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ABSTRACT: During the spring and summer of 1996 and 1997, we examined the whole-body energy content (WBEC) of Pacific herring *Clupea pallasi* ≤165 mm standard length (SL) from Prince William Sound, Alaska. From May to October, somatic energy (kJ·g^{-1} wet weight) exhibited a wide range of values relative to length. Young-of-year recruits, which appeared in July of both years, typically had WBEC of 2–3 kJ·g^{-1} wet weight after metamorphosis, and older fish had WBEC of 4–6 kJ·g^{-1} wet weight. By October the WBEC of juvenile herring was typically 4–6 kJ·g^{-1} wet weight. The consequences of the large seasonal and size-related variability in WBEC in juvenile herring are discussed relative to the transfer of energy to predators.

INTRODUCTION

In Prince William Sound (PWS) and throughout the Gulf of Alaska Pacific herring *Clupea pallasi* support important subsistence and commercial fisheries and are a major prey for several species of fish, marine mammals, and birds. Herring are seasonal feeders that build up fat stores during the spring to fall feeding season to sustain them during winter when food is scarce (Blaxter and Holliday 1963; Paul et al. 1998). This feeding and fasting cycle causes considerable seasonal variation in whole-body energy content (WBEC). Pacific herring in PWS reach sexual maturity at age 3, or at about 170 mm standard length (SL; Paul et al. 1996), and WBEC of adults and juveniles is markedly different (Paul et al. 1998). During spring and summer months several species of fish-eating sea birds migrate to PWS to nest. These birds prey mostly on younger stages of herring <165 mm SL and other small fishes (Hatch and Sanger 1992; Irons 1992). To estimate the energetic value of consumption of herring by birds and other predators, the seasonal changes in WBEC of prey species must be understood (Logerwell and Hargreaves 1997). The only published values for WBEC of juvenile herring from PWS, or anywhere in Alaska, are for fall and spring (Paul and Paul 1998; Paul et al. 1998). The objective of this study was to examine WBEC of herring ≤165 mm SL during spring and summer when nesting birds and other predators are relying on them to feed their young.

METHODS

During the spring and summer of 1996 and 1997 Pacific herring were captured from 4 sites in PWS, Alaska: Simpson Bay, Eaglek Bay, Whale Bay, and Zaikof Bay (Figure 1). Samples from all sites were pooled by collection date because there was considerable temporal variability in the number and length of fish caught at the different sites. Collection dates were 10–15 May, 10–15 June, 3–11 July, 1–6 August, and 3–10 October of 1996; and 5–8 May, 9–14 July, 9–13 August, and 22–26 October 1997. Juvenile herring were captured with 50-m-diameter by 4-m-deep purse seines with 3-mm stretch mesh. At each collection site the nets were set at least 3 times to capture specimens. All captured herring were immediately frozen in seawater aboard ship and kept frozen until processing.

In the laboratory herring were partially thawed, measured for standard length to the nearest millimeter and weighed to the nearest 0.1 g. Each herring was freeze-dried whole until no moisture was apparent. Next it was dried further in a convection oven at 60˚C until it reached a constant weight. Individual tissue wet and dry weight values were used to calculate mois-

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ture content of every herring. Dried tissues were ground in a mill, and measurements of caloric content were made using bomb calorimetry. All calorimetric samples were weighed to the 0.0001 g level with a single sample burned per fish. WBEC (kJ·g^{-1} wet weight) was plotted against standard length because many herring predators prey on specific size ranges. Also, in predator stomachs, often the only remains from which size of herring prey can be determined are skeletal parts, from which length estimates can be more precise than other parameters, such as weight.

A Kruskal–Wallis One Way Analysis of Variance on Ranks (ANOVA) and the Mann–Whitney Rank Sum test (MW) were used to compare the WBEC from different samples.

