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U.S. DEPARTMENT OF COMMERCE
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A Bioenergetics Model of Walleye Pollock (Theragra chalcogramma) in the Eastern Bering Sea: Structure and Documentat-ion

by
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ABSTRACT

The need for developing a bioenergetics model for walleye pollock in the eastern Bering Sea has been previously established. The Fish Bioenergetics Model 2 of Hewett and Johnson was adapted to walleye pollock. Appropriate submodels for consumption, respiration, egestion, and excretion were selected and parameterized. Seasonal aspects of growth, reproduction, caloric density, and diet composition of walleye pollock are described, as well as the seasonal water temperature and the caloric density of walleye pollock prey. The synthesis of published and unpublished data required for parameter estimates and seasonal descriptions is documented and discussed for each aspect of the bioenergetics model.

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INTRODUCTION

Walleye pollock (Theragra chalcogramma) support the world's largest single-species fishery and comprise 67% of the total groundfish biomass in the eastern Bering Sea (Wespestad 1993). Cannibalism by adult walleye pollock has been identified as the major source of predation mortality for juvenile walleye pollock in the eastern Bering Sea (Livingston et al. 1986, Livingston 1991, Livingston et al. 1993).

Estimates of predation mortality exerted by adult walleye pollock on economically important species in the eastern Bering Sea are based on estimates of daily ration (Dwyer et al. 1987, Livingston 1991, Livingston et al., 1993). Gastric evacuation models and observed stomach fullness have been used to estimate seasonal daily ration by size (Dwyer et al. 1987), but these are biased low (Livingston et al. 1986, Dwyer et al. 1987). Livingston (1991) estimates more realistic daily rations by size based on observed annual weight gain and a generalized food conversion efficiency for fish. However, these estimates do not incorporate seasonal differences, and they could be improved by applying a bioenergetics model that accounts for seasonal variation in water temperature and prey energy content (Livingston 1991).

Developing a bioenergetics model for walleye pollock in the eastern Bering Sea required a synthesis of information on physiological processes and how they are affected by age and the environment. The focus of our paper was to document and justify the submodels, parameters,, and seasonal aspects of this bioenergetics model. To facilitate future improvements to this model, we describe in detail the methods used to calculate the parameters and to approximate the seasonal patterns that influence walleye pollock consumption in the eastern Bering Sea. We also discuss some of the potential biases that may be introduced by our methods and assumptions.

THE BIOENERGETICS MODEL

Bioenergetics models can be used to predict growth from a specified feeding regime, or 'to predict consumption from specified growth patterns. The Hewett and Johnson (1992) "Fish Bioenergetics Model 2" (an improved and updated version of their earlier generalized bioenergetics model of individual fish growth) was parameterized for walleye pollock in the eastern Bering Sea to predict daily consumption for walleye pollock.

Bioenergetics models are based on a balanced energy equation which states that energy in the consumed food must be used for respiration, reproduction, or growth; or be egested or excreted. The basic unit of this model's daily accounting of energy input and output is the calorie, which is translated to and from weight-dependent processes using the caloric density (calories per gram wet-weight, or $cal * 9^{-1}$) of the predator and the prey.

Applying the Hewett and Johnson (19.92) bioenergetics model to walleye pollock requires choosing submodels and estimating parameters for consumption, respiration, egestion and excretion. Incorporating seasonal variation in our model is made posible by including seasonal patterns in reproduction, growth, diet composition, predator and prey caloric densities, and water temperature.

Bioenergetic Submodels and Parameters

Justification for submodel selection and derivation of parameters for the consumption, respiration, egestion, and excretion submodels are explained in this section. These weight- and temperature-dependent processes are generally assumed to be physiological constants for a species over time and among populations (Hewett and Johnson 1992). Some of the following descriptions of submodels and parameters used in the bioenergetics model are paraphrased from Hewett and Johnson (1992). Their manual is very complete, but in the course of parameterizing their generalized model for walleye pollock, we felt that a few parameters needed clarification. In addition, we noted a few inconsistencies and errors in the walleye pollock literature.

Consumption

Consumption (C), in "grams-prey- * 'grams-predator' * day^{-1}", is described by the general equation;

$$c = c_{max} * P * f(T),$$

where C_{max} is the maximum specific feeding rate (in $g * g^{-1} * d^{-1}$), f(T) is the water temperature (°C) dependence function of the specific feeding rate, and P is the proportion of the maximum specific feeding rate that is achieved by the predator. In the model, C_{max} is an allometric function of-the form'

$$C_{max} = CA * W^{CB},$$

where CA is the intercept (for a 1g fish at 0°C), CB is the weight dependence coefficient, and W is the predator weight in grams

There is a choice of three equations for the form of temperature dependence in the consumption submodel. We chose consumption model Equation 1,

$$f(T) = e^{CQ * T},$$

where CQ is the water temperature dependence coefficient. This is a simple exponential function and is only appropriate when the water temperatures are below "optimum" (the temperature at which consumption is highest) or stressful levels. For walleye pollock, the optimum temperature for consumption is notknown, but is probably greater than 7.8°C because maximum consumption increases from 3° to 7.8°C for 30 to 60 g walleye pollock (Smith et al. 1986). The average seasonal temperature regime for walleye pollock in the Bering Sea does not exceed 5°C (Chen 1983, Dwyer, et al. 1987), which appears to be well below the optimum temperature for consumption. Consumption model Equation 2 is recommended for warm-water species, and consumption model Equation 3 requires more information than is currently available on the changes in maximum consumption at higher temperatures, so these two equations were not selected.

The parameter estimates required for the submodel of consumption are CA, CB, and CQ. Curves of the form required by the model were fit to raw data from Smith et al., (1986,. 1988) relating C_{max} to weight (W) and C_{max} to temperature (T). Smith et al. (1986, 1988) fit a different form of weight dependent curve[1],

$$C_{max} = 2.58 * e^{-0.005 * W}, \ r^2 = 0.88,$$

(using consumption as percentage of body weight) for 16 to 440 g walleye pollock at 5.0° and 5.5°C. To satisfy the parameter requirements of this bioenergetics model, we fit the curve

$$C_{max} = 0.02075 * W^{-0.6292}, \ r^2 = 0.82 \qquad \text{(Eq. A)}$$

to the same data. The fit of this curve was only slightly poorer than the fit obtained using Smith et al.'s (1986, 1988) form.

Smith et al. (1986) show a linear relationship between C_{max} (percent body weight) and temperature for 30 to 60 g walleye pollock,

$$C_{max} = -2.04 + 0.929 * T, \ r^2 = 0.98;$$

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[1] The number e is omitted from this equation in Table 2 and. Figure 1 of Smith et al. (1986) 'and in Smith et al. (1988). The number e is also omitted from the equation relating maximum growth to initial weight in Table 2 and Figure 8 of Smith et al. (1986).

however, the exponential curve used in this model,

$$C_{max} = 0.003088 * e^{0.3763 * T}, \; r^2 = 0.99, \qquad \text{(Eq. B)}$$

fits slightly better.

The weight intercept in Equation A was corrected for temperature- to arrive at an intercept for a 1 g fish at 0°C. In essence, we solved for CA by dividing 0.02075 (which represents CA * e^{cQ*T} in Equation A) by $e^{0.3763*5.25}$ (which represents e^{cQ*T} in Equation B). The values of the consumption parameters are CA = 0.02878, CB = ,-0.6292, and CQ = 0.3763, and the resulting consumption submodel is,

$$c = 0287.8 * w^{-0.6292} * p * e^{0.3763 * T}$$

Respiration

The total metabolic rate, in ,"grams-energy * grams-predator-' * day^{s1}" , is described by the general equations,

$$R = RA * W^{RB} * f(T) * Activity$$

and

$$S = SDA * (C - F).$$

Respiration (R) is calculated with an allometric function (RA * W^{RB}) , a temperature dependence function (f(T)), and an activity dependence- function (Activity).

The specific dynamic. action (S, also known as the apparent heat increment) is added to standard respiration (R) to give the total respiration. Specific dynamic action can be described as the increase in standard respiration caused by digesting and assimilating prey into usable energy or tissue. It is expressed as a proportion (SDA) of the digested food energy (C - F), where C is the total consumption and F is the amount egested as feces (see Egestion and Excretion section below). Harris (1985) calculated the specific dynamic action to be 10% of the consumed energy and he estimated the digested food energy to be 80% of the consumed energy. Therefore,- the specific dynamic action is 12.5% of the digested food energy, and SDA = 0.125.

