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Energy and ration requirements of flathead sole (*Hippoglossoides elassodon* Jordan and Gilbert 1880) based on energy consumption and growth

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In flathead sole (*Hippoglossoides elassodon*) growth was linearly related to energy consumption (J g^{-1} day^{-1}) at 4°C by the following equation: growth (%bw day^{-1}) = 0.006 (consumption J g^{-1}) − 0.130; r^2 = 0.80. Growth was independent of size for fish between 1 and 350 g when growth was expressed as a function of consumption in J g^{-1} day^{-1}. Maintenance ration determined in feeding – growth experiments was 21.7 J g^{-1} day^{-1} at 4.0°C.

Minimum estimates for daily ration to achieve growth rates observed in the Bering Sea were ~0.4 to 6.2%bw day^{-1}, depending on fish size and prey energy content. These rations are three to 50 times higher than previous existing consumption estimates but well within the capacity of the species.

Key words: *Hippoglossoides*, flathead sole, energetics.

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Introduction

Fisheries scientists are using multispecies models to understand changes in population structure of Alaskan groundfishes (Laevastu and Larkins, 1981). A prime link between species in these models is mortality through predation. The flathead sole, *Hippoglossoides elassodon* Jordan and Gilbert 1880, is a common benthic fish in both the Gulf of Alaska and the south-east Bering Sea. While this species is generally not the specific target of a fishery, its abundance and extensive distribution make it a key member of the food web (Livingston *et al.*, 1986). One method to quantify predation by this species is by estimating its energy requirements and abundance. Abundance and distribution information is available in annual trawl surveys done by the US National Marine Fisheries Service, but there is no published information on the bioenergetic requirements for the species. The objective of this study was to measure flathead sole energy requirements and estimate consumption rates.

Methods

Flathead sole used in all experiments were captured by trawl in Resurrection Bay, an embayment of the Gulf of Alaska, near Seward, Alaska.

Growth vs. consumption

For studies on growth relative to energy consumption fish were held in pairs, having weights within 10% of each other, in 400-l tanks. They were held as pairs because single fish did not feed nearly as well when held alone. Fish were anesthetized with MS 222 and weighed to the nearest gram. The 11 pairs of fish had mean weights ranging from 1 to 350 g. Seven of the pairs contained fish between 50–149 g, which served as a standard weight range. The other four pairs were included to examine the effect of fish weight on daily weight gain. Groups of fish were fed pre-weighed herring fillets, for which the energy content was known. The energy content in joules (not adjusted for nitrogen formation) for triplicate samples of the food was measured with an adiabatic calorimeter. Herring fillets averaged 8372 J g^{-1} wet wt. Fish were offered food daily, but some pairs of fish were avid feeders while others were not. Natural variations in group feeding levels provided a variety of energy consumption levels. Experiments were done at 4°C (S.D. = 0.8), a temperature that the species normally encounters during the summer feeding season. In the south-eastern Bering Sea summer bottom temperatures are near 3°C (Livingston *et al.*, 1986), while in the Gulf of Alaska 3 to 6°C are more common (Smith *et al.*,

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1988). Photoperiod for all experiments was 9 h of light and 15 h of darkness. Fish were acclimated at the experimental temperature for 4 weeks before the experiments.

Fish growth was calculated using the formula:

$$G = (\log_e W_T - \log_e W_O) \times 100/t,$$

where G = growth in per cent body weight per day, W_O = initial mean fish weight, W_T = final mean fish weight, and t = the duration of each experiment (always 30 days). In one pair of fish where no food was offered, G was negative, the starvation weight loss. Consumption, as a per cent of body weight, was calculated by summing the weight of all food actually eaten during the experiment, dividing first by 30 days, then by the initial fish weight, then by the number of fish in the group. Energy consumption was calculated by multiplying the summed weight of food by its energy value, dividing by 30 days and initial fish weight, yielding food intake as calories per gram of fish weight per day. The energetic equations provided are for joules but could be converted to calories (1 J = 0.239 cal).