RESULTS

1996 Findings

WBEC tended to exhibit considerable variability relative to standard length in all seasons (Figures 2, 3). In May and June predators of juvenile Pacific herring had access only to fish that had overwintered (Figure 2A, 2B). The changes in the WBEC of these fish (age ≥1) showed a significant increase from May to June (MW, $P < 0.0001$) as they recovered from the winter fast; thereafter WBEC was more stable through October (Figure 4C). Average WBEC for all herring was 4.5 kJ·g^{-1} wet weight in May and 5.6 kJ·g^{-1} wet weight in

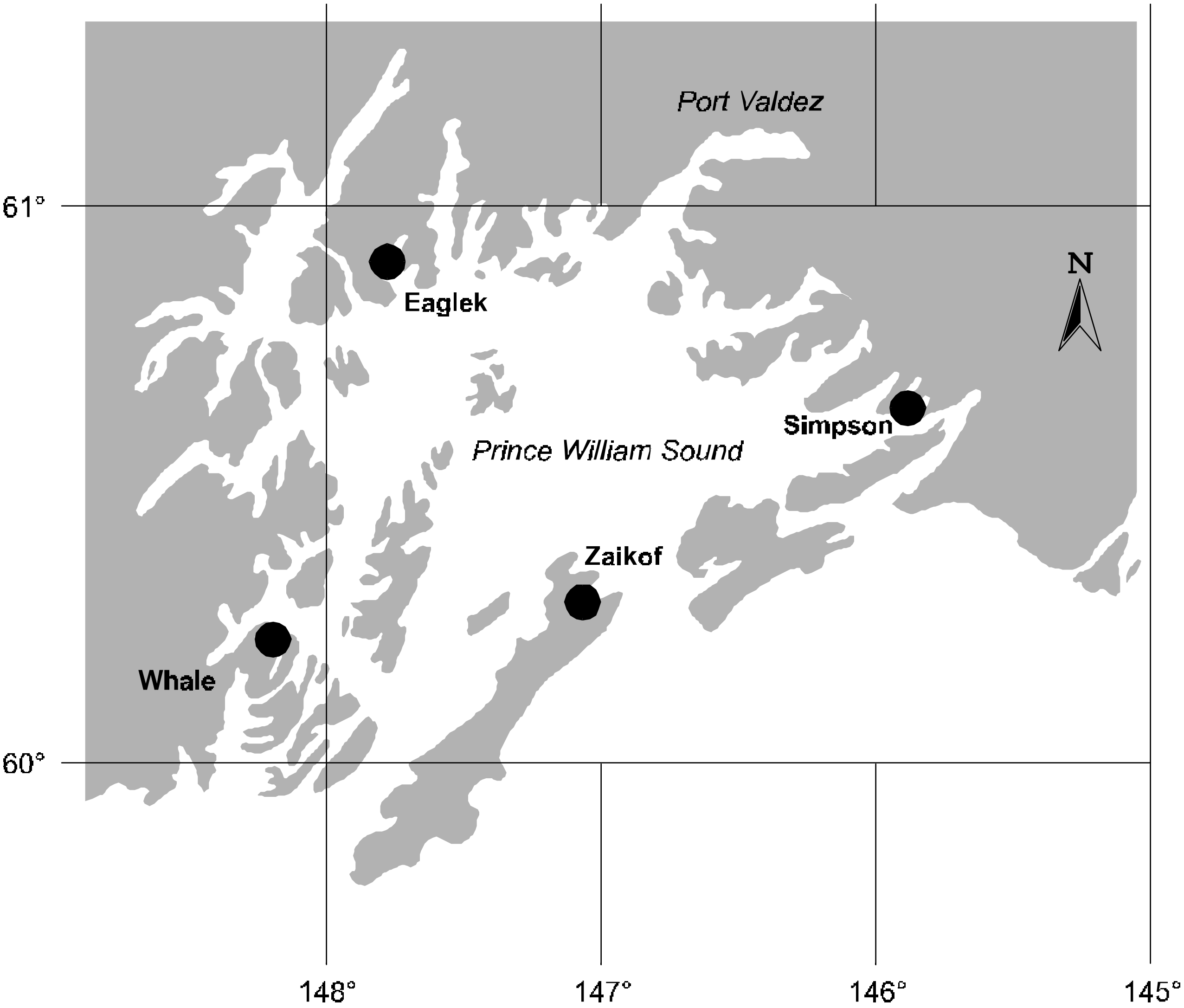

Figure 1. Areas (dark circles) in Prince William Sound, Alaska, where Pacific herring were captured for analysis of somatic energy content.