The respiration allometric function (RA * W^{RB}) describes the weight (W) dependence of respiration where RA is the intercept (for a 1 g fish at the temperature causing-the highest respiration), measured in "grams-O^2 * grams-predator" * day-'", and RB is the weight dependence coefficient.

There is a choice of two equation sets to describe the temperature dependence function in the respiration submodel. Respiration model Equation Set 2 was chosen for walleye pollock because respiration model Equation Set 1 requires information about the dependence of the metabolism on swimming-speed, which is not available for walleye pollock. The respiration model

Equation Set 2 is

$$f(T) = V^{X} * e^{(X * (1 - V))}, \text{ where}$$

$$V = (RTM - T)/(RTM - RTO),$$

$$X = (Z^{2} * (1 + (1 + 40/Y)^{0.5})^{2})/400,$$

$$Z = \ln(RQ) * (RTM - RTO),$$

$$Y = \ln(RQ) * (RTM - RTO + 2);$$

and

$$\text{Activity} = ACT$$

requires estimates for four parameters; RTO, RTM, RQ, and ACT. The parameter RTO is the optimum water temperature for respiration (the temperature at which respiration is highest), RTM is the lethal water temperature, RQ is the temperature coefficient, and ACT is a constant times the resting metabolism. The respiration temperature dependence curve described by the series of equations above is analogous to the temperature dependence curve for consumption model Equation 2, illustrated in Figure. 5 of Hewett and Johnson (1992).

Our estimates of RTO and RTM are based on the general trends among studies examining walleye pollock respiration over a fairly narrow range of temperatures. Paul (1986) shows an increase in respiration for 40 to 90 g walleye pollock from 1° to 7.5°C followed by nearly constant levels of respiration from 7.5° to 12°c. Smith et al. (1988) show a more mild increase in respiration for 345 to 750 g walleye pollock from 1.5° to 7.1°C. Harris (1985) examined the effect of temperature on respiration for 50 to 250 g walleye pollock and, although his data are biased high (Harris 1985), he found that the respiration increased more rapidly with temperature between 6° and 10°C than between 3° and 6°C. The temperature which yields the highest respiration (RTO) is likely to be between 7.5° and 10°C, therefore RTO is set at 9°c. The lethal temperature for walleye pollock is greater than 15°C (Yoshida and Sakurai 1984), and RTM is set at 16°C. Lacking further information, we make the assumption that RTO and RTM are the same for all walleye pollock 2 years of age or older.

The respiration temperature coefficient, RQ, is not clearly described in Hewett and Johnson (1992), but they say the analogous parameter in consumption model Equation 2, CQ, "approxrmates a Q_{10} for the rate at which the function increases over relatively low temperatures." Respiration equation set 2 was first used by Kitchell et al. (1977) and they describe RQ as the slope for temperature dependence of standard respiration or approximately the Q_{10} for respiration. A Q_{10} is the increase in a rate associated with a 10°C increase in temperature (Paul 1986) and is defined mathematically as

$$\log Q_{10} = 10 * (\log rate_2 - \log rate_1)/(T_2 - T_1),$$

where rate, is the rate at a temperature (T_1) and rate, is the rate at a higher temperature (T_2) (Harris 1985). A Q_{10} is independent of the units used to measure a rate, but the slope for temperature dependence is not (Appendix A). For walleye pollock, the parameter RQ is estimated by the Q_{10} of respiration-temperature relationships reported in the literature, and the parameters RA and RB are estimated using the respiration rates converted from "1-0, * g-' * h-'I' in the literature to "g-O,'* g-' * d^{-1} II in the model using "24 hr * d^{-l}", "1~ 1 * l,OOO,OOO pl-'" and "1.429 g-0^2 * (l-02)-l/

Paul (1986) found the linear increase in respiration for 40 to 90 g walleye pollock to be

$$R(g\text{-}0_2 * g^{-l} * d^{-l}) = 0.000433 + 0.000273 * T,\ r^2 = 0.98$$

between l^o and 7.5°C with a Q_{lo} of 6.04. Smith et al. (1988) found the increase in respiration for 345 to 750 g walleye pollock to be

$$R(g\text{-}0, * g^{I} * d\text{-}l) = 0.000681 + 0.000053 * T,\ r^2 = 0.999$$

between 1.6° and 7.1°C with a Q_{lo} of 1.8. Harris (1985) found intermediate respiration Q_{lo} values for intermediate-sized walleye pollock. The RQ values determined for walleye pollock decrease with increasing' size, therefore the RQ (weight) values input into the model approximately correspond to weight ranges as follows,: RQ(<100 g) = 6.04; RQ (100-299 g) = 4.5; RQ(300-400 g) = 3.0;.and RQ(>400 g) = 1.8.

The parameters RA and RB are derived from the allometric relationship defined by the equation'

$$RA * W^{RB}(g\text{-}O^2 * g^{-1} * d^{-1}) = 0.005933 * W^{-0.26}$$

for 6 to 750 g walleye pollock at 5.5°C (Smith et al. 1988).

In respiration model Equation Set 2 the specific standard metabolism, RA, should be in terms of a 1 g fish at the optimum temperature for respiration (RTO =.9°C), and the change in metabolism with the 3.5°C difference in temperature will be greater for smaller walleye pollock. Using the slopes of respiration with temperature given by Paul (1986; walleye pollock cl00 g) and Smith et al. (1988; walleye pollock >400 g), and intermediate slopes for walleye pollock (100-299 g and 300-400 g), the values for RA that correspond to approximate size ranges are calculated by

RA(<lOO g) = 0.005933 t 0.000273 * 3.5;
RA(lOO-299 g) = 0.005933 t 0.000200 * 3.5;
RA(300-400 g) = 0.005933 + 0.000127 * 3.5; and
RA(>400 g) = 0.005933 + 0.000053 * 3.5

with RA (<100 g) = 0.0069, RA(lOO-299 g) = 0.0066, RA(300-400 g) = 0.0063, and RA(>400 g) = 0.0061. The weight dependence coefficient, RB, is -0.26.

The activity multiplier, ACT, depends on the average level of active respiration above the level described by the other parts of the respiration submodel. A resting, non-feeding level of respiration is described by the above parameters, and the respiration of active, feeding walleye pollock is about double the resting, non-feeding level (Smith et al. 1988). Smith et al. (1988) calculated the metabolic rate of walleye pollock fed a maintenance ration in aquaria to be 1.55 times higher than resting, non-feeding levels. If walleye pollock respiration in the Bering Sea is 2 times the resting, non-feeding levels; and specific dynamic action accounts for respiration that is 1.55 times resting, non-feeding levels, then the activity multiplier, ACT', is 2/1.55 which equals 1.3. This is generally in agreement with Johnston and Battram (1993) who' found that the elevation of respiration above resting, non-feeding levels appears to be caused primarily by specific dynamic action.

Using the weight-specific parameters for walleye pollock greater than 400 g as an example, the equations for the respiration submodel are

$$R = 0.0061 * W^{-0.26} * f(T) * 1.3,$$

where

$$f(T) = V^{x} * e^{(x * (1 - V))}; \text{ and where}$$

$$V = (16 - T)/(16 - 12),$$

$$X = (Z^{2} * (1 + (1 + 40/Y)^{0.5})^{2})/400,$$

$$Z = \ln(1.8) * (16 - 12),$$

$$Y = \ln(1.8) * (16 - 12 + 2);$$

'and

$$S = 0.125 * (C - F).$$

Egestion and Excretion

There is a choice of three equation sets to describe the egestion of feces and excretion of nitrogenous waste, and we chose equation set 1. Egestion and excretion equation sets 2 and 3 incorporate water temperature and consumption to describe these processes. Bartell et al. (1986) conclude that this is unnecessarily complex when computing growth or consumption.

