e.g. Draulans 1984). However, these animals may be feeding in a manner that maximizes net reward conditional on constraints they face and their ability to distinguish prey. For example, Ball (1994) argued that animals foraging in highly variable environments where prey availability and profitability (net energy gain per search and handling time) change unpredictably, or where they face a wide array of choices, may be unable to distinguish small differences in profitability, and instead use “rules of thumb.” Use of such rules may cause individuals to feed in a manner that appears to be suboptimal (i.e. not choosing the most profitable prey). On the other hand, if profitability changes predictably (e.g. seasonally), animals may be better able to assess the environment and feed more selectively.

Considerable research has been conducted on prey selection by aquatic birds (e.g. Draulans 1982, 1984, 1987; Meire and Ervynck 1986;

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Bustnes and Erikstad 1990; Ward 1991; DeLeeuw and Van Eerden 1992; Ball 1994; Barras et al. 1996). Birds often eat prey that appear to be of low quality. Hypotheses to explain this include: (1) individuals minimize shell ingestion (Bustnes and Erikstad 1990) or salt intake (Nyström et al. 1991) as opposed to maximizing short-term energy intake; (2) large prey are more costly in terms of handling time and crushing resistance and therefore should be avoided, even if energetically rich (i.e. they are less energetically profitable; DeLeeuw and Van Eerden 1992); and (3) predators are unable to discriminate among prey of different sizes (Ward 1991). Hence, when attempting to determine the optimal prey for foraging animals, researchers should consider more than just energy return per prey item.

Draulans (1982, 1984) suggested that ducks select mussels of smaller than optimal size because this enables them to avoid the risk of ingesting one that is too large to handle. Draulans' (1982, 1984) hypothesis assumes that ducks are imperfect at distinguishing prey of different sizes; the better their selection skills, the less they should have to compensate in higher-risk situations (Draulans 1987). The "risk" referred to by Draulans concerns the consequences of selecting a prey item that cannot be eaten. The bird has expended energy to find and handle the prey, but obtains no reward. In this situation, where predators cannot be certain of distinguishing these risky prey from the more beneficial ones (assume, for example, that the best prey are of intermediate size), the best strategy may be to select much smaller prey. These prey items may not provide as much benefit as preferred prey, but they provide some benefit and are sufficiently different from large (i.e. risky) prey that foragers will not make a mistake. This idea may be extended beyond the case where large prey provide no benefit to situations where they are simply substantially less beneficial (because of reduced energetic profitability, increased shell content, or some other factor).

We examined predation on blue mussels (*Mytilus edulis*) by Common Eiders (*Somateria mollissima*) in two areas of Passamaquoddy Bay, New Brunswick, Canada. Common Eiders are present year-round in the area, and adults feed primarily on mussels (Hamilton 1997). Using a series of experiments, we attempted to deter-

mine whether these ducks were size-selective predators, and if so, what mechanisms they used to choose their prey (i.e. what aspect of prey quality they selected for).

We tested two hypotheses, each of which pertains to a different aspect of optimal prey choice. The shell-mass minimization hypothesis (Bustnes and Erikstad 1990) posits that Common Eiders select prey items that minimize shell intake rather than maximize short-term energy gain. Under this hypothesis, the most beneficial prey are those with the smallest shell content but not necessarily the highest energetic content. Relative tissue mass (tissue relative to shell) is highest in small mussels (Bustnes and Erikstad 1990), but differences among sizes may vary with season. At times when these differences are great, birds should choose relatively small prey, but when tissue content is more similar among mussel sizes, other selection factors (i.e. energetic profitability) may come into play. Under the risk-averse foraging hypothesis (Draulans 1982, 1984), ducks select small prey that reduce the risk of taking prey too large to be handled (or that are unfavorable for some other reason). Although we are unaware of any studies that examine the ability of Common Eiders to distinguish among length classes of prey, other species of diving ducks (Draulans 1982, 1984, 1987; Ball 1994), as well as other birds (Ward 1991), are known to be imperfect at separating similar sizes. Assuming that Common Eiders are capable of some size discrimination, but not perfect at distinguishing prey of different sizes, in areas and seasons where large mussels are less beneficial (possibly because of high shell content) and more abundant, ducks should switch to feeding on smaller prey than they would under conditions where large prey are less common. We also used our experiments to attempt to explain variation in prey sizes selected by Common Eiders in several previous studies (Raffaelli et al. 1990, Nyström et al. 1991, Guillemette et al. 1996).

#### METHODS

*Field experiments.*—We performed prey-selection experiments at two locations (Barr Road and Indian Point) approximately 3 km apart near St. Andrews, New Brunswick, Canada (45°04'N, 67°02'W) during spring (April and May), summer (June through August), and fall (September and October) 1995, and winter (January through March) and spring (April

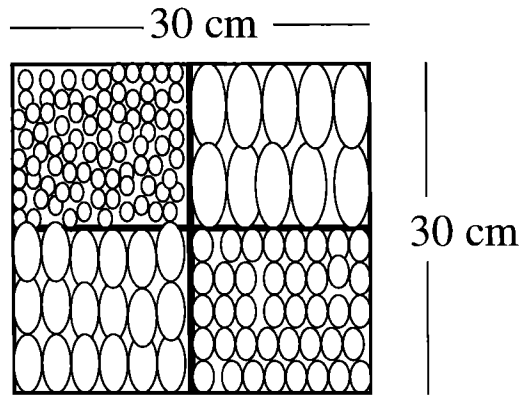
and May) 1996. The study area remained ice free throughout the experiment. Our study included foraging by only adult and full-grown juvenile (in fall) ducks. Sex ratios were approximately equal except in summer, when many females were feeding elsewhere with ducklings. Duckling feeding grounds were excluded, because ducklings and associated females have a substantially different diet than adults without ducklings (Cantin et al. 1974, Hamilton 1997). The population structure was similar in the two study locations. Analyses of ducks collected from the study areas suggest that blue mussels were the most commonly eaten prey for adult Common Eiders in all seasons (Hamilton 1997).