June (Figure 4C); a strong relationship between SL and WBEC was not evident in either month (Figure 2A, 2B; $P < 0.0001$). In July, fish >80 mm SL had WBEC of 4.5–6.5 kJ·g^{-1} wet weight and a mean of 5.4 kJ·g^{-1} wet weight (Figure 4C). In August the larger fish still had WBEC values of 4–6.5 kJ·g^{-1} ($\bar{x} = 5.2$; Figures 2D, 4C), and the relationship between standard length and WBEC was more predicable ($r^2 = 0.66$, $P < 0.0001$). The differences in the median WBEC values for the June, July, and August samples of age-1 and older herring (Figure 4C) were greater than would be expected by chance (ANOVA; $P < 0.0001$), showing there was seasonal variability in the energetic measurements after the fish recovered from the winter fast.

The 1996, young-of-year (YOY) herring became available to predators in July when their body sizes were 25–35 mm SL (Figure 3A) and their WBEC averaged 2.5 kJ·g^{-1} wet weight (Figures 3A, 4A). By August, YOY were 20–60 mm SL and their mean WBEC was 3.1 kJ·g^{-1} wet weight (Figures 3B, 4A). By October YOY herring were 40–100 mm SL and their average WBEC was 4.4 kJ·g^{-1} wet weight (Figures 3C, 4A). There was a weak linear relationship between standard length and WBEC for YOY in August ($r^2 = 0.69$; $P < 0.0001$) and October ($r^2 = 0.42$, $P < 0.0001$), but considerable variation in WBEC was evident (Figures 3B, 3C). There were significant differences in the median values for WBEC of YOY herring (Figure 4A) for the 3 times they were captured (ANOVA, $P < 0.0001$).

1997 Findings

The WBEC of herring that survived the winter of 1996–1997 typically ranged from 3.5–6 kJ·g^{-1} wet weight, but a few fish >130 mm SL were 6–8 kJ·g^{-1} wet weight