Egestion (F) and excretion (U) are modelled is constant proportions in "grams-waste * grams-predator^{-1}' * day^{-1}" in equation set 1, as

$$F = FA * C$$

and

$$U = UA * (C - F),$$

where FA is the fraction of consumed 'food (C) that is egested and UA is the fraction of the digested food energy that is excreted. Harris (1985) estimates that 20% of the food consumed by walleye 'pollock is egested (based on Winberg 1956), so FA = 0.2.

Harris et al. (1986) suggest using a nitrogen correction of 11% for ammonia-excreting predators that feed on walleye pollock. The nitrogen correction is based on the energy released during the combustion of nitrogenous compounds to N_2 that cannot be obtained when these compounds are metabolized to NH, or urea (Harris et al. 1986). The 11% nitrogen correction is represented in the excretion parameter, and UA = 0.11.

Seasonal Characteristics

Seasonal patterns in individual growth, spawning, caloric density, diet composition, and frequented temperatures have been observed for walleye pollock. Many of these seasonal patterns appear to differ substantially between the northwest and southeast areas of the eastern Bering Sea shelf (Fig. l), as -do the oceanographic conditions (Smith 1981).

Seasons in the bioenergetics model are based primarily on observed seasonal growth and caloric density patterns. When estimating consumption from observed growth of an individual, the model must calculate the amount of calories needed to get from the total body calories at the beginning of the time period to the total body calories at the end of the time period. Therefore, it is important to specify at least those points that are near observed minima and maxima of annual weight and caloric density patterns. The model has been set up with four equal seasons. with the model year beginning on 15 March:

Season	Beginning	Ending	Model Days
Spring	15 Mar.	14 Jun.	1 to 92
Summer	15 Jun.	14 Sep.	93 to 184
Autumn	15 Sep.	14 Dec.	185 to 275
Winter	15 Dec.	14 Mar.	276 to 365.

The seasonal patterns used in our model, and how they are established,- are explained for each seasonal characteristic below. Generally, these patterns are based on long-term averages and are meant to represent the seasonal conditions experienced by an average walleye pollock.- Individual and interannual differences can be explored by changing the seasonal characteristics used in the model. To aid in this, we discuss how the behavior of walleye pollock may influence the seasonal

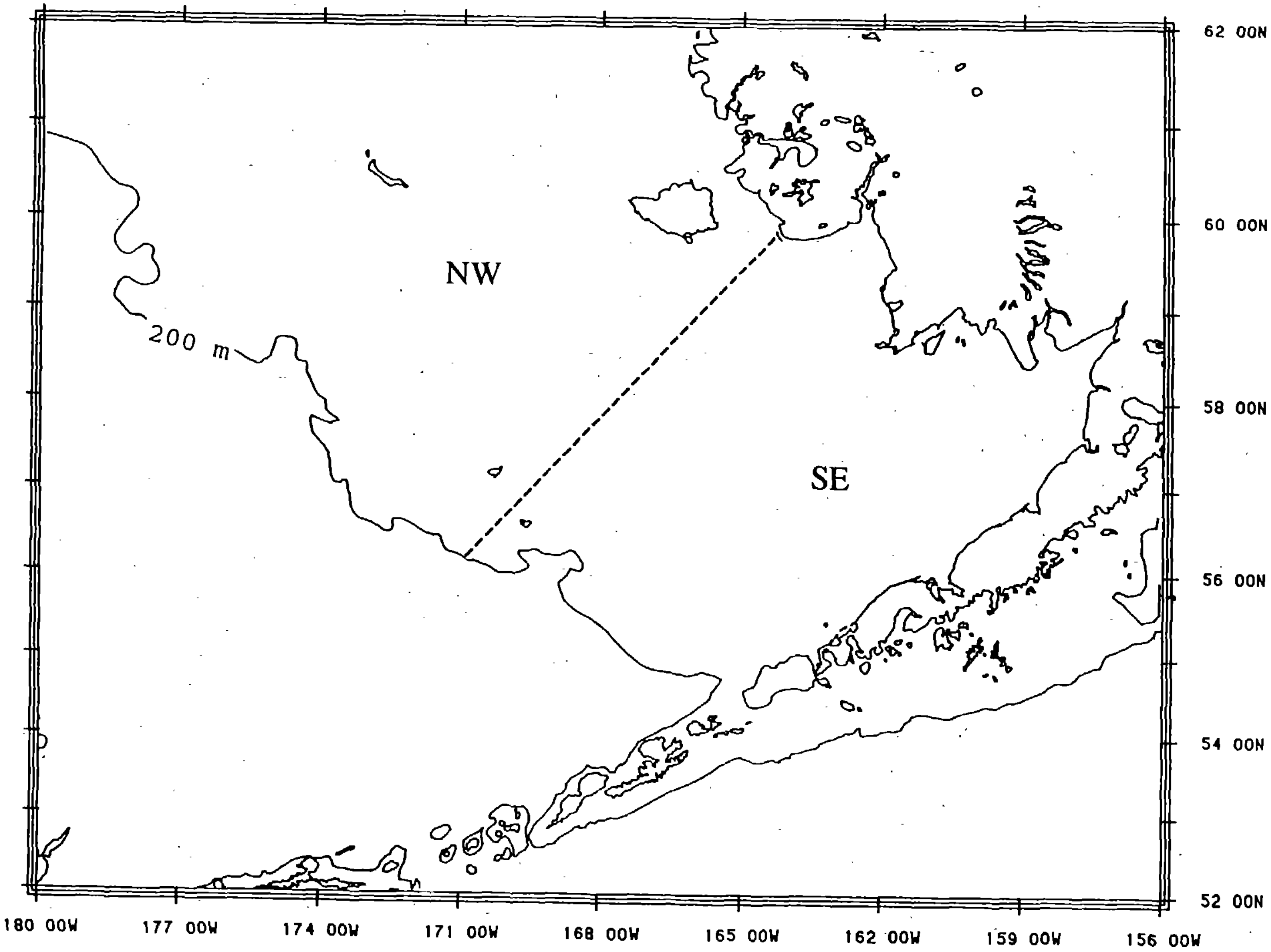

Figure 1. --Map showing the southeast (SE) and northwest (NW) areas of the eastern Bering Sea shelf and the 200 m isobath.

patterns in the data, and identify some of the potential biases introduced by our assumptions about the data. In addition, some comments are provided that may be helpful to users of the Hewett and Johnson (1992) bioenergetics model and we attempt to correct a few of the errors that we found in the literature.

Growth

Growth of walleye pollock is given to the model in "grams" for the beginning and ending weight of each time period for an individual. Seasonal variations in walleye pollock growth were proposed by Maeda (1972) and investigated by Chen (1983). Chen's (1983) results indicate that the monthly weight increment in the "feeding season" (June-September) was greater than the weight increment in the "transitional season" (October-May). Seasonal differences in growth (with negative growth in some areas and seasons) were found in length-at-age data from 1976 through 1983 by Lynde et al. (1986). They concluded that the observed pattern could be due to seasonal migration and length-dependent swimming speed of the migrating' walleye pollock.

The growth rate of walleye pollock inhabiting the southeast shelf of the eastern Bering Sea is faster than that of walleye pollock inhabiting the northwest shelf (Lynde et al. 1986, Hinckley 1987). The seasonal growth patterns of walleye pollock from these two areas were examined using monthly weight-at-age data from 1981 through 1990, provided by Vidar Wespestad (pers. commun.[2]). The-variance of the monthly weight-at-age data is high for each year, as it, is in other studies (Chen 1983), and a consistent seasonal trend in the growth among years is unclear. The weighted mean of the monthly weight-at-age was calculated for all years combined. For March, June, September and December, the mean was calculated using monthly weight-at-age data for these and their respective preceding and following months (e.g., the mean for March was calculated using weighted means of the monthly weight-at-age data from February, March, and April),. An area-specific seasonal pattern of growth emerged for the northwest and southeast areas of the eastern Bering Sea shelf (Fig. 2) that is consistent with the seasonal observations by Chen (1983) and with the areal differences found by Lynde et al. (1986) and Hinckley (1987). The general seasonal pattern is visible by age 2, but it breaks down in these data at ages 8 and 10 in the northwest and southeast areas respectively. This is apparently due to low sample sizes and increased measurement error for older walleye pollock.

