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MANAGEMENT IMPLICATIONS OF VARIABILITY IN REPRODUCTION AND GROWTH OF COMMERCIAL MARINE FISHES

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Management Implications of Variability in Reproduction and Growth of Commercial Marine Fishes

by

Peter H. Dygert

A dissertation submitted in partial fulfillment
of the requirement for the degree of

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to offer degree School of Fisheries

Date 3 February 1986

Doctoral Dissertation

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Abstract

MANAGEMENT IMPLICATIONS OF VARIABILITY IN REPRODUCTION AND GROWTH OF COMMERCIAL MARINE FISHES

By Peter H. Dygert

Chairperson of the Supervisory Committee: Professor Donald R. Gunderson
School of Fisheries

The relation between reproductive effort and natural mortality rate was examined for 15 species of marine fish. The observed correlation relating the wet gonad somatic index (WGSI) to M was r = .831. For most species reproductive effort can be determined during a single spawning season. The described method therefore can provide a quick preliminary estimate of the rate of natural mortality.

Special problems concerning the reproductive biology of copper rockfish (*Sebastes caurinus*), northern anchovy (*Engraulis mordax*) and English sole (*Parophrys vetulus*) were considered. It was estimated that a relatively small proportion (11.5%) of the energy consumed by copper rockfish embryos during gestation was contributed by the mother, particularly in relation to comparable estimates pertaining to black rockfish (*S. melanops*, 70%). It has been suggested that northern anchovy may spawn 20 or more batches of eggs per year. Alternative analysis techniques were used to show that spawning at this high rate may not be energetically feasible. Results for English sole show that the expected net somatic growth increment of a 6-year-old fish is 12 g dw compared to a seasonal weight loss of 62 g dw and a reproductive energy expenditure of nearly 30 g dw. The implications related to management strategy for English sole are then discussed.

An analysis of variability in the growth and reproduction of fish of similar size and age suggests that much of the observed variability results from inherited dissimilarities in individual abilities to obtain and process food. Additional consideration of how energy allocation patterns change with size and age suggests that declining physical condition was coincidentally related with increasing relative reproductive effort, but that the two were not necessarily causally related.

Finally, a method was developed which uses measures of the inter-annual variability in production indicators and other biological parameters to analyze how stocks respond to changes in their environment. The method was applied to a time series of Pacific herring data leading to the conclusion that fishing, poor recruitment and an increase in the rate of natural mortality have all contributed to the severe decline in stock abundance. It is also apparent that during the observed decline, the entire complex of life history parameters has undergone significant change.

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PREFACE

I have organized my dissertation into three chapters, each of which deals with a related topic. In the first chapter I evaluate whether measures of reproductive effort could be used to predict the natural mortality rate of commercial fishes. If reproductive effort is to be used as a predictor of natural mortality, then it is important to understand the components of variability that affect reproduction. The second chapter therefore contains an exploratory analysis of the variability in reproductive effort and its relation to somatic growth and physical condition. The three components of variability considered include: 1) intra-annual variability associated with the seasonal cycles of growth and reproduction, 2) the variability in reproduction and growth between fish of similar size and age, and 3) the changing relationship between growth and reproduction with size and age groups. The final chapter is devoted to a consideration of a fourth level of variability. In particular I describe a proposed monitoring program which would use measures of the interannual variability in production parameters and other biological characteristics to analyze how stocks respond to changes in their environment. The method is then applied to a time series of herring data to demonstrate the potential benefits that could be derived by using a perspective of analysis which emphasizes the use of these measures of interannual variability.

CHAPTER 1.

REPRODUCTIVE EFFORT AS A PREDICTOR OF NATURAL MORTALITY

Introduction

The first objectives of my dissertation research are to evaluate whether measures of reproductive effort could be used to predict the rate of natural mortality, and in so doing, to develop a suitable standard methodology.

Estimates of natural mortality (M) are necessary for the management of commercial fisheries. Among the standard techniques requiring natural mortality estimates are yield per recruit analysis, cohort or virtual population analysis, estimation of recruitment selectivity functions, and determination of maximum sustainable yield. These models can be sensitive to errors in the mortality parameter. When possible, mortality is therefore estimated using several independent techniques or data sets.

Unfortunately, natural mortality is a difficult parameter to estimate. The usual estimation methods involve either mark-recapture studies or the aging of fish. Both are expensive and time-consuming. Often, it is not possible to age fish using standard methods of growth ring analysis. Tropical fish, for example, grow in an aseasonal environment, and therefore, do not have annual growth rings analogous to those found in temperate fishes. Even among temperate species, determining the ages of long-lived fishes, such as Pacific rockfish and sablefish, and even some relatively short-lived fishes such as Pacific cod can be difficult (Power 1978; Beamish 1979).

An examination of some of the assumptions of life history theory suggests that mortality rate and reproductive effort may be correlated (Williams 1966; Schaffer 1974a,b; Stearns 1976; Calow 1979; Roff 1982). It is assumed that assimilated energy beyond that needed for respiration is apportioned between growth and reproduction. Bigger fish have greater competitive ability and are subject to a smaller range of potential predators. Mortality, therefore, will be inversely related to the amount of energy allocated to growth. Conversely, there are physiological and behavioral costs associated with reproduction. In the extreme, senescence, to a large degree, may be an expression of excessive reproductive effort (Orton 1929; Love 1970; MacKinnon 1972). Mortality, therefore, is directly related to reproductive effort.

There is also considerable empirical evidence demonstrating that higher reproductive effort is associated with increased mortality. Stearns (1976) and Calow (1979) summarize much of the pertinent literature for a variety of taxonomic groups. Additional evidence can be found from studies of fish species. Laboratory work on medaka (Hirshfield 1980) clearly demonstrated that fish with higher reproductive effort do die at higher rates because of increased weight loss. Gunderson (1980) correlated the life history parameters of marine fishes with mortality estimates and also found that the gonad index provided the best fit. There were no mortality rates available in Miller's (1979) study of small (10 cm or less) bony fishes, but his data on gobiids suggested that the close correlation between mortality rate and reproductive effort also extends to short-lived species which release several batches of eggs per year. Total annual ovarian production for

Gobius paganellus (maximum age = 10 years) was "somewhat less" than one-half the dry body weight, while that of *Pomatoschistus microps* (maximum age = 1.6 years) was "at least twice" the average adult body weight. Adams' (1980) correlative analysis of life history parameters also showed good agreement between the observed and expected results, although there were no explicit measures of reproductive effort included.

As indicated above, the suggestion that natural mortality and reproductive effort are correlated is supported both by theoretical analysis and empirical evidence. The first objectives of my research are to examine the relationship between the two parameters and to evaluate whether measures of reproductive effort could serve as a reliable estimator of natural mortality rates and to develop a standard methodology for quantifying reproductive effort.

Methods

General Approach

All of the fish in this study exhibit seasonal cycles in gonadal development, and often show an increase in reproductive effort with size. In order to make an interspecific comparison of reproductive effort it is therefore necessary to have a standard method for identifying the size of an "average" fish for each species. The approach taken here was to estimate the average size of a mature female fish for the pre-exploitation stock. Historical maturity-length data was used to identify the size at 50% maturity. If size frequency data were available they were used to calculate the average length of fish greater than or equal to the maturation size.

When size frequency data were not available the average size of a mature female ~~-~~was calculated using the formula

$$\text{average age} = \frac{\int_{t=a}^{\infty} tN_t \, dt}{\int_{t=a}^{\infty} N_t \, dt}$$

where

$N_t = Noe^{-m(t-a)}$

a = age of maturity

M = instantaneous rate of natural mortality.

This formula can be simplified after evaluating the intergrals to

$$\text{average age} = \frac{(Ma)+1}{M}$$

Average age was then converted to average length using a von Bertalanffy length at age function.

Samples of the five species considered directly during this study (English sole, Pacific cod, Pacific herring, dogfish, copper rockfish) were stratified by size and taken immediately prior to the spawning season. The fish were categorized by development stage and those with fully developed gonads were used for subsequent analysis. In the cases of Pacific cod, English sole and copper rockfish, a more detailed analysis of egg size was required to identify adequately those fish that were in the final stages of gonad maturation. Copper rockfish presented a special problem because they are a live-bearing species. It was therefore necessary to estimate maternal contribution during gestation (see

Appendix A) as well as the the energy content of the gonads at the time of fertilization.

The initial processing of fish occurred while they were still fresh. Each fish was measured, the gonads were then removed and the stomachs were emptied. Lengths for most species were measured from the tip of the jaw to the end of the center of the caudal fin, although standard length was used for herring to conform with the methods of Washington Department of Fisheries (WDF). Separate weight determinations were made for the gonad and remaining somatic tissue. The gonads and bodies were then labeled, bagged separately, and frozen for later analysis. Whole bodies of the individuals used for caloric analysis were either chopped by hand or ground in a Hobart meat grinder and homogenized with a known amount of distilled water in a Waring blender. The water content was determined by taking three replicate subsamples (two in the case of herring) from the homogenate and drying at 80°C for 24 hrs. The dry tissue was then weighed and ashed at 500°C for 4 hrs. The gonads were chopped, subsampled and treated as above using the same number of replicates. The caloric content of the two tissue types for each fish was determined using a Parr Instruments adiabatic bomb calorimeter. The protein and lipid content of English sole gonad and somatic body tissues were also analyzed as part of a study of seasonal energy cycling. Total protein was estimated using the Kjeldahl method (Assoc. Off. Anal. Chem. 1965). Lipid content was determined by Soxhlet extraction with diethylether.

Gonad-somatic tissue (GSI) ratios were used as indices of relative reproductive effort. Four different GSI's were calculated (Table 1). The index based on wet weights (WGSI) requires the least processing and is the one most commonly available in the literature. The dry weight index (DGSI) corrects for the variability of water content in the tissues. The two caloric-based indices (CGSI - based on calorie per g dry weight, and CAGSI - based on calorie per g ash free dry weight) were needed to compare the reproductive effort estimates of fishes with different modes of reproduction (i.e., live-bearing species, single batch spawners, and multiple batch spawners) and to account for species differences in the calorie and ash content of gonad and body tissue.

A standard procedure was used to calculate the four indices for each species. The length of the average mature fish was determined as described above. The corresponding body weight (Bwgt) was estimated from a length-weight function

$$\mathrm{Bwgt} = a\ \mathrm{Lgth}^{b}$$

derived from my own data. The gonad weight (Gwgt) for a fish of average length was estimated from a similar function

$$\mathrm{Gwgt} = a\ \mathrm{Lgth}^{b}$$

again derived from my own data. In both cases the coefficients were estimated by applying a least squares linear regression analysis to the log transformed data. The WGSI was calculated as the Gwgt to Bwgt ratio. The other three indices were derived by transforming the basic

Table 1. The computation formulae used to derive the gonad-somatic tissue indices based on gonad weight (Gwgt), somatic body weight (Bwgt), gonad and body tissue percent dry matter (__DRY), ash (__ASH), and calorie content (__CAL).

$$\mathrm{WGSI} = \mathrm{Gwgt}/\mathrm{Bwgt}$$

$$\mathrm{DGSI} = \mathrm{WGSI} \times (\mathrm{GDRY}/\mathrm{BDRY})$$

$$\mathrm{CGSI} = \mathrm{DGSI} \times (\mathrm{GCAL}/\mathrm{BCAL})$$

$$\mathrm{CAGSI} = \mathrm{CGSI} \times \frac{(1-\mathrm{BASH})}{(1-\mathrm{GASH})}$$

WGSI ratio (Table 1). Estimates of percent dry matter, ash content, and caloric content of the gonad and body tissues were correlated with body length and weight. If the correlation for a given species was significant (p = .05) a linear regression equation was used to estimate the appropriate value for the representative fish of average weight. If the variables did not vary significantly with size, the arithmetic mean of all observations was used. Estimates of natural mortality were derived from the literature.

English Sole

English sole samples were used for assessing reproductive effort, and as part of study concerning seasonal energy cycling. Samples were collected every 4 to 6 weeks from January 1983 through March 1984 from the catch of day-trip trawlers landed in Blaine, Washington. A total of 317 fish were retained for analysis.

It became apparent during the sampling that gross examination of gonad development was not sufficient to differentiate fish with developing gonads from those that were fully developed and close to the time of hydration and spawning (i.e., those needed to assess reproductive efforts). As a result, average oocyte diameter was used to select the fish needed for subsequent analysis. Like winter flounder (Dunn and Tyler 1969), English sole have three size classes of developing oocytes. Only the largest size class of yolked and maturing oocytes was measured. A small segment was clipped from the anterior dorsal corner of one of the gonads from each fish. Average oocyte diameter was estimated by first teasing individual eggs away from the tissue sample. Twenty to 40 of the separated, undamaged eggs were chosen arbitrarily and measured using an ocular micrometer. The micrometer orientation remained unchanged and the axes of the oocytes were measured as they came into the field of view.

Several fish were collected that had both hydrated and unhydrated oocytes. These fish permitted the estimation of the size of oocytes just before hydration and therefore provided an objective standard for the selection of "mature" fish.

Pacific Cod

Cod were also sampled from the catches of "day trawlers" landed in Blaine, Washington. Fifty-nine female cod were collected and retained for tissue analysis between December 10, 1982 and March 3, 1983. An additional 41 were weighed and measured. During March 1984, 14 cod were retained and during February 1985, length, body weight and gonad weight data were collected from 201 mature females.

The fish collected in 1983 were all judged by visual inspection to be in the final stages of gonad maturation. However, as with English sole, it was again necessary to measure oocyte diameters in order to provide an objective standard of relative gonad maturity. Small tissue samples were taken from frozen gonads and the maximum diameters of 20-40 individual oocytes were measured using the method described for English sole. The oocyte diameters of 10 fish were measured both fresh and frozen to provide a correction for the increase in egg size that resulted from freezing. Fish with some oocyte hydration were used to determine the size of mature, but still unhydrated eggs. Four such fish were available.

During 1984 I worked on a method for field identifications of mature fish based on egg size. As a result of the 1983 analysis I determined that mature cod eggs were at least .735 mm in diameter. I used a piece of .750 mm Nitex mesh attached to the back of a glove to aid in the identification of mature eggs. The inspection was sometimes aided with a small hand lens. The fish collected in 1984 using this method all were later shown to be mature by measuring the eggs with an ocular micrometer. In 1985 all maturity identifications employed the Nitex sorter since fish were not kept for later analysis.

Herring

Herring samples were taken from the catch of the Washington Department of Fisheries (WDF) herring trawl surveys. The surveys are conducted each year, twice per week for about 6 weeks during April and May. WDF personnel sort samples from each survey for sex, size, and maturity composition. During 1982 325 fish were collected from these samples as they were sorted. No egg size determinations were made. In 1984 150 mature females were taken from the trawl samples and from part of the unsorted catch of the surveys. Egg dry weight determinations were done on about 100 fish to define the relation between egg size and the size of the fish. Egg weights were determined by weighing 100-150 eggs, drying for 24 hours at 80°C and then reweighing.

Dogfish

Dogfish samples were taken from the trawl catch landed in Blaine, Washington and the set net catch landed in Seattle, Washington from October 1983 through January 1984. Fifty fish were retained for analysis. The diameter of all mature oocytes in the ovaries of these fish were measured to provide an objective criterion for determining the stage of reproductive development.The length and reproductive condition of 300 additional fish were noted on 6 different sampling dates during this period to monitor the timing of reproductive events. Length, body weight and gonad weight samples from 201 dogfish were collected from the trawl fishery during December 1984.

Copper Rockfish

Estimating the reproductive effort of copper rockfish required some additional analysis because of an uncertainty concerning their reproductive biology. Wourms (1981) surmized that members of the genus *Sebastes* are primitive live-bearers and, as such, do not make any energy contribution during embryonic development. However, Boehlert and Yoklavich (1984) found that 70% of the energy consumed during gestation was contributed by the mother. It was therefore necessary to determine whether copper rockfish also contributed energy to the embryos during development. Details pertaining to this analysis are discussed in Appendix A.

The copper rockfish used for assessing the gonad weight-length and body weight-length relationships and tissue characteristics were collected during the 1984 spawning season. Thirty-three were taken by spearfishing from three locations (Mukilteo, Point Heyer, and Misery Point) on four different dates (February 29, March 13 and 20, and April 27, 1984) by Washington Department of Fisheries personnel.

The procedures used to process the gonad and body tissues of copper rockfish were similar to those already described for other species. In addition, while the gonads were still fresh the state of reproductive development was determined for each fish using the Stahl-Johnson (1984) staging index. Egg diameters were estimated for all fish that had unfertilized or recently fertilized eggs by measuring a sample of 30-40 eggs using an ocular micrometer. Egg dry weights were also determined for all fish with fertilized eggs or large eggs that were judged to be close to fertilization.

The information on egg diameter was used to determine whether the gonads of each individual with unfertilized eggs were fully developed. Those that were close to fertilization were included in the computation of the gonad somatic tissue indices.

It was also necessary to determine the relationship between embryo weight and development stage during gestation. Since embryo weight declines during gestation the total gonad weight must also decline from the time of fertilization to birth. Measurements relating embryonic weight to development stage were therefore used to correct the gonad weight data for fish that had embryos in the later stages of development and which had therefore lost weight.

There were no size frequency data for copper rockfish in the historical record. It was therefore necessary to calculate the average size of a mature fish using the formula described above.

Other Species

Other species were included in the analysis if there were sufficient data available in the literature concerning necessary parameter estimates. Gunderson's (1980) review of the relationship between natural mortality and life history parameters (which provided the impetus for this part of my research) contains 11 sets of parameter estimates for 10 different species of fish including Northern plaice, North Sea sole, American plaice, Pacific halibut, North Sea cod, Pacific cod, North Sea herring, Pacific herring, North Sea haddock, Grand Banks haddock, and capelin. Recently published information permitted the consideration of 2 additional species (northern anchovy and northern sand lance). My own data provide updated estimates of reproductive effort for Pacific cod and Pacific herring. Capelin were subsequently excluded from the analysis because of uncertainties concerning the reproductive effort data (Prokhorov 1968) and the recently reported finding that capelin may be largely semelparous (Hamre and Tjelmeland 1982).

All parameter estimates for the remaining species were derived from the literature. The preferred standard for selecting estimates was that they be representative of the pre-exploitation condition. If two series of data were available, the earliest reliable parameter estimates were used. In some cases only more recent data were available and it was therefore necessary to assume that the parameters had not been seriously affected by exploitation. A firm prerequisite was that all of the required parameters for a given species be derived for a restricted geographic area to minimize stock dependent differences.

The gonad-somatic tissue index (WGSI) had to be derived in a number of different ways depending on the form of the available data. In some cases (North Sea sole, North Sea herring, North Sea plaice, sand lance) the WGSI was given or could be derived directly from tabulated data. Reported values of gonad-somatic tissue indices can be used if adequately defined. In general it must be clear that the gonads are fully developed but still unhydrated. The form of the body weight (whole, somatic, gutted, etc.) must also be specified. Gonad indices (GI) are often calculated by dividing gonad weight by whole body weight. An equivalent WGSI estimate can be derived by subtracting the proportional weight of the gonad from 100 and redividing.

That is, if $GI = A$, $WGSI = \frac{A}{100-A}$

WGSI estimates for North Sea cod, Pacific halibut, and American plaice were derived using a variety of empirical functions relating body size to fecundity, ovary weight and age data. North Sea cod was one of two species (the other being anchovy) where there was sufficient information to also calculate dry weight and caloric based indices. For the remaining species (northern anchovy, pollock, North Sea haddock, and Grand Banks haddock) it was necessary to estimate reproductive effort using fecundity and egg size data.

In the cases of pollock, other forms of gonad weight data were unavailable and the fecundity approach provided the only option. For multiple batch spawners however reproductive effort must be estimated using fecundity data. Anchovy, for example, may spawn 30 or more times per year depending on their size and age (Anon. 1984). However, at each spawning half the weight of a ripe gonad is lost indicating that egg development is a continuous process.

Haddock and pollock are also serial spawners, although in their cases all the eggs to be spawned in a given year are yolked at the start of the spawning season and are distinct in size from the clear pre-vitillogenic eggs. Once spawning begins, a batch of eggs is hydrated and released every few days.

Using fecundity data presents some particular problems. What is required is the equivalent wet weight of all spawned eggs just before hydration. Determining total annual fecundity can be a problem. For either single time spawners or serial spawners, a count of all yolked eggs is sufficient although this does require the assumption that egg resorption is minimal. For species like anchovy, however, it is necessary to determine the number of eggs spawned per batch as well as the number of batches per year. This problem has been addressed by Hunter and Goldberg (1980), Hunter and Macewicz (1980), Hunter and Leong (1980) and Anon. (1984), and is discussed in more detail below.

The second problem is converting the available egg size data to an appropriate wet weight value. Egg size is most often reported in terms of dry weight or diameter, usually of the hydrated egg. Egg dry weight can be converted to an equivalent wet weight by dividing by an estimate of the proportion of dry matter in a ripe gonad. Species specific data is desirable but generally not available. I have therefore chosen to use a dry to wet conversion factor of .32 based on my observations of English sole (.32), Pacific cod (.32), sablefish (.30) (pers. observation), Pacific herring (.27), and anchovy (.35) (Hunter and Leong 1980). This value is the estimated dry matter content of ripe gonads containing unhydrated eggs.

Direct estimates of egg dry weight are sometimes available, but diameter of hydrated (i.e., spawned) eggs is the most commonly reported measure of egg size. Egg diameter can be converted to egg dry weight in 2 different ways. Hislop (1984) calculated an empirical function relating egg dry weight to the diameter of hydrated eggs for North Sea haddock and whiting.

$$\text{Egg dry weight} = .0269(D)^{3.35}$$

where D = egg diameter (mm).

The equation is valid over a size range from 0.9 to 1.5 mm. The second method involves converting diameter to volume ($4/3\pi(\frac{D}{2})^3$; assuming the egg is spherical), and multiplying by the specific gravity to get the equivalent weight of a hydrated egg. The weight derived by converting diameter to volume to weight is that of a hydrated egg. This can be converted to dry weight using Hislop's (1984) observation that hydrated eggs are about 95% water. Obviously, it would again be desirable to have a species-specific estimate for the water content of hydrated eggs if possible. Direct observations of the specific gravity of pollock (Kim, pers. communication) and haddock eggs (Templeman et al. 1978) are 1.015 and 1.023, respectively. In fact, all pelagic eggs must be very close to that of ambient seawater (about 1.025 depending on conditions).

A comparison of gonad weight estimates derived using both direct and indirect methods suggests they give comparable results. I calculated that the expected gonad weight of a 390 mm English sole was 87.8 g using a gonad weight-length regression (i.e., direct estimation, see below). Gonad weight was then estimated using egg diameter (.99 mm, Orsi 1968) and fecundity estimates ($F = 5.202L^{3.328}$, Harry 1969) by the two methods described above (diameter-dry weight function and diameter, volume, hydrated weight, dry weight algorithms). Both techniques led to an estimated gonad weight of 83.5 g. It should be noted that the dry egg weight estimates derived using the two methods will be nearly identical for eggs around 1.0 mm in diameter, but do diverge somewhat as egg size increases. There is a 15% difference in the egg weight estimates at 1.5 mm.

Two cautions should be noted about using these methods. First, neither method applies to demersal eggs, which have different densities and thus diameter-weight characteristics. Direct egg dry weight observations probably could be used without incurring substantial error if they were available. The second caution is that egg diameter should be known with reasonable certainty since volume, and thus egg weight, varies as a cubic function of the radius. Errors in the diameter estimates are therefore magnified and could lead to unacceptable errors in the estimates of reproductive effort. This method was not used on Pacific halibut, for example, because the range in the reported egg diameter values was large (Forrester and Alderdice 1973, range 2.95-3.52 mm; Thompson and Van Cleve 1936, range 2.05-3.85 for live material and 2.90-3.80 mm for preserved).

Body weight data are generally reported as whole, gonads removed, gutted, or gutted and gilled. If whole body weight is reported, WGSI can be calculated by subtracting the estimated gonad weight from the whole body weight before dividing. The gutted, and gutted and gilled weight estimates present a problem in that their use will lead to an overestimate of WGSI if not corrected. I have found an approximate correction factor for Grand Bank haddock (estimated from data in Templeman et al. 1978) which suggests that the viscera and gills are equivalent to about 13.5% of the dressed body weight. I used this correction factor when calculating the WGSI for Grand Bank haddock.

Similar correction factors are available for flatfishes. The gut comprised 3.8 and 4.1% of somatic weight in plaice (Pleuronectes platessa, Dawson and Grimm 1980) and American plaice (Hippoglossoides platessoides, MacKinnon 1972), respectively. The estimated gutted weights of halibut were therefore elevated by 4% when estimating WGSI based on the reasoning that different flatfish species have similar body form. The body weights of North Sea sole and American plaice were reported as gutted and gilled. The 4% correction factors were also used in this case since I was unable to find the desired flatfish gutted and gilled adjustment estimate. The North Sea herring data were also reported using gutted body weight. However, my own observations indicate that the gut of herring is quite small during spawning and therefore of minimal importance. A similar observation was made by Hickling (1940). In fact, the effects of all of these minor corrections on WGSI are relatively small. However, the objective is to maintain a consistent procedure for parameter estimation that can be applied without ambiguity as data on additional species become available.

A final problem associated with estimating WGSI relates to the fact that relative reproductive effort varies with size and age. There is therefore the general problem of selecting a particular WGSI value for each species. If the data were such that reproductive effort could be calculated as a function of age, then the WGSI value used was the one associated with the calculated age of the average female derived using the formula (see above)

$$\text{Average age} = \frac{M(a)+1}{M}$$

In some cases gonad weight or fecundity could not be related directly to age. Under these circumstances the WGSI value used was the average of those derived for the full size range of mature females.

Certain standards also were used in selecting species-specific estimates of other life history parameters (i.e., natural mortality, age of maturity, longevity, growth parameters). It has been assumed for the purposes of this study that adult natural mortality rates are constant even though it is probably fairly common for mortality to increase with age, particularly as fish approach senescence (Beverton 1963; Cushing

1975). However, the potential variability that could result from this assumption h~~as~~ probably been minimized since both mortality and reproductive effort are estimated for adults in early age groups. Sex-specific estimates of M were often not available in the literature, so combined estimates were used in all cases.

Maturation age, longevity, and the growth parameters were evaluated along with measures of reproductive effort as potential predictors of M. The age of 50% maturity (a) provides a comparative measure of maturation age. Between sex differences in maturity are common. As a result, only female maturation estimates were used, except for Pacific and North Sea herring for which sex specific information was unavailable.

Longevity (T.01) was determined by identifying the age at which abundance declined to 1% of the level present at the age of maturity. The information used to estimate T.01 was generally age or size frequency data from the commercial catch. Since this kind of data is rarely sex specific, the estimates were consistently derived for sexes combined.

The Bertalanffy growth parameters (K, L_∞) were also derived from combined data, since the sex-specific estimates were often not available. American plaice was an exception because Bertalanffy parameter estimates were only available for females.

Results

English Sole

Samples of English sole were taken over a period of 15 months. However, only mature fish were used for assessing reproductive effort.

During the 1983 spawning season 59 of the English sole collected were judged by visual inspection to be in the late stages of gonad maturation. Ninety-three such fish were collected in 1984.

When I first began sampling it became apparent that there was considerable variability in egg size among these seemingly fully mature fish. For fish showing no hydration, oocyte diameters ranged from .40 to .60 mm. Although this range in diameters seems relatively small, it represents more than a three-fold increase in volume and clearly demonstrates that oocyte measurements are needed to identify maturity state with the precision required for this study.

Seven fish containing oocytes with some degree of hydration were used to provide a standard for fish selection based on egg size. Of these fish, four had relatively few hydrated eggs. The other 3 showed more hydration although none of the fish were "ripe and running." The size range of unhydrated oocytes from ovaries with few hydrated eggs was .582 to .600 mm. The unhydrated oocytes from ovaries with a higher incidence of hydration ranged from .601 to .678 mm. Using this information, an oocyte diameter of .550 mm was set as the criteria for determining which fish were in the final stages of gonad maturation. Based on this standard, 17 fish were judged to be mature from the 1983 sample of spawners and 78 from the 1984 sample.