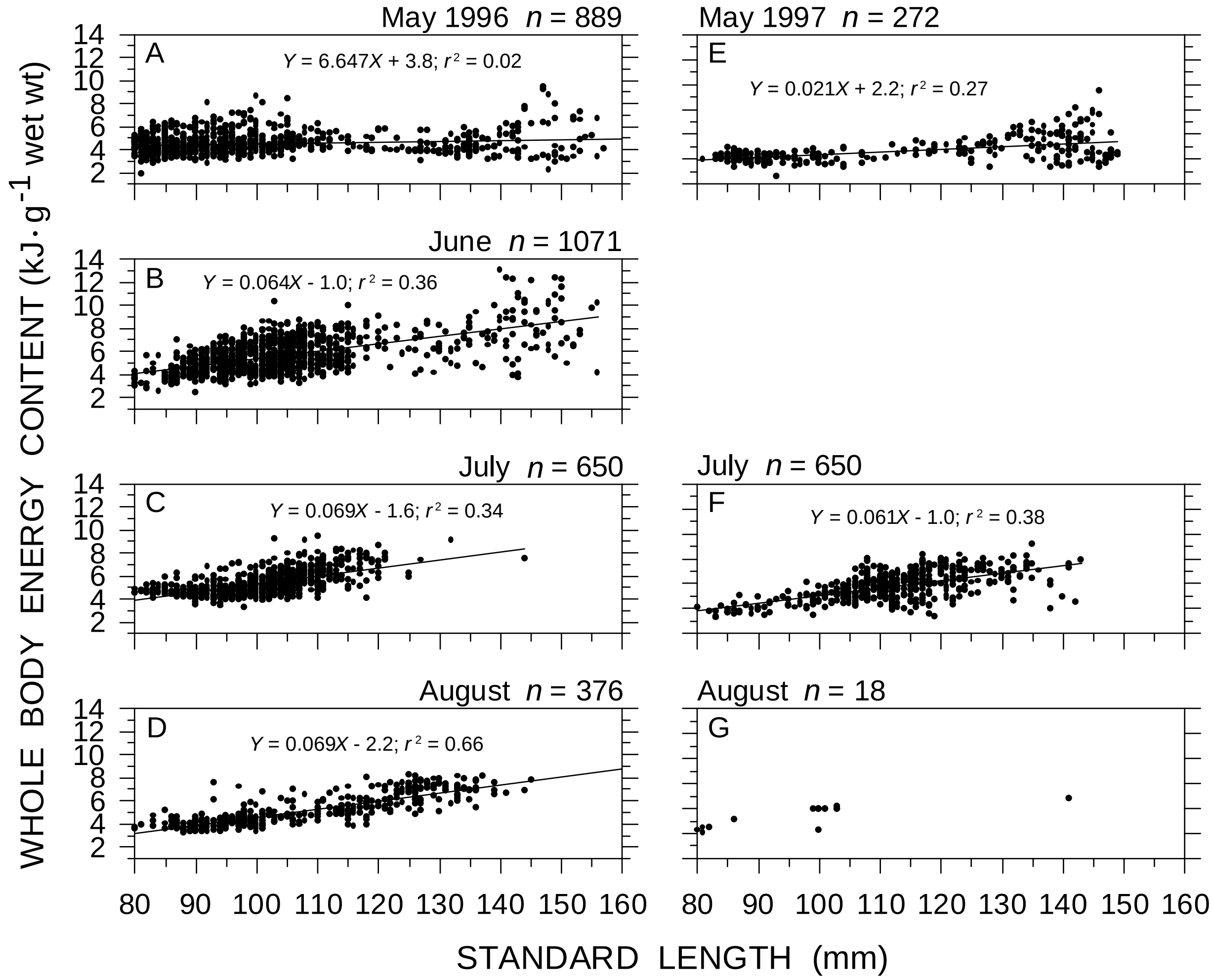

Figure 2. Whole body energy content kJ·g^{-1} wet weight relative to standard length for juvenile Pacific herring that had overwintered prior to capture in Prince William Sound, Alaska, May to October 1996 and 1997.

(Figure 2E). No fish older than age 1 were captured in June. By July those >80 mm averaged 5.7 kJ·g^{-1} wet weight. In August and October few fish >80 mm SL were captured. As in 1996, the only linear relationships between standard length and WBEC were weak and occurred during May ($r^2 = 0.27$, $P<0.0001$) and July ($r^2 = 0.38$, $P<0.0001$; Figures 2E, F). Too few older fish were captured in August for regression analysis. The ANOVA indicated that WBEC values for these collections of older fish (Figure 4D) were significantly different ($P<0.001$), and the MW tests indicated that fish from May and July were significantly different ($P<0.0001$).

In July, 2 YOY herring groups were present: about 25–35 mm SL and 45–60 mm SL (Figure 3D). All YOY fish had a mean WBEC of 2.4 kJ·g^{-1} wet weight (Figure 4B). In August, YOY were 30–65 mm SL (Figure 3E) and averaged 3.4 kJ·g^{-1} wet weight (Figures 3E, 4B). By October most YOY were 60–100 mm SL (Figure 3F) and averaged 5.5 kJ·g^{-1} wet weight (Figure 4B). The WBEC of YOY herring shown in Figures 3D, 3E, and 3F were significantly different ANOVA ($P<0.0001$). During 1997 the YOY had significantly higher WBECs (MW data from Figure 4A versus 4B) in August ($P = 0.0001$) and October ($P<0.001$) than did the 1996 cohorts.

DISCUSSION

This study was restricted to the summer period, and the data does not illustrate the full seasonal energetic cycle of Pacific herring. In PWS, YOY have the lowest WBEC, and summer somatic energy stores tend to increase until the herring reach sexual maturity. The average October WBEC of YOY herring in PWS is