It is likely that seasonality in the growth of walleye pollock exists based on the seasonality in condition factor (Harris et al. 1986) and feeding rates (Dwyer et al. 1987, Maeda 1972), but the potential influence of seasonal and lifetime movement patterns should be considered. Lynde et al. (1986)

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[2] Alaska Fisheries Science Center, 7600 Sand Point Way N.E., BIN C15700, Seattle, WA 98115-0070, U.S.A., March 1993.

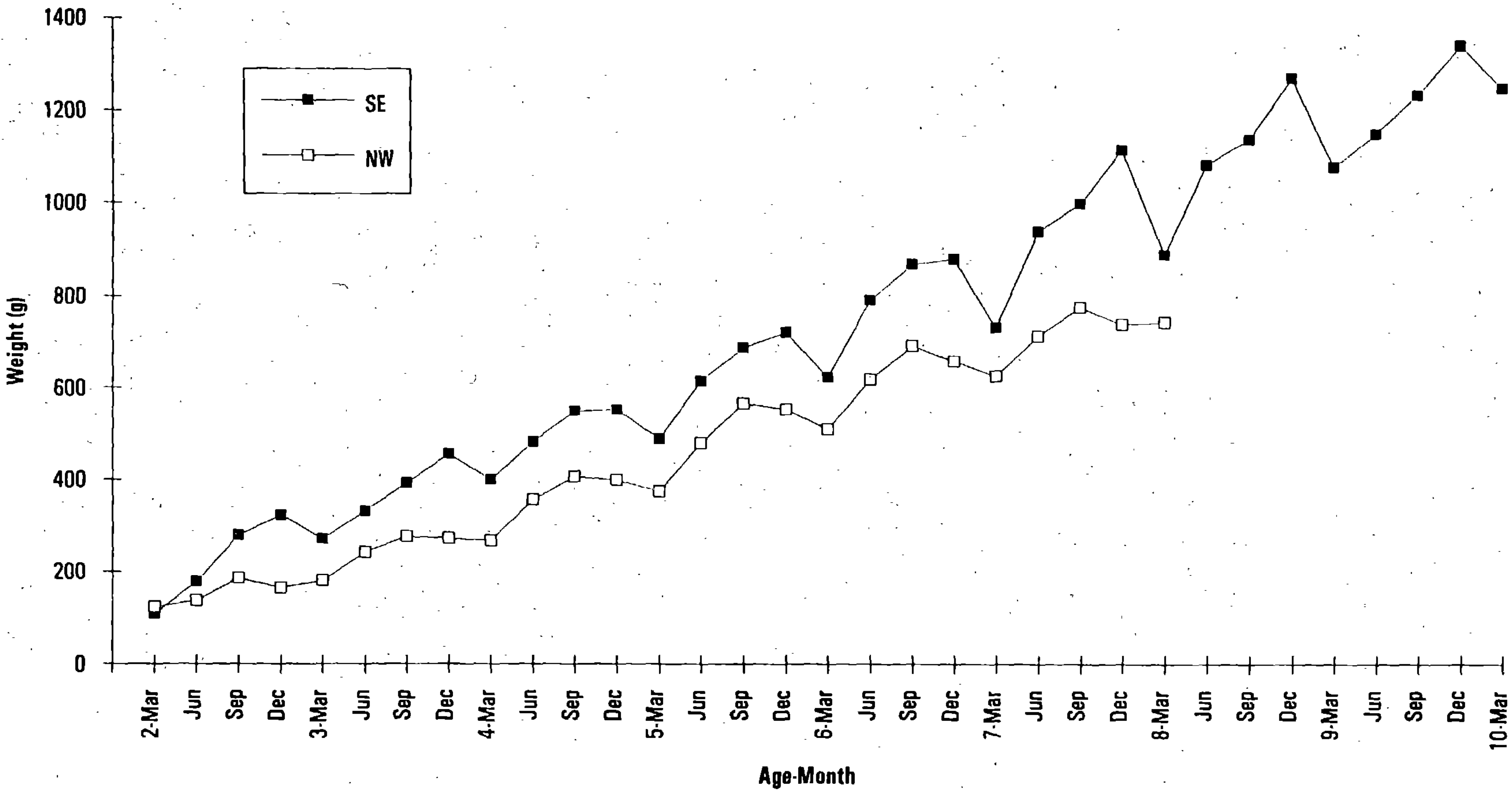

Figure 2.--The weight (g) of walleye pollock by season from age 2 to age 8 in the northwest (NW) area and to age 10 in the southeast (SE) area of the eastern Bering Sea shelf as calculated from monthly weight-at-age data.

describe how seasonal on- and off-continental shelf migrations, stratified by size, can affect the observed size-at-age in areas with migrating fish. It is likely that the apparent extremely negative winter growth in the southeast area is the result of slower growing walleye pollock immigrating from the Aleutian Basin in the spring (Lynde et al. 1986), and we think it may be more conservative to assume there is no winter weight loss in the southeast area.

While seasonal movements may have a large effect on the apparent growth pattern, long-term movements can also have some influence. A general southeastward movement (or dispersal) with age was inferred from the spatial distribution of walleye pollock by age over the eastern Bering Sea shelf (Pierre Dawson, pers. commun.[3]). The growth curve for walleye pollock in the southeast area will be biased low as smaller size-at-age fish immigrate from the northwest area. In addition, if this general movement is size-dependent with larger size-at-age fish moving faster, then the growth curve for walleye pollock in the northwest area will be biased low as well.

It may be impossible to determine the degree of influence that movement patterns, size-dependent movement rates/and spawning losses (see Reproduction section below) have on the actual seasonal growth pattern of walleye pollock. In the model, the weights in Appendix Table B-l can be input as the beginning

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[3] Alaska Fisheries Science Center, 7600 Sand Point Way N.E., BIN C15700, Seattle, WA 98115-0070, U.S.A., June 1993.

and ending weights for each season. This seasonal pattern of, growth is in general agreement with seasonal patterns in frequency of empty stomachs (Dwyer et al. 1987); in mean stomach weight (Dwyer et al. 1987), in condition factor (Chen 1983) and in caloric density (Harris et al. 1986) of walleye pollock, and these may all be related to prey availability (Cooney 1981). A reasonable but unlikely lower bound on the seasonality of growth may be to assume that growth is constant among seasons (however, fluctuations in caloric density will retain some of the seasonality in the model).. This assumption will- generally cause' the consumption to be underestimated in seasons of high growth and overestimated in seasons of low or negative growth:

Predator Caloric Density

The caloric density (using wet weight) of the predator, in "calories * grams-predator'", can be modelled as a linear function of body weight or input as a seasonal function for each age class. The caloric density (using- dry weight) of juvenile walleye pollock has been shown to vary seasonally, and to a lesser extent, vary with body size, (Harris et al. 1986). Several sources of data on the caloric density of walleye pollock (using wet weight) from different areas were examined and a seasonal pattern emerged (Appendix Table B-2). Although the data are limited, the seasonal pattern. appeared to be somewhat independent of body size for walleye pollock, age 2 and older. Therefore, seasonal caloric density changes were input into the model, but weight-dependent change's in caloric density were not.

The seasonal pattern for the caloric density of walleye pollock is given as a low of 950 cal * g^{-1} on 15 March (day 1 in the model year) and a high of 1,400 cal * g^{-1} on 15 September (day 185 in the model year). All intermediate values are calculated by linear interpolation in the model (see Prey Caloric Density section below).

The energy content of organisms is measured in several different units in the literature and most conversions to cal * g^{-1} (wet weight) are easily obtainable. The following conversions may be useful in some instances: 1 cal = 4.1868 absolute joules (J), and 1 British thermal unit (Btu) = 251.996 cal = 1055.07 J. In addition, the caloric density, or heat of combustion, is commonly expressed in "cal * g^{-1}", "J * g-'" and "Btu * lb^{-1}", and 1 cal * g^{-l} = 1.8 Btu * lb^{-1}.

Reproduction

Energy lost to reproduction is modelled as a fraction of weight (or total body energy) lost on a given day, beginning at a given year of life. Spawning dates of 1 April (day 17) on the southeast shelf (Smith 1981, Hinckley 1987) and 15 July (day 123) on the northwest shelf (Hinckley 1987) were set in the model. The age at first spawning was set at 4 years (Wespestad 1993).