Blue mussels were collected from these areas and placed in aquaria with a flow-through seawater system in a laboratory at Huntsman Marine Science Centre. Square ceramic floor tiles (900 cm<sup>2</sup>) served as a substrate for mussel attachment in the lab. Mussels were divided into four length classes: (1) 10 to 19 mm, (2) 19 to 28 mm, (3) 28 to 37 mm, and (4) 37 to 50 mm. All classes were within the range ducks were physically capable of ingesting (Hamilton 1997). We divided tiles into four equal sections using corrugated plastic dividers (height ca. 3 to 4 cm) attached with silicone. Two types of tiles were set up (Fig. 1). "Regular" tiles were those in which each section contained a different length class of mussels (i.e. one class per section). The surface area covered by mussels in each section was held constant so that ducks did not perceive differential mussel cover (145 mussels in class one, 66 in class two, 40 in class three, and 21 in class four). "Manipulated" tiles had six large mussels added to each section containing one of the three smaller length classes. In order to maintain constant surface area both within manipulated tiles and between manipulated and regular tiles, we also reduced the number of mussels in the three smaller length classes on manipulated tiles (110 in class one, 52 in class two, 30 in class three, and 21 in class four). For both types of tiles, we randomized the location of sections containing different length classes on each tile. Use of two tile types allowed us to compare prey selection under conditions of equal cover of all length classes with choices made when large prey were more abundant. This provided a direct test of the risk-averse foraging hypothesis.

We placed tiles in aquaria with aeration and a flow-through seawater system for three to seven days, until mussels attached by means of byssal threads. Aquaria were drained and left empty for approximately 2 h daily to simulate a tidal cycle and to accelerate attachment (VanWinkle 1970). Mussel attachment was checked by turning tiles upside down. After attachment was complete, we recounted mussels in each tile section (sometimes a few mussels died or failed to attach).

We placed tiles (in groups of three to six) in the intertidal zone in areas where ducks were known to

### Regular tile



### Manipulated tile

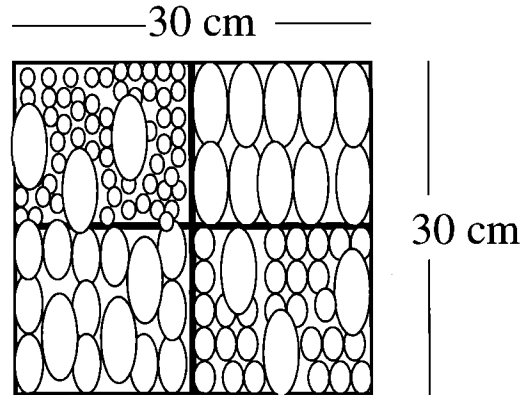


FIG. 1. Diagram of typical regular and manipulated tiles with mussels of the four length classes. The number of mussels in each section does not reflect the actual number used in experiments (see text). Positions of the four size classes were randomized for each tile.

feed. Distance between tiles within groups varied, but all were usually within 50 to 75 m of each other. Locations of groups of tiles set out at each study area depended on where ducks had last been observed feeding. At Indian Point, tiles were placed along a 2-km length of beach, whereas at Barr Road the study area was approximately 1 km long. All tiles were at about the same depth (5.5 to 7 m underwater at high tide, depending on the moon phase) to reduce potential effects of diving depth on prey selection (Draulans 1982, Beauchamp et al. 1992, DeLeeuw and Van Eerden 1992). Tiles were near the low-tide line and were exposed for a very short time each day. This minimized possible predation by gulls (which

were common) and crows (which were much less common), because they did not feed underwater. However, we also placed several tiles higher in the intertidal zone and observed them using a spotting scope to determine whether gulls attempted to remove mussels from these tiles. In all cases gulls avoided the tiles, so we concluded that their possible effects as predators were minimal.

We placed a single tile from each group under a predator-exclusion cage designed to prevent ducks from feeding under it. These cages were 30 cm high, with a roof made of  $3 \times 3$  cm plastic mesh, and had no sides. In most of the Indian Point study area, cages were permanently anchored structures of  $1.5 \times 1.5$  m. These enclosures were used in conjunction with a predator-exclusion experiment (Hamilton 1997) and have been shown to effectively exclude ducks (Hamilton et al. 1994). At Barr Road and a small part of the Indian Point site (when tiles were positioned far from the permanent cages), a portable cage, approximately  $75 \times 75$  cm, was used. Cages did not attract or exclude other predators and offered no protection from wave action (Hamilton 1997). Cages therefore acted as controls for mussels lost due to wave action or other predators (e.g. crabs and seastars) that also feed on mussels in the area. The different sizes of the two cage types almost certainly did not influence our results because observations of effects of duck exclusion on the mussel bed suggested that birds avoided cages completely, not even reaching under the edges of them in an attempt to retrieve mussels (D. Hamilton pers. obs.). Control tiles were located among experimental tiles with the control associated with each group never more than about 40 m from any tile in the group.

We used a spotting scope to check for ducks feeding in areas where tiles were positioned. Tiles were checked daily at low tide. When it became clear that mussels were missing from tiles in at least one length class (or within three days if no mussels were missing), we recovered tiles and removed and counted the remaining mussels. The number of missing mussels that could be attributed to duck predation was determined by subtracting the number of mussels in each length class missing from the control (protected) tiles from those missing from the experimental tiles that were exposed to predation during the same time period.

We estimated the natural availability of mussels (hereafter "ambient") of different length classes by collecting all mussels from 20 100-cm<sup>2</sup> samples in each area during summer 1995. Mussels from each sample were counted and classified into length classes. We obtained size-frequency distributions of mussels for Indian Point in the remainder of 1995 and 1996 using data collected from another experiment (Hamilton 1997). We also periodically (July, August, and December 1995; March and May 1996) collected sets of approximately 40 mussels (10 to 50

mm long) from the study area to assess relative tissue and shell mass at different times of the year. Mussels were opened and the tissue and shell dried separately for 20 h at 90°C, then weighed. We measured shell thickness (at the top of the valve near the attachment site of the posterior adductor muscle) and crushing resistance during one collection period. Force (N) required to crack mussels of different lengths was assessed using a Hounsfield tensometer. Mussels were placed width wise in the tensometer with one valve in contact with each of the crushing surfaces. Tension was increased slowly and the force at which mussels first cracked was recorded as crushing resistance.