Harry (1959) found that the size at 50% maturity was 310 mm for female English sole taken off the coast of Oregon. Ketchen (1947) reported a value of 295 mm for female English sole taken in the Strait

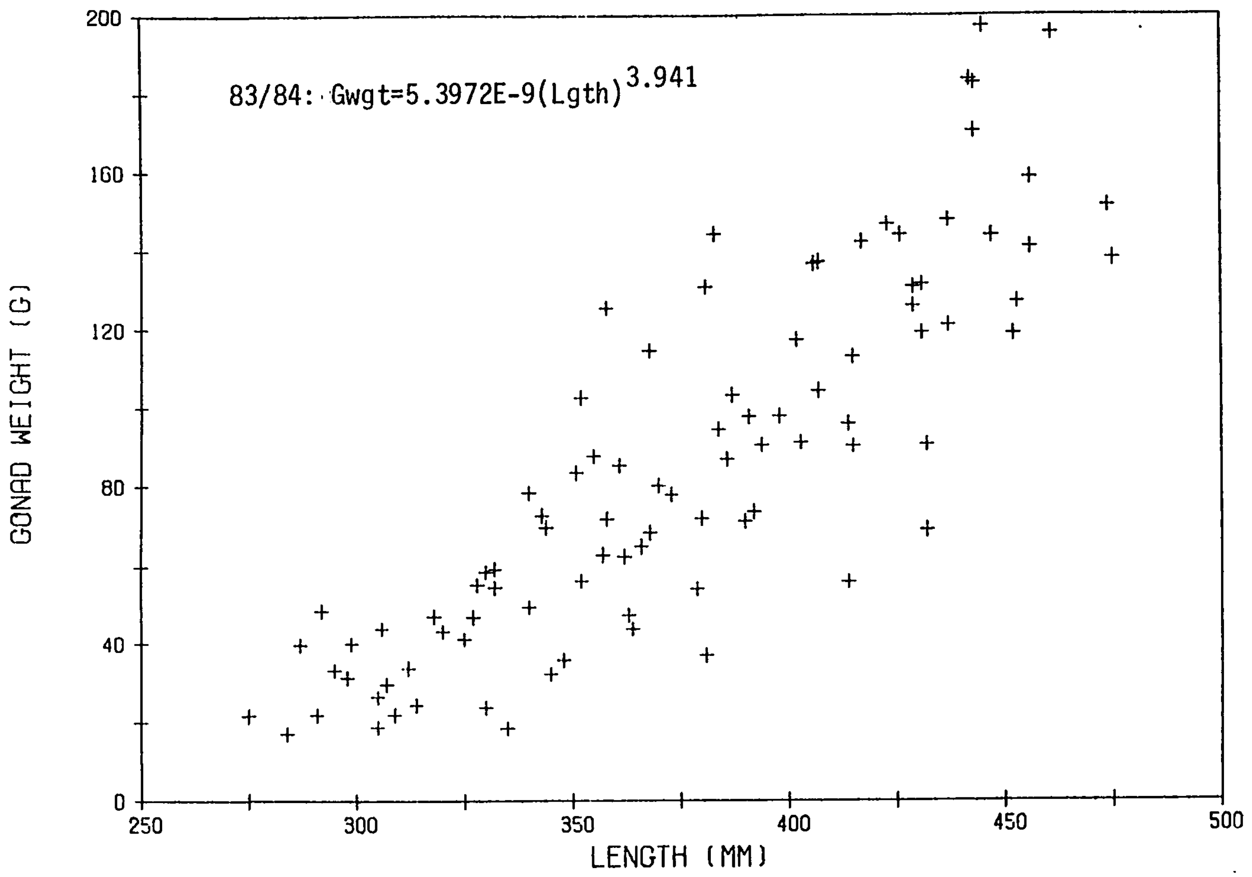


Fig. 1. Gonad weight-length plot for English sole with 1983 and 1984 data combined.

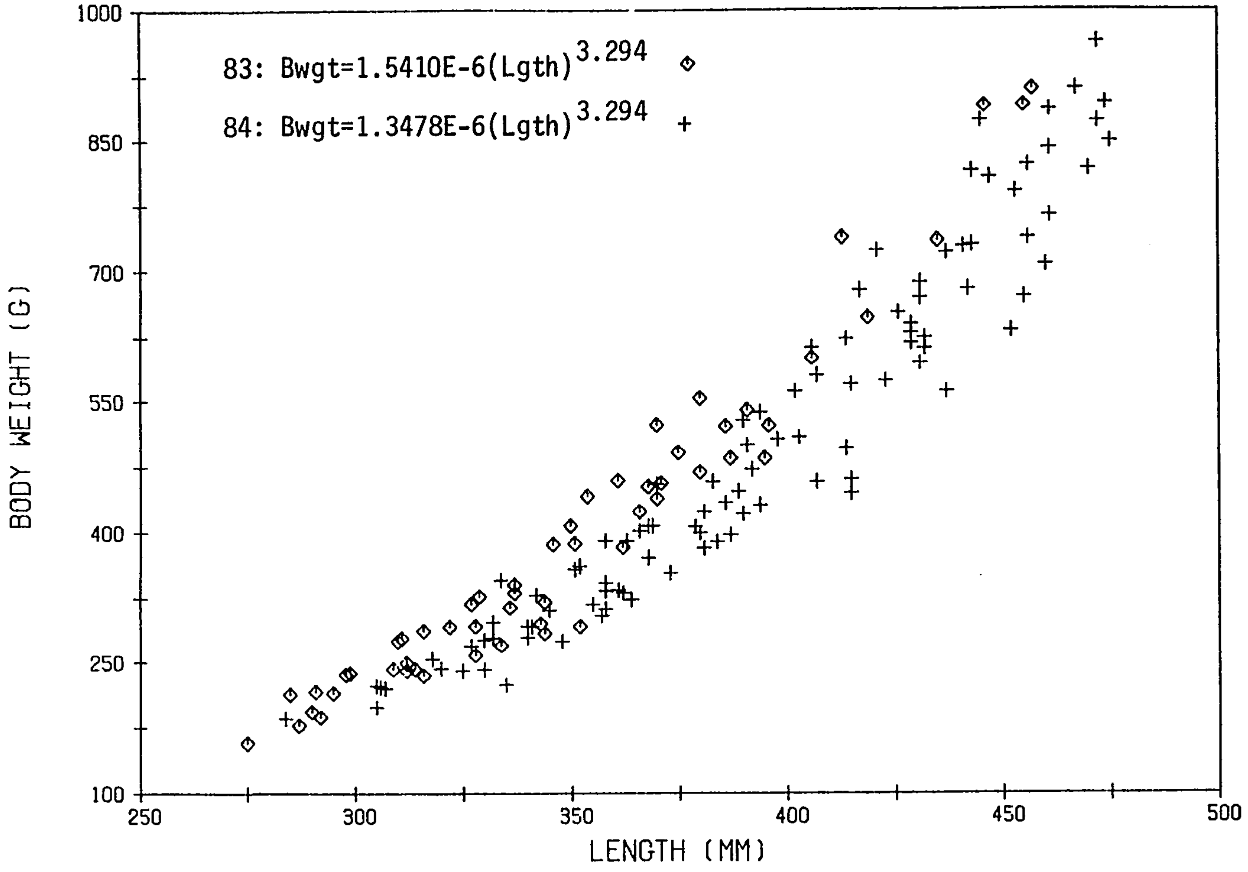


Fig. 2. Body weight-length plot for English sole with separate estimates for 1983 and 1984 data.

Table 2. Gonad-length and body weight-length regression equations and corresponding derived weights for mature English sole of average length (390 mm) by year.

English sole		n	Derived weight
1983/84	$Gwgt = 5.3972 \times 10^{-9} (Lgth)^{3.941}$	95	87.8 g
1983	$Bwgt = 1.5410 \times 10^{-6} (Lgth)^{3.294}$	59	528.2
1984	$Bwgt = 1.3478 \times 10^{-6} (Lgth)^{3.294}$	100	461.9

Table 3. The mean, standard deviation and sample size (first column) and correlation matrix for the tissue characteristic variables of English sole.

		Bwgt	Gwgt	BDRY	BASH	BCAL	GDRY	GASH	GCAL
Lgth	387.4	r=.952	.826	.036	-.134	-.124	-.147	-.143	.156
	47.8	p=.001	.001	.753	.242	.278	.199	.219	.542
	79	n=79	78	78	78	78	78	76	17
Bwgt	476.4		.852	.157	-.227	-.060	-.045	-.240	.132
	197.0		.001	.169	.046	.604	.698	.037	.613
	79		78	78	78	78	78	76	17
Gwgt	96.3			.198	-.154	-.003	-.265	-.130	.213
	51.0			.082	.177	.978	.019	.261	.411
	78			78	78	78	78	76	17
BDRY	.214				-.541	.636	.239	-.345	-.209
	.022				.001	.001	.035	.002	.420
	78				78	78	78	76	17
BASH	.149					-.769	-.380	.226	.192
	.024					.001	.001	.050	.461
	78					78	78	76	17
BCAL	4894.3						.290	-.099	-.090
	371.5						.010	.393	.730
	78						78	76	17
GDRY	.316							-.393	-.126
	.047							.001	.629
	78							76	17
GASH	.059								-.367
	.014								.148
	76								17
GCAL	5849.5								--
	231.7								--
	17								--

Table 4. Calculated gonad-somatic tissue indices for English sole by year with the necessary parameter regressions required for their computation.

English sole	WGSI	DGSI	CGSI	CAGSI
1983	.166	.245	.293	.265
1984	.190	.280	.335	.303

BASH = .1622 - .00003(Bwgt) = .148
r = -.227
p = .046

GASH = .0670 -.00002(Bwgt) = .058
r = -.240
p = .037

of Georgia. In a later paper Ketchen (1956) recorded the length frequency distribution (by 1-cm size class) of English sole taken in Hecate Strait, British Columbia from 1944-53. Assuming a knife-edge size of maturity at 300 mm, the calculated average length of mature females in his sample was 390 mm.

Analysis of covariance of the 1983 and 1984 gonad weight-length regressions showed that the lines were not significantly different. The data were therefore pooled to yield a single regression equation (Figure 1, Table 2). This relation was used to estimate the gonad weight for a fish of average size (87.8 g). Between year comparisons of the body weight-length regressions showed that the slopes were equivalent but that the intercepts were significantly different (Figure 2, Table 2). The estimated weights of a fish of average length were 528.2 g in 1983 and 461.9 g in 1984. A correlation analysis relating the water, ash and calorie content of body and gonad tissues to the body weight and length data showed that only body ash and gonad ash content were significantly correlated with body size (Table 3). Because of the between year differences in body weight, separate estimates of the gonad-somatic tissue indices were calculated for each year (Table 4).

The total mortality rate (Z) for English sole of ages 6-9 was estimated to be 0.494 (Hayman et al. 1980) using 1971-74 catch data for the stock off the Columbia River (PMFC Area 3A). The estimated exploitation rate (E) for English sole taken during the same time and from the same area was 0.156 (Demory et al. 1976) which corresponds to an average

Table 5. The average corrected oocyte diameter of Pacific cod in relation to sampling date.

Date	Mean oocyte diameter (mm)	n
1/13/83	.620	5
1/30/83	.674	14
2/03/83	.692	10
3/03/83	.762	10

annual fishing mortality (F) of 0.20. Subtracting F from Z (and rounding) gives an estimate of the annual natural mortality rate (M) of 0.3. The estimate seems reasonable given the fact that there are few fish in the catch older than 15 years of age.

Forrester and Ketchen (1963) report a slightly different estimate of natural mortality (M = 0.26) for English sole within the commercial size range. This estimate has been used in this analysis since it is derived from a variety of sources, including observations of the age composition of the virgin stock in Hecate Strait.

Pacific Cod

The estimated relationship between fresh and frozen oocyte diameters was

$$\text{Fresh} = .3012 + .5855\ (\text{frozen})$$

$$N = 10$$

$$r = .740$$

All egg size data reported below has been transformed to a corrected fresh egg diameter.

Oocyte diameter again proved to be an important criteria for identifying "mature" fish. In 1983 the average diameter of oocytes increased continuously with sampling date (Table 5). Four fish collected on March 3rd, 1983 had gonads containing some hydrated oocytes. The average diameter of unhydrated eggs from these gonads ranged from .785 to .836 mm. The criterion for identifying fully-developed fish was therefore set at .735 mm. On this basis, 27 fish were identified as mature from the 1983 sample and 14 from 1984. One hundred forty-six

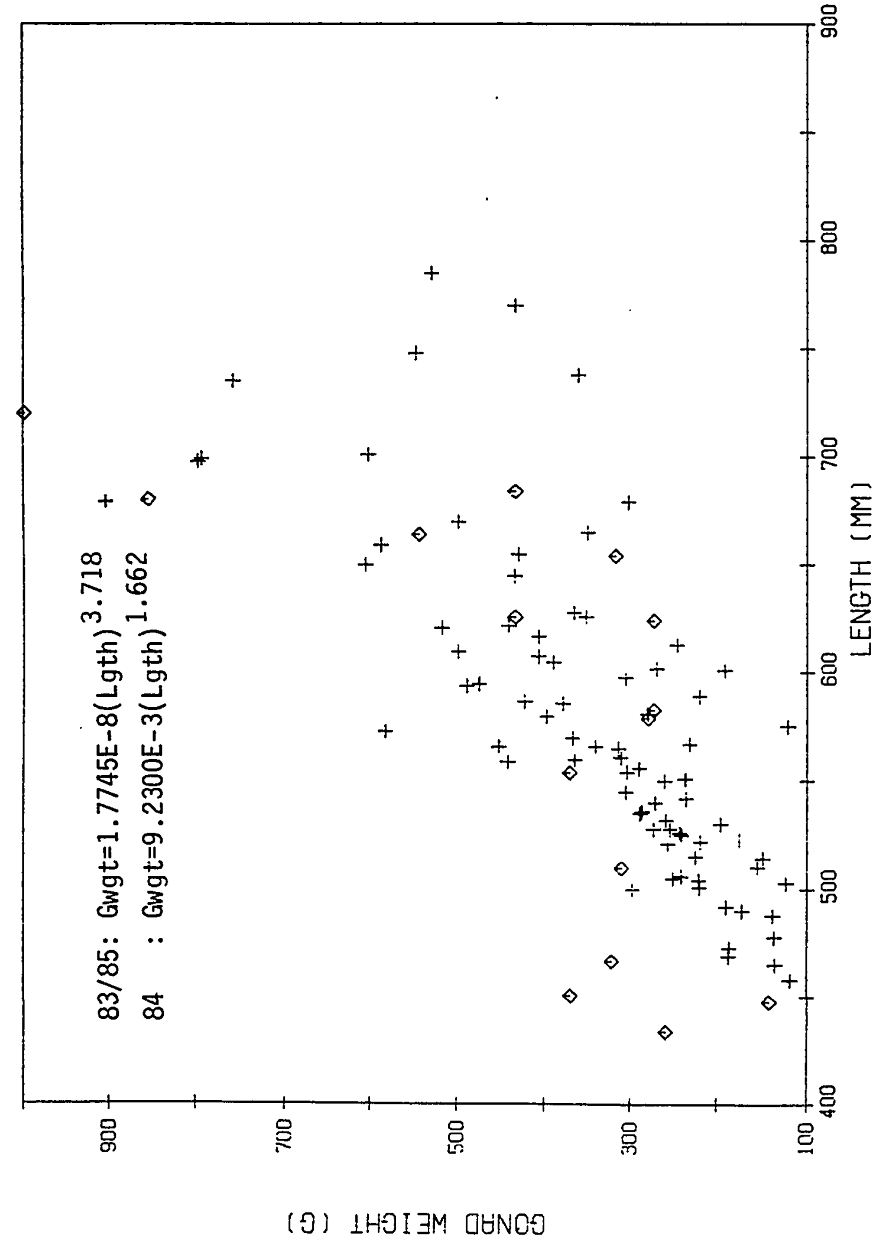


Fig. 3. Gonad weight-length plot for Pacific cod for years 1983-1985.

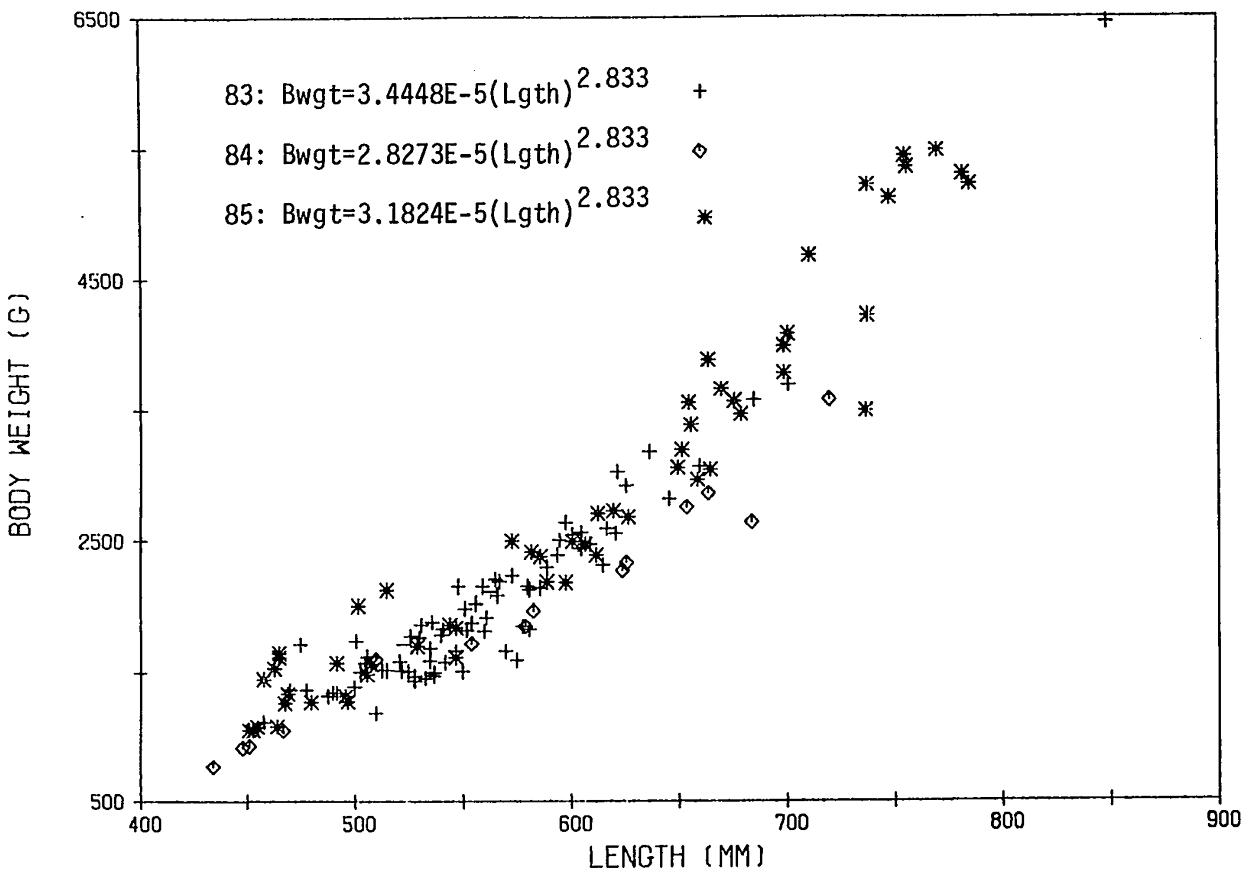


Fig. 4. Body weight-length plot for Pacific cod for years 1983-1985.

fish were measured in the field in 1985. Of these, 33 were spent. The rest were all judged to be mature based on the use of the Nitex mesh egg size sorter.

The size at 50% maturity for female cod in the Strait of Georgia is 550 mm (Ketchen 1961; Thomson 1962). Westerheim (1977) reported a value of 560 mm for females in Hecate Strait, B.C., Canada.

Ketchen (1961) tabulated the average length frequency distribution of Pacific cod caught in the Strait of Georgia during the years 1956-1960. Using this distribution the average length of fish 550 mm or larger was calculated to be 622 mm. Catches from the same area during 1954 and 1955 showed similar values of 624 to 622 mm, respectively (Ketchen 1961). WDF catch records taken during 1982 showed a corresponding length of 616 mm. The 622 mm value was used as the comparative size for estimating relative reproduction effort.

Covariance analysis of the gonad weight-length data (Figure 3) for the 3 years showed that the 1983 and 1985 data were not significantly different, but that the 1984 data had both a different slope and intercept when compared with the other two years combined. The exponent in the 1984 relationship (1.662) is atypical, however (it should be in the neighborhood of 3.0), and is probably not a reasonable estimate of the true population value. In 1984 both the sample size and size distribution within the sample were inadequate. A statistical analysis of the body weight-length data (Figure 4) showed that there were significant differences in the estimates of the 3 intercept values. The gonad weight estimates for a fish of average size were 434 g in 1983 and 1985,

Table 6. Gonad weight-length and body weight-length regression equations and corresponding derived weights for mature Pacific cod of average length (622 mm) by location and year.

Strait of Georgia		n	Derived weight (g)
1983	$Gwgt = 1.7745 \times 10^{-8} Lgth^{3.718}$	27	434
1984	$Gwgt = 9.2300 \times 10^{-3} Lgth^{1.662}$	14	406
1985	$Gwgt = 1.7745 \times 10^{-8} Lgth^{3.718}$	111	434
1983	$Bwgt = 3.4448 \times 10^{-5} Lgth^{2.833}$	56	2831
1984	$Bwgt = 2.8273 \times 10^{-5} Lgth^{2.833}$	14	2325
1985	$Bwgt = 3.1824 \times 10^{-5} Lgth^{2.833}$	146	2617
Vancouver Island			
1976	$Gwgt = 1.5794 \times 10^{-8} Lgth^{3.766}$	32	525
	$Bwgt = 6.1343 \times 10^{-6} Lgth^{3.086}$	32	2567
Hecate Strait			
1976	$Gwgt = 8.6927 \times 10^{-6} Lgth^{2.737}$	43	385
	$Bwgt = 6.1343 \times 10^{-6} Lgth^{3.086}$	43	2567
Gulf of Alaska			
1982	$Gwgt = 1.9142 \times 10^{-9} Lgth^{4.020}$	509	326
	$Bwgt = 3.1668 \times 10^{-6} Lgth^{3.189}$	509	2571

Table 7. The mean and standard deviation (first column) and correlation matrix for the tissue characteristic variables for Pacific cod. N = 11 in all cases.

		Bwgt	Gwgt	BDRY	BASH	BCAL	GDRY	GASH	GCAL
Lgth	642.8	r=.963	.893	.180	.017	.210	.162	-.428	-.206
	70.0	p=.001	.001	.596	.962	.536	.634	.189	.543
Bwgt	3154.9		.899	.149	-.091	.253	.120	-3.99	-.264
	1147.7		.001	.663	.790	.453	.726	.224	.432
Gwgt	555.0			.034	.129	.111	.029	-.106	-.259
	232.1			.920	.706	.745	.932	.756	.442
BDRY	.216				-.382	.765	.643	-.374	.367
	.008				.246	.006	.033	.257	.267
BASH	.152					-.807	-.056	.351	.322
	.012					.003	.871	.290	.335
BCAL	4816.9						.420	-.396	-.106
	191.1						.198	.228	.756
GDRY	.322							-.480	.533
	.008							.135	.091
GASH	.072								-.160
	.012								.638
GCAL	5510.2								
	37.0								

Table 8. Calculated gonad-somatic tissue indices of Pacific cod by location and year.

--	WGSI	DGSI	CGSI	CAGSI
Strait of Georgia				
1983	.153	.228	.261	.239
1984	.174	.259	.296	.270
1985	.166	.247	.283	.259
Vancouver Island				
1976	.205	.306	.350	.320
Hecate Strait				
1976	.150	.224	.256	.234
Gulf of Alaska				
1982	.127	.189	.216	.197

and 406 g in 1984. The corresponding body weights were 2833, 2325, and 2617 g for years 1983-85, respectively (Table 6). The correlation analysis of tissue constituents with body size (Table 7) showed no significant relationships. The calculated gonad-somatic tissue index values for each of the three years is shown in Table 8.

There are several published estimates available for the natural mortality (M) rate of Pacific cod. Wespestad et al. (1982) considered stocks in the eastern Bering Sea. A first approximation of the upper level of natural mortality came from estimates of total mortality (Z) derived from a regression analysis of 1976-81 survey age composition data. The regression of natural log of average numbers at ages 2-9 resulted in a Z value of 0.71 ($r^2 = .977$). This estimate indicates that the average M for all ages is less than 0.71. A second approximation of M was derived for this same stock by using 1979 survey age specific population estimates as a starting point and varying M between 0.6 and 0.8 to find a value that most closely approximated abundance estimates shown by 1980 and 1981 surveys. A value of 0.7 provided the best results. Wespestad et al. (1982) concluded that 0.7 was a resonable estimate of M. The true value may be lower but is unlikely to be any higher than 0.7.

The eastern Bering Sea stock is quite distant from the Puget Sound stock, but it appears that the age compositions of Pacific cod stocks throughout the northeast Pacific are roughly comparable (Foucher et al. 1981). Although some doubt exists as to the validity of existing age determination methodology, few fish appear to live longer than 10 years in the eastern Bering Sea and Gulf of Alaska or 7 years in Hecate Strait. In 1980, commercial catches in the eastern Bering Sea and Gulf of Alaska were dominated by 3- and 4-year-olds (Foucher et al. 1981). This compares with Ketchen's (1964) observation that the fishery in Hecate Strait is dependent on fish that have completed 3-4 years of growth.

Ketchen (1964) provides independent estimates of M for Pacific cod stocks in Hecate Strait. The estimates ranged from .83 to .99, depending on the assumptions of the analysis. Karp (1982) discussed Ketchen's work and concluded that some of his results were probably biased.

Karp (1982) estimated natural mortality for Pacific cod in the Port Townsend area, using the method of Alverson and Carney (1975). With T_c = 2.5 years (Maximum age = 7 years) M was estimated to be within the range of 0.7 to 0.8. However, this was a misapplication of the technique. Although Alverson and Carney speak in terms of estimating natural mortality (M), the derived estimate actually is for total mortality (unless, of course, the stock is unexploited). Given the other available information .75 (the average) seems an unreasonably low estimate of Z.

Karp (1982) derived an independent estimate of total mortality from an extensive tagging study and concluded that Z was about 1.50. He also was able to estimate that between 24 and 34% of the harvestable stock was taken during the intensive winter fishery. The equivalent instantaneous fishing mortality rates (F) are .27 and .41. Most but not all of the total annual fishing mortality occurs during this spawning ground fishery. This analysis therefore places a reasonable upper bound on M (1.23 to 1.09). but does not provide a useable estimate of the true value.

Fournier (1983) estimated the natural mortality of cod using an age structured model. The age distribution was derived from a length-frequency analysis of 20 years worth of commercial catch data from Hecate Strait. The advantage of this approach is that it does not depend on the use of aging structures. Their best estimate of M using this technique was .65 which has been accepted for use in this analysis.

Herring

The maturity state of herring was determined by WDF personnel and myself by visual inspection. Oocytes were not measured as part of the sorting process and therefore cannot be used as a selection criteria as was done for English sole and Pacific cod. Although egg size determinations are desirable, there is probably less variability in the relative development of a synchronous spawner like herring than a species like English sole, which has a more protracted spawning season. The egg dry weight data were part of a separate analysis and will be discussed elsewhere.

Of the 325 fish sampled in 1982, 87 were stage five females needed for the reproductive effort analysis. In 1984, all of the 150 fish collected were mature females.

