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ABSTRACT: Ovarian energy content (OEC; measured in kilojoules) of ripe whole ovaries and per gram of ovary wet weight (OEC·g^{-1}) were examined for Pacific herring *Clupea pallasi* from Prince William Sound, Alaska. Specimens were collected in 1995 and 1996. The OEC of whole ovaries was related linearly to whole body weight, but OEC·g^{-1} of ovary was not. Just prior to spawning OEC was typically between 5 and 7 kJ·g^{-1} of ovary. There were no significant differences in OEC·g^{-1} of ovary between groups of females from different capture sites in the 1995 collections, but in 1996 there were small but significant differences in OEC values related to capture site. When the OEC values from all fish collected in 1995 were pooled and compared to all those collected in 1996, there was no significant difference in OEC·g^{-1} of ovary between years. The number of ova present just prior to spawning exhibited no clear relationship to OEC·g^{-1} of ovary. About 97% of OEC was expended during spawning. The OEC of whole ovaries was used to estimate the energy from herring spawn added to Prince William Sound beaches from 1988 to 1995. Since 1989, when there was a massive oil spill, the annual amount of energy added to the Prince William Sound ecosystem by herring eggs has decreased from 68 x 10^9 kJ to 10 x 10^9 kJ in 1995, which in addition to being a concern for recruitment, could also be important to species relying on herring spawn as an energy source.

INTRODUCTION

Following the *Exxon Valdez* oil spill in 1989 there has been increased prevalence of disease and poor recruitment of Pacific herring *Clupea pallasi* in Prince William Sound, Alaska, and commercial fisheries were curtailed or reduced between 1993 and 1997. As a result a suite of projects were funded that examine fecundity, models of egg mortality due to oil, physical factors, and avian and fish predation (Rooper 1996; Brown and Debevec *in press*). These projects are ongoing and few publications have resulted as yet. Additionally, the Sound Ecosystem Assessment (SEA) project is examining the trophic relationships that support Pacific herring and other species injured by the oil spill.

Many of the species injured by the oil spill are linked to herring as predators or competitors. Herring store fat during spring and summer to survive winter declines in the abundance of their zooplankton prey (Blaxter and Holliday 1963). During late winter stored energy is also allocated to gonadal products for the spring spawning (Hay et al. 1988), when eggs are deposited in intertidal and shallow subtidal areas. During recruitment the largest loss to a herring year class occurs in the egg stage, mortalities effected by waves, anoxia, desiccation, and predation (Rooper 1996). Herring eggs on kelp are harvested commercially and for subsistence use. Ongoing companion studies to this project found that hexagrammid fish ate 2–9% of the herring eggs at Prince William Sound study sites and sea birds in other North Pacific sites have consumed 3–95% of herring eggs deposited in the intertidal zone (Rooper 1996). The method used to estimate egg loss to avian predators was a bioenergetic model linking predator metabolic requirements, prey selection information, and predator abundances to food item energy content. A key component of such models is an esti-

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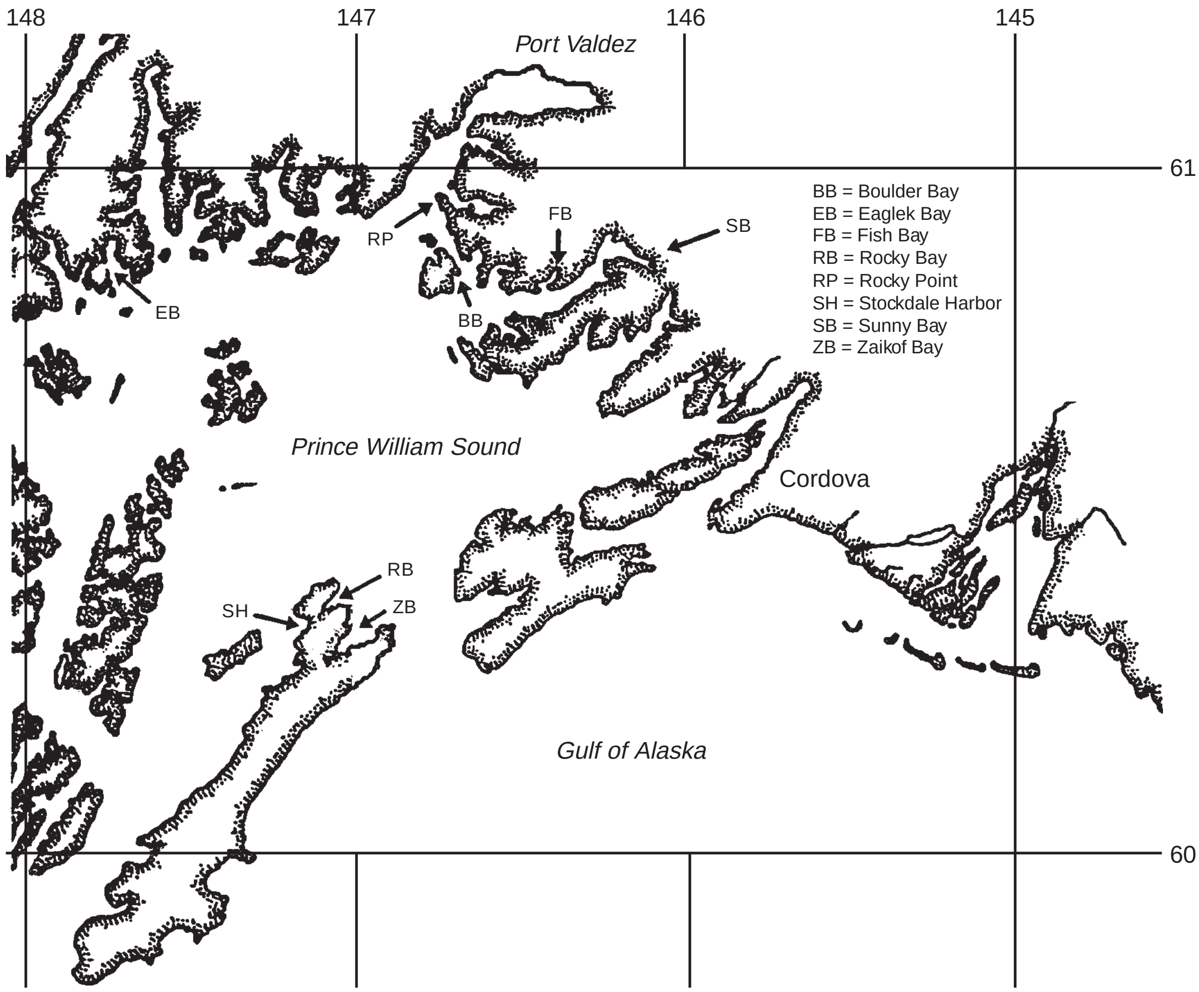