We assessed benefits of different prey-length classes for ducks using several means. Energy (J) gained and shell mass consumed by eating mussels of each length were estimated for all seasons using estimates of energy content of mussel tissue (1 g dry tissue = 20.511 kJ; Bustnes and Erikstad 1990) and predicted average shell mass for each mussel length class. As estimates of costs associated with feeding on different sized mussels, we calculated the amount of work (in J; force  $\times$  distance compressed) required to crack mussels of each length, and we determined force required to pull mussels off tiles using a Pesola scale. From literature estimates of daily food requirements for Common Eiders (Bédard et al. 1980, Bustnes and Erikstad 1990, Egerrup and Laursen 1992, Hilgerloh 1997), we estimated an average dry-tissue biomass requirement of 130 g per day. We then calculated for each season the mass of shell that would be consumed per day from each length class if a Common Eider obtained the 130-g requirement completely from mussels of that length. The estimate of 130 g per day is likely to be an overestimate in summer and an underestimate in winter (Hilgerloh 1997), but this seasonal variation does not affect our interpretation because the relevant comparisons of shell ingestion are among length classes within seasons, not across seasons (see Results). We set the constant requirement at 130 g per day simply to provide a uniform graphical presentation; any value would have given the same result.

*Statistical analyses.*—We used a series of chi-square analyses to test for size selectivity (based on mussel length) at different times, locations, and among tile types (regular vs. manipulated). Each treatment combination was analyzed separately using a single calculated  $\chi^2$ , although when insufficient replication was available, some seasons had to be pooled (e.g. spring and summer in a particular location). We used the following procedure to calculate  $\chi^2$  values for each combination of time, location, and tile type. For each tile within a treatment combination, corrected (for losses other than to ducks) numbers of mussels eaten from each length class were taken as observed values, and expected numbers eaten were calculated based on a null hypothesis of random removal. We

TABLE 1. Regression equations predicting dry-tissue mass from mussel length for the different months in which mussels were sampled. The relationship is log-log taking the form: tissue mass =  $10^a \times \text{length}^b$ .

| Month         | <i>b</i> | <i>a</i> | <i>r</i> <sup>2</sup> | df    | <i>F</i> | <i>P</i> |
|---------------|----------|----------|-----------------------|-------|----------|----------|
| July 1995     | 2.92     | -5.36    | 0.97                  | 1, 82 | 2,543.7  | <0.0001  |
| August 1995   | 2.53     | -4.80    | 0.96                  | 1, 41 | 1,135.0  | <0.0001  |
| December 1995 | 2.67     | -5.00    | 0.97                  | 1, 39 | 1,172.9  | <0.0001  |
| March 1996    | 2.78     | -5.23    | 0.98                  | 1, 39 | 1,920.5  | <0.0001  |
| May 1996      | 2.45     | -4.63    | 0.94                  | 1, 39 | 660.3    | <0.0001  |

summed observed and expected numbers across all tiles in an experimental group to generate single observed and expected values for each length class, and an overall  $\chi^2$  value. We used this particular computational approach because Common Eiders selected mussels at the level of the individual tile. However, because approximately the same number of mussels was available on each tile, we could equally have summed all observed values and calculated expectations based on those totals without changing the results appreciably. We then tested for differences in prey selection by Common Eiders among times, locations, and tile types using a series of heterogeneity  $\chi^2$  analyses (Zar 1996). This procedure compared deviation of observed from expected values (i.e. results of the simple  $\chi^2$  analysis) among different experimental manipulations (e.g. regular versus manipulated tiles in a given season and location) and was approximately analogous to testing for an interaction between main effects in a two-factor ANOVA (see Zar [1996] for computational details). All  $\chi^2$  values reported in the text are from heterogeneity analyses.

This nonparametric analysis was necessary because when data were converted to a form that would accommodate ANOVA or other parametric techniques, assumptions of normality and homogeneity of variances were severely violated. We pooled tiles within treatments because in many cases too few mussels were removed, resulting in violation of chi-square assumptions if each was considered separately (Zar 1996). Our approach was conservative because it resulted in reduced degrees of freedom and potentially minimized observed effects by combining observations (different tiles) taken under slightly different conditions. It did, however, provide an estimate of overall prey selection by Common Eiders over the range of conditions they encountered. Our approach also had the advantage of giving greater weight to tiles on which more predation had occurred.

All parametric analyses were performed using SAS version 6.11. Data were examined for conformity to assumptions and, when necessary, were transformed. We determined the relationship between mussel length, total mass, and dry tissue mass using analysis of covariance (ANCOVA), with season as the classification variable. Average tissue mass

and relative tissue content (dry tissue mass/total dry mass) of mussels in each length class were calculated using predicted (from regressions of biomass on length) total and tissue biomass (Table 1). We used predicted as opposed to raw values to ensure that a true and consistent mean for each length class was achieved (because the mean length of mussels sampled from each length class may have varied slightly from sample to sample and was not necessarily the arithmetic mean length of all mussels in that class). Our approach likely introduced very little bias into the analysis, because  $r^2$  values for each regression exceeded 0.94 and intercepts were zero (by definition because the regression was log-log). We then compared relative tissue content (arcsine transformed) across length classes and seasons using two-way ANOVA and the *a posteriori* Tukey's HSD test (Zar 1996). We regressed shell thickness and crushing resistance on shell length and compared attachment strength of mussels to tiles across length classes using ANOVA and Tukey's test.

## RESULTS

*Prey-selection experiments.*—Common Eiders were size-selective predators on both regular and manipulated tiles during all seasons at both locations (Table 2). Total observed and predicted numbers of mussels consumed in each treatment combination are provided in Table 3. Preferred length classes differed among treatment groups. At Indian Point, preferences differed among seasons ( $\chi^2 = 267.4$ ,  $df = 9$ ,  $P < 0.0001$ ) and tile types (regular vs. manipulated; spring,  $\chi^2 = 13.6$ ,  $df = 3$ ,  $P = 0.004$ ; summer,  $\chi^2 = 22.5$ ,  $df = 3$ ,  $P < 0.0001$ ; winter,  $\chi^2 = 74.8$ ,  $df = 3$ ,  $P < 0.0001$ ). During spring, summer, and fall, ducks generally preferred smaller length classes, especially 19 to 28 mm, and avoided larger classes (Table 2). However, in winter, large mussels were selected (Table 2). During all seasons in which comparisons could be made, ducks tended to take smaller mussels from manipulated tiles than they did from corresponding regular tiles (Table 2).