Although the spawning loss is modelled as a l-day event, walleye pollock have a protracted spawning period (about 4 to 6 weeks) during which they apparently do not feed (Smith 1981). However, when the total spawning energy loss is known, the average daily ration for the time period will be very similar whether the total energy loss of spawning is modelled as a l-day loss of energy or a protracted loss of energy (Hewett and Johnson 1992). 1

The energy lost during the spawning event, including any starvation that may occur, is about 25.2% of the total body energy (Smith et al. 1988)[4]. This is composed of a 14.35% weight loss from the pre-spawning weight accompanied by a reduction in caloric density. We assumed that the weight loss due to spawning was included in the quarterly weight-at-age data (see Growth section above). We made an additional assumption that the reduction in caloric density resulting from spawning was not represented in the seasonal predator -caloric density file; known post-spawning caloric densities were omitted from the calculated averages (see Predator Caloric Density section above).

The measurement of energy losses due to spawning were conducted in the Gulf of Alaska (Smith et al. 1988.) where the walleye pollock spawn at about the same time as in the 'southeast area of the eastern Bering Sea shelf (Hinckley 1987, Smith et al. 1988), and they appear to follow a similar seasonal caloric density pattern (Appendix Table B-2). Therefore, the spawning loss parameter was first, calculated for walleye pollock on the southeast shelf-. The total energy loss is 25.2% and we assumed that 14.35% was accounted for by lost weight, so the remaining 10.85% must be accounted for by the spawning loss parameter.

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[4] Due to calculation errors, this paper concludes that about 46% of the body energy is lost during spawning. The' correct calculation of their published data is presented in Appendix C.

This 10.85% of the pre-spawning, total body energy divided by the remaining body weight (85.65%) yields the proportion of the remaining body energy (0.127) that is lost. Hence, the spawning loss parameter was set at 0.127 for walleye pollock on the southeast shelf.

The weight-fecundity relationship appears to be similar in the southeast and northwest shelf areas (Hinckley 1987). Therefore, the weight-specific energy loss that resulted in the southeast area due to spawning,

$$0.127 * 994 \text{ cal} * g^{-1} = 126 \text{ cal} * g^{-1},$$

was applied in the northwest area to correct for differences in the specified seasonal caloric density on the day of spawning,

$$126 \text{ cal} * g^{-1} / 1249 \text{ cal} * g^{-1} = 0.101,$$

and the spawning loss parameter for the northwest shelf was set at 0.101.

Different values of the spawning loss parametermay be used under alternative assumptions. If we assume the total spawning energy loss is already represented, then the spawning loss parameter would be set at 0.0. If we assume none of the spawning energy loss is represented, then the spawning loss would be set at 0.252. The spawning loss values of 0.127 and 0.101 for walleye pollock on the southeast and northwest shelf are intermediate of these two extreme possibilities.-

Under- or overestimation of the spawning losses may result respectively in under- or overestimation of the consumption by walleye pollock. Setting the first year of spawning at age 4 may underestimate the average energy loss during the spawning season for age-3 walleye pollock, especially on the southeast shelf, and overestimate the average energy loss for age-4 walleye pollock on the northwest shelf. Smith (1981) found 50% of walleye pollock males and females to be sexually mature at 31 cm (about 206 g) and 34 cm (about 275 g), respectively. The first spawning season when these sizes are attained, on average, is at age-3 in the southeast and age 4 in the northwest areas of the eastern Bering Sea shelf (see Growth section above) .

The effect that the weight' loss due to spawning has on the weight-at-age data can only be estimated, and it may cause some bias in the observed seasonal growth, and therefore the predicted seasonal consumption. 'The' observed growth during the season preceding a weight estimate reduced by spawning. may be biased low and the observed growth-during the season following a weight estimate reduced by spawning may be biased high.

Temperature Regime

Seasonal temperature (°C) changes were input by specifying temperatures on chosen days. The specified temperatures (Appendix Table B-3) were based on observed mean bottom temperatures for 1953 through 1982 (Ingraham 1983) in areas where walleye pollock are-the most common (Wilson and Armistead 1991, Bakkala et al. 1992) 'in the eastern Bering Sea. The daily temperatures between the days where temperatures are specified in the input file are interpolated by the model (Fig. 3).

Although sea surface temperature and bottom temperature data are available for much of the-Bering Sea shelf throughout the year, the degree of behavioral thermoregulation in walleye pollock is unknown. The temperatures given in Appendix Table B-3 are similar to what larger juveniles and adult walleye pollock are believed to "prefer" in the eastern Bering Sea (Chen 1983).

The model also requires input of a "maintenance temperature." This is the temperature below which zero growth occurs and the predator consumes food at a rate equal to its energy expenditure each day. This temperature must be, set above the above input temperatures to have any effect on the model's output. The maintenance temperature will be set at 0.0°C and will have no effect on the model because the temperature regime that we input into the model never drops below 1.5°C.

Prey Caloric Density

Model inputs of caloric densities of the prey (up to 10 prey categories in the model), in "calories * grams-prey-'", were seasonally varied. The seasonal changes in caloric density for the 10 prey categories (Fig. 4 and Appendix Table B-4) were estimated from published and unpublished literature (Davis 1993) with an emphasis on values determined for Bering Sea samples (Harris 1985), as well as estimates based upon the trophic level of the prey category. The seasonal trend in caloric density for the prey categories of walleye pollock, other Gadidae and other

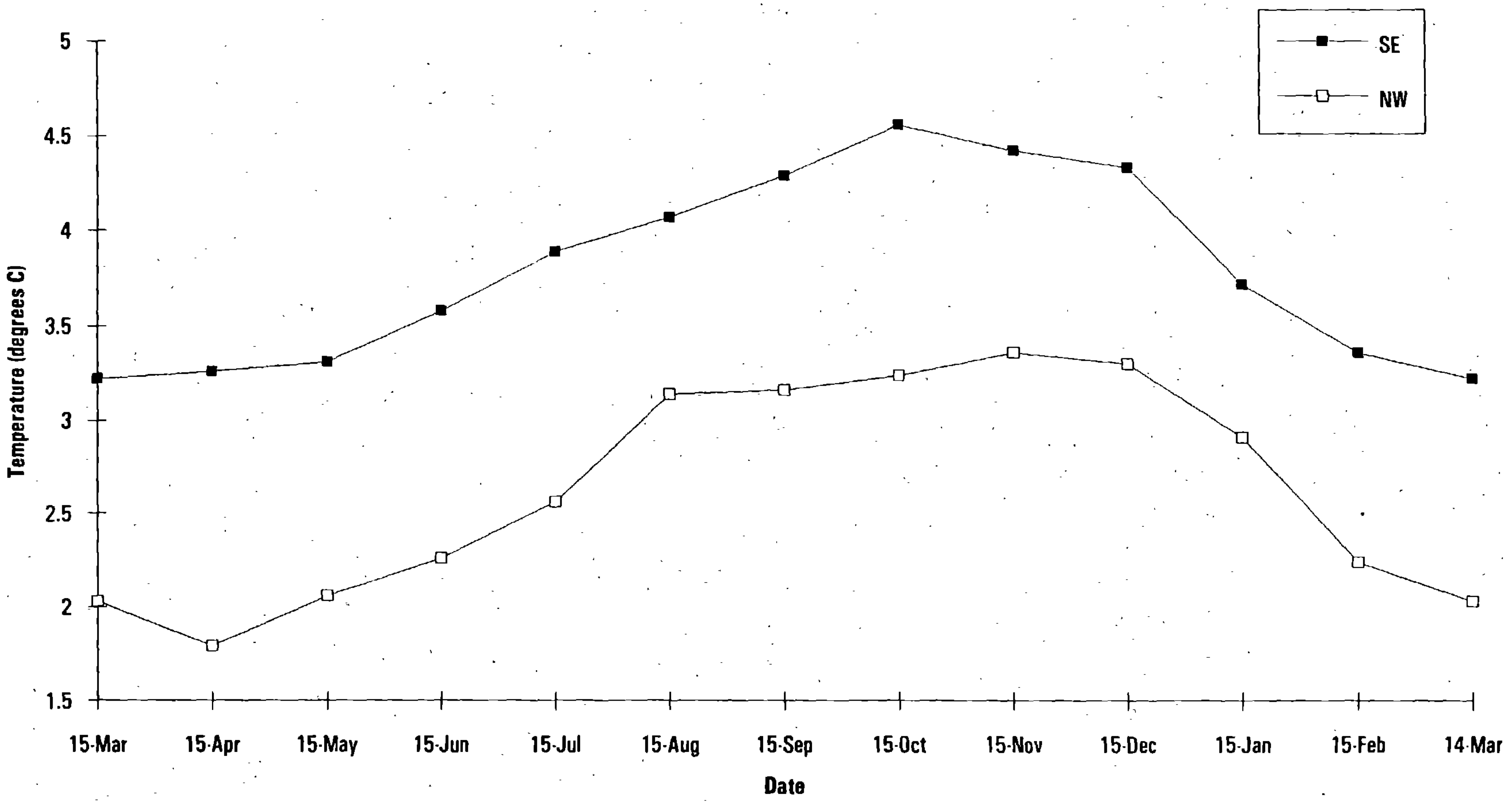

Figure 3.--The average near bottom water temperature (°C) in areas of high walleye pollock density in the southeast (SE) and northwest (NW) areas of the eastern Bering Sea shelf.