Figure 1. The 1995 and 1996 locations in Prince William Sound, Alaska, where Pacific herring were captured to measure ovarian energy content. Sampling sites are marked with arrows and initials.

mate of the amount of energy in the herring spawn. Because information on the amount of energy released during spawning of Pacific herring was lacking, this became the objective of our study. In herring, ovary size is related to body weight, and thus age (Blaxter and Holliday 1963), so we quantified the relationship of ovarian energy content (OEC) to size and age. We also examined geographic and interannual differences in OEC·g^{1}.

METHODS

Colleagues in the Alaska Department of Fish and Game, who were monitoring gonad ripeness of the herring run in Prince William Sound for a possible roe fishery opening, collected adult herring just prior to and after spawning. We used some of those fish in this study and selected females from several sites (Figure 1) when the product quality was at its peak, indicating spawning was imminent. Females were frozen immediately upon collection. In 1995, females were collected from 14 April to 14 May at 3 sites: Eaglek Bay in northern Prince William Sound (n = 35), Fish Bay in Port Fidalgo (n = 29), and Rocky Bay on Montague Island (n = 46). Just after the spawning was completed 26 spent females were also collected from Zaikof Bay on Montague Island. In 1996, females were collected on 15–16 April at 5 sites: Boulder Bay (n = 40) on Bligh Island, Rocky Bay (n = 50) on Montague Island, Rocky Point (n = 50) in northeastern Prince William Sound, Stockdale Harbor (n = 50) on Montague Island, and Sunny Bay in Port Fidalgo (n = 47). No postspawned (spent) females were collected in 1996.

Each fish was partially thawed in the laboratory for measurement but not enough so that the carcass lost fluids. The females were measured for whole-body wet weight to 0.1 g. Both ovaries were removed and weighed to the nearest 0.1 g. Then a subsample weighing about 0.1 g was removed from 1 ovary and weighed, and all eggs in it were counted. These subsamples typically contained about 100 eggs. The number of ova in the ovaries was estimated from the number of ova in the subsample expanded by the entire ovary weight. In Pacific herring, subsamples from both ovaries are unnecessary because fecundity estimates from either ovary usually agree to within 4% (Hay and Brett 1988). Because the fish were ready to spawn, the clumps of eggs could be separated by physical manipulation and then counted under a dissecting microscope. The gonosomatic index was determined by dividing ovary weight by wet body weight. The relationship of gonosomatic index to OEC was examined to illustrate the variability associated with differing degrees of ripeness inherent in the samples and attributable to slight gonadal maturation differences.

Ovarian subsamples of 10–15 g measured to the nearest 0.1 g were removed from each ripe female for OEC measurements. After freeze drying for 24 h, ovarian tissues were placed in a convection oven at 60°C until they reached a constant weight. These wet and dry weights were used to calculate the moisture content. Dried tissues were then ground in a mill and OEC measurements in kilojoules were made by bomb calorimetry. OEC per gram of wet weight ($OEC \cdot g^{-1}$) was calculated using the percent moisture in the ovary subsample. The energy content of whole ovaries was obtained by multiplying $OEC \cdot g^{1}$ by the corresponding ovary weight.

Energetic estimates of whole ovaries just after spawning were obtained from females collected at Zaikof Bay on 2 April 1995. The whole ovary was weighed and treated as above for energy measurement. Whole dried ovaries were combusted for each calorimetric analysis.

Scales for aging were removed from every fish just above or below the lateral line, 3 rows behind the operculum. They were cleaned manually, mounted on glass slides, and read using a microfiche reader. Annuli were counted in the conventional manner; age equals number of annuli because herring in Prince William Sound hatch in the spring.