TABLE 2. Results of simple  $\chi^2$  analysis of Common Eider prey-selection experiments. "Reps" refers to the number of tiles pooled to obtain the final result. Symbols associated with mussel length classes are as follows: --, strongly avoided; -, avoided; 0, eaten randomly; +, selected; ++, strongly selected. These classifications are based on cell  $\chi^2$  values. If the cell  $\chi^2 \geq 6.63$  ( $P = 0.01$  at 1 df), the class was strongly selected or avoided, and if  $6.63 \geq \chi^2 \geq 3.84$  ( $P = 0.05$  at 1 df), the class was selected or avoided. These divisions are not intended as *a posteriori* tests, but rather as a means of standardizing levels of preference and avoidance. For overall  $\chi^2$  comparisons,  $df = 3$  and critical value of  $P = 0.05$  was at  $\chi^2 = 7.815$ . Values in parentheses indicate percentage of the total  $\chi^2$  value attributable to that cell; high values indicate strong selection or avoidance.

| Site         | Season                | Type        | Reps | $\chi^2$ | Mussel length class (mm) |          |          |          |       |       |       |       |
|--------------|-----------------------|-------------|------|----------|--------------------------|----------|----------|----------|-------|-------|-------|-------|
|              |                       |             |      |          | 10 to 19                 | 19 to 28 | 28 to 37 | 37 to 50 |       |       |       |       |
| Indian Point | Spr 1995              | Regular     | 17   | 19.8     | 0 (3%)                   | +        | (30%)    | -        | (23%) | --    | (44%) |       |
| Indian Point | Sum 1995              | Regular     | 23   | 106.5    | ++                       | (9%)     | ++       | (17%)    | --    | (45%) | --    | (29%) |
| Indian Point | Spr/sum 1995/<br>1996 | Manipulated | 12   | 15.1     | +                        | (33%)    | -        | (28%)    | 0     | (2%)  | -     | (37%) |
| Indian Point | Aut 1995              | Regular     | 9    | 27.8     | 0                        | (5%)     | +        | (14%)    | --    | (81%) | 0     | (0%)  |
| Indian Point | Win 1996              | Regular     | 16   | 182.5    | --                       | (35%)    | ++       | (7%)     | ++    | (7%)  | ++    | (51%) |
| Indian Point | Win 1996              | Manipulated | 5    | 16.2     | 0                        | (19%)    | --       | (72%)    | 0     | (0%)  | 0     | (9%)  |
| Barr Road    | Spr/sum 1995          | Regular     | 20   | 22.4     | ++                       | (34%)    | -        | (22%)    | 0     | (0%)  | --    | (44%) |
| Barr Road    | Spr 1996              | Regular     | 9    | 84.3     | 0                        | (4%)     | ++       | (65%)    | --    | (15%) | --    | (16%) |
| Barr Road    | Spr/sum 1995/<br>1996 | Manipulated | 6    | 29.6     | --                       | (34%)    | ++       | (65%)    | 0     | (1%)  | 0     | (0%)  |

Preferences at Barr Road differed among years ( $\chi^2 = 73.7$ ,  $df = 3$ ,  $P < 0.0001$ ) and tile types (1995,  $\chi^2 = 40.8$ ,  $df = 3$ ,  $P < 0.0001$ ; 1996,  $\chi^2 = 12.6$ ,  $df = 3$ ,  $P = 0.006$ ). Common Eiders feeding on regular tiles preferred mussels in the 10 to 19-mm class in 1995 and the 19 to 28-mm class in 1996 (Table 2). They avoided the smallest mussels on manipulated tiles in both years, strongly preferred length class two, and fed randomly on larger classes (Table 2). Preferences for length classes also differed among sites on manipulated tiles ( $\chi^2 = 40.6$ ,  $df = 3$ ,  $P < 0.0001$ ) and regular tiles in 1995 (spring,  $\chi^2 = 15.0$ ,  $df = 3$ ,  $P = 0.002$ ; summer,  $\chi^2 = 46.2$ ,  $df = 3$ ,  $P < 0.0001$ ). At Indian Point, ducks feeding from manipulated tiles during spring

and summer preferred the smallest length class, whereas at Barr Road, they selected class-two mussels (Table 2). Ducks eating mussels from regular tiles in 1995 generally preferred prey of 19 to 28 mm (and to a lesser degree, 10 to 19 mm) at Indian Point and 10 to 19 mm at Barr Road (Table 2).

*Mussel characteristics.*—In 1995, mussels from Indian Point tended to be smaller than those at Barr Road, although lengths also varied within locations (Fig. 2). No samples were taken in 1996 at Barr Road, but the size-frequency distribution of mussels from enclosure experiments at Indian Point during winter 1995–1996 and spring 1996 suggest that mussel sizes remained relatively constant throughout the ex-

TABLE 3. Total observed and expected (based on a null hypothesis of random removal) number of mussels of each length class eaten by Common Eiders throughout the experiment. Numbers are corrected for losses from sources other than ducks (see text) and are rounded to the nearest whole digit.

| Site         | Season            | Type        | 10 to 19 mm |     | 19 to 28 mm |     | 28 to 37 mm |     | 37 to 50 mm |     |
|--------------|-------------------|-------------|-------------|-----|-------------|-----|-------------|-----|-------------|-----|
|              |                   |             | Obs         | Exp | Obs         | Exp | Obs         | Exp | Obs         | Exp |
| Indian Point | Spr 1995          | Regular     | 277         | 265 | 131         | 106 | 55          | 74  | 21          | 40  |
| Indian Point | Sum 1995          | Regular     | 351         | 298 | 182         | 133 | 21          | 86  | 10          | 48  |
| Indian Point | Spr/sum 1995/1996 | Manipulated | 64          | 48  | 13          | 23  | 16          | 14  | 3           | 10  |
| Indian Point | Aut 1995          | Regular     | 187         | 171 | 99          | 82  | 15          | 48  | 26          | 27  |
| Indian Point | Win 1996          | Regular     | 109         | 232 | 144         | 107 | 97          | 68  | 91          | 35  |
| Indian Point | Win 1996          | Manipulated | 90          | 75  | 16          | 37  | 21          | 20  | 21          | 16  |
| Barr Road    | Spr/sum 1995      | Regular     | 319         | 274 | 98          | 123 | 82          | 82  | 22          | 43  |
| Barr Road    | Spr 1996          | Regular     | 105         | 123 | 110         | 55  | 13          | 34  | 3           | 19  |
| Barr Road    | Spr/sum 1995/1996 | Manipulated | 16          | 35  | 32          | 15  | 10          | 8   | 7           | 7   |