Estimated consumption of common prey

Growth rates of the various age-classes of flathead sole from the Bering Sea were calculated using the instantaneous growth coefficient equation of Chapman (1978): $G_x = \log_e W_i - \log_e W_{i-1}/365$, where G_x is instantaneous growth coefficient, W_i is weight in the ith year, W_{i-1} is weight in the previous year. We expressed these coefficients as growth in %bw day^{-1}. Weights of the year classes of Bering Sea flathead sole were extracted from Niggol (1982). Once the energy–growth relationship was developed in the laboratory, we used it to estimate the energy required to achieve the growth rates predicted by Chapman's equation. These energy values were converted to equivalent rations of two typical prey of flathead sole, brittle stars, and the walleye pollock, *Theragra chalcogramma* (Pallas) (Livingston *et al.*, 1986). Brittle stars are low energy food, having a energy content of ~2121 J g^{-1} wet weight (Thayer *et al.*, 1973). Walleye pollock are higher energy food, having an energy content of ~6042 J g^{-1} wet weight (Smith *et al.*, 1988). Growth rates, minimal energy requirements, and minimal ration requirements for these two foods were all illustrated as functions of fish age.

Regressions describing the various relationships were fitted to log, power, exponential, and linear models and the best fit as indicated by the coefficient of determination (r^2) adopted.

Results

Growth vs. consumption

Growth of flathead sole was linearly related to energy consumption [equation (1)]: Growth (%bw day^{-1}) = 0.006 (consumption J g^{-1} day^{-1}) − 0.130; $r^2 = 0.80$. This equation was derived from growth trials involving fish from a large range of sizes. The r^2 value (0.80), and the fit of the data points, suggest growth for 1–350 g fish was independent of size when weight gain was expressed as a function of consumption in J g^{-1} day^{-1} (Fig. 1). At 4.0°C the estimated maintenance ration based on feeding and growth observations was 21.7 J g^{-1} day^{-1}.

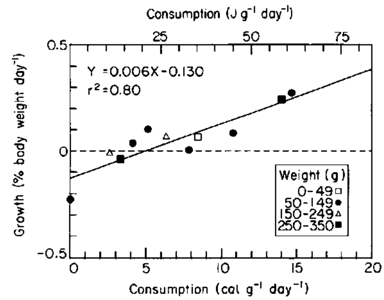

Figure 1. Growth (% body weight per day) for *Hippoglossoides elassodon* of 1 to 350 g at 4°C relative to energy consumption. Equation relates growth and consumption in J g^{-1} day^{-1}. Weight (g): □ = 0–49, ● = 50–149, △ = 150–249, ■ = 250–350. Y = 0.006X − 0.130, $r^2 = 0.80$.

Growth rate recalculated from Niggol's (1982) data conforms to the power function [equation (2)]: growth rate (%bw day^{-1}) = 0.631 (age in years)$^{-1.16}$; $r^2 = 0.97$. Based on equation (1) the energy requirement to achieve these growth rates also conforms to a power function [equation (3)]: energy requirement (J g^{-1} day^{-1}) = 96.8 (age in years)$^{-0.52}$; $r^2 = 0.93$. Converting these energy requirements to minimal rations of brittle stars and walleye pollock necessary to achieve the observed growth rates yielded the power curves seen in Figure 2. Estimates for daily ration necessary to achieve growth rates observed in the Bering Sea were calculated to be ~0.4 to 6.2%bw day^{-1} depending on fish size or age and prey energy content (Fig. 2).