The interrelationships between size/age and OEC were graphed and analyzed using SIGMASTAT[1] and

[1] Mention of a trade name is included for scientific completeness and does not imply endorsement by the authors or the Alaska Department of Fish and Game.

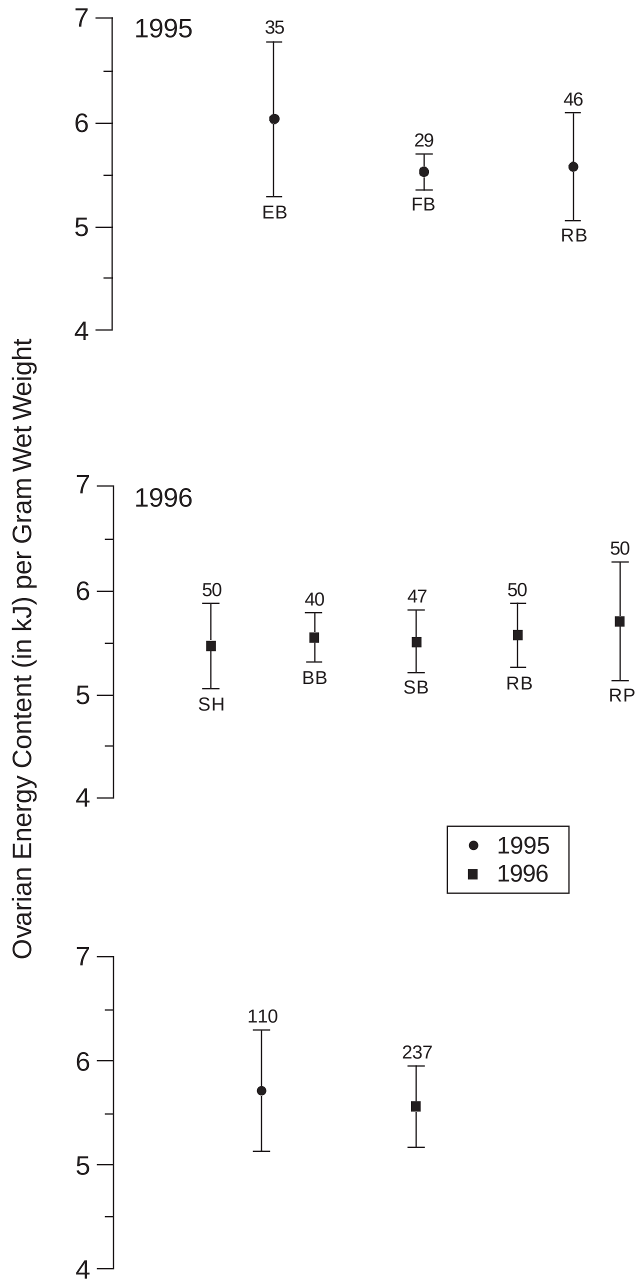

Figure 2. Energy content per gram of ripe ovaries in Pacific herring from Prince William Sound collected at 3 sites in 1995 (upper panel), 5 sites in 1996 (middle panel), and all females combined from 1995 and 1996 (lower panel). Data are mean and standard deviation; the number of fish in the sample appears over each data plot; the 2 letters under each plot represent the collection site as defined in Figure 1, except the bottom panel represents all sites combined.

SIGMAPLOT[1] software. To compare OEC by site and year the statistical tests included the Mann-Whitney Rank Sum Test (MW) and the Kruskal-Wallis ANOVA on Ranks (KWANOVA).

RESULTS

Ovarian Energy Content

In 1995 the OEC·g[1] was not significantly different (P = 0.126, KWANOVA) for females collected at the 3 sites (Figure 2). The average OEC for all ripe females (n = 110) collected in 1995 was 5.7 kJ·g^{-1} (SD = ±0.6; Figure 2). All 110 measurements for the 1995 fish were combined to improve the sample size. The pooled data for OEC·g^{-1} exhibited little relationship to age or wet body weight (Figure 3); there was also no apparent relationship between ovary weight and OEC·g[1] (r^2 = 0.13, P = 0.0001).

In 1996 the average OEC for all the ripe females (n = 237) in the 5 collections was 5.6 kJ·g[1] (SD = ±0.4;