The fishery on the Strait of Georgia herring stock began in 1973. That same year, and every year since, WDF has conducted independent

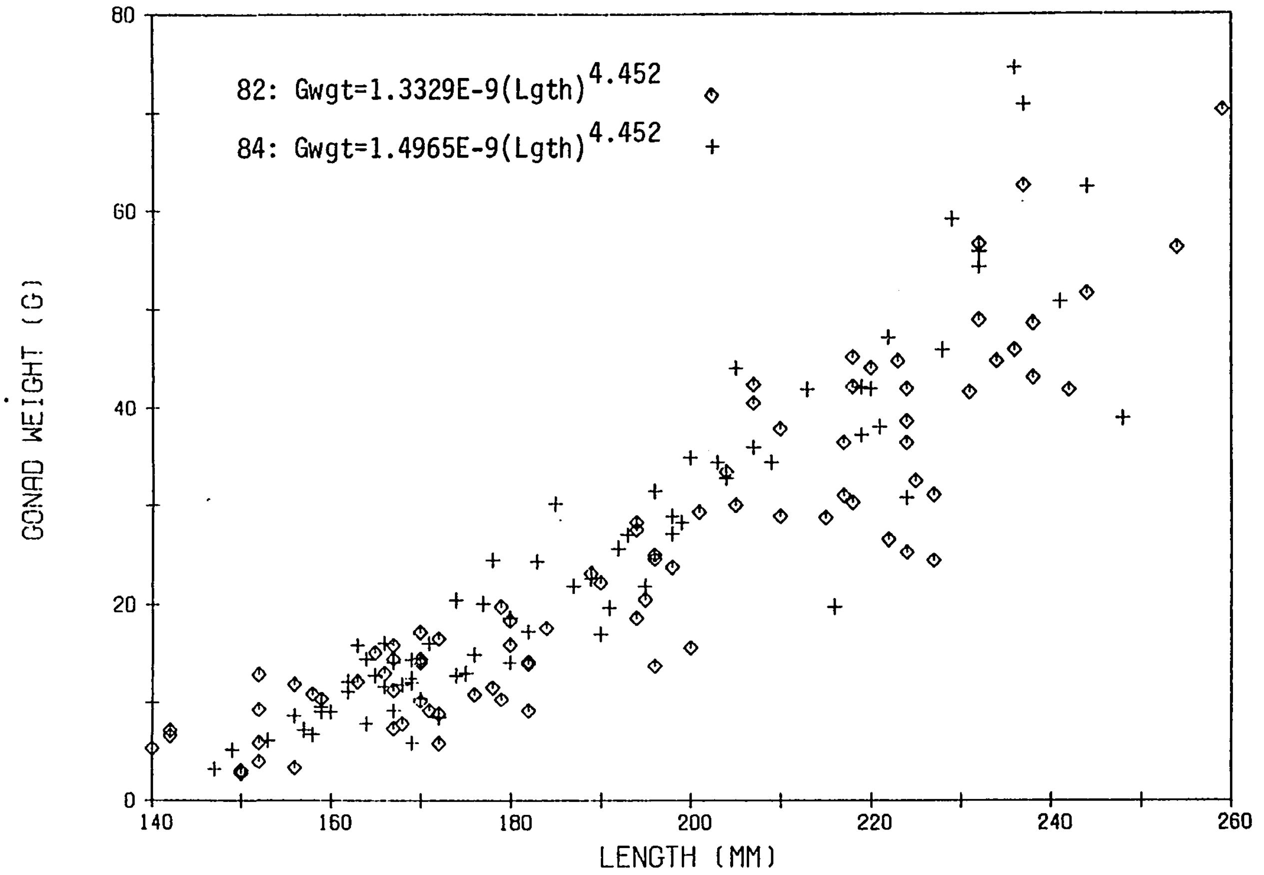


Fig. 5. Gonad weight-length plot for Pacific herring for years 1982 and 1984.

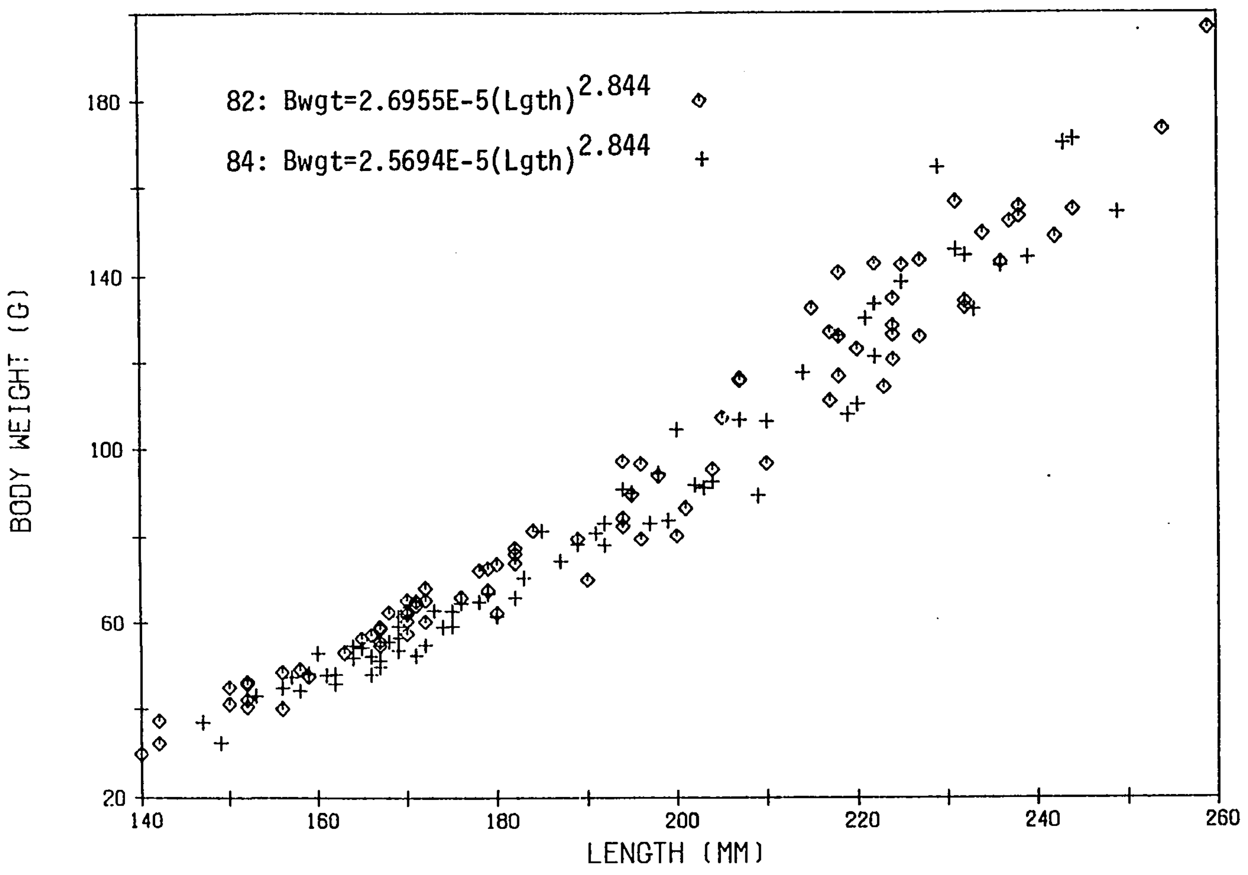


Fig. 6. Body weight-length plot for Pacific herring for years 1982 and 1984.

Table 9. Gonad weight-length and body weight-length regression equations and corresponding derived weights for mature Pacific herring of average length (209 mm) by year.

Strait of Georgia Herring		n	Derived weight
1982	$Gwgt = 1.3329 \times 10^{-9}(Lgth)^{4.452}$	87	28.5
1984	$Gwgt = 1.4965 \times 10^{-9}(Lgth)^{4.452}$	149	31.9
1982	$Bwgt = 2.6955 \times 10^{-5}(Lgth)^{2.844}$	87	106.9
1984	$Bwgt = 2.5694 \times 10^{-5}(Lgth)^{2.844}$	149	101.9

Table 10. The mean and standard deviation (first column) and correlation matrix for the tissue characteristic variables for Pacific herring. n = 25 in all cases except for BASH, n = 18.

	Lgth	Bwgt	Gwgt	BDRY	BASH	BCAL	GDRY	GASH	GCAL
Lgth	196.9	r=.982	.914	-.334	.164	-.669	-.329	.261	.594
	34.3	p=.001	.001	.097	.515	.001	.108	.218	.002
Bwgt	96.4		.918	-.338	.248	-.655	-.281	.211	.558
	44.0		.001	.098	.320	.001	.173	.322	.004
Gwgt	26.9			-.560	.343	-.615	-.328	.126	.571
	18.1			.004	.163	.001	.110	.559	.003
BDRY	.279				-.454	.423	.182	.064	-.312
	.025				.059	.035	.383	.768	.129
BASH	.091					.093	-.007	-.640	-.365
	.013					.713	.979	.004	.137
BCAL	5751.8						.480	-.688	-.351
	367.6						.014	.001	.085
GDRY	.273							-.326	-.102
	.021							.120	.628
GASH	.080								.116
	.024								.589
GCAL	5651.1								--
	89.0								--

Table 11. Calculated gonad-somatic tissue indices for Pacific herring by-year with the necessary parameter regressions required for their computation.

Strait of Georgia Herring	WGSI	DGSI	CGSI	CAGSI
1982	.266	.260	.260	.257
1984	.313	.306	.306	.302

GCAL = 5347.4 + 1.543(Lgth) = 5669.9

$r = .594$

$p \leq .002$

BCAL = 7165.2 - 7.179(Lgth) = 5664.8

$r = -.669$

$p \leq .001$

trawl and/or market surveys of the spawning stock. The 1974 data were taken as representative of the unexploited condition since there were no maturity estimates available for 1973. The WDF commercial seine catch data were analyzed to determine that the average length of mature females was 209 mm. The data were weighted to account for biases in the sampling of a size-dependent spawning run, since large fish spawn earlier in the spawning season.

The 1982 body length-weight relationship was derived using all stage 5 (mature), 6 (ripe), and 7 (spent) female herring sampled during our analysis. The gonad weight-body weight regression employed only stage 5 fish. The analysis of covariance tests showed significant between year differences in both the gonad weight-length (Figure 5, Table 9) and body weight-length (Figure 6, Table 9) regression equations. The estimated gonad and body weights for fish of average size in years 1982 and 1984 were 28.5 and 31.9 g, and 106.9 and 101.9 g, respectively.

The correlation analysis (Table 10) indicated that both body and gonad calorie content varied significantly with body size. The GSI index estimates for years 1982 and 1984 are shown in Table 11.

A review of recent estimates of instantaneous natural mortality rates suggests that the value (M = .67) obtained by Tester (1955) was somewhat high. Canadian workers have used a value of 0.36 in their stock assessment work (Schweigert and Hourston 1980) while estimates of natural mortality for the Gulf of Georgia herring stock range from 0.4 - 0.5 (Trumble, WDF, personal communication). A more recent report from

Ware (1985) also suggests that the natural mortality rate of Pacific herring in the Strait of Georgia is .45.

In Chapter 3, which deals with between-year differences, I reanalyzed the WDF Strait of Georgia herring data. When I averaged my estimates of cohort-specific mature mortality rate over the years I obtained the same result as did Trumble (i.e., M = .45). However inspection of the age-frequency data for individual cohorts suggests that natural mortality has increased in recent years (from about .37 to .56) starting with the 1974 cohort which first appeared in the fishery as 3-year-olds in 1977. The analysis also shows that expected changes in other life history characteristics including reproductive effort have occurred in conjunction with the increase in M. My samples were taken after the suggested change in life history and they therefore reflect the higher reproductive effort rates. For that reason I have chosen to use the value of .56 as the most applicable current estimates of M.

Dogfish

Analysis of the 1983 egg size data suggested that 46 of the 50 fish kept for processing had fully developed eggs. Three of the remaining fish had recently ovulated and one had smaller eggs that probably were still in the first year of the 2-year ovarian development cycle. No egg size determinations were done on the 201 dogfish sampled in 1984. It was apparent from the sampling of the previous year that ovulation occurs within a few weeks of parturition and that fish which are a year out of phase in their development can be easily distinguished from those giving birth in the current year.

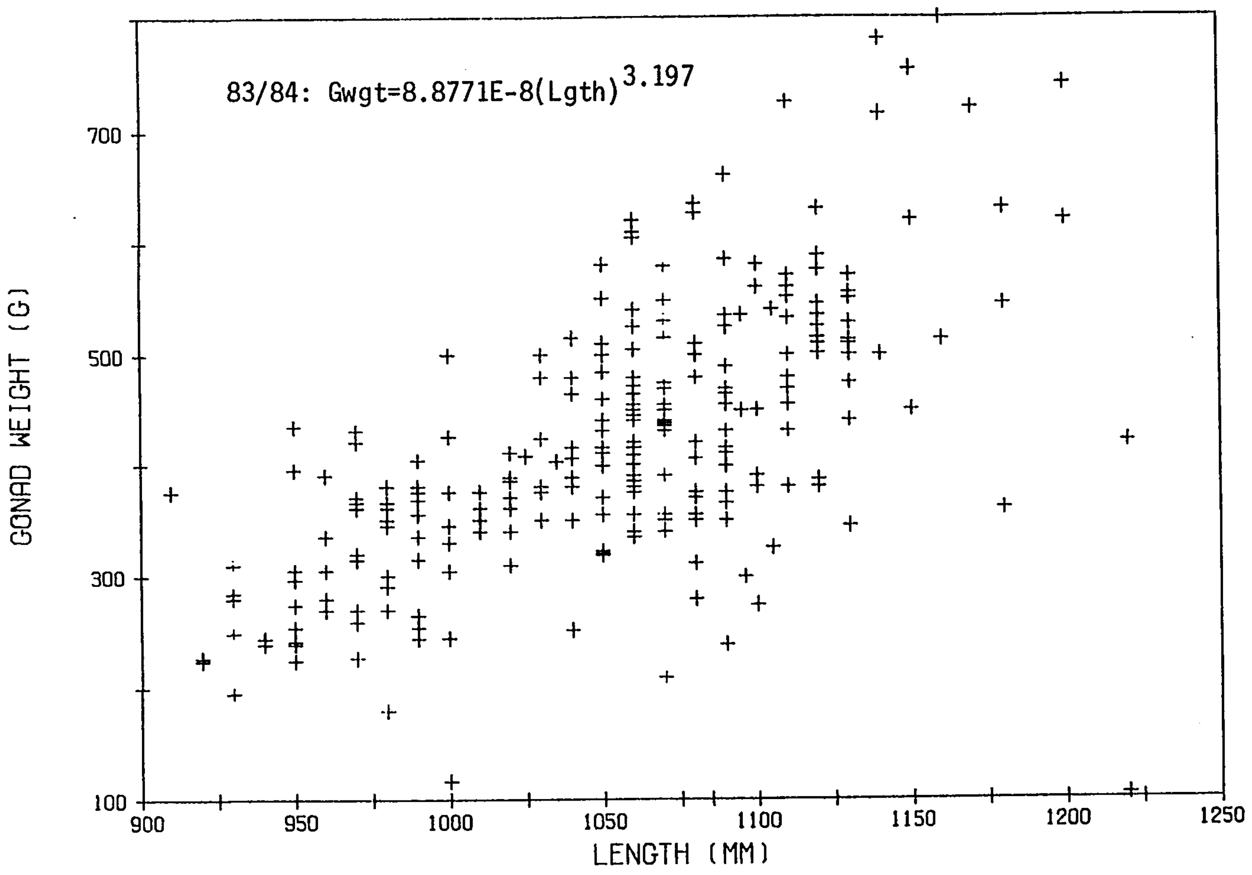


Fig. 7. Gonad weight-length plot for dogfish, 1983 and 1984 data combined.

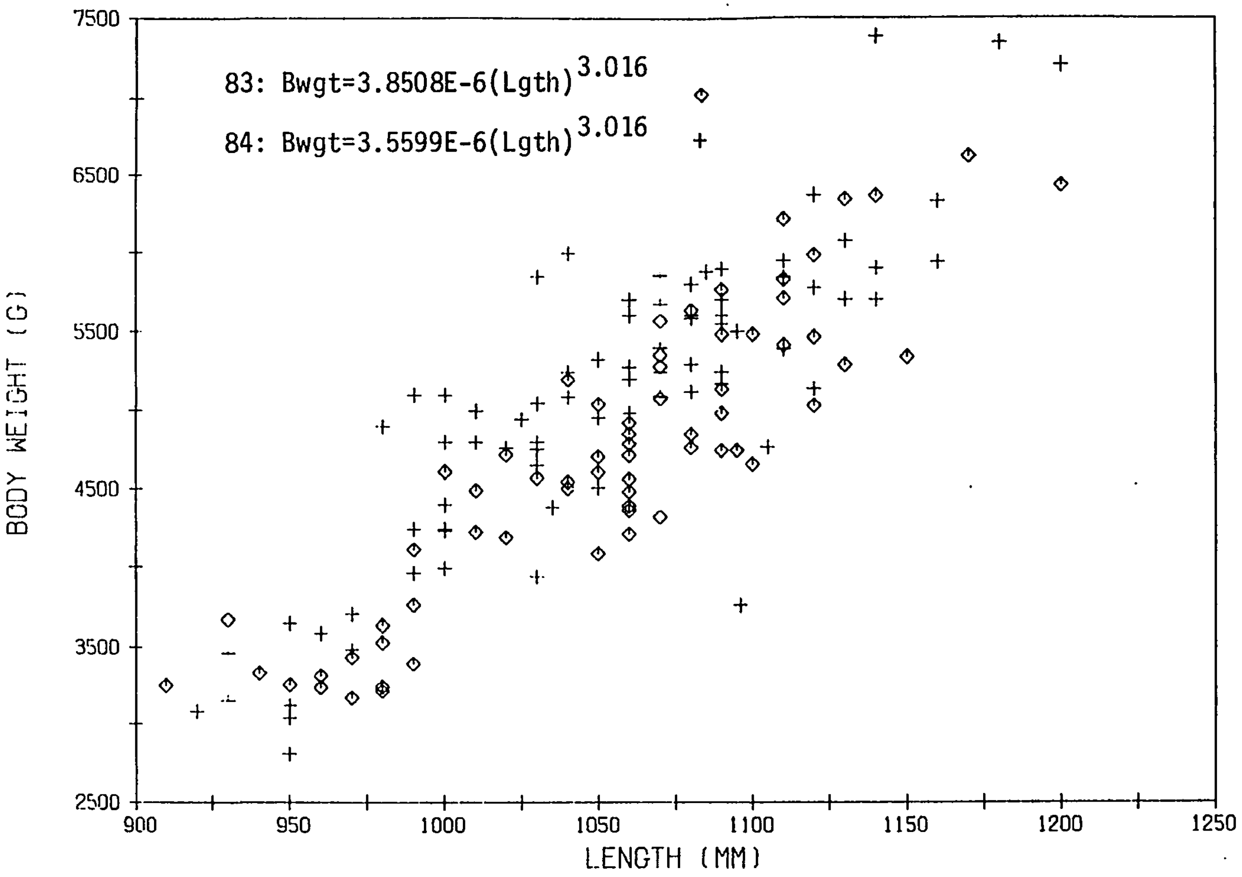


Fig. 8. Body weight-length plot for dogfish for years 1983 and 1984.

Table 12. Gonad weight-length and body weight-length regression equations and corresponding derived weights for mature dogfish of average length (1026 mm).

Dogfish		n	Derived weight
1983/84	$Gwgt = 8.8771 \times 10^{-8} Lgth^{3.197}$	247	376
1983	$Bwgt = 3.8508 \times 10^{-6} Lgth^{3.016}$	78	4647
1984	$Bwgt = 3.5599 \times 10^{-6} Lgth^{3.016}$	201	4296

Table 13. The mean and standard deviation (first column) and correlation matrix for the tissue characteristic variables for dogfish.

		Bwgt	Gwgt	BDRY	BASH	BCAL	GDRY	GASH	GCAL
Lgth	1049.7	r=.902	.774	.413	-.352	.263	-.309	-.299	.116
	71.3	p=.001	.001	.008	.026	.101	.185	.201	.628
		n = 46	46	40	40	40	20	20	20
Bwgt	4890.6		.742	.546	-.523	.319	-.345	-.282	.167
	1170.3		.001	.001	.001	.045	.136	.228	.482
			46	40	40	40	20	20	20
Gwgt	410.7			.348	-.171	.180	-.007	.008	.135
	132.9			.028	.291	.265	.977	.972	.571
				40	40	40	20	20	20
BDRY	.343				-.806	.616	-.326	-.078	.087
	.026				.001	.001	.255	.791	.768
					40	40	14	14	14
BASH	.066					-.678	.477	.111	.019
	.009					.001	.085	.707	.949
						40	14	14	14
BCAL	6633.2						-.224	.113	.168
	296.7						.441	.700	.566
							14	14	14
GDRY	.519							.504	.322
	.026							.024	.167
								20	20
GASH	.085								.338
	.029								.146
									20
GCAL	6672.4								--
	93.6								--

Table 14. Calculated gonad-somatic tissue indices for dogfish by year with the necessary parameter regressions required for their computation.

Dogfish	WGSI	DGSI	CGSI	CAGSI
1983	.041	.062	.063	.065
1984	.044	.067	.068	.070

$\text{BDRY} = .1846 + .00015(\text{lGTH}) = .339$

$r = .413$

$p \leq .008$

$\text{BASH} = .1143 - .00005(\text{Lgth}) = .063$

$r = -.352$

$p \leq .026$

$\text{BCAL} = 6233.0 + .0803(\text{Bwgt}) = 6606.2$

$r = .319$

$p \leq .045$

The size of 50% maturity for female dogfish was estimated to be 920 mm by Bonham (1949) and 935 mm by Ketchen (1975). The length frequency data (by centimeter size class) used to estimate the average length of a mature female came from a tagging study conducted in central and south Puget Sound by the Washington State Department of Fisheries during November 1972 (unpublished data). The average length of mature females (assuming a size at 50% maturity of 930 mm) was 1026 mm (n = 473).

The gonad weight-length relationships from 1983 and 1984 were not significantly different. The data were therefore pooled (Figure 7, Table 12). A covariance analysis of the body weight-length regressions did show significant between year differences (Figure 8, Table 12). The gonad weight of a fish of average size was 376 g and the corresponding body weights were 4647 g in 1983 and 4296 g in 1984.

The correlation analysis of body and gonad constituents (Table 13) showed that body dry weight and body ash and calorie content were correlated with body size. The appropriate linear regressions were therefore determined and incorporated into the estimates of the separate 1983 and 1984 GSI calculations (Table 14). It should be recalled that because dogfish are biannual spawners, the original index estimates had to be divided by two. The natural mortality rate was estimated to be .094 based on an analysis of an age structured population model (Wood et al. 1979).

Although dogfish are viviparous, there apparently is no maternal contribution during gestation. Pritchard et al. (1958) found that respirometry data for both pregnant and non-pregnant females fell on a common line described by $Y = aX^b$, where Y = oxygen consumption per minute and X = body weight. Gilbert (1981) injected radioisotopes into the bloodstream of a pregnant female and found that within 12 hours radioactive phosphate and sulphate had found their way into the uterine cavity. The developing pups did not incorporate any of these materials into their own tissues, however.

Copper Rockfish

I estimated that 11.5% of the energy consumed during gestation by embryos was contributed by the mother (see Appendix A). However, the precision of that estimate was such that I could not reject the null hypothesis of no maternal contribution. As a result, I did not incorporate the estimate into the calculation of the gonad-somatic tissue indices for copper rockfish.

The parameters needed to calculate the average age of mature fish using the previously described formula are average age-at-maturity and the natural mortality rate.

Gowan (1983) estimated that 35.3% of all 3 year old copper rockfish had spawned once and 72.8% of all 4 year olds had spawned at least once. The average age of fish spawning for the first time was therefore taken to be 3.5 years.

Gowan (1983) used an age-frequency analysis to estimate the total mortality rate (Z = .233) for the central Puget Sound copper rockfish. Additional work on tagged fish led to an estimate of natural mortality (M = .131). Barker (1979) studied a copper rockfish population in northern Puget Sound where fish were older, smaller for a given age, and had a lower total mortality rate ($Z = .181$). Barker's estimate of natural mortality ($M = .113$) however, was similar to that found by Gowan. Gowan (1983) suggested that all of the above observations were consistent with the idea that the central Sound fish were being more heavily exploited. Since our reproductive effort estimates were from fish collected in the central Sound, .113 was used as the estimate of natural mortality.

Computation of the average age of mature fish using the formula $\frac{(Ma)+1}{a}$ led to an estimate of 10.6 years. Gowan (1983) reported values of 9.25 and 11.61 for the average age of copper rockfish taken by hook and line from central and northern Puget Sound, respectively. Although these values are affected by problems of gear selectivity and varying rates of fishing mortality, they suggest that the artificially derived estimate is reasonable.

The length of a fish that is 10.6 years old was calculated to be 391 mm using the von Bertalanffy length at age function

$$L = 460\ (1-e^{-.16(t+1.3)})$$

derived for female copper rockfish (Gowan 1983). Length was converted to weight (1094 g, Figure 9) using the relationship

$$\text{Bwgt} = 5.480 \times 10^{-6}(\text{TLTH})^{3.202}$$

$$n = 42$$

$$r^2 = .958$$

which was derived from my own data.

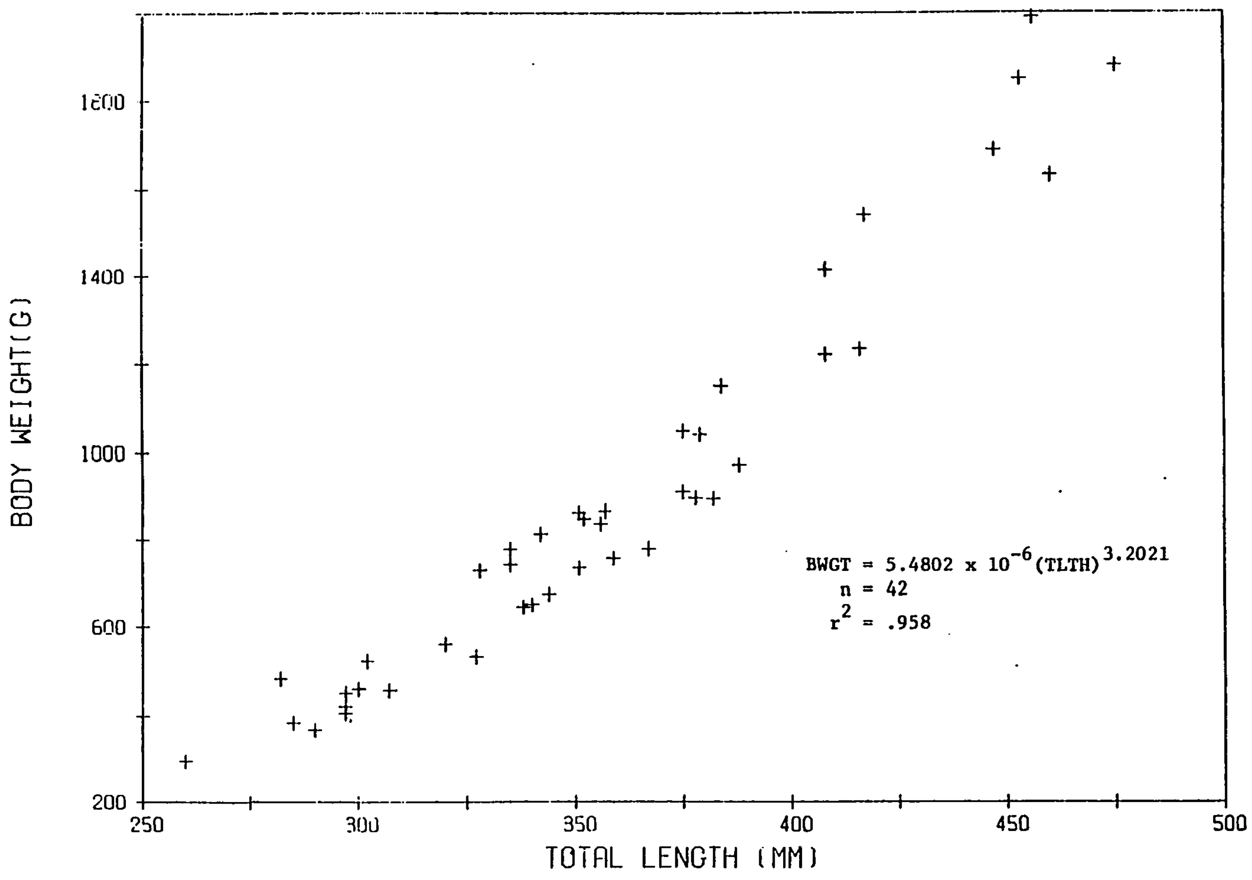


Fig. 9. Body weight-length regression for copper rockfish.