Discussion

Growth vs. consumption

Flathead sole between 1 and 350 g were similarly efficient at converting energy to body weight, as indicated by the linearity and the fit of the data in Figure 1. Juveniles of both *Pleuronectes asper* and walleye pollock, *Theragra chalcogramma*, the most common fish found with flathead sole, also have conversion efficiency rates similar to their adult stages (Smith *et al.*, 1988; Smith *et al.*, 1991). These observations suggest that for a variety of Alaskan fish

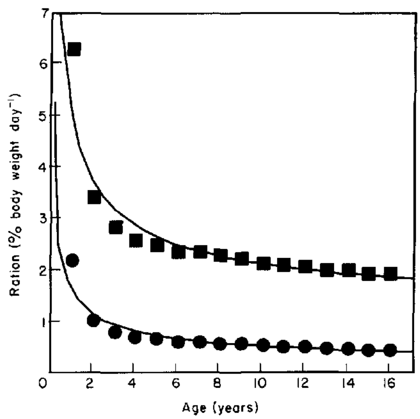

Figure 2. Minimal rations of brittle stars and walleye pollock for *Hippoglossoides elassodon* to achieve observed growth rates in the Bering Sea. ■ = brittle stars as food ($Y = 4.56X^{-0.52}$), ● = pollock as food ($Y = 1.60X^{-0.52}$). $r^2 = 0.93$.

species conversion efficiency is not markedly changed by the maturation process. The existence of similar conversion efficiencies for juveniles and adults will simplify modeling energy flow through their populations.

There is only one previous bioenergetic study of a flatfish species that lives in the Bering Sea. *Pleuronectes asper* at 3°C (Smith *et al.*, 1991) and flathead sole at 4°C have nearly identical conversion efficiency rates. With a consumption of $50\,J\,g^{-1}\,day^{-1}$, flathead (4°C) and *P. asper* (3°C) would have growth rates of 0.19 and 0.18%bw day^{-1}, respectively. Thus, our conversion efficiency values appear to be similar for these coexisting species. Most of the bioenergetic studies of flatfish from the Atlantic were done at temperatures too warm to be directly comparable to this study. Growth data for plaice (*Pleuronectes platessa* L.) and common dab (*Limanda limanda* L.) at 10°C, presented in Edwards *et al.* (1969), were recalculated using the above equations for energy intake and growth. The resulting equation for growth (%bw day^{-1}) as a function of energy intake ($J\,g^{-1}\,day^{-1}$) is:

$$Y = 0.0071X - 0.561\ (r^2 = 0.84, n = 8).$$

The equation for dab is:

$$Y = 0.0096X - 1.00\ (n = 2).$$

Maintenance rations for the two species would be 79 and $104\,J\,g^{-1}\,day^{-1}$ for plaice and dab, respectively. These maintenance rations were about 3.5 and 4.7 times that of flathead sole at 4°C. Much of this difference is probably attributable to the thermal habitat, but this is speculation without further studies.

Energy and ration estimates

No other information on the bioenergetics of flathead sole is available, but because this species is abundant, estimates of consumption are needed to quantify multispecies interactions (Livingston *et al.*, 1986). Using low and high energy prey, we estimate the minimal requirement of flathead sole to range from 2.2 to 6.2%bw day^{-1} in its first year (Fig. 2). The minimal rations required to achieve observed growth declines with increased age and body size, so that by age 16 they range from 0.4 to 1.2%bw day^{-1} (Fig. 2). Since they consume a variety of prey a value between these extremes, 0.8%bw day^{-1} seems likely for this initial estimate of minimal ration for these older fish. The only previously existing ration estimate, 0.12%bw day^{-1} at 3°C (Livingston *et al.*, 1986), is based on stomach content weights and an evacuation rate for another species using the Elliott and Persson (1978) model. This value is only 15% of our minimal ration estimate above. The preliminary model we present (Fig. 2) predicts the minimal ration required by any age (or weight) fish, whereas the previous estimate (Livingston *et al.*, 1986) would seriously underestimate minimal rations for small (young) fish. It appears that the previously existing estimate for daily consumption of 0.12%bw day^{-1} (Livingston *et al.*, 1986) is far too low to balance a realistic energy budget for the species and additional field work is necessary to improve the ration estimate for this abundant benthic predator.

Obviously, there are several factors which modify energy requirements and a single estimate of ration is not reasonable in any comprehensive bioenergetic model. Continued examination of predator–prey interactions will be needed to improve on these first consumption estimates for an energy flow model.

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