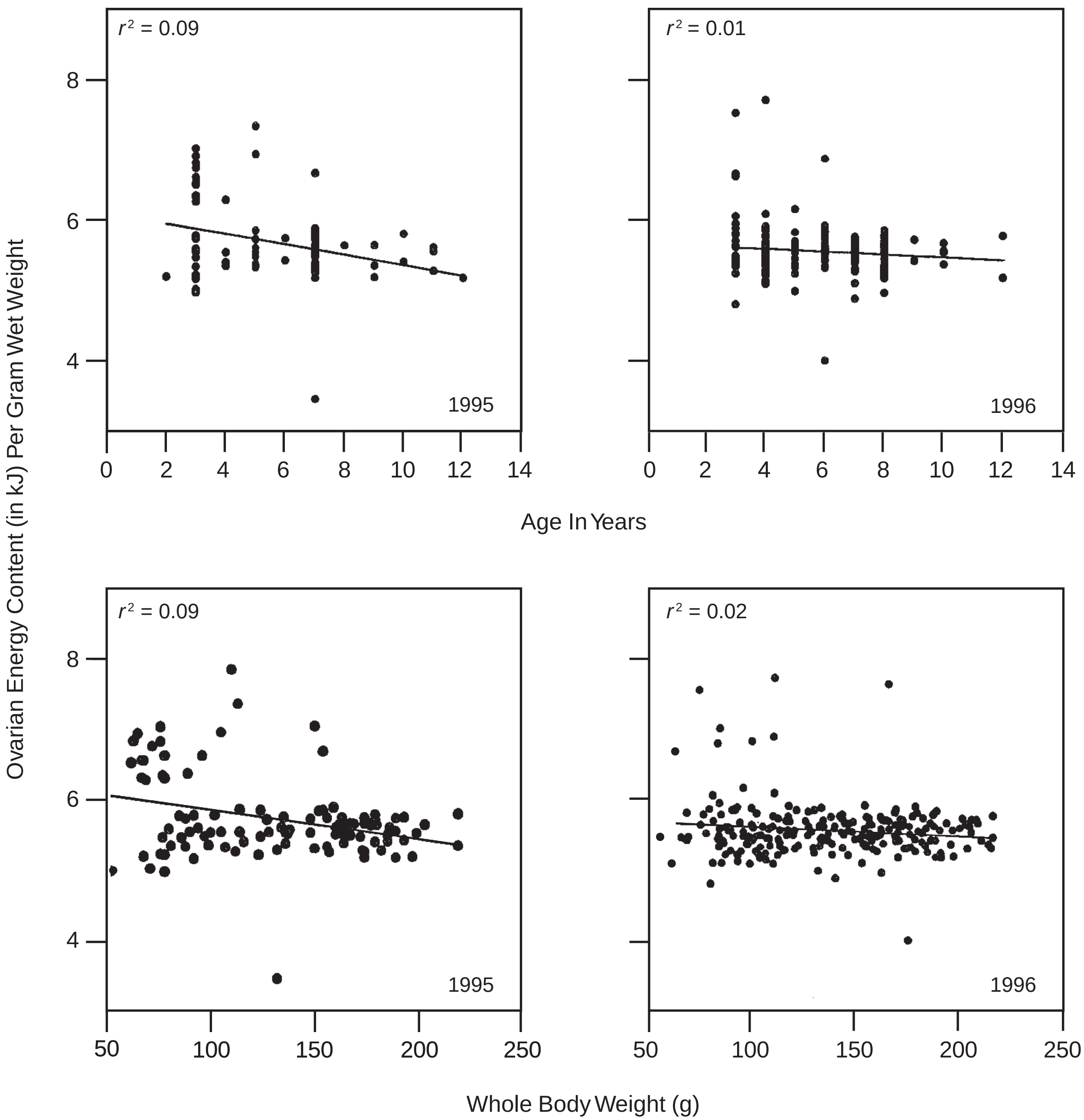

Figure 3. Energy content per gram in ripe Pacific herring ovaries from Prince William Sound collected in 1995 (left panels) and in 1996 (right panels) relative to age (upper panels) and body weight (lower panels).