The next step was to estimate gonad weight for a fish of average size. Fish with both fertilized and unfertilized eggs were used in this analysis. However, before a gonad weight-body weight regression could be calculated, three problems had to be addressed. First, as was the case with English sole and Pacific cod, egg size criteria had to be used to select those fish with unfertilized eggs that were close to the time of fertilization. The other 2 problems concern fish with fertilized eggs for which it was also necessary to account for the decreasing trend in egg dry weight, and the increasing trend in gonad water content of developing gonads.

Seventeen of the 34 fish collected by spearfishing in 1984 had unfertilized eggs. Egg diameter was used as the selection criteria for determining which of these fish were close to the time of fertilization. Egg diameters were determined for all fish from the 1984 collection with both unfertilized or recently fertilized eggs. In addition, the two fish held at Manchester during 1984 provided a time series of egg size measurements which began several weeks before fertilization and continued through the late stages of development. Based on these observations, it was concluded that eggs are approximately .850 mm in diameter at the time of fertilization. As a result, all fish with eggs greater than .800 mm could be included in the gonad weight-body weight analysis. Eight fish with unfertilized eggs met this selection criterion.

Sixteen fish taken by spearfishing had fertilized eggs. Two were ripe and running and were therefore excluded from the analysis. One additional fish was spent. The gonad weight-body weight relationship was determined using the 14 fish with fertilized eggs in addition to the 8 fish which met the selection criteria. However, it was first necessary to account for the weight loss of embryos during gestation. The estimated dry weight of embryos was .160 mg at the time of fertilization and .127 mg at birth (Figure 10). This indicates that there was a 21% loss of weight over the course of the full gestation period. Corrected gonad weights were therefore calculated for all fish with embryos that were more than 6 days past the time of fertilization. Gonad weight (Gwgt) was corrected by using the relationship

$$\text{corrected Gwgt} = \text{Gwgt} + F\,\frac{(.160 - \text{observed egg weight})}{\text{GDRY} \times 1000}$$

where F is fecundity and 1000 is a conversion factor for mg to g. Fecundity was estimated from the function

$$F = 5.816 \times 10^{-9} L^{5.216}$$

derived by Washington et al. (1978) for copper rockfish taken in central Puget Sound. The effects of the gonad weight correction procedure were relatively small. In all cases but one the observed gonad weight was increased by 10% or less.

An analysis of the gonad percent dry matter data (GDRY) indicated that the water content of the gonad increased continuously (percent dry matter decreases) from the time of fertilization to birth (Figure 11). Gonads containing eggs that were within a day or two of fertilization were 60% water. At fertilization (probably over a period of only a few hours), the water content increased to about 72%. It then continued to increase, and at the time of parturition the gonads were 90% water. In

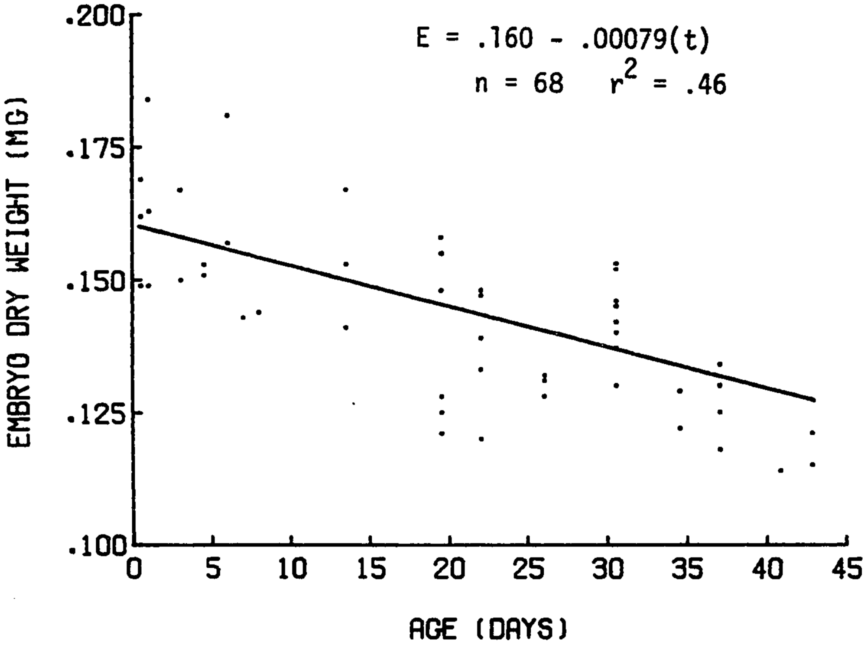


Fig. 10. Copper rockfish embryo dry weight shown as a function of embryonic age.

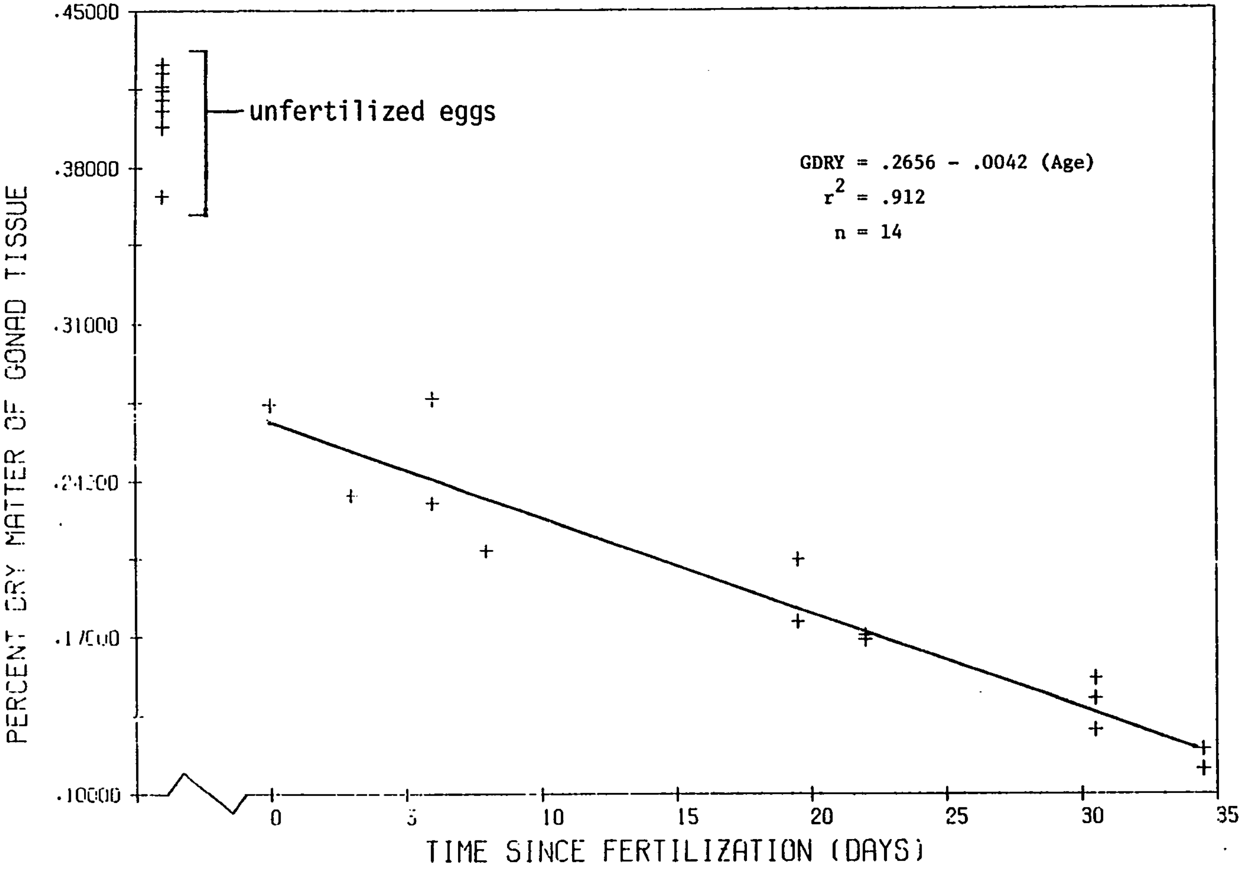


Fig. 11. The relationship between percent dry matter (x 10^{-2}) of gonad tissue and time since fertilization in copper rockfish. The unfertilized eggs are all greater than .800 mm and are therefore close to the time of fertilization. The regression analysis excludes unfertilized eggs.

order to remove water content as a source of variability, length was plotted as a function of dry gonad weight (using the 8 fertilized and 14 unfertilized fish) (Figure 12) yielding the relationship

$$\mathrm{DGwgt} = 4.517 \times 10^{-12}(\mathrm{Lgth})^{5.043} \qquad n = 22,\ r^2 = .948.$$

Dry gonad weight can be reconverted to a standardized wet weight by dividing by .274, the observed percent dry matter of embryos at the time of fertilization.

The observed wet gonad weight-length relationship (Figure 13)

$$\mathrm{Gwgt} = 1.155 \times 10^{-7}(\mathrm{Lgth})^{3.562} \qquad n = 22,\ r^2 = .600$$

had a much lower correlation coefficient. This indicates that the water content of the gonad tissues did account for a large proportion of the variability in the gonad weight-length relation.

The estimated dry gonad weight of a fish of average size (391 mm) is 53.4 g. A corresponding wet gonad weighs 194.9 g.

The gonad and body tissues of the above described 22 fish were analyzed for water, ash and calorie content. The body tissues of 1 additional fish were also analyzed. The correlation analysis (Table 15) of the tissue characteristics shows that percent body dry matter (BDRY) was correlated with body size. The calculated linear relationship between BDRY and body weight was

$$\mathrm{BDRY} = .246 + 2.850 \times 10^{-5}\ \mathrm{Bwgt}.$$

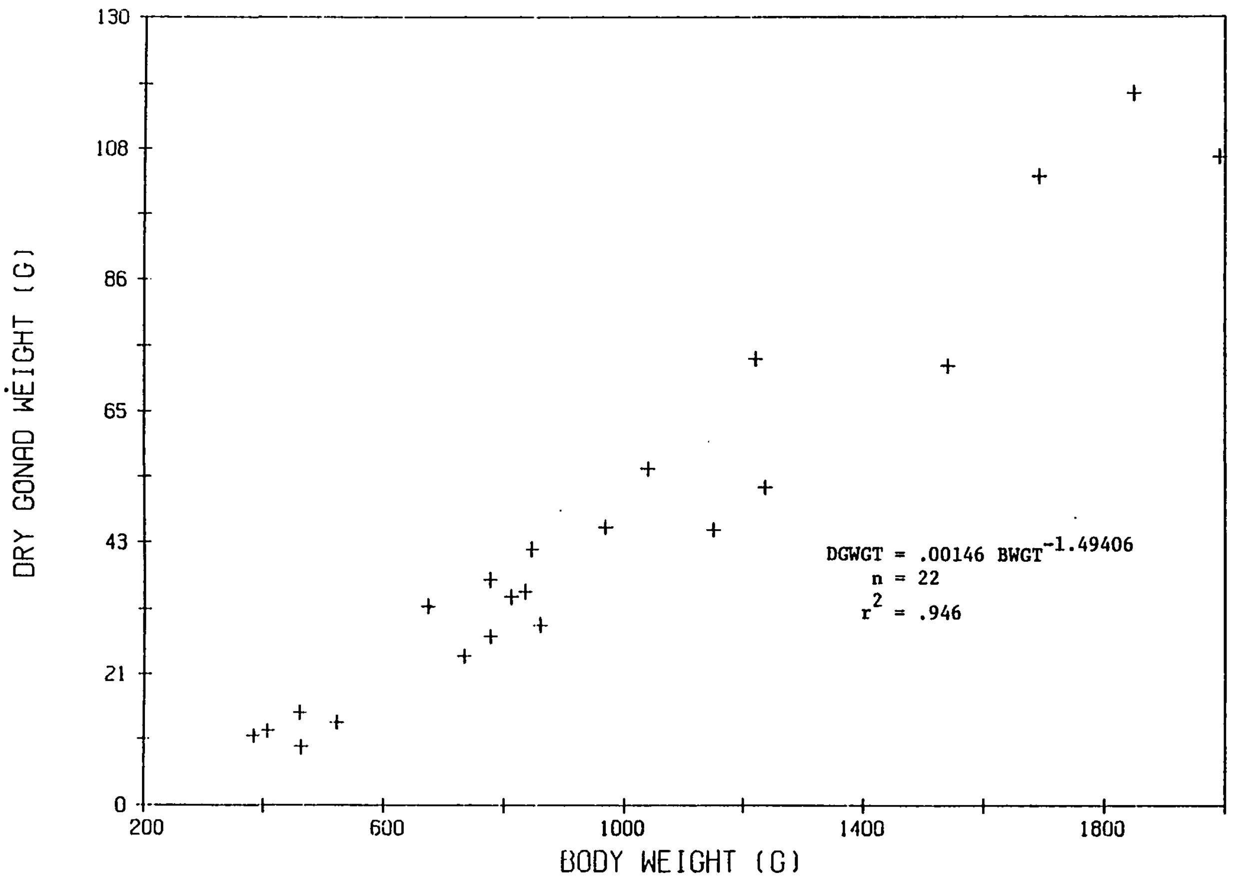


Fig. 12. Dry gonad weight-body weight plot for mature copper rockfish.

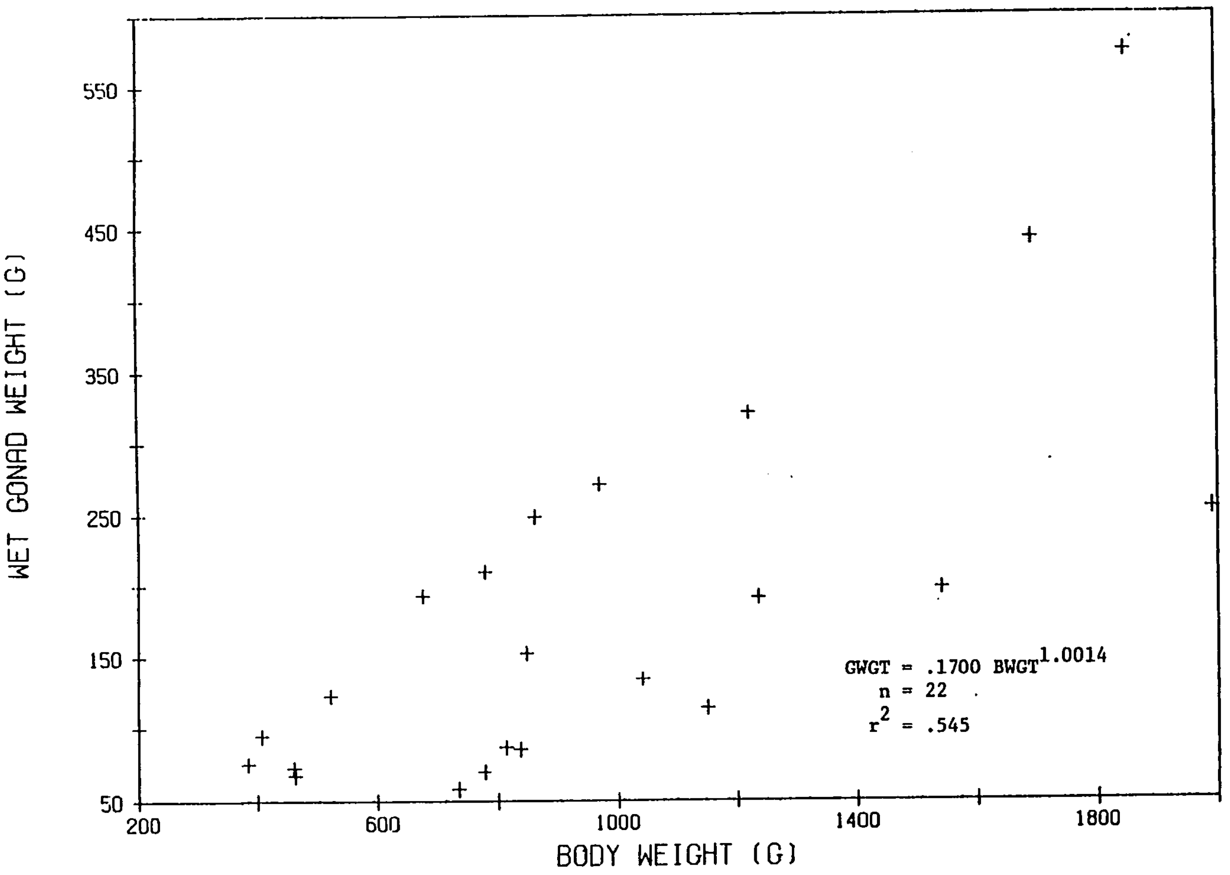


Fig. 13. Gonad weight-body weight plot for mature copper rockfish.

Table 15. The mean, sample size and standard deviation (first column) and correlation matrix for the tissue characteristic variables for copper rockfish.

	Lgth	Bwgt	Gwgt	DGwgt	BDRY	BASH	BCAL	GDRY	GASH	GCAL
Lgth	357.6	r=.966	.767	.950	.584	-.344	.372	.356	-.313	.569
	42	n=42	22	22	23	23	23	22	22	22
	53.5	p=.001	.001	.001	.003	.108	.081	.104	.157	.006
Bwgt	902.8		.750	.972	.565	-.297	.374	.376	-.324	.552
	43		22	22	23	23	23	22	22	22
	445.1		.001	.001	.005	.169	.078	.085	.142	.008
Gwgt	183.4			.837	.228	.049	-.019	-.222	.160	.285
	22			22	22	22	22	22	22	22
	131.4			.001	.308	.829	.934	.320	.477	.198
DGwgt	45.5				.447	-.195	.253	.278	-.234	.589
	22				22	22	22	22	22	22
	31.6				.037	.384	.256	.211	.294	.004
BDRY	.273					-.484	.767	.472	-.230	.360
	23					23	23	22	22	22
	.023					.019	.001	.027	.304	.100
BASH	.175						-.636	-.460	.444	-.486
	23						23	22	22	22
	.013						.001	.029	.036	.022
BCAL	5024.5							.486	-.352	.329
	23							22	22	22
	330.9							.022	.108	.135
GDRY	.266								-.760	.602
	22								22	22
	.017								.001	.003
GASH	.070									-.539
	22									22
	.019									.010
GCAL	6338.8									--
	22									--
	331.4									--

Gcal was also correlated with body size (Table 15). However, there was an additionl complication in that the calorie content of embryos decreases with age (Figure 14). As a result, instead of using a standard gonad calorie content weight regression, gonad weight was converted to calories using the calculated gonad calorie content at the time of fertilization (6554). Since body calorie content was not significantly correlated with size the average observed Bcal value was used to convert body weight to calories (5024).

The ash content of embryos also increased with embryonic age from .051 at fertilization to .090 at an age of 34 days (latest available estimate). As a result, the value of .051 was used to convert gonad calories to gonad calories per g AFDW rather than the average value (.070) reported in the correlation analysis.

The above mentioned parameter conversions for BDRY, GCAL, and GASH were used to calculate the gonad-somatic tissue indices for copper rockfish (Table 16).

Northern Anchovy

The estimated size at 50% maturity is 96 mm (Hunter and Macewicz 1980). The instantaneous natural mortality rate (M) for northern anchovy has been estimated from information provided in Hanan (1981) and MacCall (1974), using the relation $F = \frac{CZ}{Ba}$

where F = Instantaneous rate of fishing mortality

Z = Instantaneous rate of total mortality

C = Catch

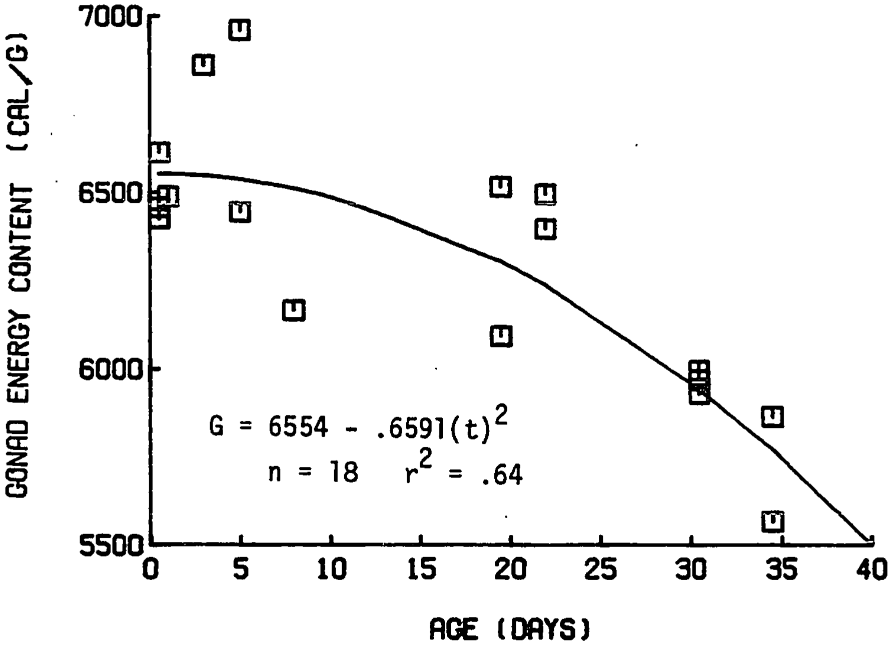


Fig. 14. Whole gonad calorie content (G) shown as a function of embryonic age.

Table 16. Computation formulae for the copper rockfish gonad-somatic tissue indices.

$$\mathrm{WGSI} = \frac{\mathrm{DGwgt/EDRY}}{\mathrm{Bwgt}} = \frac{53.4/.274}{1094} = .178$$

$$\mathrm{DGSI} = \frac{\mathrm{DGwgt}}{(\mathrm{Bwgt})(\mathrm{BDRY})} = \frac{53.4}{(1094)(.277)} = .176$$

$$\mathrm{CGSI} = \mathrm{DGSI} * \frac{\mathrm{GCAL}}{\mathrm{BCAL}} = .176 \times \frac{6554}{5024} = .230$$

$$\mathrm{CAGSI} = \mathrm{DGSI} * \frac{\mathrm{GCAL(1-BASH)}}{\mathrm{BCAL(1-GASH)}} = .230 \times \frac{(1-.175)}{(1-.051)} = .200$$

$$\mathrm{BDRY} = .2457 + 2.8497 \times 10^{-5}\ \mathrm{Bwgt} = .277$$

$r = .565$

$P \leq .005$

B = Stock biomass

a = Annual mortality rate

Using Z = .97, a = 0.621 for the 1966-76 period (Hanan 1981) and $\bar{C}$ = 108,336 tons, $\bar{B}$ = 3.24 million tons for 1966-76 (Stauffer and Picquelle 1981; Anon. 1978).

$$F = \frac{(108{,}412)(0.97)}{(3{,}240{,}000)(0.621)} = 0.052$$

Subtracting F from Z gives an estimate of M = .92.

This is somewhat lower than the value of M = 1.06 previously reported by MacCall (1974), but is still the highest of any of the six species dealt with during the course of our study.

The average age of a mature female was calculated using the relationship $\frac{(Ma)+1}{a}$ to be 2.25 years. This corresponds to a length of 114.9 mm and weight of 14.3 g (Table 17). Picquelle and Hewitt (1984) reported the mean weight of mature females from CALCOFI surveys for 1980-1983 (including 2 estimates for 1981) to be 17.4, 13.4, 16.2, 18.8, and 11.2 g. There is considerable variability in these estimates, much of which may be due to year-class strength and density-dependent growth phenomena. The estimate of 14.3 g derived from the average age formula seems reasonable given these independent empirical observations.

Hunter and Leong (1981) summarize the details of the reproductive biology of the anchovy. The most notable feature of their reproduction is that they are multiple batch spawners. To estimate reproductive effort, it is therefore necessary to determine the number of eggs spawned per batch for a fish of a given size and then multiply by the number of

Table 17. Documentation for sources of parameter estimates used in calculating the gonad-somatic tissue indices for northern anchovy.

Average age of mature female	2.25 yrs	Artificial cohort
Average length of mature female	114.9mm	von Bertalanffy function (Spratt 1975)
Fat free dry body weight (without gonad)	2.61 g	Equation 2 (Hunter and Leong 1981)
Lipid weight	.46 g	Assuming lipid is 15% of total
Total wet body weight	14.30 g	Equation 1 (Hunter and Leong 1981)
Number of eggs in 1 spawning batch	7926	Eggs = -313.4 + 576 (wet weight) Hunter (pers. comm.)
Dry weight-one spawned egg	.0000301 g/egg	Hunter and Leong (1981)
Number of spawnings per year	20	Hunter and Leong (1981)
Caloric content of anchovy eggs	5450 cal/g	Table 2 (Hunter and Leong 1981)
Caloric content fat free body tissue	4129 cal/g	Table 2 (Hunter and Leong 1981)
Caloric content anchovy fat	9227 cal/g	Table 2 (Hunter and Leong 1981)
Dry matter content of ovary just prior to hydration	35%	Figure 7 (Hunter and Leong 1981)

batches per year. Hunter and Leong estimated that a fish of average size spawns 20 times per year. This number is therefore the primary determinant of relative reproductive effort. A more recent analysis suggests that spawning frequency is strongly age dependent and that 1, 2, 3 and 4 year old fish spawn 6.8, 15.2, 22.8, and 31.9 times per pear, respectively (Anon. 1984). For now I will continue to use an estimated spawning frequency of 20, although this will be discussed in more detail below.

The number of eggs spawned per batch was originally estimated by Hunter and Macewicz (1980) but has subsequently been updated. The batch fecundity equation used here is

$$F = -313.4 + 576 \text{ (wet weight)}$$

and was derived by combining all available estimates through 1982 (Hunter, pers. communication). The procedure for estimating the gonad-somatic tissue indices is outlined in Tables 18. Table 17 provides documentation concerning the source of each parameter estimate.

The most important estimate for determining the reproductive effort of northern anchovy is the number of spawnings per year. I considered problems associated with these estimates in Appendix B. My conclusion was that the reported values of spawnings per year are probably too high. The northern anchovy estimate was therefore excluded from the final reproductive effort-mortality relationship. However, the complete and rather complicated procedures for assessing reproductive effort were reported here because of my hope that the spawning frequency question

Table 18. Calculated gonad-somatic tissue indices for northern anchovy. Sources for parameter estimates shown in Table 18.

$$\mathrm{WGSI} = \frac{(7926 \times 20 \times .0000301)/.35}{14.30} = .95$$

$$\mathrm{DGSI} = \frac{(7926 \times 20 \times .0000301)}{2.61 + .46} = 1.55$$

$$\mathrm{CGSI} = \frac{(7926 \times 20 \times .0000301)\ (5450)}{2.61(4129) + .46(9227)} = 1.73$$

---

will be resolved, permitting eventual inclusion of northern anchovy. The species is of particular interest because there are so few with comparable high rates of mortality.

