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Reprinted from the Alaska Fishery Research Bulletin Vol. 6 No. 1, Summer 1999 $The Alaska Fishery Research Bulletin can found on the World Wide Web at URL: \ \underline{http://www.state.ak.us/adfg/geninfo/pubs/afrb/afrbhome.htm} \,.$

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ABSTRACT: The energy content of whole bodies (WBEC), ovaries (OEC), and ova taken from ripe Pacific herring *Clupea pallasi* collected from one site in Prince William Sound, Alaska was measured to determine how female nutritional status influenced ova energy content and OEC. The average female WBEC was 23.86 kJ·g⁻¹ dry weight (SD = ± 1.19), and the average energy content of one ovum was 8.1 J (SD = ± 0.9). The WBEC of spawning females varied considerably. No clear relationship was found between either female body weight or WBEC and the mean energy content of ova or OEC·g⁻¹. Well-fed females, those identified by high WBEC, did not have a higher average energy content in their ova. Apparently Pacific herring allocate energy to somatic growth rather than enriching OEC·g⁻¹. This strategy would improve their chances to successfully propagate because bigger females spawn more eggs.

INTRODUCTION

Pacific herring *Clupea pallasi* growth rates, age at maturity, weight at age, and whole-body energy content (WBEC) are highly variable and respond to environmental changes and population size (Ware 1985; Paul et al. 1998). As body weight increases, WBEC (kJ·g⁻¹) tends to increase although there is considerable variability in WBEC relative to fish weight (Paul et al. 1996). In Pacific herring, fecundity increases with body weight (Ware 1985), and intense feeding of captives promoted higher gonad weights (Hay et al. 1988). However, the effect of nutritional state on the energy content of herring ova has not been studied. This information would improve our understanding of herring reproductive strategies.

Fish larvae hatching from eggs with higher yolk content hatch at bigger sizes and have a better chance of survival (see Trippel 1998 for a review). Herring larvae with larger yolk reserves can manage a longer first-feeding phase which enhances their chance of surviving the critical transition from subsisting on yolk to becoming a predator (Blaxter and Hempel 1963). In freshwater walleye (*Stizostedion vitreum*), egg mass dry weight is related to female size, but in white suckers (*Catostomus commersoni*) it is not (Johnson 1997). Larval size is related to egg energy reserves in both those freshwater species (Johnson 1997). In Pacific herring, the relationship between female size and egg energy content is undescribed. Our objective in this study was to determine if herring with high OEC or WBEC allocated more energy to ova to increase larval survival potential, or if they produced more eggs without enhancing ova energy content. We measured the mean ova energy content of Pacific herring relative to female weight, ovarian energy content (OEC) and WBEC.

METHODS

Fish Collection

Adult female herring (n = 49) were collected with commercial herring purse seines (182 m diameter, 22 m deep, 3 cm mesh) deployed on 15 April 1997 in Port Chalmers, on the west side of Montague Island in Prince William Sound (PWS). The Alaska Department of Fish and Game continually monitored ovarian ripeness in the spring. Their staff collected adult fish for this study when herring aggregated near the spawning beaches, but before spawning commenced. Females were fro-

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Acknowledgments: J. Wilcock, Alaska Department of Fish and Game — collected fish for the study. P. Shoemaker, C. Adams and R. Schmidt — helped with laboratory procedures. This is Institute of Marine Science Report 2568.

Project Sponsorship: This study was funded by the *Exxon Valdez* Oil Spill Trustee Council through the Sound Ecosystem Assessment project.

zen immediately upon collection. None of the 49 fish exhibited any obvious evidence of debilitating disease or parasites.

Tissue Energy

The fish were partially thawed in the laboratory for measurement, but not enough so that the carcass lost fluids. The partially-thawed fish were measured for standard length to the nearest millimeter and weighed to the nearest 0.1 g. The ovaries were removed from the body cavity and weighed to the nearest 0.01 g. A 20- to 50-g subsample of one ovary was taken and

set aside for later analysis. In Pacific herring, sampling both ovaries is unnecessary because fecundity estimates from either ovary usually agree to within 4% (Hay and Brett 1988). Because the fish were collected prior to the spring zooplankton bloom during a period when herring are not actively feeding (Wootton 1985), prey contribution to WBEC was assumed to be minimal. None of the fish stomachs were distended. In our fish, the ripe ovaries filled the body cavity leaving little room for filling the stomach. The remainder of the ovary and the body were recombined and ground while partially frozen, then made into a paste in a mortar. A 30-g subsample of the whole body was freeze dried until no