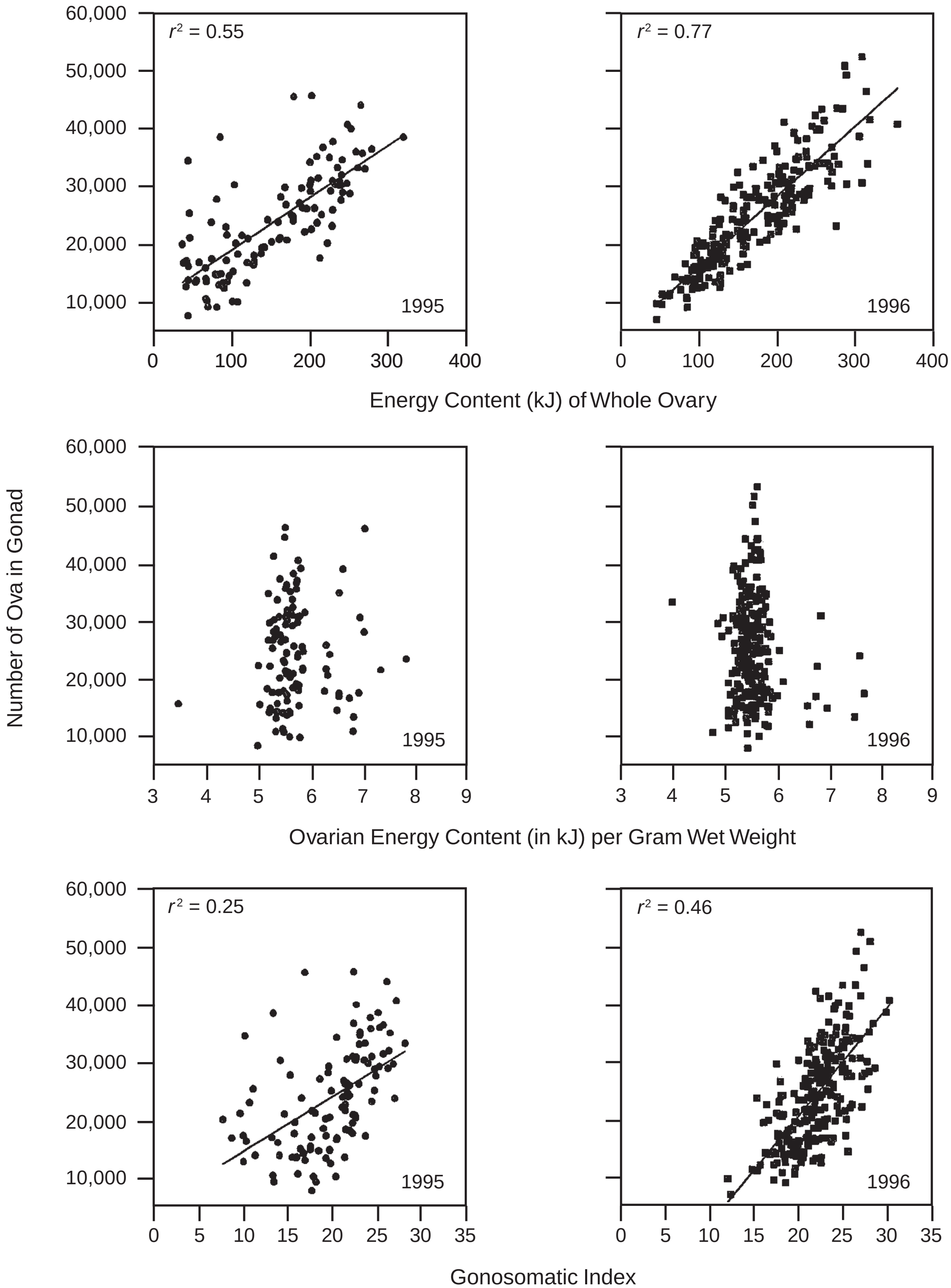

Figure 4. Number of ova in gonads of prespawning Pacific herring from Prince William Sound collected in 1995 (left panels) and in 1996 (right panels) relative to whole ovary energy content (upper panels), ovarian energy content per gram wet weight (middle panels), and gonosomatic index (lower panels).

Figure 2). The differences in the median OEC·g^{-1} values between the 1996 collection sites were greater than would be expected by chance (P = 0.0000006, KWANOVA), but the site-related variations were relatively small (Figure 2). There was no apparent relationship between age or wet body weight and OEC·g^{-1} in the 1996 samples (Figure 3). As in 1995 there was no obvious relationship in 1996 between ovarian weight and OEC·g^{-1} (r^2 = 0.02, P = 0.016) for the 237 values. There was no significant difference (MW test) between the OEC·g^{-1} for ripe females collected in 1995 and 1996 (P = 0.070; Figure 2 lower panel).

Number of Ova

The number of ova in ripe ovaries showed no predictable relationship to the OEC·g^{-1} or to the gonosomatic index (Figure 4). The number of ova in prespawning ovaries showed a relatively weak relationship to the energy content of whole ovaries in 1995