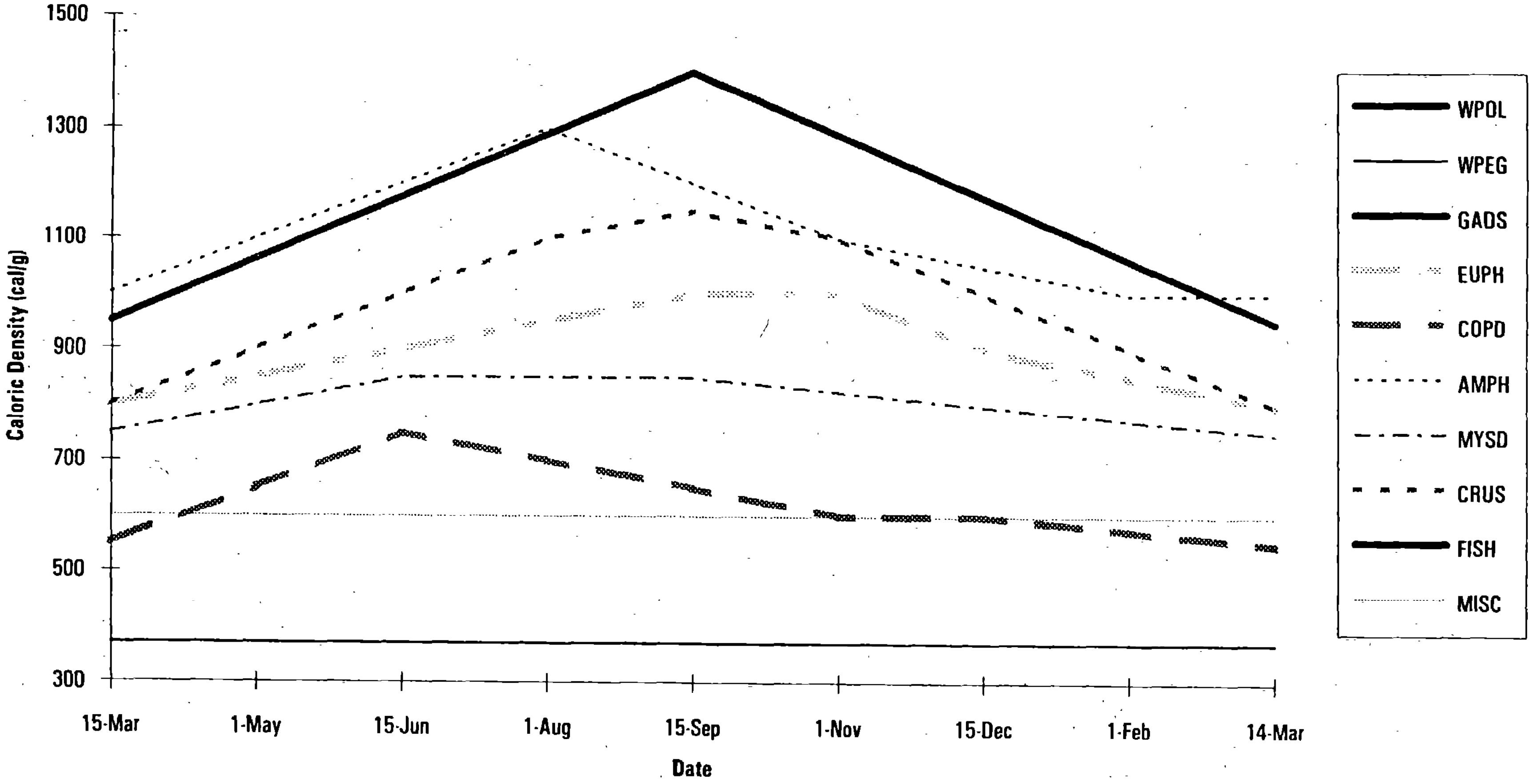

Figure 4.--The seasonal caloric density (cal * g^{-1} wet weight) of major prey categories of walleye pollock. (WPOL - walleye pollock, WPEG - walleye pollock eggs, ,GAD - gadidae that are not walleye pollock, EUPH - euphausiids,. COPD - copepods, AMPH - amphipods, MPSD - mysids, CRUS - crustaceans not included in the above categories, FISH - fishes not included in the above categories, MISC - miscellaneous prey not included in the above categories)

fish was taken from the caloric density of predator walleye pollock. No distinction was made between the southeast and northwest shelf areas in the timing or magnitude of changes in the caloric densities, however differences probably do exist.

-The model interpolates the caloric density between days where it is specified in the prey caloric density input file. However, the overall caloric density of the diet on a given day is dependent on the prey composition, therefore large changes in the caloric density of the diet can occur if the compositionof the diet changes.

Diet Composition

The proportion by weight of each prey in the diet (up to 10 prey categories in the model), can be seasonally varied for each walleye pollock age group. The model will interpolate between the days where diet proportions are specified. The methods used to collect the diet, data and to calculate the proportion by weight for the prey categories can be found in Livingston (1991). The four time periods used to calculate the diet composition begin on the 1st of January, April, July and October. These time periods are offset by about 15 days from the growth seasons. The diet composition was maintained as a constant mean over the time period for which it was calculated by specifying the mean diet composition at both the beginning and, end of the, time period. To ensure complete coverage in all seasons for all ages in each area, the proportion by weight of each prey category was calculated using the diet data pooled from 1985 through 1989.

Fork length intervals were used to approximate the age o-f the predator walleye pollock in the food habits database:

Length Interval (cm)	Age Group
25 to 32	2
33 to 38	3
39 to 43	4
44 to 48	5 to 6
49 and up	7 and up.

Diet proportions of walleye pollock ages 2 through 4 were pooled. The seasonal diet composition of the three age groups in the southeast and northwest shelf is presented in Appendix Tables B-5 and B-6.

CONCLUSIONS

This model can be used to provide insight into the effects of different conditions on walleye pollock consumption. The physiological processes are described as well as the data available will allow. As more data on the physiological processes of-walleye pollock become available, the parameter estimates (Table 1) may be improved, or perhaps different submodels may be used. One benefit to our choice of the submodels available in the "Fish Bioenergetics Model 2" is that they require the fewest parameter estimates.

The seasonal characteristics experienced by walleye pollock in the eastern Bering Sea are also 'described as well as the data

Table 1.--Parameter values for the bioenergetics model' of walleye pollock in the eastern Bering Sea. See text for explanation of the parameters and bioenergetic equations.

Consumption:	
CA	0.02878
CB	-0.6292
CQ	0.3763
Egestion and Excretion:	
FA	0.20
UA	0.11

Respiration:	
RA(100-299 g)	0.0066
RA(300-400 g)	0.0063
RA(>400 g)	0.0061
RB	-0.26
RQ(100-299 g)	4.5
RQ(300-400 g)	3.0
RQ(>400 g)	1.8
RTO	9.0
RTM	16.0
ACT	1.3
SDA	0.125

Reproduction:	Southeast	Northwest
age of first spawn	4	4
spawning date	1 April	15 July
proportion of energy spawned (= -126 cal/g)	0.127	0.101

will presently allow. The seasonal patterns observed for many of these characteristics must be considered in terms of the behavior of walleye pollock and also in terms of interactions between the characteristics. As we have discussed, some of the observed seasonal characteristics may be somewhat biased, and thus estimates of consumption generated by the bioenergetics model may be somewhat biased. However, we feel that the bioenergetics model, in its present form, will allow us to make relatively good seasonal estimates of daily rations for walleye pollock in 'the eastern Bering Sea.