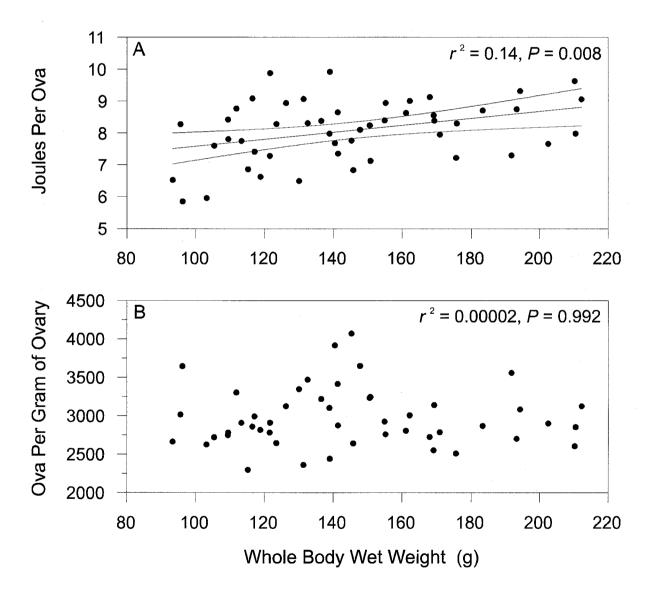


Figure 1. Average energy content of ova (Joules per ova; A) and the number of ova per gram of dried ovary (B) relative to the whole body wet weight (grams) of ripe Pacific herring females. The linear regression line ±95% confidence lines are plotted (A).

moisture was apparent, then it was dried to a constant weight in a convection oven at 60°C. Dried tissues were ground in a mill and measured for caloric content using bomb calorimetry. The WBEC of each individual (minus the ovary subsample) was determined as kJ·g⁻¹ dry weight. All calorimetric samples were weighed to the 0.0001-g level with a single 1-g WBEC sample burned per fish. The wet ovary subsample was weighed to the nearest 0.0001 g, and all ova in it were counted. These subsamples typically contained about 50 to 100 ova. Because the fish were ready to spawn, the clumps of ova could be separated by physical manipulation and then counted using a dissecting microscope. Then the ovary subsample was dried to a constant weight using the above methods. The number of ova in one gram of dried ovary was estimated from the number of ova in the dried subsample.

Dried ovarian tissues were then ground in a mill and OEC measurements in kilojoules were made by bomb calorimetry. The whole ovarian subsample was burned in the calorimeter. This procedure provided estimates of OEC g^{-1} dry weight and the average energy content of one ovum.

Linear regression analysis was used to examine the relationships between weight, WBEC and energy content of ovaries and ova.

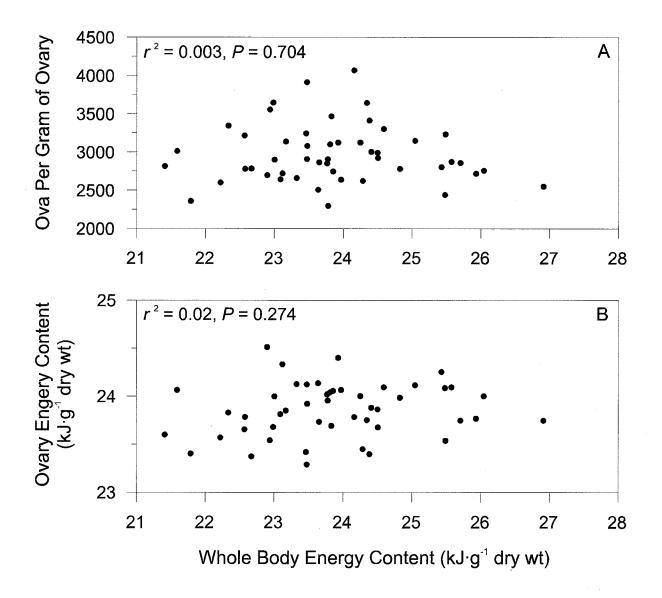


Figure 2. The number of ova in one gram of dry ovary from ripe Pacific herring (A) and the energy content of ovarian tissue (kJ·g⁻¹ dry weight; B) relative to female whole-body energy content (kJ·g⁻¹ dry weight).

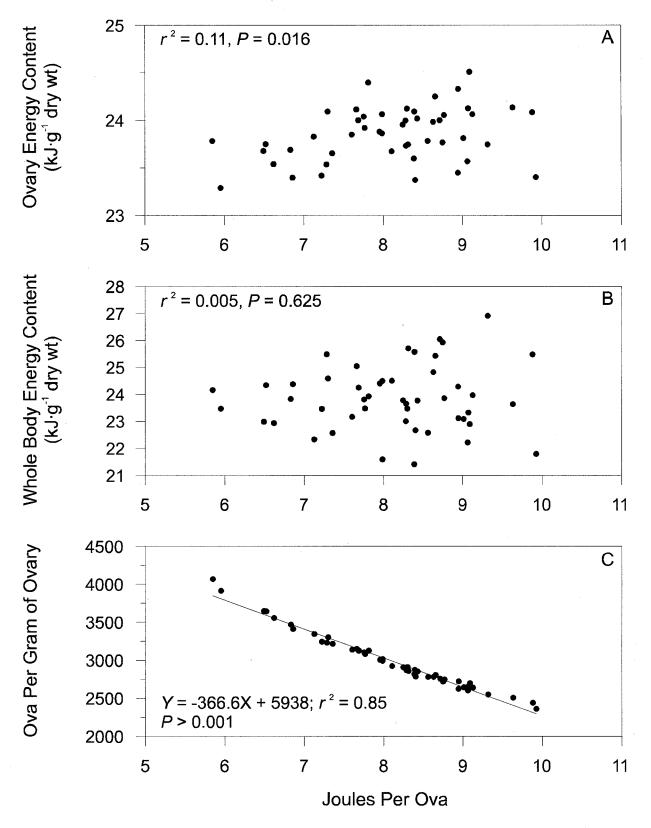


Figure 3. The energy content of ovarian tissue (kJ·g⁻¹ dry weight; A), female whole body energy content (kJ·g⁻¹ dry weight; B), and number of ova in one gram of dried ovary (C) relative to the average energy content (Joules) of ova of ripe Pacific herring.