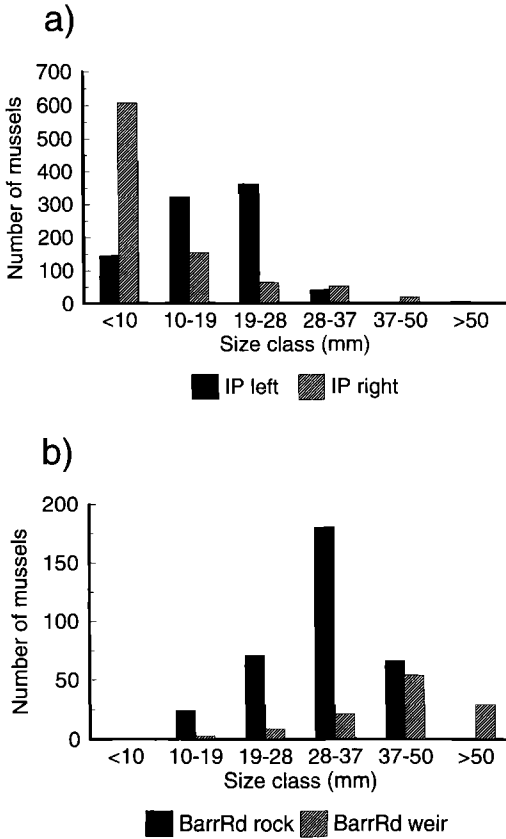


FIG. 2. Length frequency distributions of mussels collected from (A) Indian Point and (B) Barr Road in summer 1995. Within each site, mussels were collected from two areas (Indian Point left and right, Barr Road rock and weir). Different bars represent the different areas at each site.

periment, with only a small increase in the proportion of large mussels in the population in spring 1996 (D. Hamilton unpubl. data).

Mussel density was very high at both study sites throughout the experiment. On tiles, density was approximately 3,000 mussels per m<sup>2</sup>. In samples collected in summer 1995 (Fig. 2), densities were 3,420 ± SD of 968 and 1,170 ± 263 at two areas of Barr Road, and 7,330 ± 2,422 and 2,870 ± 1,509 at two areas of Indian Point (excluding mussels <10 mm long). Densities declined but still remained high at Indian Point in 1996, with approximately 1,700 mussels per m<sup>2</sup> (D. Hamilton unpubl. data). Although these ambient densities were highly variable, densities on tiles were within the range of those found naturally. The high den-

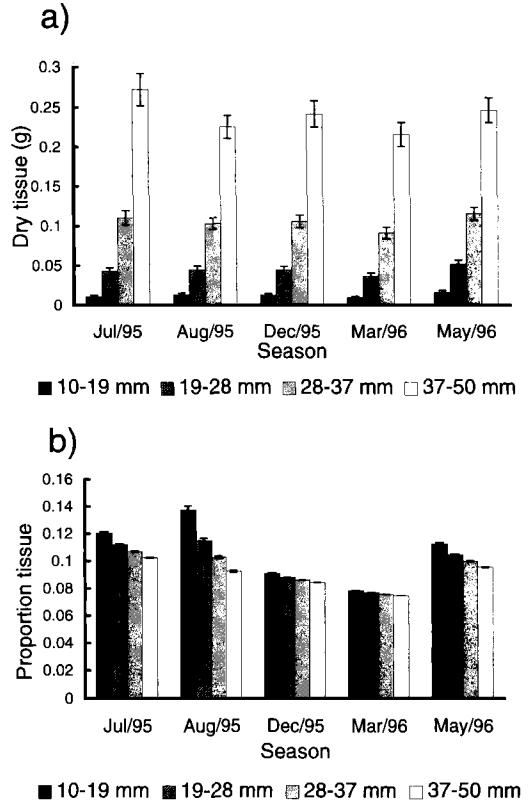


FIG. 3. Tissue content of mussels collected during each sampling period. Values for (A) average dry-tissue mass of mussels were calculated as an average of predicted (from regression) dry-tissue content for mussels in each length class. (B) Proportion tissue biomass was calculated using values from part (A) and similar ones predicting total dry-mussel biomass. Error bars represent ± 1 SE.

sities of mussels found throughout the study area suggested that variation in underwater search time would be small (see Discussion).

Dry-tissue mass of mussels increased exponentially with length (Table 1), and the relationship varied with collection period (ANCOVA, length × date interaction  $F = 7.5$ ,  $df = 4$  and  $240$ ,  $P < 0.0001$ ), although trends appeared consistent across seasons (Fig. 3A). Generally, mussels contained the most tissue in July (just before spawning) and the least in March and August (Fig. 3A). However, when predicted length-class means were considered using ANOVA, although the main effect of season was significant ( $F = 2.64$ ,  $df = 4$  and  $197$ ,  $P = 0.035$ ), the result was due primarily to a difference between July and March (Tukey's

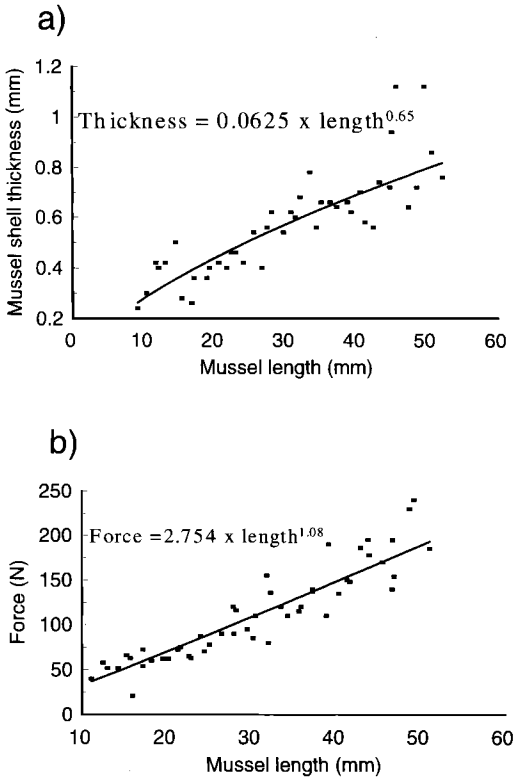


FIG. 4. (A) Regression of shell thickness on mussel length. (B) Regression of force (in Newtons) required to crush mussels on mussel length. Results of significance tests are provided in text.