Other Species

The parameter estimates for the species reported by Gunderson (1980) were reviewed and updated to ensure consistency, although few were changed significantly (Table 19). Capelin was excluded from the analysis as discussed above; northern sand lance and Gulf of Alaska pollock were added. New information on the reproductive effort of Pacific herring and Pacific cod were derived from this study. More recent estimates of the Bertalanffy growth parameters and the natural mortality were also included for Pacific cod. Recalculation of the North Sea cod and Grand Bank haddock reproductive effort indices also led to values that were higher than previously reported.

Discussion

A correlation analysis of all estimated life history parameters (Table 20) indicates that the wet weight gonad-somatic tissue index (WGSI) explains the greatest proportion of the natural mortality variability (r^2 = .69, Figure 15). The dry weight and caloric based indices were calculated in order to account for some of the between species variability in tissue composition. Unfortunately, I was only able to obtain the appropriate conversions for North Sea cod and the five species sampled directly during this study. As a result the number of observations of DGSI, CGSI, and CAGSI are too small to evaluate as potential predictors of M.

Table 19. Life history parameter estimates.

										References					
	M	WGSI	DGSI	CGSI	CAGSI	L	k	Tm	T.01	WGSI	M	L	k	Tm	T.01
Pacific herring	.56	.29	.28	.28	.28	26.3	.36	3	10	-	2	1	1	3	3
Pacific cod	.65	.16	.24	.28	.25	86.6	.33	3	8	-	4	5	5	6	7
Dogfish	.09	.04	.06	.07	.07	125.3	.048	23	50	-	8	9	9	9	8
Copper rockfish	.13	.18	.18	.23	.20	46.0	.16	3.5	-	-	10	10	10	10	-
English sole	.26	.19	.28	.33	.30	43.2	.25	4.3	11	-	11	12	12	12	13
Northern anchovy	.92	.95	1.55	1.73	-	16.5	.299	1.2	5	-	14,15	16	16	16	17,18
North sea plaice	.10	.12	-	-	-	68.5	.10	5	22	19	20	20	20	21	22
American plaice	.22	.12	-	-	-	59.4	.09	13	30	23	24	24	24	24	25
North Sea cod	.20	.16	.18	.25	-	114.8	.30	4	10	26,28	27	28	28	27	29
North Sea sole	.10	.10	-	-	-	36.7	.39	3	14	30	30	30	30	30	31
North Sea herring	.23	.24	-	-	-	30.0	.38	4	12	32	33	34	34	35	36
North Sea haddock	.20	.14	-	-	-	52.5	.20	3	8	38	20	37	37	38	39
Grand Bank haddock	.20	.19	-	-	-	66.3	.15	6	12	40,43	41	43	43	42	41
Pacific halibut	.19	.11	-	-	-	109.6	.13	12	23	46	44	45	45	46	44
Sand lance	1.00	.50	-	-	-	26.2	.34	3	8	47,48	49	50	50	49	49
Gulf of Alaska pollock	.35	.14	-	-	-	52.2	.32	3	13	51	52	53	53	53	54

1. Trumble, pers. comm.
2. Pers. observation (see text)
3. Taylor (1964)
4. Fournier (1983)
5. Karp (1982)
6. Westerheim (1977)
7. Ketchen (1964)
8. Wood, Ketchen & Beamish (1979)
9. Ketchen (1975)
10. Gowan (1983)
11. Forrester & Ketchen (1963)
12. Van Cleve and El Sayed (1969)
13. Holland (1969)
14. Hanan (1981)
15. MacCall (1974)
16. Spratt (1975)
17. Spratt (1972)
18. Spratt (1973)
19. Simpson (1951b)
20. Beverton & Holt (1957)
21. Hefford (1916)
22. Cushing (1973)
23. Pitt (1964)
24. Pitt (1975)
25. Pitt (1973)
26. Oosthuizen & Daan (1974)
27. Daan (1975)
28. Daan (1974)
29. ICES (1977a)
30. DeVeen (1976)
31. ICES (1977b)
32. Hickling (1940)
33. Cushing & Bridger (1966)
34. Beverton & Holt (1959)
35. Cushing (1968)
36. Gulland (1972)
37. Jones (1962)
38. Raitt (1933)
39. Blacker (1971)
40. Hodder (1963)
41. Halliday (1971)
42. Templeman et al. (1978b)
43. Templeman et al. (1978a)
44. IPHC Staff (1960)
45. Southward (1967)
46. Schmitt & Skud (1978)
47. Scott (1972)
48. Smiglelski et al. (1984)
49. Winter (1983)
50. Winter (1981)
51. Miller et al. (1985)
52. Megery, pers. comm.
53. Hughes & Hirschhorn (1979)
54. Smith (1981)

Table 20. Correlation matrix of life history parameter estimates.

	M	--WGSI	DGSI	CGSI	CAGSI	L∞	K	Tm	$T_{.01}$
M		r = .831 n = 15 p = .001	.678 6 .139	.544 6 .264	.612 5 .265	-.443 16 .086	.497 16 .060	-.400 16 .125	.503 15 .056
WGSI			.870 6 .024	.782 6 .066	.847 5 .070	-.568 16 .022	.494 16 .052	-.474 15 .075	-.541 14 .046
DGSI				.956 6 .003	-.996 5 .001	-.770 6 .073	.839 6 .037	-.845 6 .034	-.888 5 .044
CGSI					.989 5 .001	-.660 6 .153	.816 6 .048	-.917 6 .010	-.949 5 .014
CAGSI						-.819 5 .090	.873 5 .053	-.902 5 .036	-.967 4 .033
L∞							-.480 17 .051	.662 16 .005	.596 15 .019
K								-.712 16 .002	-.736 15 .002
T_m									.960 15 .001
$T_{.01}$									

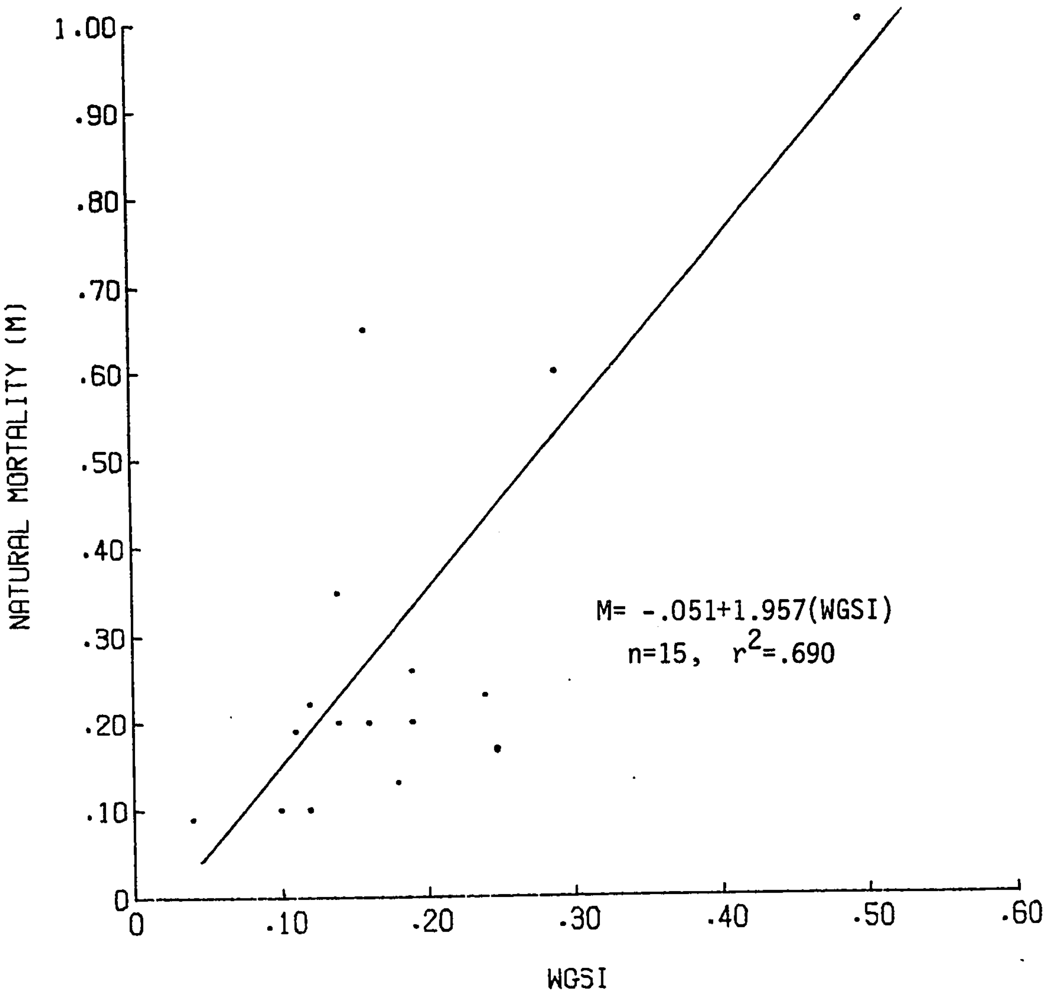


Fig. 15. Relation between WGSI and natural mortality.

The available data does indicate that there are significant species-specific differences in the water, calorie and ash content of gonad and body tissues (Table 21). A comparison of the correlation coefficients relating M to each of the reproductive effort indices using similar sample sizes (Figure 16) shows that the DGSI is actually the best predictor of M. The correlations are not significant for any of the indices but this is not surprising given the small sample sizes and the fact that Pacific cod seems to be a notable outlier (see below). Log conversions provide a better fit to the data (Figure 17) but selection of a particular predictive model needs to be based on a more complete data set.

These results suggest that the predictive power of the WGSI could be improved by accounting for the differences in water and calorie content of the tissues. However, until more data becomes available, the predictive power of these more detailed indices will remain unclear.

Although the growth parameter (K) did not correlate well with M (r^2 = .25) a plot of the data does indicate that it contains useful information (Figure 18). When the growth rate was high (> .26) mortality was unpredictable. But if K was less than .26 mortality was always low as well. It is intuitive perhaps that low growth rate is incompatible with high mortality. However, these results suggest that fast growing fish can also live a long life.

A consideration of the between year differences in the WGSI data indicates that the index is fairly consistent (Table 22). Reproductive effort is not a constant and can be expected to vary depending on the

Table 21. Calorie, dry weight and ash content estimates for the gonad and body tissues of six species of fish.

	Gonad			Body		
Species	Dry wt (%)	Calorie ($g^{-1}dw$)	Ash (%)	Dry wt (%)	Calorie ($g^{-1}dw$)	Ash (%)
Herring	.27	5670	.08	.28	5665	.09
Cod	.32	5510	.07	.22	4817	.15
Dogfish	.52	6672	.09	.34	6606	.06
Copper Rockfish	.27	6554	.05	.28	5025	.18
English sole	.32	5850	.06	.21	4894	.15
Anchovy	.35	5450	--	.30	4893	--

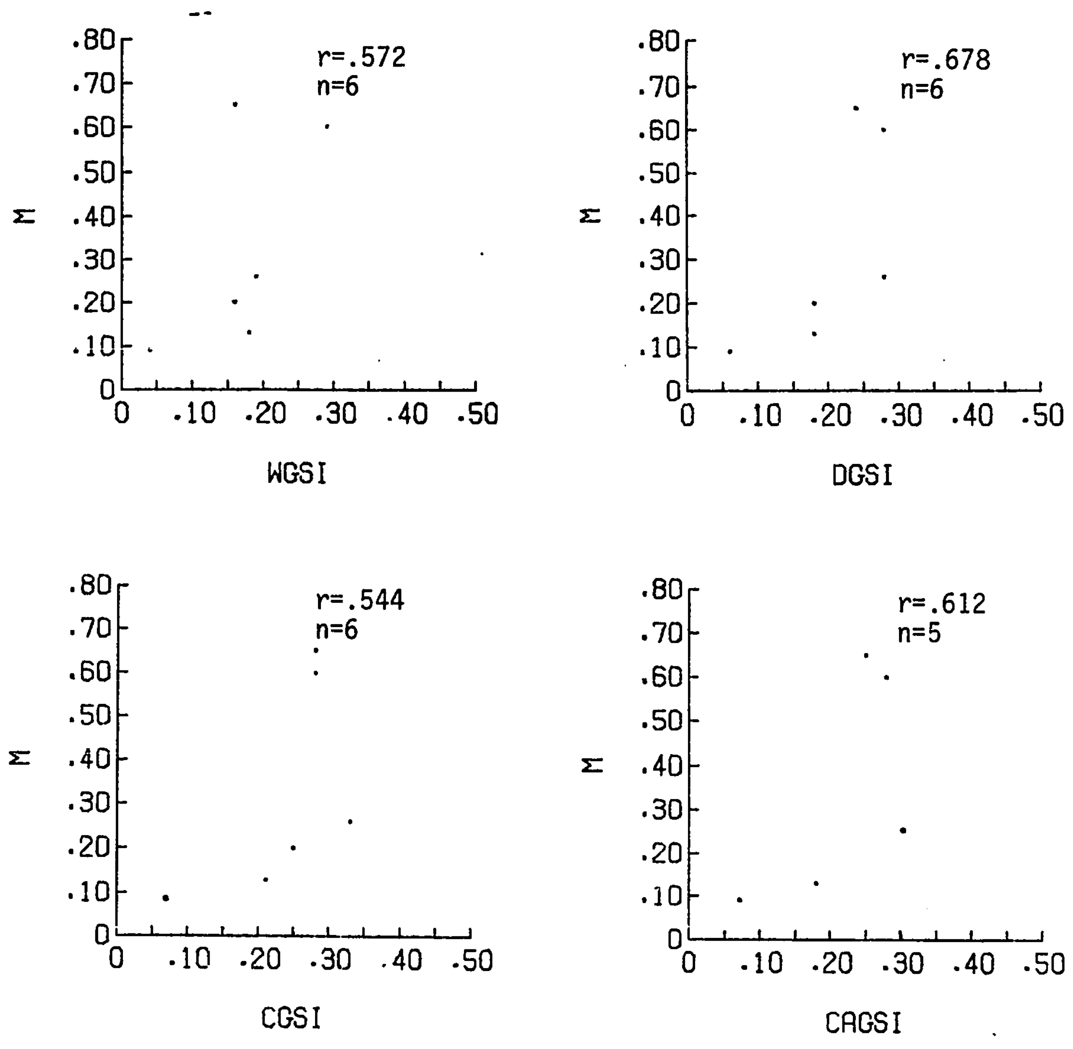


Fig. 16. Plots of the 4 reproductive effort indices versus natural mortality (M) using equivalent sample sizes.

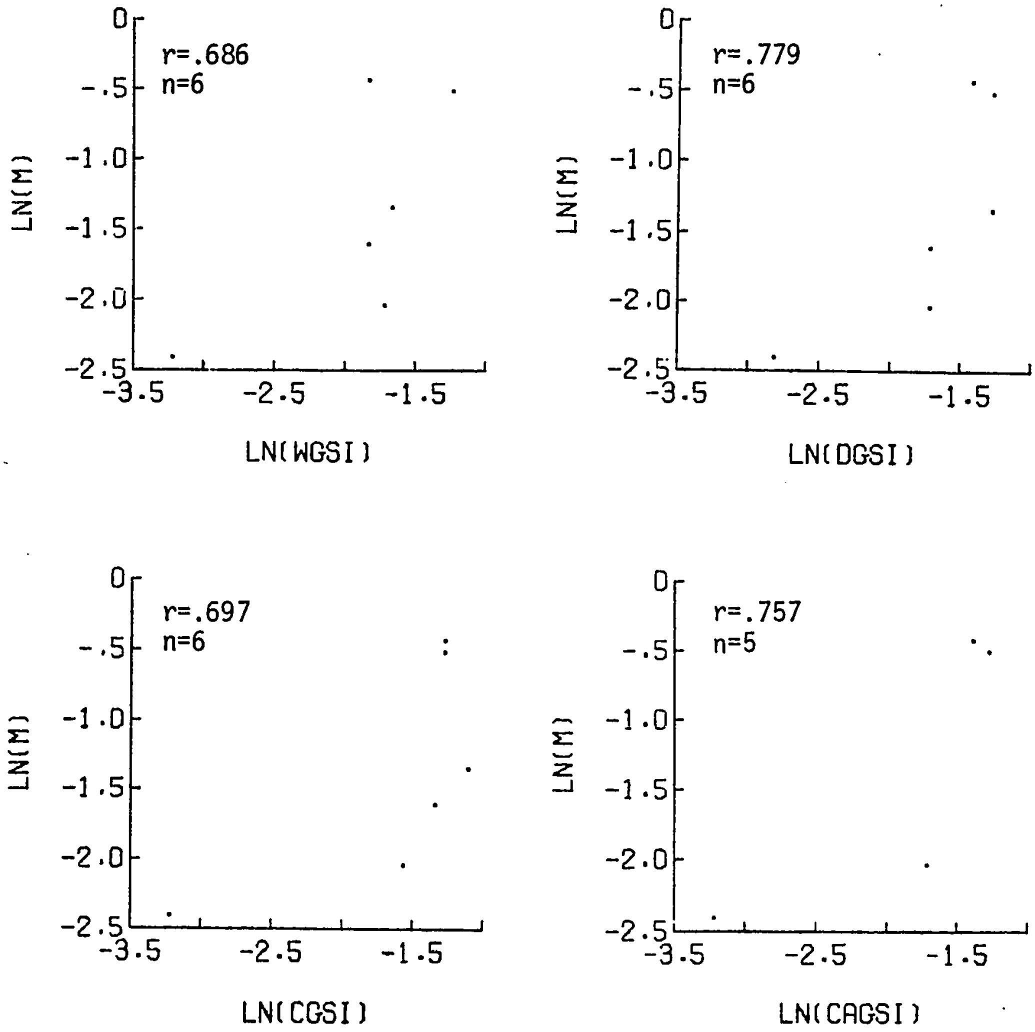


Fig. 17. Plots of the 4 transformed (ln) reproductive effort index estimates versus the transformed (ln) M estimates using equivalent sample sizes.

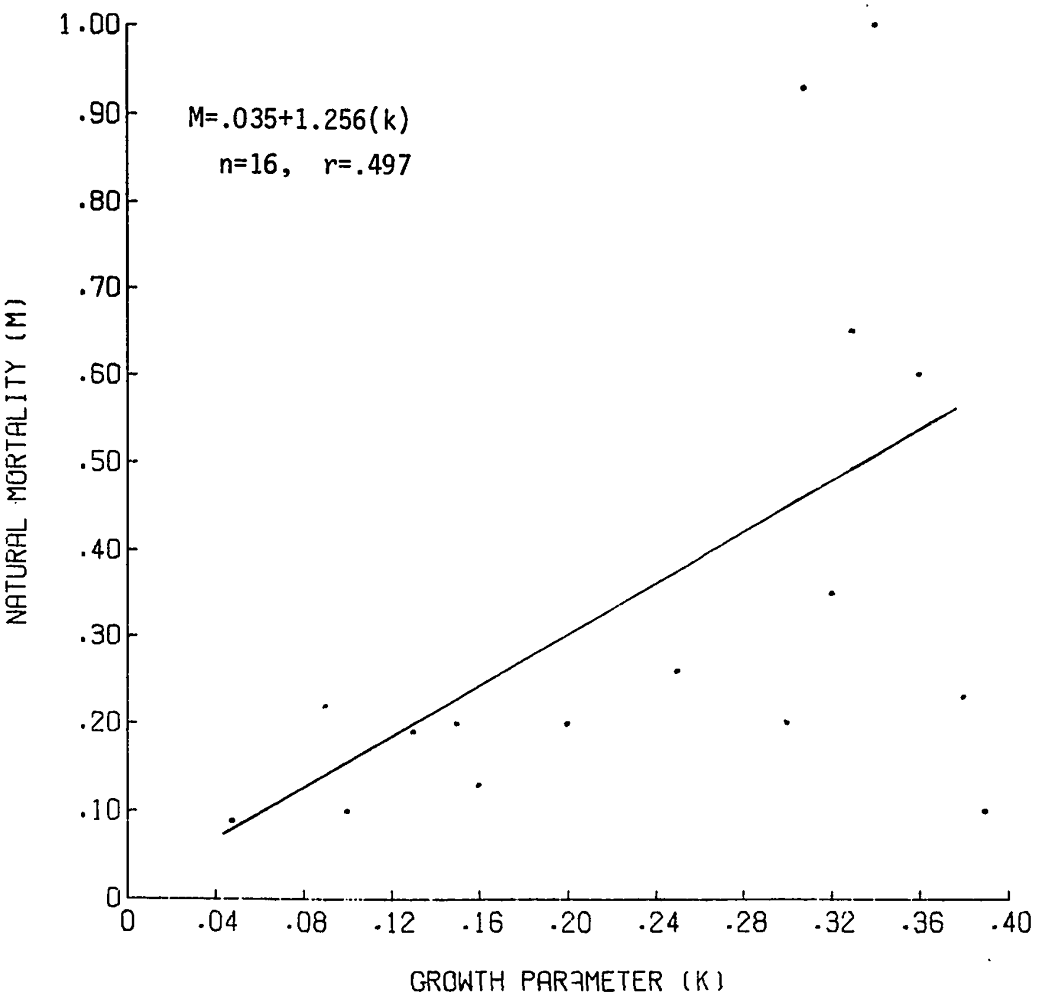


Fig. 18. Plot of the growth parameter (K) versus natural mortality (M).

Table 22. Between year and location comparisons of the WGSI values for 4 species.

Species	Year	Location	WGSI
Pacific herring	82	North Puget Sound	.266
	84	"	.313
Pacific cod	83	North Puget Sound	.153
	84	"	.174
	85	"	.166
	76	West Vancouver Island	.205
	76	Hecate Strait	.150
	82	Gulf of Alaska	.127
Dogfish	83	North Puget Sound	.041
	84	"	.044
English sole	83	North Puget Sound	.166
	84	"	.190

feeding and growth conditions during the previous year, as well as the strategy of energy allocation for growth and reproduction. (This topic will be reviewed in more detail below). Herring, for example, had significantly larger gonads in 1984, and the length-specific body weights were lower. Either change would lead to a higher estimate of the WGSI. Even so, the 2 estimates for herring are within reasonable limits of each other. The difference between the 2 observations for herring is .05 units while the range of values for all species varies from .04 to .50 (Table 19).

The cod data also provides estimates for 5 different years and 4 different locations. Despite both year and stock differences, the WGSI estimates for the species range from .127 - .205.

It is important to note here the WGSI is being used as a predictor variable in a regression analysis. One of the assumptions of regression is that the independent variable (WGSI in this case) be known without error. Unfortunately, WGSI is itself a random variable which can only be estimated. It is therefore desirable to obtain the best estimate possible for each species by using observations from several different years. The methods for estimating the WGSI are not time consuming. Multiple observations are therefore a reasonable expectation for any species that is already being routinely monitored for management purposes.

A number of other predictors of M have been considered that are based on correlative methods or analytical models. The theoretical support for the correlative methods is derived from life history theory which predicts that certain parameters will be associated. There is some debate about which mechanisms of selection are most important (see Stearns 1976 for review) but there is general agreement that high adult mortality will be associated with low age of first maturity, low maximum age, high growth rates (k), low maximum size (L_∞) and high reproductive effort. These are r-selected species. k-selected species have low adult mortality which is associated with high age of first maturity, high maximum age, low growth rates, high maximum size, and low relative reproductive rates.

There is a large volume of literature which pertains to life history theory. I will not attempt to review it here, but will just say that although there appear to be innumerable exceptions to any rule derived from life history theory, there does seem to be some general validity to the concept that these 2 groups of parameters are associated. Adams (1980) conducted a correlation analysis of five life history parameters (M, k, L_∞, age-at-maturity, and maximum age) for five different taxonomic groups of fishes and found the sign of every parameter pair was as predicted and that 87% of the individual taxa parameter correlations were significant at the 5% level.

Beverton and Holt (1959) were the first to consider the relationship between mortality and the von Bertalanffy growth parameters for fishes (their work was actually done in the absence of the more recent perspective of life history theory). They also considered taxonomic groups separately and found that k was generally closely associated with mortality. Even when taxonomic groups were considered together, the association was still evident. Their presentation, however, was graphical in nature and was not developed as a predictive model.

Murphy (1968) related the variability of recruitment success to reproductive life span for pelagic baitfish. Roff (1981) reexamined Murphy's results after including some new data. He concluded that the Murphy's suggested correlation was not significant, but that age at maturity was related to reproductive life span for both baitfish and flatfish species. Jensen (1981) concluded that age at maturity and growth rate were the life history parameters most able to compensate for changes in total mortality and confirmed his analytical findings using data on lake whitefish.

Pauly (1982) has taken the correlative approach to its logical extreme. He compiled a list of mortality, growth parameter (k and $L\infty$) and average annual water temperature estimates for 175 stocks representing 84 species. He then used multiple regression methods to develop an empirical model for predicting M which contained the 3 variables. The correlation was highly significant, explaining 72% of the variability in the observed values of M.

Other researchers have used analytical reasoning to develop models describing the relationship between natural mortality and various life history parameters. Alversen and Carney (1975) related the age of maximum biomass for a cohort (T_{mb}) to the growth rate parameter (k) and a mortality rate estimate (M).

$$T_{mb} = (\frac{1}{k}) \ln [(M+3k)/M]$$

They then concluded that an approximate estimate of T_{mb} could be derived from an empirical relationship between T_{mb} and an estimate of maximum age (T_{max}) thereby permitting one to solve for M. Despite the terminology used in the original paper, this method actually gives an estimate of total mortality (Z) unless the stock is unexploited since both T_{mb} and T_{max} will be influenced by fishing.

Myers and Doyle (1983) developed a model that is dependent on more complicated analytical techniques. Basically, their approach was to find a solution to the discrete form of the Lotka equation

$$\sum_{x=1}^{T} \exp\ (-r_x)\ l_x m_x$$

which maximized r given 2 constraints that were themselves derived mathematically (methods not specified). The constraints dealt with the reproductive effort-mortality trade-off, and the relationship between reproduction and the efficiency of energy conversion to reproductive products. The method requires estimates of the growth rate, reproductive effort, age-at-maturity and estimates of surplus energy as defined by Ware (1980). Once this data is incorporated into the model, an iterative search algorithm is used to find parameter estimates giving a local maxima. The resulting M value is referred to as the "best adapted" estimator. A test correlation with "known" values of M gave an r^2 value of .91 (n=8).

Roff (1984) has developed a different model but also begins his analysis with the discrete form of Lotka's equation and the assumption that natural selection will maximize fitness. Fitness is defined in terms of the Malthusian parameter in the general case, or lifetime fecundity if the population is stable (in which case r equals 0). The outcome of his analysis is a 3 parameter nonlinear model relating M to k, $L\infty$ and length at maturity L_T. A test correlation with known values led to a significant r value of .683 ($p < .01$, $n = 30$).

The drawback of all of the predictive methods discussed above is that they are dependent on good estimates of the von Bertalanffy growth parameters and in some cases, require even more detailed information concerning the stock of interest. Growth parameter estimates are derived from either size-at-age data or tagging studies, the same information sources used in developing traditional mortality estimates. The data requirements for growth parameter estimation are not as burdensome as those for mortality, but the technical and time/cost problems associated with the methods still apply. That is, the aging of fish is time consuming, technically difficult, and sometimes impossible. Tagging studies are not always feasible and are both expensive and time consuming.

The suggested inverse relationship between reproductive effort and natural mortality is a prediction derived from life history theory that is strictly analogous to similar predictions concerning the relations between size, growth, age of maturity and mortality. An independent rationale which purports to explain the trade-off between mortality and reproductive effort has been developed from energetics concepts. The basic argument is that higher reproductive effort leads to increased somatic depletion and as a result, greater susceptibility to the mortality factors of disease and predators (Orton 1929; Templeman and Andrews 1956; Gerking 1959; MacKinnon 1972; Jones and Johnston 1977; Mann and Mills 1979; Woodhead 1979; Bell 1980; Roff 1982). Ware (1980, 1984) and Myers and Doyle (1983) have incorporated the concept of the reproductive effort mortality trade-off into their quantitative models. Although this argument is often made in a within-species context, life history theory uses similar reasoning in making between-species comparisons.