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We are grateful to A.J. Paul for digging up and sharing raw data that substantially improves our confidence in some of the parameter estimates: Nancy Davis provided helpful comments on an early draft of this paper, and later versions were thoughtfully reviewed by Sarah Hinckley, Vidar Wespestad, and Richard Brodeur.

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APPENDIX A

Q_{lo} versus Slope

The Q_{10} of a rate. (k) is the increase in that rate associated with a 10°C increase in temperature (T) and is defined mathematically as

$$\log Q_{10} = 10 * (\log k_2 - \log k_1)/(T_2 - T_1).$$

A Q_{10} will approximate the slope of the change in respiration (R) with temperature if respiration is measured in "$\mu l\text{-}O_2 * g^{-1} * hr^{-1}$" as in Kitchell et al. (1977), but not if respiration is measured in "$g\text{-}O_2 * g^{-1} * d^{-1}$" as in the bioenergetics model of Hewett and Johnson (1992). Respiration rates are converted between these two units of measure using "$24\ hr * d^{-1}$", "$1\ l * 1{,}000{,}000\ \mu l^{-1}$", and "$1.429\ g\text{-}O^2 * (l\text{-}O^2)^{-1}$". Paul (1986) found the linear increase in respiration for 40 to 90 g walleye pollock between 1° and 7.5°C to be

$$R(\mu l\text{-}O_2 * g^{-1} * hr^{-1}) = 12.617 + 7.961 * T$$

or

$$R(g\text{-}O_2 * g^{-1} * d^{-1}) = 0.000433 + 0.000273 * T.$$

The Q_{10} of the first equation can be calculated for T_1 = 1.0°C and T_2 = 7.5°C as follows:

$$\log Q_{10} = 10 * (\log R_2 - \log R_1)/(T_2 - T_1)$$

$$\log Q_{10} = 10 * (\log 72.3245 - \log 20.5780)/(7.5 - 1.0)$$

$$\log Q_{10} = 0.83982$$

$$Q_{10} = 6.915.$$

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The slope of the first equation (7.961) approximately equals the Q_{10} (6. 915) .

The Q_{10} of the second equation can be calculated for T_1 = 1.0°C: and T_2 = 7.5°C as follows:

$$\log Q_{10} = 10 * (\log R_2 - \log R_1) / (T_2 - T_1)$$

$$\log Q_{10} = 10 * (\log 0.0024802 - \log 0.0007057)/(7.5 - 1.0)$$

$$\log Q_{10} .= 0.83980$$

$$Q_{10} = 6.915.$$

The slope of the second equation (0.000273) is not approximately equal. to the Q_{10} (6:915), but the Q_{10} of both respiration equations is the same.

APPENDIX B

Growth, walleye pollock caloric density, temperature, prey caloric density, and diet composition data.

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Table B-1.--Weight-at-age data input into the bioenergetics model for walleye pollock from the southeast (SE) and northwest (NW) areas of the eastern Bering Sea shelf. Weight is in grams and age is the number of December 31sts survived.

		Weight (g)		
Age	Month	SE	NW	Model Quarter
2	Mar.	108	122	1
2	Jun.	177	136	2
2	Sep.	278	185	3
3	Dec.	323	163	4
3	Mar.	323	180	5
3	Jun.	331	242	6
3	Sep.	393	275	7
4	Dec.	456	272	8
4	Mar.	456	267	9
4	Jun.	482	356	10
4	Sep.	550	407	11
5	Dec.	552	399	12
5	Mar.	552	374	13
5	Jun.	615	480	14
5	Sep.	688	566	15
6	Dec.	722	554	16
6	Mar.	722	510	17
6	Jun.	791	618	18
6	Sep.	868	692	19
7	Dec.	879	658	20
7	Mar.	879	625	21
7	Jun.	938	713	22
7	Sep.	998	775	23
8	Dec.	1,114	737	24
8	Mar.	1,114	742	25
8	Jun.	1,081		26
8	Sep.	1,138		27
9	Dec.	1,270		28
9	Mar.	1,270		29
9	Jun.	1,149		30
9	Sep.	1,232		31
10	Dec.	1,337		32
10	Mar.	1,337		

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Table B-2.--Caloric density values (cal * g^{-1} wet weight) of walleye pollock. Monthly averages omit known post-spawning samples (lb). BS = Bering Sea samples.

	Month							
Source	FEB	MAR	APR	JUN	JUL	AUG	SEP	OCT
1a.	922	922	922					
1b.	798	798	798					
2a.		867						
3a.		1,247						
3b.		1,108	1,108					
4a.		1,120						
4b.						1,085		
5.				1,573	1,573	1,573		1,573
2b.BS	937	937	937	1,216	1,216	1,216	1,216	
3c.BS							1,563	
4c.BS					1,280			
6. BS					1,408	1,408	1,408	
Avg.	930	1,034	989	1,394	1,369	1,321	1,396	

Sources (showing collection area and walleye pollock size):

1. Smith et al. (1988)
   a. Gulf of Alaska, Resurrection Bay to Kodiak shelf; pre-spawning adults
   b. Gulf of Alaska, Resurrection Bay to Kodiak shelf; post-spawning adults
2. Harris et al. (1986)
   a. Gulf of Alaska, Resurrection Bay; 7-140 g
   b. Bering Sea, southeast shelf - based on seasonal condition factors from Chen (1983); age 2
3. NMFS, National Marine Mammal Laboratory (unpublished data)[*]
   a. Aleutian Islands, Unimak Pass; 343-1,077 g
   b. Gulf of Alaska, Shelikof Strait; 40-1,428 g
   c. Bering Sea, southeast slope; 900-1,350 g
4. Perez (1994)
   a. Gulf of Alaska, Shelikof Strait; 577-1,065 g
   b. Gulf of Alaska, Shelikof Strait; 42-107 g
   c. Bering Sea, southeast shelf; 151-470 g
5. Harris (1985), Table III-5
   Gulf of Alaska, Resurrection Bay; 65-360 g
6. Miller (1978)
   Bering Sea; mean size = 288 g

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[*] Alaska Fisheries Science Center, 7600 Sand Point Way N.E., BIN C15700, Seattle, WA 98115-0070, U.S.A.

Table B-3.--Dates, corresponding model day and the temperature input for the southeast (SE) and northwest (NW) areas of the eastern Bering Sea shelf.

Date	Model Day	Temperature (OC)	
		SE	NW
15 Mar	1	3.22	2.03
15 Apr	32	3.26	1.79
15 May	62	3.31	2.06
15 Jun	93	3.58	2.26
15 Jul	123	3.89	2.56
15 Aug	154	4.07	3.14
15 Sep	185	4.29	3.16
15 Oct	215	4.56	3.24
15 Nov	246	4.42	3.36
15 Dec	276	4.33	3.30
15 Jan	307	3.72	2.91
15 Feb	338	3.36	2.24
14 Mar	365	3.22	2.03

Table B-4.--The date and caloric densities (cal * g^{-1}, wet weight) for 10 prey categories specified in the model. A 'description of each prey category and the major information sources are described below.