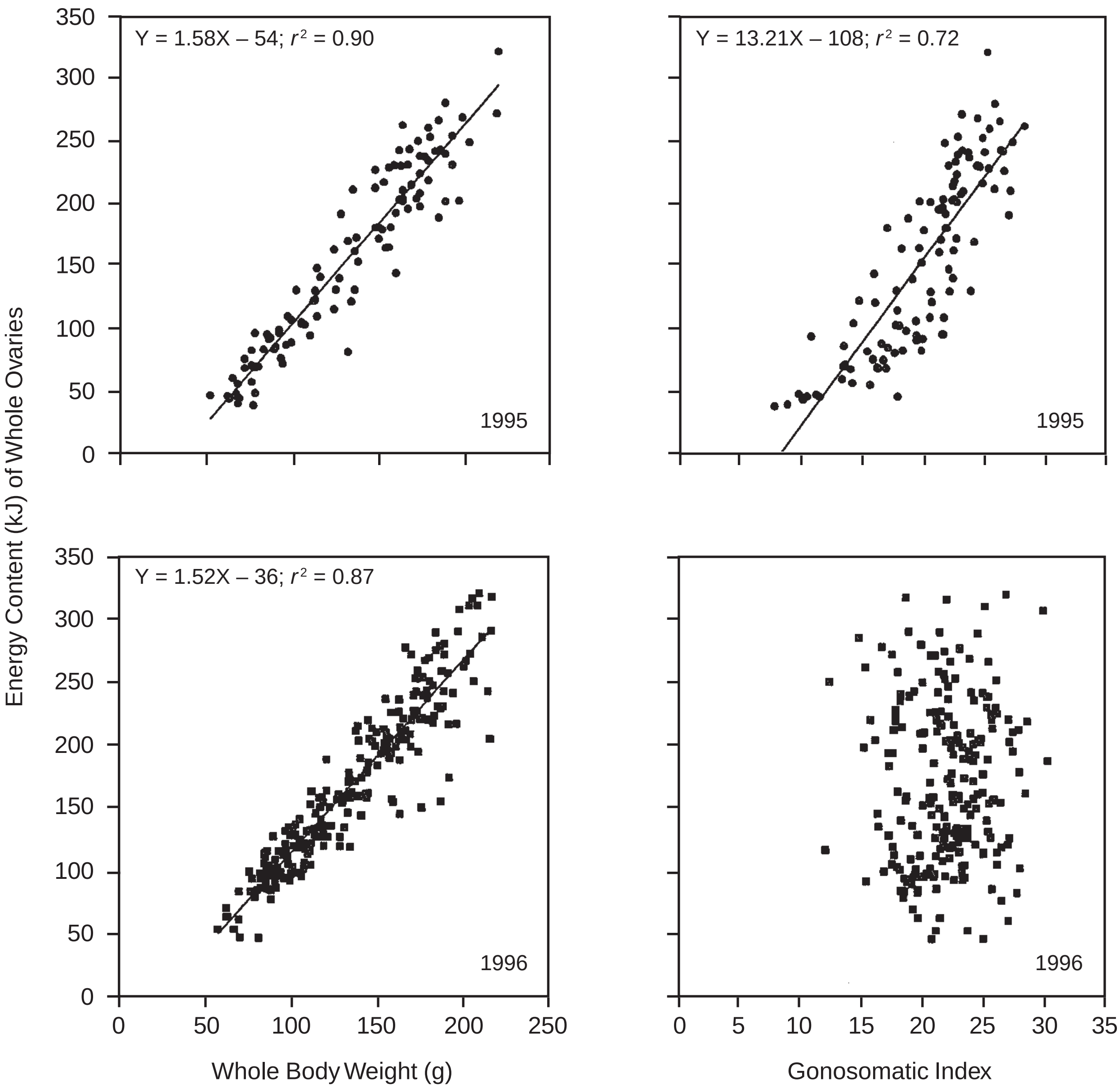

Figure 5. Energy content of whole ovaries in ripe Pacific herring from Prince William Sound collected in 1995 (upper panels) and in 1996 (lower panels) relative to wet body weight (right panels) and gonosomatic index (left panels).

($r^2 = 0.55$, $P < 0.0001$) and a stronger one in 1996 ($r^2 = 0.77$, $P < 0.0001$; Figure 4). The ovaries of spent females were very small and contained almost no unspawned eggs.

Whole Ovarian Energy Content

Whole ovarian energy content was correlated with body weight ($r^2 \geq 0.76$, $P < 0.0001$; Figure 5). Whole ripe ovaries typically contained 50–300 kJ (Figure 5). The linear relationships between the energy content for whole ovaries and fish weight in 1995 and 1996 had slightly different regression equations, but the differences were small (Figure 5). In 1995 whole ovarian energy content (Y) was related ($r^2 = 0.99$, $P < 0.0001$) to ovary weight (X) by the equations: Y(kJ) = $5.4X + 4.8$. In 1996 this relationship, Y(kJ) = $5.4X + 3.7$, was also correlated ($r^2 = 0.98$, $P < 0.0001$). Whole ovarian energy content was not strongly related to the gonosomatic index (Figure 5).

Whole ovarian energy content of spent females averaged 0.9 kJ (range 0.1–6.0) showing that most of the energy contained in the ovaries was expended with spawning (Figure 6). The spent ovaries consisted primarily of structural tissues and very few eggs. In 1995 a typical 150-g female, during spawning, expended about 97% of the energy stored in the ovary.

DISCUSSION

Ovaries of spawned-out Pacific herring typically weigh <1 g because most of the material in the ovary is expended upon spawning (Hay and Brett 1988). However, no previous measurements of OEC were located in the literature for ripe or spent Pacific herring; our measurements indicated about 97% of the prespawning OEC was expended during spawning.

In Pacific herring, weights of both ovaries and eggs tend to increase with body wet weight (Ware 1985) and ration (Hay and Brett 1988; Hay et al. 1988). Thus, conditions that promote larger-than-average females allow for more reproductive output for those individuals. If large eggs have more energy reserves than small ones, then our OEC data hints that this is due simply to the egg weight, not some increase in OEC·g[1]. However, this is speculative because the relationship between Pacific herring egg size and its energy content per gram has not yet been measured.