Reproductive effort has not been considered in the past to the same degree as the other life history parameters because comparable reproductive effort data is generally not available. Fecundity data is the most common measure of reproductive effort. However, partly because of large differences in egg size between species, fecundity is an inappropriate comparative measure of reproductive effort (Roff 1982).

Gunderson (1980) was the first to compile data on reproductive effort and consider it as predictor of mortality. This study confirms that reproductive effort indices correlate well with estimates of mortality. In fact, WGSI explains a greater proportion of the variance than k or any of the other parameters taken either in their linear or log-linear forms. As mentioned earlier, it seems likely that the use of dry gonad and body weight data (DGSI) would further reduce the proportion of unexplained variance. Dry weight conversions are relatively easy to obtain. Calorie data would be desirable, but is unlikely to be routinely available.

I did investigate the possibility of using more than one independent variable as a predictor of M. However, a multiple regression analysis indicated that the inclusion of additional variables was not justified. The probabilities associated with the independent partial F-tests for the entry of L∞, k, T_m, and $t_{.01}$ once WGSI was already in the model ranged from .32-.92. It is conceivable that the form of the best fit model will change given a larger data set, but for the present a linear model relating WGSI to M is the most suitable choice.

Outliers seem to be a fairly common feature in plots showing the relations between life history parameters (see for example, Beverton and Holt 1959; Roff 1981; Jensen 1981;, Pauly 1980 (plotted in Roff 1983)). In my own data, the reproductive effort estimate for Pacific cod was unexpectedly low (Figure 15) as was the growth parameter k for North Sea sole (Figure 18). However, it is reasonable to expect that such outliers will occur. A fundamental limitation of the methods of using correlative estimators of life history parameters is that it cannot account for the fact that a given life history tactic is the result of a compromise of selective forces acting on all traits. In general, certain sets of life history parameters tend to reoccur Occasionally, however, a particular species may encounter an unusual combination of selective forces. The North Sea sole, for example, is a comparatively small fish (L∞ = 39.7) with a high growth rate (.39) and early maturity (3 yr). However, it has a low mortality rate (.10) and therefore tends to live a long time (T.01 = 14 yrs). One can speculate that this combination of traits occurs because there is low adult mortality, unusually high predation pressure on juveniles and a critical size refuge from predation. As a result, there would be strong selective pressure for a high juvenile growth rate, but once fish reach the size refuge, it would be logical to mature and then continue to reproduce at a low rate since the adults could "expect" to live a long time. Under such circumstance, k is a very poor predictor of natural mortality because it has been forced out of conformity with other life history parameters by an atypical selection force.

Pacific cod from Puget Sound are also enigmatic in that they have a high mortality rate (.65), short life span (8 yrs), high growth rate (k = .33), and early age of maturity (3), but are a relatively large fish (L_∞ = 86.6g) with low reproductive effort (WGSI = .16). Their size may be related to their position on the food chain as a large mouthed semi-dermersal predator. As such, size is both a prerequisite and a result of their ability to eat large energy rich food items. Relative reproductive effort is low compared to other species, but fecundity is very high. Larger fish typically spawn 2-3 million eggs per year (Thomson 1962). In this case, because the fish are large, fecundity is high and there may be no further selective advantage to having greater relative reproductive effort in terms of body mass. For whatever reason, reproductive effort is a poor estimator of the natural mortality of cod, whereas k correlates quite well.

The use of more than one predictor variable may lead to a reduction in the magnitude of outlier deviation. However, in general, the parameter coefficients are derived from the dominant trends in the data. As a result, those species which violate the general rules of parameter association will continue to be outside the main cluster of points.

Roff (1983) commented that empirical or analytical models should not in general be depended on for estimates of M because the errors of estimation could be quite large. However, parameter estimation in fisheries almost always involves some degree of subjectivity. Standard estimation procedures often lead to unrealistic estimates and it is therefore generally necessary to make a judgment about whether a given value is reasonable. Mortality estimates derived from these correlative or analytical models should be used conservatively and viewed with some skepticism until they can be corroborated by independent methods. However, it can easily take several years to obtain a reliable estimate of natural mortality using tag or aging data, whereas reproductive effort estimates of fish can be obtained for most species during a single spawning season.

The proper use of reproductive effort as a predictor of M does require some knowledge about the reproductive biology of the species of interest. Incorrectly assuming that a species is a single batch spawner would lead to an underestimate of reproductive effort and thus mortality. If the spawning behavior of a species is unfamiliar, a reasonable initial judgment could be made from consideration of the reproductive biology of congeners, inspection of the gonads of mature and spent fish, and an analysis of egg size frequencies from ripe fish. If species are multiple batch spawners, a more detailed study of their reproductive habits may be necessary before the gonad indices can be determined.

CHAPTER 2.

VARIABILITY IN THE GROWTH AND REPRODUCTION OF FISH

Variability in Growth and Reproduction of Fish

If reproductive effort is to be used as an indicator of natural mortality, then it is important to develop an understanding of the sources of variability that might affect those estimators. As a result I have conducted an exploratory analysis and general review of the variability in reproductive effort and its relation to somatic growth. The three levels of variability considered here include 1) the seasonal cycling of energy storage products and their use for growth and reproduction; 2) the variability in reproduction between fish of similar size and age; and 3) the changing relation between growth and reproduction with size and age. Chapter 3 is devoted to a consideration of the between-year variability in production dynamics.

These topics are to some degree independent of one another, each having its own context and associated literature. However, taken together they provide a broad overview of the strategies of energy allocation, thus providing valuable insight into the relation between reproductive effort and natural mortality.

Seasonal Energy Cycles

Introduction

One of the mechanisms that presumably relates reproductive effort to natural mortality is the process of somatic depletion. Somatic depletion is a result of the seasonal energy cycles that are characteristic of most temperate fishes. Fish that spawn in the late winter or spring depend on energy stores laid down the previous summer. Because parents must in part supply both reproductive and maintenance costs from their somatic energy stores, they are at the bottom of their seasonal condition cycle (somatic depletion) immediately after spawning. Seasonal cycles, somatic depletion, reproductive effort and natural mortality are all interrelated. Consideration of seasonal energy cycles should therefore help elucidate some of the important mechanisms which presumably underlie the correlative relationship between reproductive effort and natural mortality.

There is a great deal of qualitative information concerning seasonal cycles, and in particular the coincident changes in body condition and gonad weight (Milroy 1908; Bruce 1924; Lovern and Wood 1937; Wood 1958; Templeman and Andrews 1966; Mannan et al. 1961; Love 1970; and Shevchenko 1972). However, there are relatively few studies which quantify the magnitude of these seasonal fluctuations in any detail (Le Cren 1951; MacKinnon 1972; Craig 1977; Dawson and Grimm 1980). I therefore conducted an analysis of the seasonal growth and reproductive dynamics of English sole.

Methods

English sole were the subject of the investigation concerning the relationship between seasonal energy cycling, and reproduction and growth. A size stratified sample of fish was collected every 4-6 weeks for 13 months (Table 23). The somatic tissues of the 257 fish collected from March 1983 through March 1984 were analyzed for water, ash, calorie, lipid, and protein content using the methods described earlier. In

Table 23. Sampling dates and sample sizes for English sole.

Sampling dates	N	Condition
Feb. 1, 1983	17	Ripe
Mar. 3 and 15	20	Spent
June 6	20	Resting
July 22	20	Resting
Sept. 12	19	Resting
Oct. 18	20	Developing
Nov. 29	10	Developing
Dec. 15	20	Developing
Jan. 13, 1984	12	Developing
Feb.-Mar.	15	Developing
Feb.-Mar.	78	Ripe

addition, each of the fish was aged by counting the rings on the interopercular bone. (The aging was done by Ruth Mandapat of the Washington Department of Fisheries aging group.) Relative gonad development was characterized by measuring the average egg diameter of the largest size mode of eggs for each fish. The ash and water content of all gonads were also determined. Calorie and protein estimates were made on 40 gonad samples and lipid content on 65. The gonad samples selected for these more detailed analyses were stratified by egg size in order to define the changes in tissue composition during development.

Seasonal trends in the proximate components were analyzed by converting % composition to total constituent content (for example, total lipid content = body weight x % dry matter x % lipid content of dry tissue). The alternative of reporting % composition can be misleading unless size is held constant since changes in the content of any one component will affect the % composition of all others.

Each sample includes fish from a range of sizes. As a result total composition of each component on each date was expressed as a log-linear function of length. The evaluation of seasonal trends was then accomplished by using analysis of covariance techniques. Computations were performed using a dummy variable approach (Kleinbaum and Kupper 1978) and an SPSS Regression subroutine. Presuming that the assumption of homogeneity of slope can be justified, the outcome of the analyses for each constituent was therefore a family of parallel lines (e.g., total dry body weight vs. length) where each line represents a given sampling date (for example see Figure 19). The use of analysis of covariance

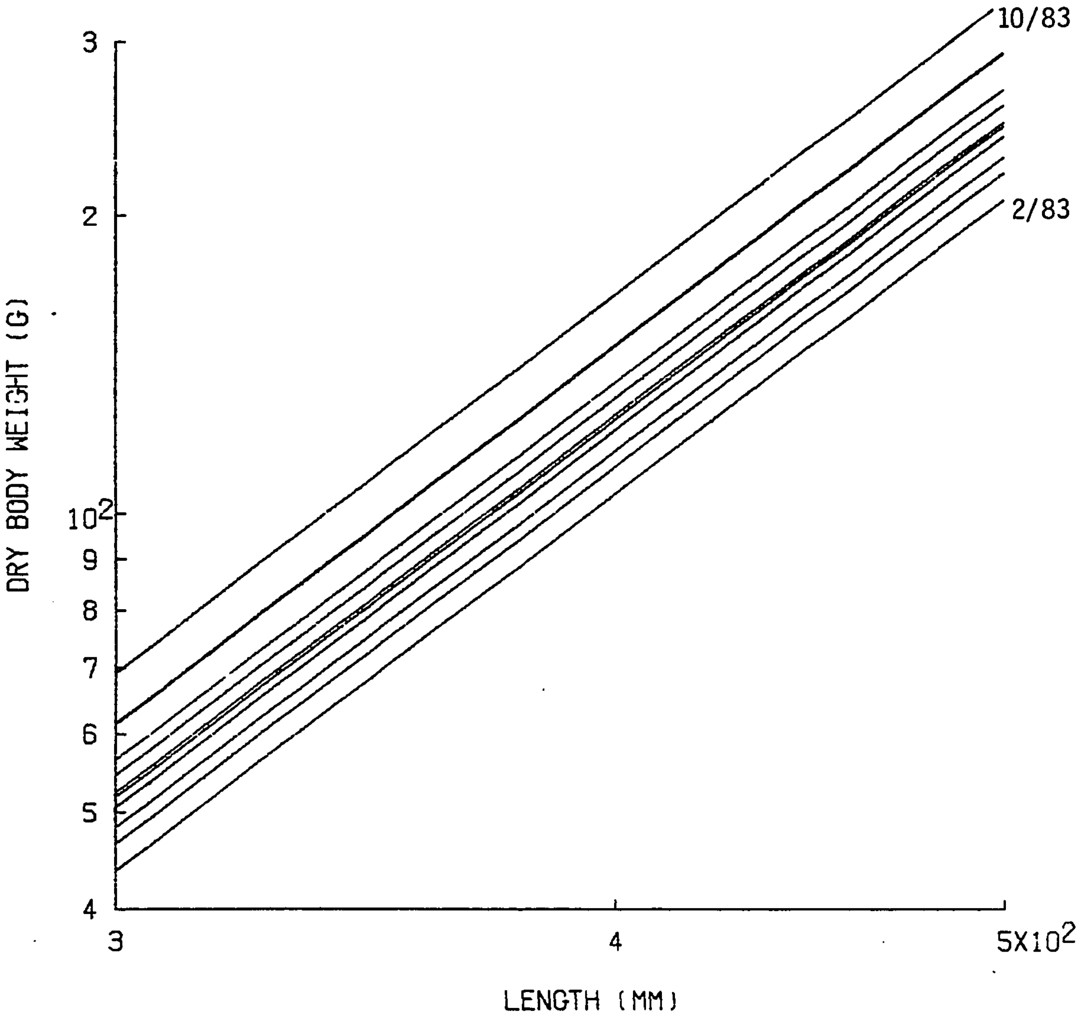


Fig. 19. Total dry body weight versus length plots for each of the 11 English sole sampling dates.

greatly simplifies the consideration of seasonal trends although the required homogeneity of slope assumption may obscure potential size-dependent effects. However, such effects have been considered more directly and will be discussed in a later section.

Presentation of the results of this analysis of seasonal trends can be simplified by selecting a fish of average size and examining the time series of estimates derived from the linear equations. It is also necessary, however, to allow for seasonal growth. The following analysis, therefore, describes the seasonal trends for a fish that was 6 years old in February 1983. I assumed that all linear growth occurred during the spring and summer months, so that by October the fish had the equivalent length of a 7-year-old which then did not change through the remainder of the year. Growth was assumed to occur at a constant rate during the spring and summer months. The estimated age on any given sampling date was converted to length using a Bertalanffy length-at-age function.

Results

The estimated relationship between length and age (Figure 20)

$$\text{Lgth} = 485.09\ [1-e^{-.1712(t+3.3200)}]$$

was derived using the SPSS Nonlinear subroutine. Average length-at-age was calculated from the 240 available observations which were distributed over 19 age-classes. Each observation was weighted by both sample size and the inverse of the variance.

The covariance analysis used in defining the seasonal trends assumes that slopes are homogeneous. A multiple partial F-test conducted

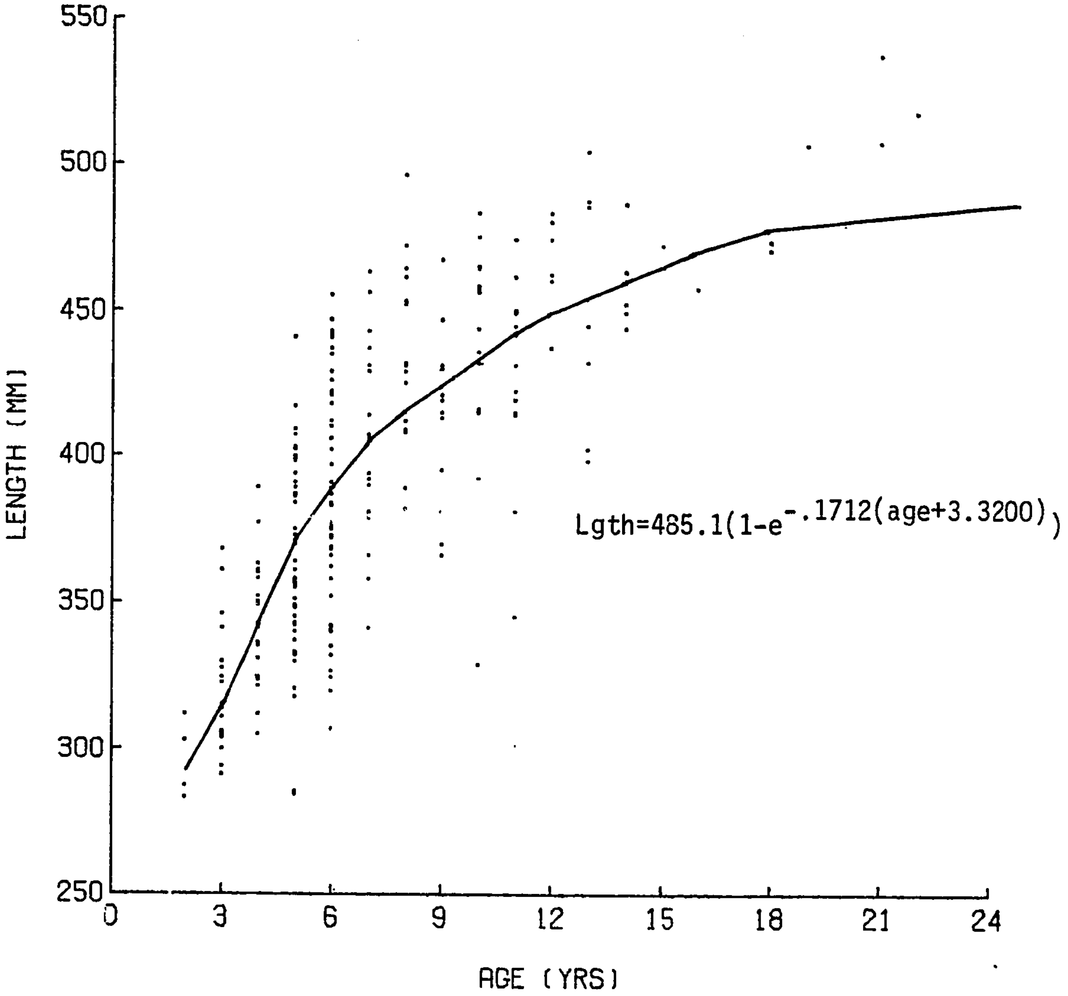


Fig. 20. Length at age plot for English sole.

for each constituent confirmed that the contribution of 10 slope terms (11 sampling dates) taken as a group was not significant ($p \geq .05$) once the intercept terms had been entered into the equation. Figure 19 is a plot of log dry body weight (DBwgt) versus log length for each sampling date, and is an example of the results derived from the covariance analysis from which the seasonal trend data was determined.

The estimated dry body weight (DBwgt) of a 6-year-old fish in February 1983 was 94.5 g and 387 mm (Table 24, Figure 21). Dry body weight increased rapidly after the initial spawning and reached a peak of 168.5 g by October. Fish then lost body weight through the remainder of the year. Ripe fish that were 7 years of age in 1984 weighed 106.5 g and were 402 mm long, suggesting that the net gains in length and dry weight were 15.5 mm and 12 g, respectively.

Similar cyclic patterns were also shown by the other body constituents (Table 24). Total body lipid content (TBLP) increased over 4 fold (Figure 22) and total calorie content more than doubled (Figure 23) from February to October, even though the gain in dry body weight was only 78%. These differences are the result of an increase in the concentration of lipids in the body tissues. The results also showed that there was significant (50%) seasonal fluctuation in total body protein (TBPR) and more modest trends in ash content (Figure 22).

The trends in body constituents can be contrasted to the seasonal changes in the dry weight of the gonad (Table 24, Figure 24). Gonad development peaked in February or March. After spawning, gonad weight remained low and relatively constant until the fall when eggs gradually

Table 24. Age, size, total proximate and caloric content for an English sole of representative size for each samping date (DBwgt = dry body weight, DGwgt = dry gonad weight, TBASH = total body ash content, TBLP = total body lipid content, TBPR = total body protein content, TBCAL = total body calorie content).

Sampl-ing date	Age	L	DBwgt	DGwgt	TBash	TBLP	TBPR	TBcal x 10^3
2/83	6.0	386.7 mm	94.5 g	26.0 g	13.9 g	- g	- g	461.1 cal
3/83	6.0	386.7	100.6	1.6	16.4	8.0	68.8	477.1
6/83	6.4	393.2	115.1	1.7	16.9	11.1	82.7	559.7
7/83	6.6	396.2	126.8	1.7	17.0	14.2	87.8	631.3
9/83	6.8	399.3	146.6	3.1	19.9	23.9	97.9	765.5
10/83	7.0	402.2	168.5	8.4	17.7	40.6	103.1	950.0
11/83	7.0	402.2	149.6	13.3	17.5	33.8	91.6	823.2
12/83	7.0	402.2	137.6	8.5	16.6	24.9	89.6	738.5
1/84	7.0	402.2	127.5	24.0	15.4	22.3	85.8	654.9
2-3/84	7.0	402.2	126.4	25.8	16.6	22.3	84.7	640.3
2-3/84	7.0	402.2	106.5	30.3	15.7	14.4	71.6	520.0

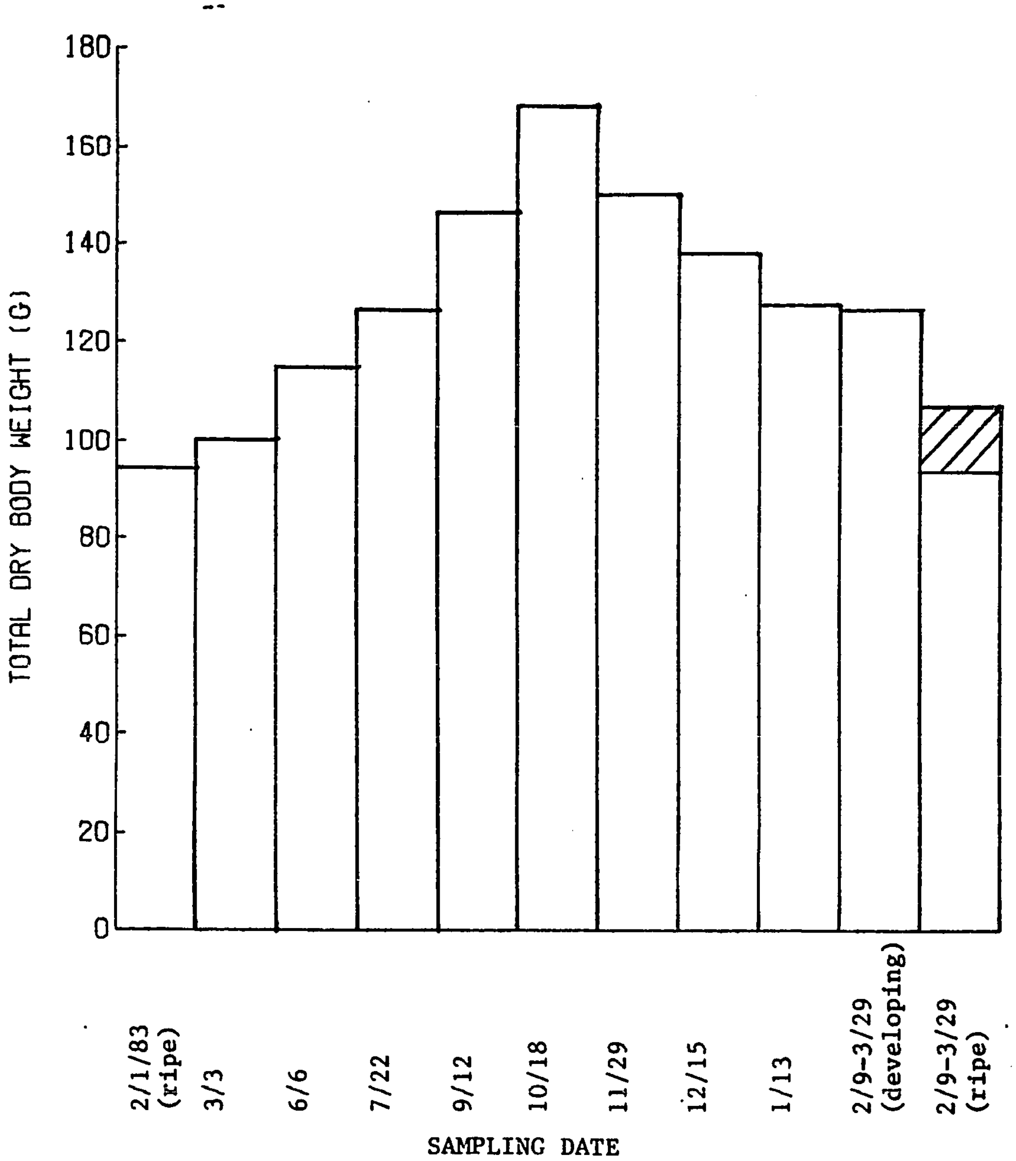


Fig. 21. Total dry body weight of an English sole of representative size for each sampling date. Hatched area shows annual somatic growth increment.

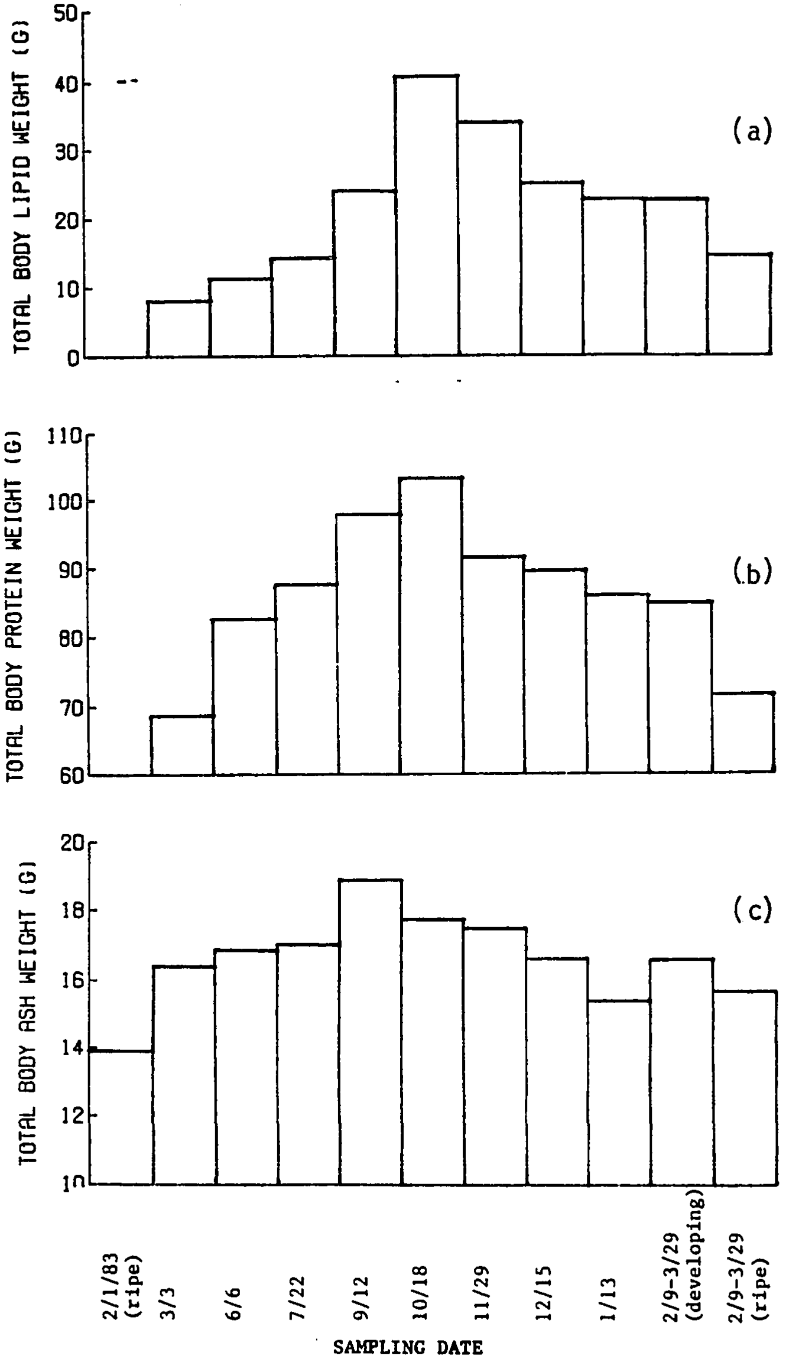


Fig. 22. Total body lipid (a), protein (b) and ash (c) content of an English sole of representative size for each sampling date.