Date	WPOL	WPEG	GADS	EUPH	COPD	AMPH	MYSD	CRUS	FISH	MISC
	Prey categories*									
15 Mar	950	370	950	800	550	1,000	750	800	950	600
1 May	1,063	370	1,063	850	650	1,100	800	900	1,063	600
15 Jun	1,175	370	1,175	900	750	1,200	850	1,000	1,175	600
1 Aug	1,288	370	1,288	950	700	1,300	850	1,100	1,288	600
15 Sep	1,400	370	1,400	1,000	650	1,200	850	1,150	1,400	600
1 Nov	1,288	370	1,288	1,000	600	1,100	825	1,100	1,288	600
15 Dec	1,175	370	1,175	900	600	1,050	800	1,000	1,175	600
1 Feb	1,063	370	1,063	850	575	1,000	775	900	1,063	600
14 Mar	950	370	950	800	550	1,000	750	800	950	600

*Prey category definitions and data sources:

WPOL	Walleye-pollock caloric densities are taken directly from the predator caloric densities.
WPEG	Walleye pollock egg caloric density is derived from the. average caloric. density of Harris (1985).
GADS	Gadidae, that are not walleye pollock, have caloric densities taken directly from the walleye pollock caloric densities.
EUPH	Euphausiid caloric densities are derived. from the seasonal caloric densities given in Harris (1985).
COPD	Copepod caloric densities are 'derived from the average caloric density given in Harris (1985) and seasonal changes are inferred from the May and June spring "bloom" (Cooney 1981).
AMPH	Amphipod caloric densities are based on Harris (1985).
MYSD	Mysid caloric densities are based on Harris (1985).
CRUS	Crustaceans not included in the above categories are mostly decapods and some isopods, and their caloric densities were. based on Harris (1985) and Davis (1993) .
FISH	Fishes not included in the above categories have caloric densities taken directly from walleye pollock.
MISC	Miscellaneous prey include molluscs, echinoderms, other invertebrates and unidentified prey, and their caloric densities were based on Davis (1993), Steimle and Terranova (1985), and Tyler (1973).

Table B-5.--Diet proportions by weight and season of the 10 prey categories and three age groups used in the model of walleye pollock on the southeast shelf of the eastern Bering Sea. (WPOL - walleye pollock, WPEG - walleye pollock eggs, GADS - gadidae that are not walleye pollock, EUPH - euphausiids, COPD - copepods, AMPH - amphipods, MYSD - mysids, CRUS - crustaceans not included in the above categories, FISH - fishes not included in the above categories, MISC - miscellaneous prey not included in the above categories)

	Prey categories									
Age & Season*	WPOL	WPEG	GADS	EUPH	COPD	AMPH	MYSD	CRUS	FISH	MISC
2-4										
Winter	.0023	.0346	.0000	.7758	.0182	.0510	.0013	.0186	.0713	.0269
Spring	.0000	.0000	.0060	.5352	.3588	.0430	.0050	.0119	.0080	.0321
Summer	.0231	.0000	.0045	.4438	.2861	.0199	.0007	.0644	.0500	.1075
Autumn	.2215	.0000	.0000	.2688	.0242	.0249	.0407	.0623	.3271	.0305
5-6										
Winter	.0086	.0119	.0000	.7380	.0344	.0395	.0021	.0579	.0769	.0307
Spring	.0000	.0000	.0000	.6429	.2539	.0288	.0041	.0099	.0268	.0318
Summer	.0298	.0000	.0002	.6255	.1575	.0274	.0005	.0437	.0574	.0580
Autumn	.3166	.0000	.0000	.3455	.0067	.0187	.0013	.1174	.1757	.0181
7+										
Winter	.0976	.0457	.0000	.5670	.0344	.0609	.0002	.0526	.1136	.0280
Spring	.0295	.0000	.0019	.5226	.0869	.0383	.0282	.1156	.1339	.0431
Summer	.0912	.0000	.0033	.5364	.0878	.0267	.0224	.1066	.0823	.0433
Autumn	.3275	.0000	.0002	.2816	.0127	.0259	.0150	.0827	.2201	.0343

*Winter = 1 January to 31 March- (model days 293 to 17).
Spring = 1 April to 31 June (model days 18 to 108).
Summer = 1 July to 30 September (model days 109 to 200).
Autumn = 1 October to 31 December (model days 201 to 292).

Table B-6.--Diet proportions by weight and season of the 10 prey categories and three age groups used in the model of walleye pollock on-the northwest shelf of the eastern Bering Sea. (WPOL - walleye pollock, WPEG - walleye pollock eggs, GADS - gadidae that are not walleye pollock, EUPH - euphausiids, COPD -copeppds, AMPH - amphipods, MYSD - mysids, CRUS - crustaceans not included in the above categories, FISH - fishes not included in the above categories, MISC - miscellaneous prey not included in the above categories.)

	Prey categories									
Age & Season*	WPOL	WPEG	GADS	EUPH	COPD	AMPH	MYSD	CRUS	FISH	MISC
2-4										
Winter	.0000	.0000	.0000	.7938	.0079	.0513	.0000	.0000	.1315	.0155
Spring	.0061	.0001	.0000	.5411	.2396	.0118	.0000	.0243	.1263	.0507
Summer	.0422	.0000	.0047	.2342	.4853	.0791	.0007	.0570	.0312	.0656
Autumn	.1759	.0000	.0312	.2781	.1518	.0474	.0000	.0091	.2630	.0435
5-6										
Winter	.0000	.0000	.0000	.8167	.0000	.0000	.0000	.0000	.1833	.0000
Spring	.0263	.0000	.0000	.5896	.2589	.0276	.0000	.0003	.0612	.0361
Summer	.0805	.0000	.0090	.3162	.2947	.0771	.0010	.0837	.0446	.0932
Autumn	.2503	.0000	.0136	.1802	.0835	.0711	.0236	.1096	.1954	.0727
7+										
Winter	.3908	.0000	.0053	.3880	.0001	.0001	.0000	.0365	.1665	.0127
Spring	.1090	.0022	.0005	.5186	.0711	.0117	.0208	.0678	.1524	.0459
Summer	.1631	.0000	.0197	.2290	.1526	.0653	.0227	.1268	.1211	.0997
Autumn	.5317	.0000	.0594	.0597	.0255	.0135	.0034	.0585	.2261	.0222

*Winter = 1 January to 31 March (model days 293 to 17).
Spring = 1 April to 31 June (model days 18 to 108).
Summer = 1 July to 30 September (model days 109 to 200).
Autumn = 1 October to 31 December (model days 201 to 292).

APPENDIX C

Corrected calculations of energy losses due to spawning by walleye pollock.

Table C-1.--Table II of Smith et al. (1988) is reproduced below with the corrected values underlined. Based on the corrected values, adult walleye pollock will lose about 14.4% (males, 7.3%; females, 21.4%) of their pre-spawning body weight and about 25.2% (males,. 14.1%; females, 36.3%) of their total body energy during spawning.

TABLE II. Energy content and partitioning of that energy in ripe and spent adult walleye pollock. In this exercise, [Smith et al. (1988)] assumed a ripe weight of 1,000 g for both males and females; corresponding lengths (49.6 cm for males, 48.3 cm for females) were calculated for ripe fish, based on average condition of ripe males (0.82) and ripe females (0.89) in March 1986; weights of spent adults were predicted based on lengths and average condition of spent fish (0.76 for males; 0.70 for females) in April, 1986; liver, gonad and somatic indices were those calculated for ripe fish in March 1986 and for spent fish in April 1986

Compartment	% body	g	g (dry)	kcal/g (dry)	kcal	% total
Ripe male: 1,000 g, 49.6 cm						
Whole body	100	1,000	200	4.4	880	100
Liver	4.8±3.03	48	28.3	7.1	201	23
Gonad	8.1±2.17	81	12.2	4.3	52	6
Somatic	87.1±3.52	871	159.5		627	71
Muscle				4.3		
Spent male: 927 g, 49.6 cm						
Whole body	100	927	189	4.0	756	100
Liver	3.3±1.55	31	16	7.4	119	16
Gonad	0.8±0.15	7	1	4.3	5	<1
Somatic	95.9±1.52	889	172		632	84
Muscle				4.4		
Ripe female: 1,000 g, 48.3 cm						
Whole body	100	1,000	214	4.5	963	100
Liver	4.1±1.22	41	25.8	7.5	193.5	20
Gonad	20.0±4.41	200	42	4.8	201.6	21
Somatic	75.9±4.40	759	146.2		567.9	59
Muscle				4.2		
Spent female: 786 g, 48.3 cm						
Whole body	100	786	157	3.9	613	100
Liver	3.4±1.23	27	15	7.6	110	18
Gonad	1.1±0.52	9	1	4.2	6	1
Somatic	95.5±1.31	75	141		497	81
Muscle				4.5		

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