HSD test). Relative tissue biomass also varied among mussel length classes (Fig. 3B), and the variation differed among seasons (ANOVA, season  $\times$  length class interaction,  $F = 68.4$ ,  $df = 12$  and  $185$ ,  $P < 0.0001$ ). During all sample months, the main effect of length class was highly significant ( $F \geq 141.6$ ,  $df = 3$  and  $37$ ,  $P < 0.0001$  for each sample). All length classes differed from each other; the smallest mussels had the highest relative tissue biomass and the largest mussels the lowest proportion of tissue (Tukey's HSD test). However, differences among length classes were substantially higher in May, July, and August than they were in December and March (Fig. 3B).

Both shell thickness ( $r^2 = 0.75$ ,  $df = 1$  and  $41$ ,  $P < 0.0001$ ; Fig. 4A) and resistance to crushing ( $r^2 = 0.86$ ,  $df = 1$  and  $46$ ,  $P < 0.0001$ ; Fig. 4B) were positively correlated with shell length. When crushed, shells usually failed first in the middle or toward the rear (away from the

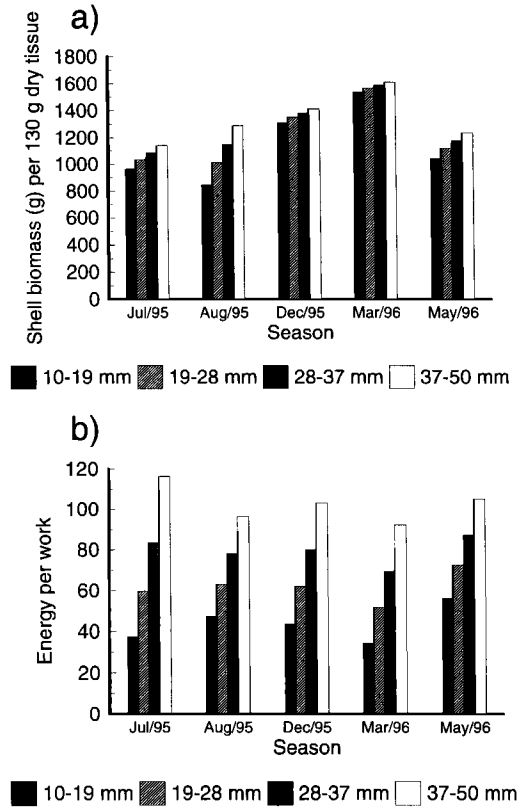


FIG. 5. (A) Estimated shell mass consumed per day by Common Eiders based on average consumption of 130 g dry tissue. Values were calculated based on predictions from regression of tissue and shell on mussel length. (B) Ratio of energy gained to work done by Common Eiders eating mussels of each length class during a day. Work is based on cost associated with crushing 130 g dry tissue of mussels of each length class.

umbo) of one valve or the other. Attachment of mussels to the substrate differed among length classes (ANOVA,  $F = 140.1$ ,  $df = 3$  and  $556$ ,  $P < 0.0001$ ); the smallest mussels were the easiest to detach and largest ones the most difficult.

*Costs and benefits.*—In any season, Common Eiders that met their energetic requirements by feeding on large mussels would have to consume more shell biomass than ducks that fed on small ones (Fig. 5A). However, as described above, differences among length classes in shell mass consumed while eating a set amount of mussel tissue varied among seasons. In December and March, the difference in shell masses consumed by eating equivalent dry-tissue bio-



mass of the smallest versus largest length classes of mussels was relatively small (7.8 and 4.9%, respectively) (Fig. 5A). During other months, however, the differences were larger, ranging from 18.5% in May and July to 52.5% in August (Fig. 5A). Energy intake relative to work was always highest when large mussels were taken (Fig. 5B). The ratio of energy gain relative to cost (estimated as the work required to crack a mussel) increased steadily across length classes, and trends appeared similar for all seasons, although the increase in benefit was somewhat lower during May and August than it was at other times of the year (Fig. 5B).

#### DISCUSSION

Common Eiders feeding in our experiment were size-selective predators. This has been shown before, although preferred sizes of prey vary among studies (Raffaelli et al. 1990, Nys-tröm et al. 1991, Guillemette et al. 1996). However, unlike earlier studies of prey selection in this species, we attempted to quantify and control availability of prey of different lengths. This could be achieved only on tiles; we had no control over the ambient size distribution of prey in the mussel bed, which could strongly influence our results (see below). However, our experiment provided standard prey composition and equal search time for all length classes once a tile was encountered by a foraging Common Eider (because each class covered an equivalent surface area). Thus, our study offers a starting point for assessing size-selective predation. This is important, because prey selection is influenced by availability of both profitable (Stephens and Krebs 1986) and unprofitable prey size classes (Elner and Hughes 1978, Ward 1991). Although differences in mussel size distributions between tiles and the surrounding area may have influenced prey selection by Common Eiders, differences in mussel density probably had little effect. Mussels in the experimental area were superabundant, and ambient densities of mussels were similar to those on tiles, so birds never had to look for prey during a dive once they reached the bottom. Hence, variation in patch quality related to prey density was eliminated from consideration.

Relative abundance of different-sized mussels on tiles changed somewhat as trials pro-

gressed because ducks removed more mussels of some length classes than others. This was unavoidable, but it probably had only a small effect on the results. Tiles were checked daily and removed as soon as noticeable predation had occurred. In most cases, this meant that tiles were removed before any size class was completely eliminated or even substantially reduced. Hence, foraging ducks still had a relatively equal choice of all four classes in the same immediate area. In situations where ducks quickly removed all or most prey of one length class (mostly in winter 1996; see below), the change in prey availability as the trial progressed may have had some effect on selection. However, this effect would be a conservative bias (following a null hypotheses of random prey removal) because elimination of preferred prey would force a switch to the next best choice, hence broadening the diet and reducing the apparent degree of selectivity. Therefore, because we found significant prey selection, this artifact of our experimental design was not a serious problem.