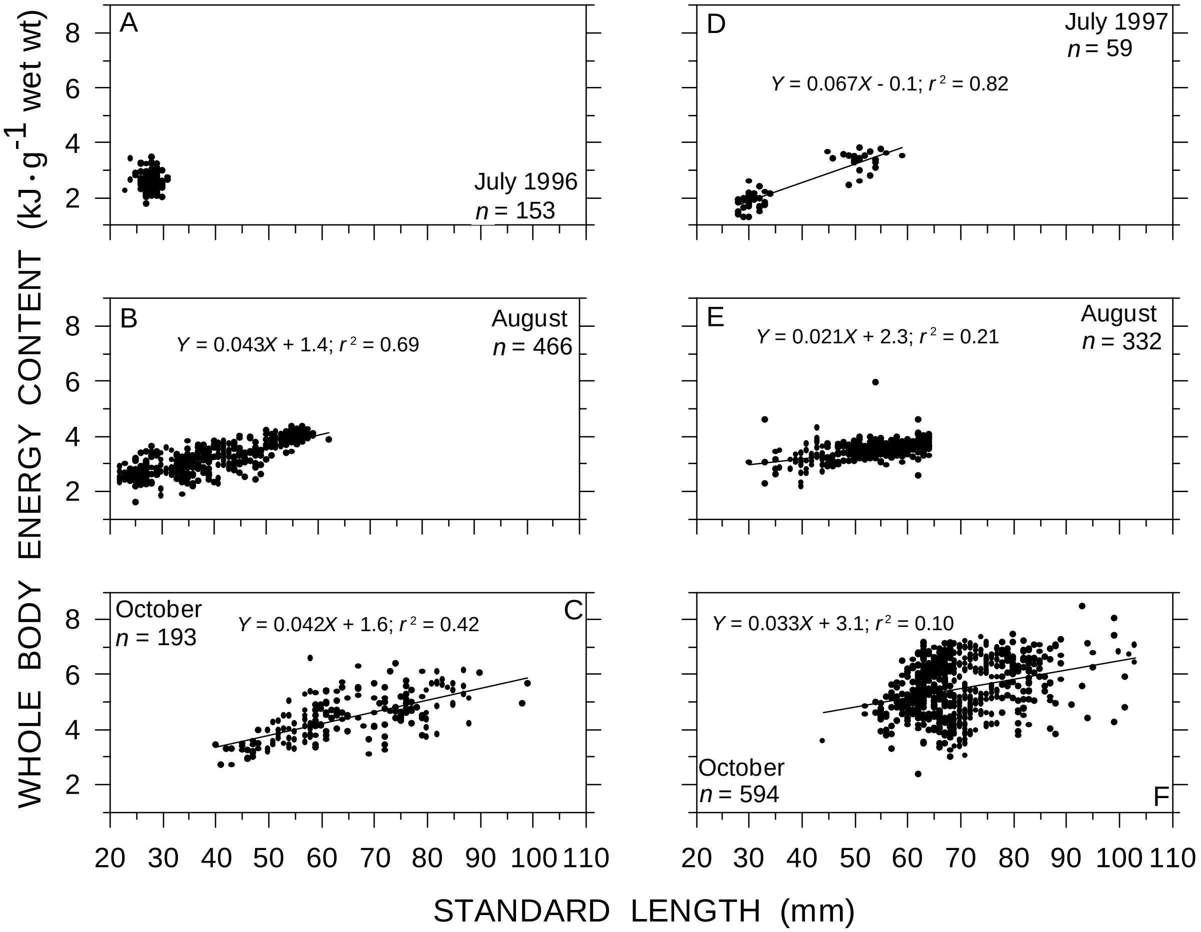

Figure 3. Whole body energy content kJ·g^{-1} wet weight relative to standard length for young-of-year juvenile Pacific herring captured in Prince William Sound, Alaska, May to October 1996 and 1997.

about 4–6 kJ·g^{-1} versus 8–10 kJ·g^{-1} for age 1 and ages 2–7 (Paul et al. 1998). In winter the WBEC of all age classes declines considerably as herring fast. For example, adult herring lose about 40% of their stored energy between October and March (Paul et al.1998).

Tufted *Fratercula cirrhata* and horned puffins *F. corniculata* consume herring <45 mm total length (Hatch and Sanger 1992). In PWS, herring this small would not occur until July when they typically have WBECs of about 2–4 kJ·g^{-1} wet weight. Kittiwakes *Rissa tridactyla* in PWS eat primarily YOY (67%) and some age-1 herring (16%; Irons 1992). So apparently all 3 avian predators target size groups with the lowest WBEC. This selectivity may be related to the size of fish they can catch or the energetic cost of catching them.