RESULTS AND DISCUSSION

The examination of whole body weight and OEC identified females with the most energy-rich ova. We found poor relationships between body weight and the average energy content of ova ($r^2 = 0.14$, P = 0.008; Figure 1A), and body weight and the number of ova per gram of dry ovary ($r^2 = 0.00002$, P = 0.992; Figure 1B). The average WBEC of the 49 females was 23.86 kJ·g⁻¹ dry weight (SD = ± 1.19), and the average energy content of one ovum was 8.1 J (SD = ± 0.9). Ware (1985) found egg weight tended to increase when the body weight of female Pacific herring increased. However, Ware reported much variability in the relationship of egg and body weights. In our single PWS collection, there was no indication heavier females consistently produced energy-rich ova (Figure 1A). Further sampling from other sites is needed to verify the accuracy of this finding.

Ova counts and OEC kJ·g⁻¹ dry weight could not be predicted from female WBEC. No significant relationship was detected between the number of ova per gram of dry ovary and WBEC kJ·g⁻¹ dry weight ($r^2 =$ 0.003, P = 0.704; Figure 2A). Similarly, a relationship between OEC kJ·g⁻¹ dry weight and WBEC kJ·g⁻¹ dry weight $(r^2 = 0.02, P = 0.274)$ was not apparent (Figure 2B). Neither the energy content of one ovum $(J \cdot ova^{-1})$ relative to OEC kJ·g⁻¹ dry weight (Figure 3A) nor the WBEC $kJ \cdot g^{-1}$ dry weight (Figure 3B) were strongly correlated. The number of ova in one gram of ovary (Y) and the average energy content of an ovum (X) were linearly correlated (Y = -366.6X + 5.938); $r^2 = 0.85, P < 0.0001$; Figure 3C). Females with fewer energy-rich ova per gram of ovary (Figure 3B) could not be identified by their weight (Figure 1) or WBEC (Figure 2).

Pacific herring females with high WBEC levels, or heavy body weights, did not allocate more energy to OEC·g⁻¹, nor was the average energy content of their ova consistently higher than females in poorer nutritional condition (Figures 1, 2, 3). This is also the situation for another clupeid, the northern anchovy *Engraulis mordax*. In that species, the egg energy content is not altered by either food quantity or quality (Hunter and Leong 1981). Ware (1985) reported that the reproductive rates of Pacific herring in Canadian management areas were remarkably constant, but he did not examine egg energy content. In other species like *S. vitreum* and *C. commersoni*, the quality of eggs produced varies interannually (Johnson 1997).

In PWS, there appears to be only slight differences in OEC·g⁻¹ between groups of females and between years (Paul et al. 1996). The average energetic content of dried ripe herring ovaries in this study was 23.86 (SD = ± 0.28) kJ·g⁻¹ dry weight, a value identical to our average WBEC measurements. Pacific herring OEC was also similar to egg energy values reported for other species. The average energy content of newly spawned eggs and ovaries for 50 other teleost species was 23.48 kJ·g⁻¹ dry weight (Wootton 1985).

There are 2 methodological considerations in interpreting our characterization of WBEC and OEC relationships. Because we did not separate ovary from other body tissue, we could not determine the relationships between somatic energy content and OEC. Combining somatic and ovarian tissues could mask small differences in the reported relationship between WBEC and OEC. Additionally, the energy values of ovarian tissue in some fish species differ from that of recently spawned eggs (Wootton 1985). The average ovary energy content in *E. mordax* is 23.89 kJ·g⁻¹, but the egg energy content is 22.80 kJ·g⁻¹ (Hunter and Leong 1981). Without similar measurements for Pacific herring, we do not know if ova and spawned eggs have similar energy content.

Pacific herring maximize reproductive output when feeding conditions are good by maturing early and increasing overall body weight (Ware 1985). This is advantageous because larger females produce more eggs than smaller ones (Ware 1985; Paul et al. 1996). Increasing body size and somatic energy reserves has additional survival value for Alaskan herring because adults rely heavily on stored energy to overwinter (Paul et al. 1998). Obtaining a high body weight or WBEC does not insure ova will be energy rich (Figures 1, 2). This finding suggests the production of energy-rich ova may be genetically determined, with some females producing fewer high-energy ova per gram of ovary (Figure 3C) regardless of their nutritional status as measured by WBEC (Figure 3B).

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