*Seasonal variation.*—Common Eiders selected mussels of different lengths at different times of the year. For most of the year at Indian Point, ducks feeding from regular tiles preferred the two smallest length classes, 10 to 19 mm and 19 to 28 mm, and avoided large mussels. However, in winter this trend was reversed; ducks strongly avoided 10 to 19-mm mussels and selected others (Table 2). The largest mussels (37 to 50 mm) were the most preferred, although others were also selected, probably after all large mussels had been removed from tiles. This switch may have been related to changes in costs and benefits of feeding on prey of different lengths at different times of the year (see below).

If Common Eiders selected prey that maximized short-term energy gain, they should always have fed on large prey. The ratio of energy gained to work done (Fig. 5B) varied little across seasons. Notwithstanding the increase in shell thickness and force required to crush large mussels, energy intake appeared to be maximized by taking the largest prey. This was a consistent trend across seasons, because although crushing resistance was measured only once during the experiment, shell mass relative to length (and therefore thickness) varied little through the year. Because we did not attempt

to quantify handling time, which probably is higher for large mussels (Draulans 1982, DeLeeuw and VanEerden 1992), the relative benefits of consuming large prey may be somewhat lower than indicated. However, based on relative tissue biomass (Fig. 3A) and costs associated with crushing mussels (Fig. 5B), Common Eiders would have to consume 15 to 20 small mussels in less time than it takes them to eat one large mussel to reverse the order of energetic profitability of the length classes. Costs associated with detaching prey from the substrate may also have slightly reduced the relative benefits of large prey because these required the greatest force to remove. This effect would have been minimal, however, if the force required to remove mussels from the substrate did not alter profitability of different size classes, as was found for Tufted Ducks (*Aythya fuligula*) feeding on zebra mussels (*Dreissena polymorpha*) in Europe (Draulans 1982). Common Eiders have a nail on the upper bill, and a strong grasping action, allowing them to easily remove even large mussels from the substrate (Meire 1993). Therefore, even with the inclusion of handling time and costs of mussel detachment, large prey would probably remain the most energetically profitable when considered on an individual mussel basis.

The overall benefits of prey to foraging animals depend on more than just energetic profitability per prey item. Foraging ducks must simultaneously consider benefits of different prey and costs, such as those associated with ingestion of shell. The presence of food in the digestive tract limits consumption of other food (Ball 1990, 1994), so if Common Eiders consume a high proportion of shell in a feeding bout, less room will be available for mussel tissue. Consumption of less mussel tissue per foraging bout will probably require more feeding bouts, and certainly more feeding time, to obtain the necessary food intake each day. In all seasons, small mussels had the highest proportional tissue biomass (more shell per tissue), but variation in tissue content among length classes in winter was lower than during the rest of the year (Fig. 3B). During most of the year, Common Eiders could therefore reduce shell ingestion substantially by feeding on smaller length classes. Notwithstanding the high individual value of large prey, lower shell content may have made small mussels the most bene-

ficial prey for most of the year. However, during winter little variation existed among length classes of mussels in the amount of shell consumed by ducks while acquiring their daily requirement of mussel tissue. Thus, because the added cost of high shell ingestion associated with large mussels was reduced, it may have been most beneficial for Common Eiders to feed on larger prey, which offered more energetic benefit on a short-term basis, during winter.

Our results appear to be consistent with the shell-mass minimization hypothesis of Bustnes and Erikstad (1990). Ducks selected prey that allowed them to minimize shell ingestion when large differences between length classes were evident (most of the year). However, when shell mass was least variable among mussel length classes, Common Eiders appeared to switch tactics in an attempt to maximize short-term energy intake by taking large mussels. This suggests that shell content was an important component of overall prey value. Our results are also consistent with those of Barras et al. (1996), who studied acorn selection by Wood Ducks (*Aix sponsa*), and of Zwarts and Blomert (1992), who studied preferences of Red Knots (*Calidris canutus*) for *Macoma balthica*. In both cases, birds selected prey that minimized shell intake relative to the amount of tissue ingested.

However, our results do not provide conclusive proof of the shell-minimization hypothesis. Even in spring and summer, the difference among mussel length classes in the ratio of energy intake relative to work (Fig. 5A) was considerably higher than the difference in shell content (Fig. 5B). As discussed above, if other costs such as handling time and detachment of mussels from the substrate were factored in, larger mussels would likely still be more energetically profitable on a per prey basis. By suggesting that ducks are attempting to minimize shell ingestion, we assume that total energy intake is sufficiently limited by shell accumulation and passage time to offset any benefit of feeding on more energetically profitable length classes. We have no data to support this assumption. Our results indicate that energy maximization appears not be the primary factor influencing prey selection by Common Eiders. However, to fully test the shell-minimization hypothesis, researchers should combine an experimental study such as ours with ana-

lyses of shell retention time and effects of shell accumulation in the digestive tract on prey ingestion rates. It would also be useful to consider seasonal variation in lipid, protein, and ash content of different length classes of mussels.

*Geographic variation.*—Selection of prey by Common Eiders varied among locations. At Indian Point in 1995, mussels in the 19 to 28-mm class were the most preferred by ducks, although they also selected smaller prey during summer. At Barr Road during the same time, Common Eiders strongly preferred the 10 to 19-mm length class. Tiles had the same length composition at each site, but naturally occurring mussels at Indian Point were smaller than those at Barr Road (Fig. 2). This result lends support to the risk-averse foraging hypothesis. In an environment (Barr Road) where mussels were generally large and therefore unprofitable in terms of shell ingestion (but not energy yield), ducks selected smaller prey that minimized the risk of inadvertently taking large mussels.

Draulans (1984) found that as the proportion of large, unprofitable prey in the population increased, ducks took smaller mussels, either to reduce the risk of taking one too large to handle (and therefore unprofitable), or because large mussels were more highly variable in profitability, and therefore presented a higher risk (the risk-averse foraging hypothesis). Draulans' suggestion that birds took small prey to avoid those that were too large is supported by our data. Ducks in our study could eat the larger mussels, but these mussels may have been less beneficial during most of the year because of large shell masses.