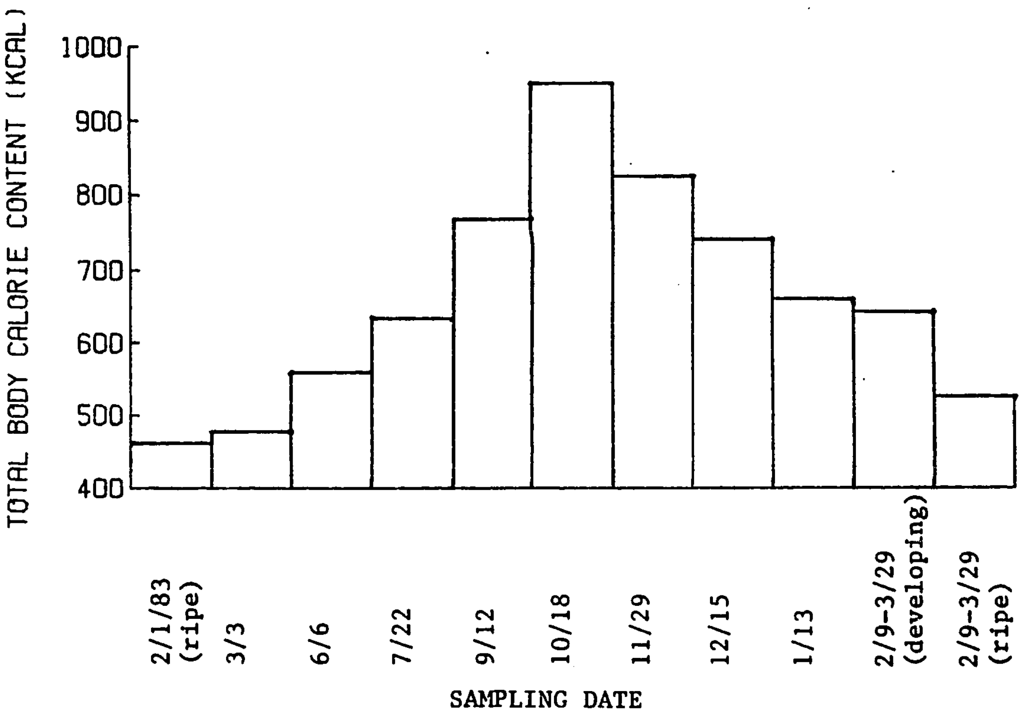


Fig. 23. Total body calorie content of an English sole of representative size for each sampling date.

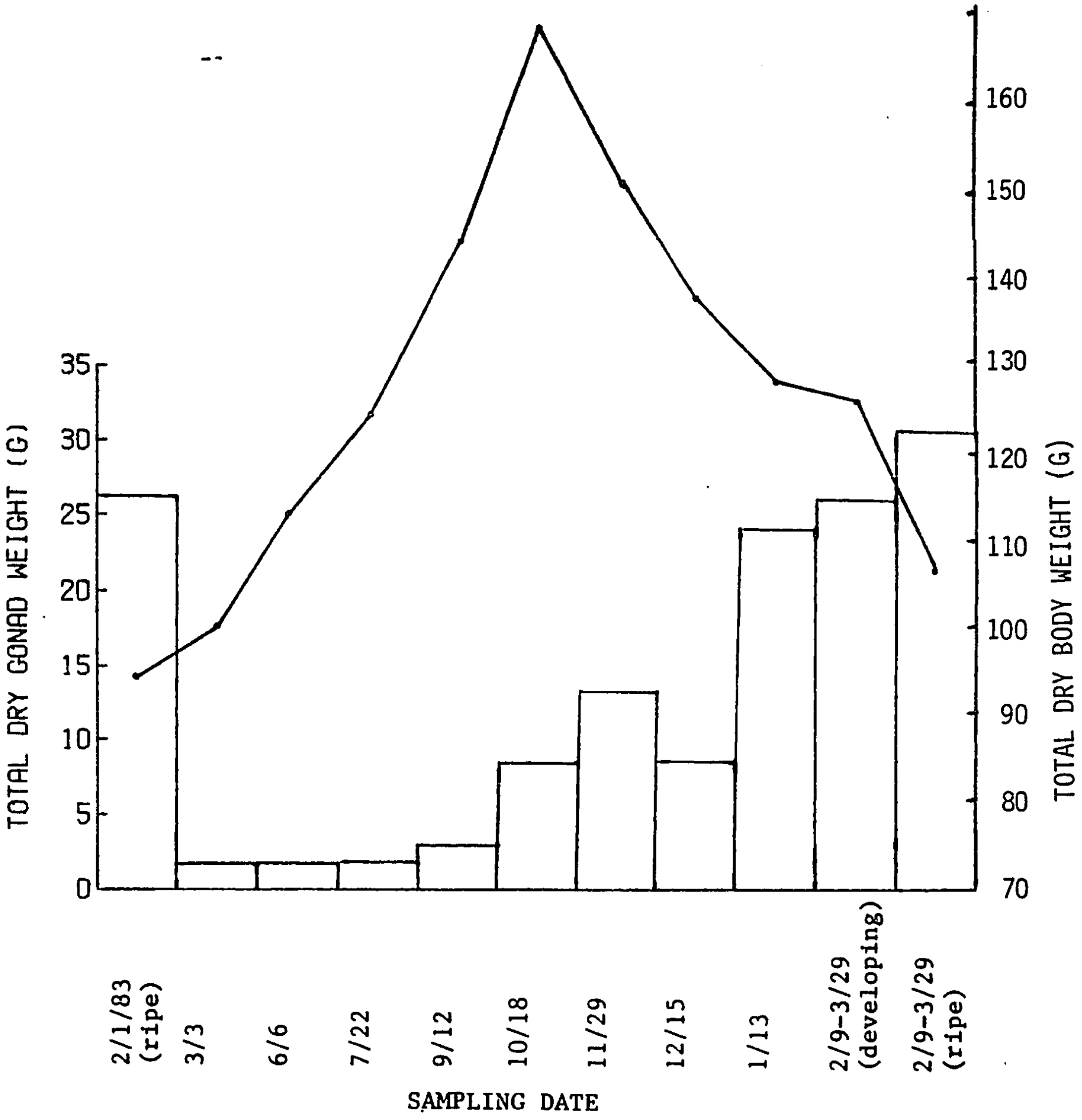


Fig. 24. Total dry gonad weight of an English sole of representative size for each sampling date (bars) and coincident trend in total body dry weight (points).

began to accumulate yolk. The increase in gonad weight was coincident with the decline in body weight.

The seasonal trends in the proximate composition of the gonads can be inferred from a consideration of how each component changed with egg size. The water content of spent gonads initially was high, decreased during development, and reached a minimum when eggs were between .5 and .6 mm (Figure 25). Thereafter, hydration began and the water content of the gonads again went up. This result provides independent support for the use of the .55 mm criteria for selection of fish with fully developed gonads.

The ash content (Figure 26) of the gonad tissues generally decreased over the course of development. The concentration of lipids (Figure 26) in spent gonads was uniformly low at about 3% of dry weight. Lipids increased during maturation but then became quite variable in the fully developed and hydrating gonads. Attempts to explain this variability in the lipid concentration of mature eggs were unsuccessful. It was unrelated to fish size or other proximate components. As will be discussed later, body condition does have some effect on the gonad composition, but the differences do not involve the lipid data. The protein content (Figure 26) was variable, but did suggest a slight decline with egg size. The gonad calorie content (Figure 25) increased during development from about 4600 calories per g dry weight (g dw) for spent gonads to 5700 calories g dw·for maturing eggs, then remained constant through late development and hydration.

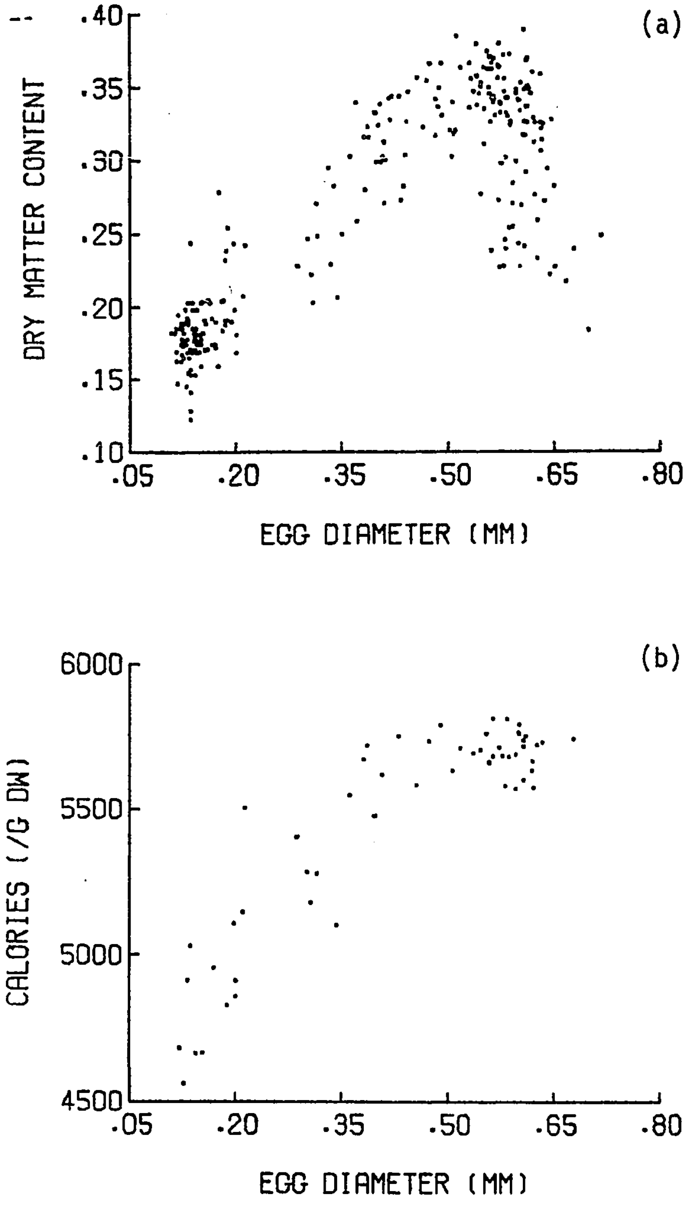


Fig. 25. Percent dry matter (a) and calorie content (b) of English sole gonads plotted versus egg diameter.

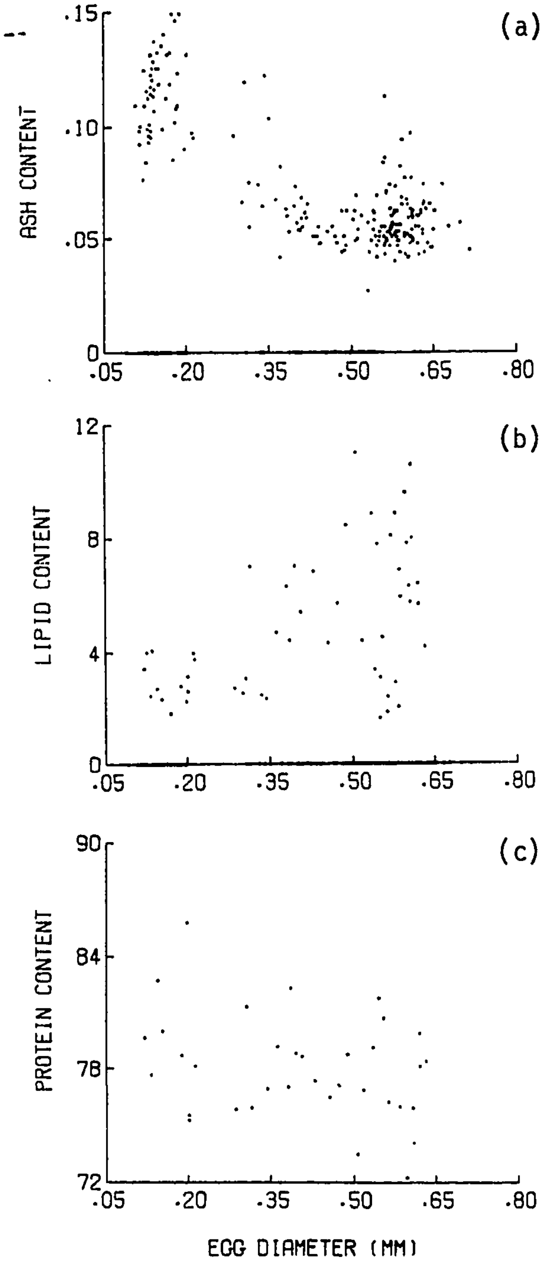


Fig. 26. Percent ash (a), lipid (b) and protein (c) content (percent of dry weight) of English sole gonads plotted versus egg diameter.

A more general impression of the constituent changes which accompany gonad development can be obtained by comparing the average observed values for spent and resting gonads (egg diameter ≤ .24 mm) and ripe gonads ((egg diameter ≥ .55 mm), Table 25). The magnitude of the absolute change in gonad weight emphasizes the fact that although the relative proportions of the constituents may increase or decrease, the absolute abundances all go up as development proceeds.

Discussion

Results of the preceding analysis show that the expected annual growth increment of a 6-year-old fish is 15.5 mm and 12 g dw (about 54 g ww). However, the seasonal fluctuations in body weight were much larger. The representative fish gained 74 g dw over the course of the spring and summer but subsequently lost 62 g dw during the 5 months from October-March (Table 24). Since the average percent dry matter of body tissues in October and March were 25.5 and 21.4%, respectively, this seasonal weight loss is equivalent to 163 g ww [(168.5/.255)-(106.5/.214) = 163)] or more than 1/3 of a pound. Even this figure is misleading since the fish have maintained wet body weight by increasing their water content. The 62 g of lost dry weight represents nearly 37% of the total weight of the fish in October.

Dawson and Grimm (1980) observed similar seasonal fluctuations in the body weight of plaice (Pleuronectes platessa). The dry weight of 6-year-old plaice increased from 73.0 g dw in May to 127.3 g in November and then declined to 102.9 g the following May. American plaice (Hippoglossoides platessoides) showed a seasonal gain in somatic energy con-

Table 25. Proximate composition and caloric content of resting and ripe English sole gonads for a fish of representative size.

	Resting (egg size ≤ .24 mm)		Ripe (egg size ≥ .55 mm)	
	% composition	Constituent wt (g)	% composition	Constituent wt (g)
GDRY	18.5	1.55	31.7	30.3
GASH	11.2	.17	5.8	1.76
GLP	3.0	.05	5.6	1.70
GPR	79.3	1.23	76.8	23.27
GCAL	4910 cal/g	7611 cal	5706 cal/g	172892 cal

tent of 143.2 kcal, but subsequently utilized 92 kcal for overwintering metabolism and gonad development (MacKinnon 1972). In fact, seasonal cycles of this type are to be expected of temperate fishes and their existence is well documented, at least to the extent that it is known that such cycles exist for many species (Nikolskii 1969; Templeman and Andrews 1956; LeCren 1951; Bagenal 1957; and Shulman 1974; MacKinnon 1972; Craig 1977; Dawson and Grimm 1980).

Seasonal cycles are a common feature of the biology of temperate fishes and are related to the production cycles in their environment. Fish do most of their feeding and growth during the spring and summer months when food is most abundant. However, they must also develop energy stores to meet both metabolic and reproductive demands which occur during the seasons of low productivity. Most temperate species have adapted to spawning in the late winter or spring, which may be disadvantageous from the parents' point of view since it requires that at least some gonad development occur at a time when food availability is low. However, winter/spring spawning is probably necessary so that the larvae and juveniles can take advantage of the seasonal maxima in food abundance during this critical period in their early life history.

It is appropriate to consider whether the magnitude of the estimated seasonal fluctuations in body weight of English sole are reasonable based on a consideration of expected energy utilization. In conducting such an analysis of seasonal energy or mass transfer, it is preferable to consider the proximate components independently (rather than mass or calorie units) since lipids and proteins serve different functions. Lipids are primarily an energy storage product, while the bulk of the stored proteins are utilized for gonad development (Love 1970; Dawson and Grimm 1980; Iles 1984).

It will be useful to note before proceeding with the analysis that the sum of the proximate components (lipid, protein and ash) is generally less than the estimated total dry weight (see Table 24). This discrepancy results in part from the fact that carbohydrates have not been accounted for, although the concentration of carbohydrates in most fishes is typically quite low (Shevchanko 1972; Dawson and Grimm 1980). An additional reason for the discrepancy is that the standard methods for estimating "total" lipid and protein levels typically give biased estimates of the true values. For example, the Kjeldahl method determines nitrogen content. Nitrogen is then converted to protein by dividing by the average nitrogen content of protein (16.0%). The actual nitrogen content varies, however, depending on species, tissue type, conditions, etc. Love et al. (1959) reported that the nitrogen concentration in the muscle tissues of Pleuronectids was 16.9% in which case the Kjeldahl method would underestimate total protein. Olly and Lovern (1954) have shown that the solubility of various kinds of lipids depends on the solvent being used. As a result, estimates of "total" lipid content derived using different methods are not directly comparable and the implication is that the use of any single extraction method probably leads to an underestimate of the true value.

An energetics analysis of the plausibility of the estimated weight loss requires a consideration of winter feeding, losses of individual proximate components, and metabolic rate. Although there are no definitive studies of the seasonal feeding rates of English sole, it is probable that feeding activity is greatly reduced during the winter. In general, many adult Pleuronectids of temperate and boreal waters migrate to deeper water during the winter months where feeding is reduced or nonexistent (Moiseev 1953). English sole fit this pattern at least to the extent that they do show definite seasonal migrations across bathymetric lines (Ketchen 1956; Alverson 1960).

Consideration of the seasonal changes in the proximate components indicates that the representative fish lost 26.2, 31.5, 2.0 g of somatic lipid, protein and ash, respectively (Table 26). Gonad development starts before the onset of the decline in body weight (DGwgt = 8.4g in October), but from October to March the lipid, protein and ash constituents of the gonad increase by 1.4, 16.6, .9 g, respectively (Tables 24 and 26). These results indicate that 32% of the lost body mass is accounted for by the increase in gonad mass. However, consideration of the fate of the individual constituents shows that 52.7% of the lost body protein, 45% of lost ash, and 5.3% of lost lipids can be accounted for by the gains during gonad development.

This disproportionate transfer of components is to be expected since the lipid concentration in gonads is typically quite low. The observed concentrations of lipid (% of dry weight) in mature gonads of English sole, plaice and coho salmon are about 6, 8, and 12%, respectively (pers. obs.; Dawson and Grimm 1980; Hardy et al. 1984). The same

Table 26. Computation of potential mass transfer of the proximate components from body to gonad tissue during maturation.

	Protein	Lipid	Ash	Total
October body composition	103.1 g	40.6	17.7	161.4
March body composition	71.6	14.4	15.7	101.6
Seasonal constituent wgt. loss	31.5	26.2	2.0	59.8
March gonad composition	23.3	1.7	1.8	26.8
October gonad composition	6.7	.3	.9	7.9
Seasonal constituent wgt. gain	16.6	1.4	.9	18.9
Percent of lost body composition accounted for by increase in gonad wgt (%)	52.7	5.3	45.0	31.6

authors reported that the proportion of lost somatic lipid accounted for by gains in the gonad for plaice and coho salmon were 22 and 8%.

It can be assumed that the lost somatic weight not accounted for by gonad uptake was utilized for overwintering metabolism. The estimated calorie content of this fraction of the weight loss is 306510 cal [(9450 cal/g x 24.8 g lipid) + (4810 cal/g x 15.0 g protein) = 306510 cal]. If we assume for the present that fish do not feed for the 151 days from October 1 to February 28 and that the average weight of the fish during that time is 137.5 g dw [(168.5 + 106.5)/2) or 642.5 g ww (137.5/.214), then the metabolic rate required to use the available energy would be .132 cal/g/hr (306510/642.5/(151 x 24)). This value is at the low end of the range of observed values for the standard metabolic rate of fishes (0.08 - 0.74 cal/g/hr) reported by Brett and Groves (1979).

The estimated metabolic rate for English sole can be compared to similar values calculated for other flatfishes. The respiration rates that are sufficient to account for the observed weight losses (assuming no winter feeding) for plaice, American plaice and winter flounder are .124, .071, and .092 cal/g/hr, respectively (Dawson and Grimm 1980; MacKinnon 1972; Tyler and Dunn 1976). Experimental temperatures for the 3 species were, in the same order, 6°, 2-3°, and 7°C, while winter temperatures encountered by English sole are typically 8-9°C (LeBlond 1983).

It is reasonable to assume the actual metabolic rates for English sole are at least .132 cal/g/hr since standard metabolism assumes a zero level of activity and since English sole undertake a full migratory cycle during this 5-month period. If I make the more conservative assumption that feeding meets metabolic needs for 61 of the 151 days, the available energy would last 90 days only if the average rate of oxygen consumption were .221 cal/g/hr. This figure is still near the low end of the range of values for standard metabolism. It is higher than the above estimates for other flatfishes. However, the figures are no longer directly comparable since I have relaxed the assumption concerning winter feeding to a greater degree than was done for the other species.

This analysis suggests that it is reasonable to conclude that English sole could lose as much weight as was estimated by the covariance analysis. One implication of this conclusion is that, when feasible, a consideration of seasonal cycles in body condition could lead to substantial increases in yield without any detrimental impact on the stock. The estimated wet weight of a 7-year-old fish was 661 g (168.5/ .255) in October and 498 g (106.5/.214) in March. However, the length, and therefore the frame weight, would not have changed appreciably. That is, the seasonal weight loss was almost all recoverable muscle tissue. As a result, the yield from a fish taken in October could be nearly twice that of the same fish taken the following March. For example, if the fillet yield in March was 35% (174 g), then the frame weight was 324 g. During the preceding October the frame weight would have been about the same, resulting in a potential fillet weight of 337 g (661 - 324). These calculations probably overemphasize the real seasonal differences since they fail to account for visceral or subcutaneous fat storage. However, MacKinnon (1972) and Dawson and Grimm (1980) came to the same general conclusions based on their analyses of seasonal cycling in other flatfishes.

Consideration of seasonal cycles in designing a harvest strategy would be appropriate in any overcapitalized fishery where seasonal restrictions are required to reduce effort and where fishes are available to the gear during times of peak condition. The frequent habit of concentrating effort on spawning aggregations may be convenient, but is probably not always the best policy since potential opportunities for both increased yield and egg production are being lost.

Finally, it is important to point out that there is still a significant component of variability in the reproductive cycle that is not adequately described by the preceding model. English sole have a very protracted spawning period. Most fish spawn between October and March, although there is a definite peak in spawning activity. However, it is possible to find fish with large gonads containing yolked eggs throughout the year (Alverson 1960, and per. obs.). Washington State Department of Fisheries personnel reported finding ripe and running females in Saratoga Passage in August. It would, therefore, be misleading to imply that all fish fit the described seasonal pattern.

The reasons for this lack of synchrony are unclear. It may simply be that food resources for the larvae and juvenile fish are more available through time so that reproductive activity is not constrained to the relatively narrow time window more typical of other temperate species. It also may be that we are making some improper assumptions about the general reproductive biology of English sole. It is clear that spawning English sole have a single size mode of ripe eggs (pers. obs.). In addition,-there does not seem to be any indication that there are partial releases of eggs during spawning. Observations of this sort are generally interpreted to mean that each fish spawns a single batch of eggs at one time each year. However, a comparative analysis of fish of similar size (covered in the next section) indicates that there is a great deal of variability in the condition of spawning fish. From an energetics point of view, some individuals have both the time (within the protracted spawning season and the energy resources to spawn more than a single batch of eggs per year.

Unfortunately, this scenario is largely speculative and would be difficult to evaluate. It is clear however that there are still some important features of the reproductive biology of English sole that are not adequately understood.

Variability between Fish of Similar Size and Age

Introduction

A number of authors have noted that, despite the generally high correlation between size and reproductive effort, there consistently is considerable variability in gonad weight or fecundity among fish within a size or age group (Simpson 1951; Bagenal 1957a, b; Nikolskii 1969; Hislop et al. 1978; Wootten 1979). My own observation is that reproductive effort typically varies by a factor of 2 or 3.

It has been suggested that the causes of the observed variability may be due to differences in egg size (Roff 1982), age, genetic composition, environmental influence, or food (Hislop et al. 1978; Wootten 1979), but the relative importance of these factors has not been specifically analyzed. The objectives of the analysis of the variation in reproductive effort between similar fish are to identify common characteristics among fish with high or low reproductive effort and to infer from these results what the causes of the variation could be. Because growth and reproduction are inextricably related, the analysis must consider factors which affect productivity as a whole as well as strategies for allocating energy between growth and reproduction.

Methods

The objective of the following analysis was to compare the relation between reproductive effort and body conditions among fish of similar size and age. Length rather than weight was used as the indicator of size because it is a less variable measure of the growth history of an individual. Fish do not lose length, whereas weight fluctuates seasonally and in relation to short term changes in food abundance. Blaxter and Hunter (1982) concluded that length growth is under greater genetic control than is weight growth, again suggesting that length is the better indicator of size, at least given the objectives of the forthcoming analysis.

One approach to analyzing fish of similar length would be to select a particular size class and do direct comparisons of the associations of reproductive effort and condition indices or other measures of somatic well being. However, since my samples were stratified by size, the number of individuals within any particular size class is small. An alternative method which permits utilization of all the size dependent data separates the fish for comparisons into 2 groups, those with high and low relative reproductive effort. This division was accomplished by fitting a regression line to the gonad weight versus length data. Those individuals above the line had high reproductive effort relative to others of similar size. Those below the line had low relative reproductive effort (Figure 27). Once the fish were stratified in this way it was possible to consider various measures of body condition.

One method used to contrast the average condition of fish with high and low relative reproductive effort was to compare the dry body weight-length regressions using analysis of covariance techniques. If the intercept terms were significantly different, then one group of fish is underweight relative to the other. This method has allowed me to consider the general question of whether high relative reproductive effort was associated with better or worse body condition. Other indicators of physical condition that can be considered include body water, lipid, protein, ash, and calorie content.

It is also reasonable to consider the inverse of the above procedure. That is, sort by dry body weight versus length and then compare the dry gonad weight versus length regressions (Figure 28). The specific question being addressed using this approach is--"Do fish in good condition have high or low relative reproductive effort?" Stratification by body weight also allowed me to consider whether fish in good condition had qualitatively different eggs. Indicators of gonad quality include gonad calorie content and proximate composition.

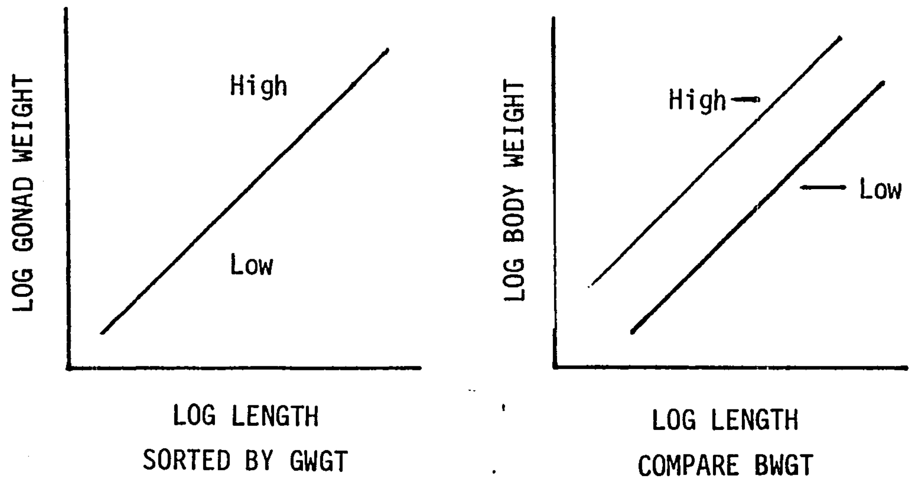


Fig. 27. Schematic representation of the method of analysis used to compare the body condition of fish with high and low relative gonad weight.