The wide variation in juvenile Pacific herring WBEC (Figures 2, 3) also occurs in Atlantic herring *C. harengus* (Blaxter and Holliday 1963; Arrhenius and Hansson 1996.) and adult Pacific herring (Paul et al. 1998). However, these temporal and life history-based differences in WBEC are often ignored in predator studies. For example, in estimating the impacts of foraging murres *Uria aalge* and sooty shearwaters *Puffinus griseus* on Pacific herring in British Columbia, Canada, the WBEC value assigned to all herring age 0–2 was 7.03 kJ·g^{-1} wet weight (Logerwell and Hargreaves 1997). This value is considerably higher than any we measured for age-0 and most age-1 herring captured in PWS. These investigators also assumed murres occupied the British Columbia study area all year, and shearwaters were there for 180 d. Over such long periods the WBEC of herring should change considerably (Figures 2, 3). From May to October, the WBEC of YOY (age-0) PWS herring increased about 1 kJ·g^{-1} wet weight per month. Over the winter adult

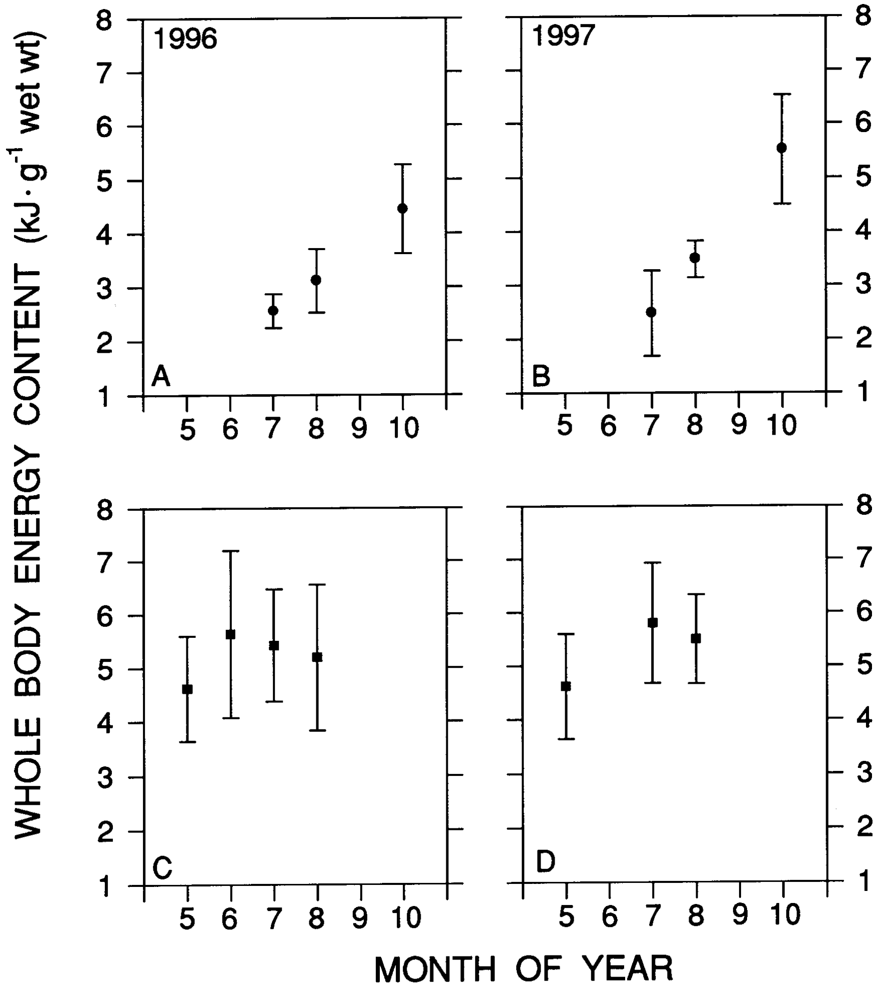

Figure 4. Whole body energy content kJ·g^{-1} wet weight for young-of-year (A, B) and older juvenile Pacific herring (C, D) captured in Prince William Sound, Alaska, May to October 1996 (A, C) and 1997 (B, D).

herring lost a total of 4 kJ·g^{-1} or more wet weight (Paul et al. 1998).

Variations in WBEC relative to age and season must be recognized in predator consumption models to obtain accurate results. Future studies also need to examine WBEC of herring eaten by avian or other predators to determine if they tend to capture herring in poorest or best condition.

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Postnote

► 99 Aug 30 — Captions for Figures 2 and 3 were inadvertently reversed in the intial full-issue printing of this article and distributed full-issue copies of this Bulletin still contain this error. The order of the figures and the captions themselves have been corrected in this online version and all reprints of this article. See also Errata.

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