During spring 1996, ducks at Barr Road preferred 19 to 28-mm mussels, contrary to results from the previous year. During 1996, all tiles were placed in the rock area of Barr Road, where mussels were somewhat smaller the previous year (Fig. 2B). The previous year, tiles were mixed evenly among the two areas. Therefore, the experimental area in 1996 probably was not as heavily dominated by very large mussels as it was in 1995; accordingly, eiders selected mid-sized prey (the same as at Indian Point). This result highlights the importance of considering the natural availability of prey in experiments such as ours. Because size-frequency distributions and feeding locations of ducks were relatively consistent among

years at Indian Point, comparisons at that site were not biased by changes in the underlying prey-size distribution to which ducks were accustomed. However, specific Common Eider feeding locations at Barr Road changed from 1995 to 1996, and the natural prey-size distribution experienced by ducks in the two years probably differed. Although it is difficult to draw firm conclusions without knowledge of the exact size distribution of prey associated with each area in each year, variation in the ambient size distribution of mussels may have led to the shift in preferred prey size.

In future studies of this type, it would be prudent to avoid study areas such as Barr Road where size distributions of prey in the environment surrounding tiles differed, and birds focused on different sections of the site in different years (although we had no way of predicting this in advance). However, comparing environments with different prey-size distributions (Indian Point vs. Barr Road) is desirable because it allows tests of the effects of ambient prey availability. It is also noteworthy that when dealing with highly mobile predators such as Common Eiders, it is virtually impossible (without radio-tagging and tracking birds) to control their exposure to different prey sizes before the experiment. Hence, if experiments are to be done under natural conditions (which is important if we want realistic estimates of prey selection), we have to accept that some level of variation in experience, which may influence results, is unavoidable.

*Variation in prey availability on tiles.*—We made a further test of the risk-averse foraging hypothesis by comparing regular and manipulated tiles at each location. At Indian Point, ducks feeding on manipulated tiles during spring and summer preferred mussels of 10 to 19 mm, as opposed to 19 to 28 mm preferred by ducks feeding on regular tiles. When the available proportion of less beneficial prey (i.e. high shell content) increased, ducks responded by selecting smaller mussels, possibly to avoid mistakenly taking a large one.

Surprisingly, selection of mussels also varied with tile type during winter. Given that large mussels were preferred on regular tiles during winter, ducks should have continued to select them on manipulated tiles. However, in this situation all length classes were taken randomly, except 19 to 28 mm, which was strongly avoid-

ed. Possibly, 10 to 19-mm mussels were taken incidentally because ducks were feeding on large mussels located in the same tile section as small prey. The smallest mussels (which are more mobile than larger individuals) sometimes attached on top of large mussels on manipulated tiles. If ducks selected these small prey, they could easily remove them without dislodging the larger mussels, which were attached more firmly to the underlying tile. However, if ducks were selecting the larger prey (as they did in winter), small mussels on top of them may have been removed at the same time. It is also possible that the small sample ( $n = 5$ ) of manipulated tiles in winter provided unclear results due to insufficient replication.

It should be noted that the problem of ducks accidentally removing mussels that were attached to others was likely only an issue for the manipulated tiles in winter. On regular tiles in all seasons, the four length classes were separated, and although mussels tended to clump (which we attempted to minimize by separating mussels when tiles were assembled), this would not influence selection because birds would be just as likely to take a clump of one length class as another. In seasons other than winter, Common Eiders selected only small- and medium-sized mussels. As indicated above, on manipulated tiles these ducks would have had no difficulty removing small prey without disturbing the underlying larger ones.

The risk-averse foraging hypothesis was not supported when manipulated and regular tiles were compared at Barr Road. Birds actually appeared to select somewhat larger mussels from manipulated tiles than they did from regular ones, especially in 1995. We have no explanation for this except that again, results may be suspect due to a very small sample at this location ( $n = 6$ ), and because we were forced to pool 1995 and 1996 data for manipulated tiles at Barr Road due to small sample sizes (note above that differences existed among years on unmanipulated tiles in this location). Hence, these results should be interpreted with caution.

*Conclusions.*—Common Eiders are size-selective predators, and their preferences vary with season and risk of taking poor-quality prey. We found support for both aspects of optimal prey selection that we studied (i.e. the shell-mass minimization hypothesis and the risk-averse

foraging hypothesis), although the latter should probably be investigated further due to questionable results in one area where we had limited replication. We examined only a few of many decisions confronting predators each time they dive. Although we controlled for other factors (e.g. diving depth and prey availability), we did not address effects of handling time, dive duration, and when during dives birds fed on mussels from our tiles, any of which could have influenced our results (Beauchamp et al. 1992, DeLeeuw and VanEerden 1992, Guillemette et al. 1992). Prey selection under natural conditions is complicated and often is difficult to explain using simple models (Ball 1994). The fact that we observed significant, interpretable patterns suggests that the factors we examined are important to foraging Common Eiders.

Some of the variability in previous estimates of prey selection by Common Eiders may be explained by these findings, and by the fact that previous studies have not incorporated seasonal variation in prey value. Raffaelli et al. (1990) found that Common Eiders preferred mussels 10 to 25 mm, and that these were large relative to the available population. They collected Common Eiders in December and January, when, according to our results, large prey should be preferred. Similarly, Guillemette et al. (1996) reported that Common Eiders fed in winter on a modal mussel length of 8 mm, when the modal availability was 3 to 4 mm (although they ascribed part of the difference to different collection times for mussels and ducks). Nyström et al. (1991) found that Common Eiders selected mussels 17 to 18 mm, but that these were smaller than the average of those available. They attributed this to attempts by the ducks to minimize salt intake by eating small mussels. However, they collected their data in September and October, when, according to our findings, selection of smaller mussels may also be favored to minimize shell ingestion.

These results highlight the importance of considering factors such as prey availability, local background conditions, and season in studies of prey selection. Foraging choices by Common Eiders are influenced by season and by the relative abundance of undesirable prey. These ducks are capable of adjusting their feeding patterns relative to seasonal changes in prey

quality. This is a regular, repeatable pattern. They apparently are less adept at handling unpredictable variation within seasons in the abundance of prey of different sizes, and they appear to respond to increased relative abundance of poor-quality prey by taking smaller mussels.

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