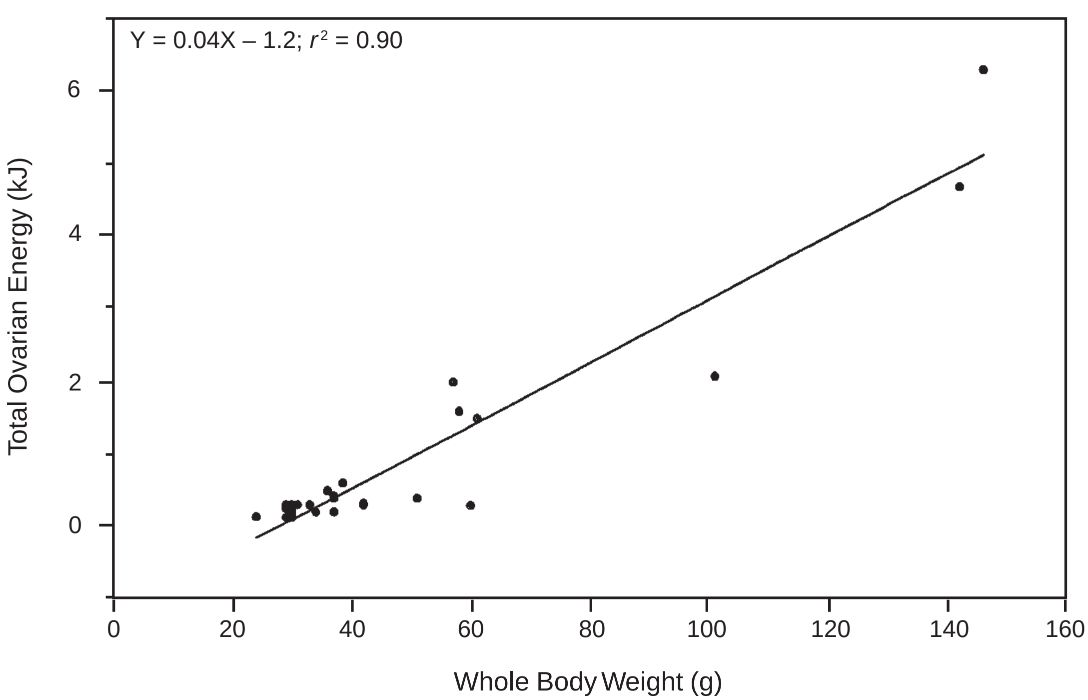

Figure 6. Energy content (kJ) of whole ovaries in spent Pacific herring from Prince William Sound collected in 1995 relative to wet body weight.

In Pacific herring, regional or interannual variations in prey availability appear as differences in body growth (Ware 1985), and hence whole ovary weights may be similarly affected. However, this study suggests there may not be large differences in OEC·g^{-1}, but examination of OEC should be conducted over more years to verify this hypothesis.

In Prince William Sound each year the population of mature herring is assessed to set the harvest levels of the roe fishery; age and body weight measurements are also recorded. That data, along with these OEC measurements, can be used to estimate the energy content of the annual spawning. We calculated spawning run OEC based on (1) mean numbers of females from the 1988–1995 Prince William Sound roe fishery spawning run samples, (2) age-specific spawning run biomass estimates (Figure 7), (3) the assumption that 97% of ovarian energy is released during spawning, and (4) the 1995 body weight equation in Figure 5. That spawning run OEC estimate shows a marked decline in the amount of energy supplied to Prince William Sound by herring spawn since 1992 (Figure 8). This decline in spawning run OEC is primarily due to decreased female biomass (Figure 7). In 1991 there was a good recruitment of age-3 fish that resulted from the 1988 pre-oil spill spawn, but comparatively few females recruited from the 1992 to 1995 year classes. The effect of such large interannual variations in the kilojoules of input to the ecosystem from herring eggs is unknown but may be significant. If egg predator populations remain stable or increase while the amount of herring spawn decreases, predation could limit recruitment. Our size-OEC relationships can be used to make more sophisticated estimates of ovarian energy input into Prince William Sound in models incorporating detailed individual fish information available in the extensive Alaska Department of Fish and Game herring fisheries database. These in turn can be used in egg-predator consumption estimates and herring recruitment models based on energetics.

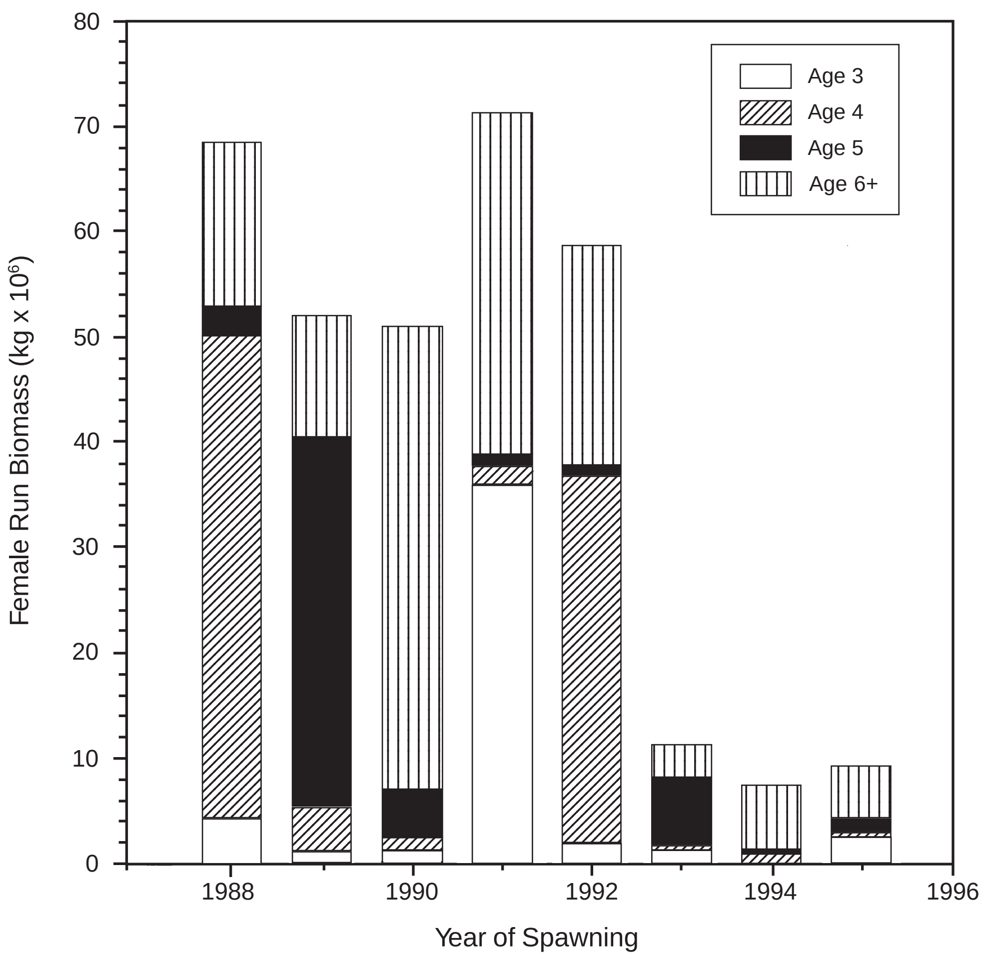

Figure 7. Spawning run biomass of adult female Pacific herring in Prince William Sound from 1988 to 1995.

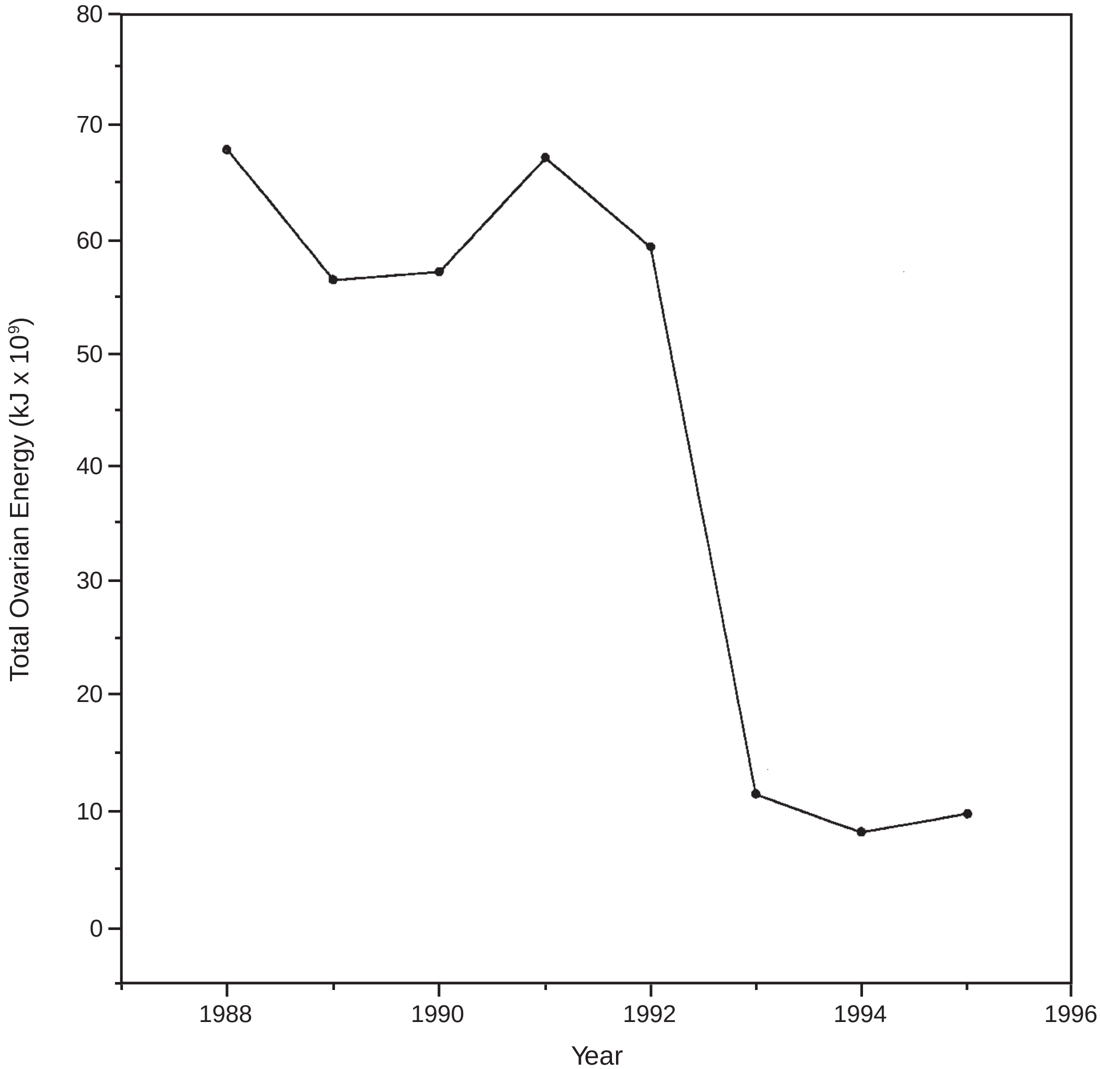

Figure 8. Estimated total ovarian energy (kJ) in Pacific herring eggs deposited each spring in Prince William Sound from 1988 to 1995.

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