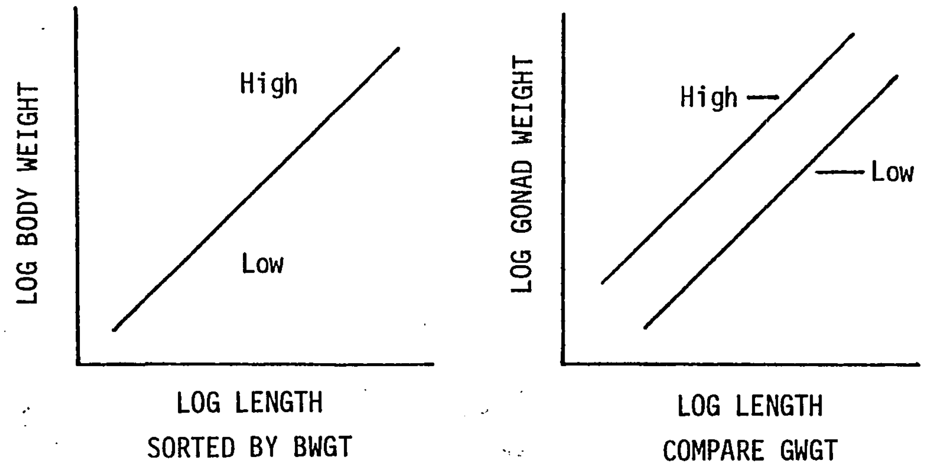


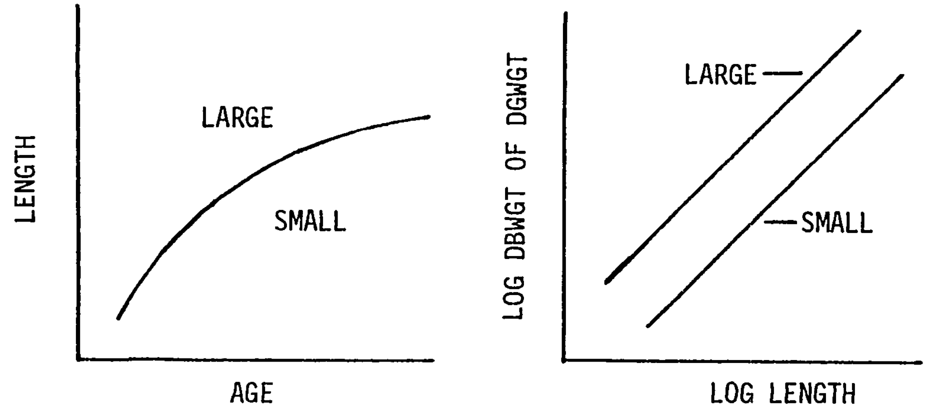
Fig. 28. Schematic representation of the method of analysis used to compare the gonad characteristics of fish with high and low relative body weight.

In addition to using the 2-way stratification described above, English sole samples were also divided into 4 strata, each of which contained approximately the same number of individuals. This permitted me to consider whether the generalizations concerning reproductive effort and body conditions held in the face of more detailed scrutiny.

The procedures described above concern the size characteristics of the fish. However, I was also interested in considering differences between fish of similar age. My approach to analyzing the age data was to compare measures of reproductive effort and body condition for fish that were either large or small for their age. This was accomplished by stratifying the data using a Bertalanffy length at age function (Fig. 29). Covariance analysis was then used to compare the dry gonad weight-length and dry body weight-length functions as described above. I also analyzed the body constituent data by comparing the average observed values for the large and small fish (those above and below the fitted line) for each age.

English sole provided the primary focus for the above described analyses although some herring, Pacific cod, and dogfish data were also considered. In February and March of 1984 78 English sole with fully developed gonads were collected. The somatic tissue of each fish was analyzed for proximate composition and calorie content. All gonads were analyzed for ash and water content, although only 17 determinations were made for lipid content and 7 for calorie and protein content.

Herring data were available for analysis from samples taken in 1982 (n=87) and 1984 (n=150). The herring samples had to be sorted using the



SORTED BY LENGTH AT AGE

COMPARE BOTH DBWGT AND DGWGT

Fig. 29. Schematic representation of the method of analysis used to compare the gonad and body characteristics of fish that were large or small for their age.

wet weight data (i.e., either wet gonad or body weight versus length) since the constituent analyses of the herring tissues were more limited in scope than those of English sole. Age data were available only for the 1984 fish. The herring scales were read by Pat McAllister of the Washington State Department of Fisheries.

A relatively large sample of Pacific cod (n = 507) collected in the Gulf of Alaska in 1982 was analyzed as was a 1985 collection of dogfish (N = 204) taken from the Strait of Georgia. In both cases only wet weight data were available.

Information on the water content of tissues is probably very important when analyzing measures of condition since fish replace utilized lipid and protein stores with water (Love 1970). This displacement tends to stabilize length specific body weight relative to the true condition of the fish. As a result, tests which depend on wet weight data are less powerful than analyses of dry weight data such as were available for English sole, but still may lead to significant results.

Results

English sole. Comparison of the dry body weight-length regressions derived by sorting on dry gonad weight indicates that there was a positive association between reproductive effort and body condition (Table 27). The body constituent analyses confirm these results. Fish with high reproductive effort also had significantly lower water, ash and protein content and significantly higher concentrations of lipids and calories (Table 28). (Low protein content is an indicator of good condition since it implies that the proportional content of lipid is high.)

Table 27. Estimated coefficients for the body weight-length functions ($Bwgt = a\ Lgth^b$, dry or wet as indicated) for English sole, herring, Pacific cod, and dogfish with high and low relative reproductive effort. P_1 and P_2 are probabilities associated with the partial F-tests for entry of intercept and slope terms (in that order) into the log-linear regression models. Also shown are fitted values for fish of 3 rep-resentative lengths.

Reprod. effort	a	b	Length classes (mm)			P_1	P_2
English sole:							
	Dry body weight		300	375	450		
High	$2.7233X10^{-8}$	3.697	39.2	89.4	175.4	.000	.005
Low	$2.6396X10^{-6}$	2.905	41.5	79.4	134.8		
Herring 1982:							
	Wet body weight		150	200	250		
High	$3.7375X10^{-5}$	2.779	41.7	92.7	172.4	.035	.898
Low	$3.8656X10^{-5}$	2.779	43.1	95.9	178.4		
Herring 1984:							
	Wet body weight		150	200	250		
High	$2.2182X10^{-5}$	2.873	39.6	90.5	171.9	.389	.627
Low	$2.1981X10^{-5}$	2.873	39.3	89.7	170.3		
Pacific cod:							
	Wet body weight		600	800	1000		
High	$3.1833X10^{-6}$	3.188	2304	5766	11745	.655	.616
Low	$3.1682X10^{-6}$	3.188	2293	5738	11690		
Dogfish:							
	Wet body weight		950	1050	1150		
High	$4.1088X10^{-7}$	3.329	3355	4681	6337	.000	.001
Low	$4.6016X10^{-5}$	2.645	3451	4496	5719		

Table 28. The body constituent characteristics (all in percent except for BCAL and GCAL which are calories per dw) of English sole stratified by relative dry gonad weight and the gonad constituent characteristics stratified by relative dry body weight. P values are probabilities associated with the ANOVA F-tests. The horizontal lines distinguish means that are significantly different in the 4-way stratification as determined by an SNK multiple range test.

	Hi	Low	p	1	2	3	4	p
	2-way stratification by Gwgt			4-way stratification by Gwgt				
BDRY	21.9	20.6	.011	22.3	21.4	20.8	20.4	.030
BASH	14.2	16.0	.001	14.2	14.3	15.5	16.5	.007
BCAL	5015	4690	.000	5023	5007	4773	4611	.001
BLP	16.8	12.1	.000	17.4	16.0	14.0	10.3	.001
BPR	66.7	69.0	.014	66.6	66.8	68.0	69.8	.057
	2-way stratification by Bwgt			4-way stratification by Bwgt				
GDRY	32.7	30.0	.010	33.5	31.6	30.4	29.5	.034
GASH	5.5	6.5	.001	.051	.060	.067	.070	.000
GCAL	5731	5585	.003	*				
GLP	5.4	8.0	.074	4.3	6.7	8.1	5.6**	.039
GPR	78.3	75.4	.264	*				

*Insufficient data.

**Only one observation in this strata, not included in multiple range test.

The 4-way stratification shows that these trends are consistent, even upon closer scrutiny. All the tissue characteristics show continuous trends with changing level of reproductive effort.

Comparison of the gonad characteristics associated with fish with high and low relative body weight also show that fish in better condition have large gonads (Table 29). Constituent analyses of the gonad data was less complete than that of the soma, but do indicate that body condition affects gonad quality. Fish in better condition had gonads with significantly ($P < .05$) lower water and ash content and a higher concentration of calories.

Analysis of the age data indicated that fish that were longer than the average length-at-age had higher relative reproductive effort and were in better condition. The estimated dry gonad weight of a fish that was large for its age was 23% greater than that of a slower growing fish (based on comparison of fish of similar lengths (Table 30)). The relative dry body weights were also usually higher for fast growing fish, although the magnitude of the differences changed with size since both the slope and intercept terms were significantly different (Table 30).

Consideration of the average body constituents of fish stratified by relative length within ages suggested a similar conclusion (Table 31, that is, within each age, fish were distinguished as being either longer or shorter than expected). The dry gonad somatic index (DGSI) was higher in the faster growing fish in 7 out of 9 age classes. Lipid concentration was always higher and ash content always lower in fast

Table 29. Estimated coefficients for the gonad weight-length functions (Gwgt = $aLgth^b$, dry or wet as indicated) for English sole, herring, Pacific cod and dogfish with high and low relative body weights. P_1 and P_2 are probabilities associated with the partial F-tests for entry of intercept and slope terms (in that order) into the log-linear regression models. Also shown are fitted values for fish of 3 representative lengths.

Body condition	a	b	Length classes (mm)			P_1	P_2
English sole:							
	Dry gonad weight		300	375	450		
High	1.4419×10^{-9}	3.979	10.4	25.2	52.0	.003	.226
Low	1.1715×10^{-9}	3.979	8.2	20.5	42.3		
Herring 82:							
	Wet gonad weight		150	200	250		
High	2.5027×10^{-9}	4.325	6.5	22.4	58.8	.222	.963
Low	2.7196×10^{-9}	4.325	7.0	24.3	63.9		
Herring 84:							
	Wet gonad weight		150	200	250		
High	9.7589×10^{-10}	4.536	7.2	26.7	73.3	.664	.390
Low	9.6127×10^{10}	4.536	7.1	26.3	72.2		
Pacific cod:							
	Wet gonad weight		600	800	1000		
High	2.1412×10^{-9}	4.008	291	922	2255	.020	.541
Low	2.0210×10^{-9}	4.008	275	870	2128		
Dogfish:							
	Wet gonad weight		950	1050	1150		
High	3.8521×10^{-9}	3.659	302	436	608	.000	.020
Low	6.3183×10^{-9}	2.576	296	383	484		

Table 30. Estimated coefficients for the dry gonad weight-length and dry body weight-length functions (dry weight = aLgth^b) for English sole stratified (big/small) by length at age. P_1 and P_2 are probabilities associated with the partial F-tests for entry of intercept and slope terms (in that order) into the log-linear regression models. Also shown are fitted values for fish of three representative lengths.

Relative size	a	b	Length classes (mm)			P_1	P_2
English sole:							
	Dry gonad weight		300	375	450		
Large	$4.0662X10^{-8}$	3.421	12.1	25.9	48.4	.025	.797
Small	$3.3105X10^{-8}$	3.421	9.8	21.1	39.4		
	Dry body weight		300	375	450		
Large	$7.1804X10^{-8}$	3.530	39.8	87.6	166.7	.011	.015
Small	$1.2778X10^{-5}$	2.646	45.7	82.5	133.7		

Table 31. Average dry gonad somatic tissue index (DGSI) and body constituent characteristics of English sole stratified by length at age. Sample sizes of each cell shown at bottom.

Parameter	Relative size	Age									
		3	4	5	6	7	8	9	10	11	12
DGSI	Large	.400	.241	.301	.301	.303	.286	.357	.241	.276	.211
	Small	.228	.147	.259	.284	.212	-	.221	.314	.213	.368
BCAL	Large	5085	4905	5094	4931	5220	4779	4849	4670	4972	4421
	Small	4551	4880	4991	4981	4846	-	5113	4178	4886	4001
BASH	Large	14.5	14.0	13.8	13.7	12.7	15.0	13.8	14.5	14.3	18.7
	Small	18.5	17.3	14.6	14.9	15.1	-	13.9	20.2	15.9	19.1
BLP	Large	19.9	13.8	16.7	17.3	19.9	12.3	21.3	12.6	15.8	11.3
	Small	11.3	11.8	15.5	16.6	14.5	-	19.8	7.7	14.0	3.6
BPR	Large	64.1	69.9	67.5	68.5	64.5	69.7	64.4	68.9	69.3	69.3
	Small	68.0	66.9	67.8	66.0	66.0	-	63.3	72.6	66.7	70.1
Sample size	Large	1	3	11	11	6	7	1	2	3	2
	Small	2	1	13	14	8	0	2	1	5	1

growing fish. Body calorie content was higher in 7 out of the 9 age classes of fish with higher growth rates. The body protein data gave mixed results. These data are therefore consistent in suggesting that faster growing fish are in better physical shape and have higher relative reproductive effort.

Herring. In contrast to the English sole, the results of the herring analyses were either nonsignificant or tended to suggest that body condition and reproductive effort were inversely correlated. The comparative analysis of the body weight versus length data for fish with high and low relative reproductive effort in 1982 indicated that fish with higher gonad weights tended to have lower relative body weights (Table 27). There were no significant differences in the limited information on body constituents (Table 32), and no additional indication of an inverse association in the 1984 data (Table 27).

The paired gonad weight-length regressions associated with high and low body weight were not significantly different in 1982 or 1984, although the trend in the 1982 data was in accord with the inverse association noted above (Table 29). Comparison of the mean gonad somatic indices for fish with high and low body weights does indicate that fish with higher body weight have lower reproductive effort ($P = .001$, Table 32). This might be expected based simply on the fact that body weights were higher, but it is in direct contrast to the parallel analysis for English sole and supports the previous conclusion that condition and reproductive effort are inversely correlated in herring.

Table 32. The body constituent characteristics of Pacific herring stratified by relative gonad weight and the gonad constituent characteristics derived by stratification by relative body weight. P values are the probabilities associated with ANOVA F test.

	1982			1984		
	High	Low	p	High	Low	p
			Stratified by Gwgt			
BDRY	27.5	28.5	.421	23.6	24.4	.291
BASH	9.1	9.2	.859	11.6	11.5	.837
BCAL	5818	5667	.369	5124	5130	.936
			Stratified by Bwgt			
GDRY	27.9	26.4	.092			
GASH	7.6	8.3	.497			
GCAL	5629	5679	.175			
GSI	.219	.279	.001			
DGSI	.228	.290	.121			

Pacific Cod. Pacific cod displayed weak or nonsignificant positive associations between body condition and reproductive effort. Comparison of the body weight regressions which resulted from sorting on gonad weight were nonsignificant (Table 27). The gonad weight data, however, did indicate that fish in better condition had higher gonad weights (Table 29).

Dogfish. Analysis of the dogfish data showed strong and highly significant effects. Both methods of comparison indicated that fish in better condition have higher reproductive effort (Tables 27 and 29).

Discussion

The above analysis suggests that the reproductive strategies of English sole, dogfish and perhaps cod are different from that of the herring. The differences observed in the English sole and dogfish data were highly significant, while those for cod were merely suggestive of a pattern similar to that of the other 2 species. Stratification of the English sole data by length using either gonad weight or body weight as a sorting factor clearly indicated that fish with large gonads were in better condition. In general, condition can be defined in terms of higher relative body weight. For English sole, however, it was possible to further demonstrate that those fish with the very highest relative reproductive effort were also in peak condition as measured by body calorie content or any of the proximate components except protein.

The proximate components, when analyzed in terms of percent composition as was done here, can be expected to vary in parallel. If lipid content goes up, percent content of ash and protein should go down. As a result, any one of the parameters can be used as an indicator of condition. It therefore should not be surprising that the components do vary in parallel, but it is significant that all of the indicators are consistent in giving the same result.

The body weight-length stratification analysis also led to the conclusions that fish in better condition had larger gonads. Although this parallel analysis of the same data (stratify by gonad weight or body weight and then analyze differences between body weight or gonad weight, respectively) is redundant to some degree, it is not always the case that both analyses give significant results. Both cod and herring provide examples where one of the analyses was significant, but the converse was not. I interpret the fact that both tests led to similar conclusions as an internally consistent, and therefore more highly significant result.

Stratification using the body weight-length data and analysis of gonad proximate components (Table 28) led to the conclusion that English sole in better condition had qualitatively different gonads. Sample sizes were relatively small for this analysis, but the indication was that fish in better condition had gonads with lower water and ash content and higher calorie levels. The gonad lipid levels were inexplicably lower in the fish with better condition, although the associated statistical probabilities were marginal. Proteins were not statistically different, but only 7 gonads were analyzed for protein content.

A number of other investigators have also found that body condition and feeding rate can affect egg quality (Bagenal 1969; Ponomarenko, V.

P. 1967; Nikolskii 1969; Ponomarenko, I. Ya. 1973; Graumann 1973; Ayles 1974; Tyler and Dunn 1976; Wootten 1977; Hislop et al. 1978; Woodhead 1979). The results related to English sole, therefore, are a further confirmation of the previously stated results concerning the relation between condition and reproductive effort.

Consideration of the characteristics of English sole that were either large or small for their particular age were perhaps more unexpected. The general conclusion was that faster growing fish are in better condition and have larger gonads, even when compared with fish of similar length (Table 30 and 31). Another way to state the same finding is that, in general, fish of a given length that are in better condition and have larger gonads are younger than those that are apparently less well off.

The results of these analyses, particularly those of English sole, suggest that much of the observed variability in the production characteristics of similar fish occurs because fish are unequal in terms of their ability to obtain and process food. An alternative explanation is that fish are basically similar but that annual rations differ due to random variation in prey encounter. This could explain the variation between individuals without having to invoke the suggestion of inherited dissimilarities. However, if random variation in prey encounter were the only factor involved, then I would not expect to see an association between higher reproductive effort, better condition and lower age. Instead, differences between years would average out and the age differences would not exist.

The premise of my argument is that variability in production characteristics occur because of differences in assimilated energy, and that assimilated energy varies because of inherited differences in competitive ability and/or metabolic efficiency. Competitive differences could result from disparities in sensory acuity or learning ability, or because of dominance hierarchies in competitive interactions.

It has been clearly demonstrated in the literature that both reproduction and growth can be regulated by food availability. Studies demonstrating the effects of food supply on reproduction have been conducted both in the laboratory (guppies, Hester 1969; rainbow trout, Scott 1962; brown trout, Bagenal 1969; winter flounder, Tyler and Dunn 1976; haddock, Hislop et al. 1978) and in the field (herring, Anokhina 1960; brook trout, Vladykov 1956; Wydoski and Cooper 1966; plaice, Bagenal 1957, 1966; lake trout, Martin 1970). The literature also provides numerous examples of changes in somatic growth rates that are interpreted as being caused by changes in relative food abundance (North Sea herring, Cushing and Bridger 1966; and Burd 1985; American plaice, Pitt 1975; North Sea sole, DeVeen 1976; North sea haddock, Jones 1983; Gulf of St Lawrence herring, Winters 1976; juvenile sockeye salmon, Hyatt and Stockner 1985; menhaden, Reish et al. 1985; Pacific halibut, Schmitt and Skud 1978). These often are reported under the general heading of density-dependent phenomena.

The more detailed laboratory work of Tyler and Dunn (1976) has shown that both reproduction and condition (or growth) increase in fish given a higher ration. Bagenal (1957a, 1966) came to a similar conclusion based on a correlation analysis of field-caught animals. These results-are in accord with my own findings concerning English sole.

Additional experiments clearly demonstrate how competitive interactions accentuate differences in growth characteristics. Grosse (1982) showed that competitive hierarchies developed within all feeding treatments during artificial rearing experiments on ling cod (Ophiodon elongatus). The result of these hierarchies was that the variation in size within a given treatment increased with time and ration level. Such growth disparities are apparently quite common in artificial rearing and hatchery settings. They have been noted for brown trout (Brown 1946), plaice and sole (Purdom 1974), medaka (Magnuson 1962), sunfish (Allee et al. 1948), European eels (Peters et al. 1980), and zebra danio (Eaton and Farlye 1974). There is some debate whether the disparities in size are caused by genetic or behavioral differences (Grosse 1982), but this seems a moot point since behavioral dissimilarities are probably inherited.

Grosse (1982) discusses 2 types of response to changes in food availability. When food is limiting, all fish show competitive dissimilarities and thus differences in growth. When food is in excess, the territorial, non-schooling fish show even greater growth disparities (as did lingcod), whereas in other fishes such as the medaka, aggressive behavior and growth variations are reduced or eliminated. These results suggest that food limiting conditions in natural populations may be indicated by decreased growth rates and by increased variability in size at age. --

A final mechanism that could contribute to the observed disparity in production characteristics among similar fish is inherited differences in metabolic efficiency. A slight advantage in any of the metabolic functions (e.g., higher assimilation efficiency and low standard metabolic rate) would mean that the advantaged individual would have more energy available for production from a given amount of food consumed.

The suggestion that inherited dissimilarities explain the difference in growth characteristics is consistent with the English sole data. The individuals that are inherently superior have higher reproductive effort and higher growth rates. They are also large for their age and in better condition.

Consideration of the dogfish data, and to a lesser degree the cod data, suggest a similar result. However, I have no age data for these species and therefore cannot conclude that the variation between similar individuals is regulated by the same mechanism suggested for English sole.

Analysis of the herring data indicate that herring may have a very different strategy of energy allocation compared to English sole and perhaps dogfish and cod. The analysis also suggests that the mechanism controlling variation between similar individuals in English sole may not be universally applicable to all species.

Inherited dissimilarities between individuals must be common to all species and therefore will always explain a portion of the observed variability. However, the magnitude of the variability will also be affected by species-specific strategies of response to varying levels of food. Some strategies may tend to reduce the variability between individuals while others will accentuate it.

Roff (1982), Tyler and Dunn (1976) and Hislop et al. (1978) all discuss strategic options for dealing with a limited food supply. The suggestions include 1) maintaining reproductive effort at the expense of growth and/or condition; 2) maintaining growth rates at the expense of current reproduction; and 3) allocating energy to both growth and reproduction in proportion to the available food. Other variations which differ in degree of response could also be suggested. The variability in length-specific reproductive effort will be reduced by the first strategy, exaggerated by the second, and unaffected by the third.

Changes in Growth and Reproduction with Size and Age

Introduction

One reason for the analysis of size- and age-dependent differences is the concern that if natural mortality is modeled as a constant rate, and if reproductive effort varies with size, then some objective criteria must be used to select a representative size for each species. Although an objective selection criterion is used (average size of a mature female), it will be useful to understand how reproductive effort varies with size. This will allow me to evaluate the potential biases in the between species comparisons.

In the remainder of this section I consider how reproductive effort, physical condition, and natural mortality are related, and in particular how they change with size and age. A specific question that is addressed is whether reproductive effort could be used to develop more refined estimates of intraspecific, age-dependent mortality. A necessary assumption of this approach for analyzing age-dependent mortality is that reproductive effort and physical condition are directly related. A second objective is, therefore, to evaluate this important assumption.

Natural mortality is usually modeled as a constant rate. Sometimes this is appropriate or at least sufficient for the underlying model, but often constant mortality rate is simply the most reasonable approximation given the available data. With more extensive data sets it is possible to estimate age-specific mortality rates and in general, it is found that mortality increases with age, beginning at some point following sexual maturity (i.e., Ricker 1949; Wohlschlag 1954; Kennedy 1954; Tester 1955; Beverton and Holt 1959; Mann 1973; Wespestad and Fried 1983).

Ware (1982a,b) specifically related mortality to reproductive effort in his energetics model. He modeled mortality as an increasing exponential function of the proportion of surplus energy allocated to reproduction. Myers and Doyle (1983) also found that a convex reproduction-mortality function was one of two conditions sufficient to stabilize their age specific population model. They note, however, that there is "unfortunately, no evidence to suggest what shape the curve of mortality as a function of the proportion of surplus energy allocated to reproduction might take." Williams (1966), Jones and Johnston (1977), and Ware (1982) also indicate there is a need for more study of the relation between mortality and reproductive effort.

One of the arguments used to explain increasing age-specific mortality concerns the mechanistic relationship between reproduction, somatic depletion, and mortality. The presumed mechanism is that higher reproductive effort leads to increased somatic depletion. It is suggested that older fish typically have higher relative reproductive effort, are more depleted after spawning, take longer to recover, and therefore experience increased mortality rates due to disease and predation (Orton 1929; Templeman and Andrews 1956; Gerking 1959; MacKinnon 1972; Jones and Johnston 1977; Woodhead 1979; Mann and Mills 1979; Bell 1980; and Roff 1982). If we can clearly establish that reproduction is related to physical condition, then perhaps measures of relative reproductive effort (which are easily obtained) might lead to more refined estimates of age-dependent mortality rates.

There are a number of studies that have considered the processes which relate reproduction to physical condition (Shevchenko 1972; MacKinnon 1972; Dawson and Grimm 1980; Tyler and Dunn 1976; Hunter and Leong 1981). However, each of the studies focuses on fish within a representative size class. As a result, the functional relation between size-specific reproduction, body condition, and natural mortality remains unclear. It is therefore my intention within this section to consider the relationships between these parameters.

Methods

The size- and age-dependent trends in reproductive effort and somatic depletion were analyzed using the English sole and herring data collected during the course of this study. All data and analysis techniques used here have been described previously.

Results

Consideration of the English sole data indicates that relative reproductive effort does increase with size. The exponent of the power function relating dry gonad weight to length is greater than the exponent of the dry weight-length function (3.942 vs. 3.249, $Z = 2.149$, $.01 < P < .05$)

The change with age of the relative importance of reproduction as a proportion of overall net production can also be demonstrated by comparing estimates of age-dependent gonad weight and the annual somatic growth increment. Age-dependent gonad weight was derived by combining the dry gonad-length and age-length functions.

$$\text{DGwgt} = 1.6596 \times 10^{-9}\ \text{Lgth}^{3.941}$$

$$\text{Lgth} = 485.09[1-e^{-.1712(t+3.320)}]$$

The annual somatic growth increment was calculated by differentiating the weight-at-age function and evaluating the result at each age.

$$\text{DBwgt} = 200.9(1-e^{-.1712(t+3.320)})^{3.249}$$

$$d(\text{DBwgt})/dt = 652.8[1-e^{-.1712(t+3.320)}]^{2.249}[.1712e^{-.1712(t+3.320)}]$$

The sum of the 2 estimates gives annual net production (Figure 30, Table 33), which conceptually is equivalent to Ware's (1980) surplus energy parameter, although it is calculated in a different way.

The point of the analysis is that once English sole reach maturity, reproduction very quickly becomes the dominant component of an individual's annual production. When English sole first mature at an age of about 4 years (Van Cleve and El-Sayed 1969), they put half of their surplus production into gonad development. In the older age classes 10% or less of annual surplus production is utilized for somatic growth. What these analyses demonstrate is that on the average, there is 1) an increase in relative reproductive effort with age, and 2) a dramatic shift in the emphasis of gonad and somatic production.

Analyses of various condition indicators along a size or age gradient indicated that there was a great deal of variability in the data. The anticipated trends were not as evident as I had expected from the above consideration of average changes with age. Simple regression analysis of body calorie content and proximate components using individual data points failed to show any significant trends. When the data were averaged by age- or size-class, general trends did become evident. If we ignore the earliest ages for the present, body calorie content does show a general decreasing trend (Figure 31). Older fish have a lower calorie content per gram dry weight. This holds true even after correcting for ash content. The condition index data (where CI = $[(\text{Bwgt} \times \text{BDRY})/(\text{Lgth}^{3.308})] \times 10^6$, and 3.308 is the exponent of the dry body weight-length relationship) show a similar decline when averaged by

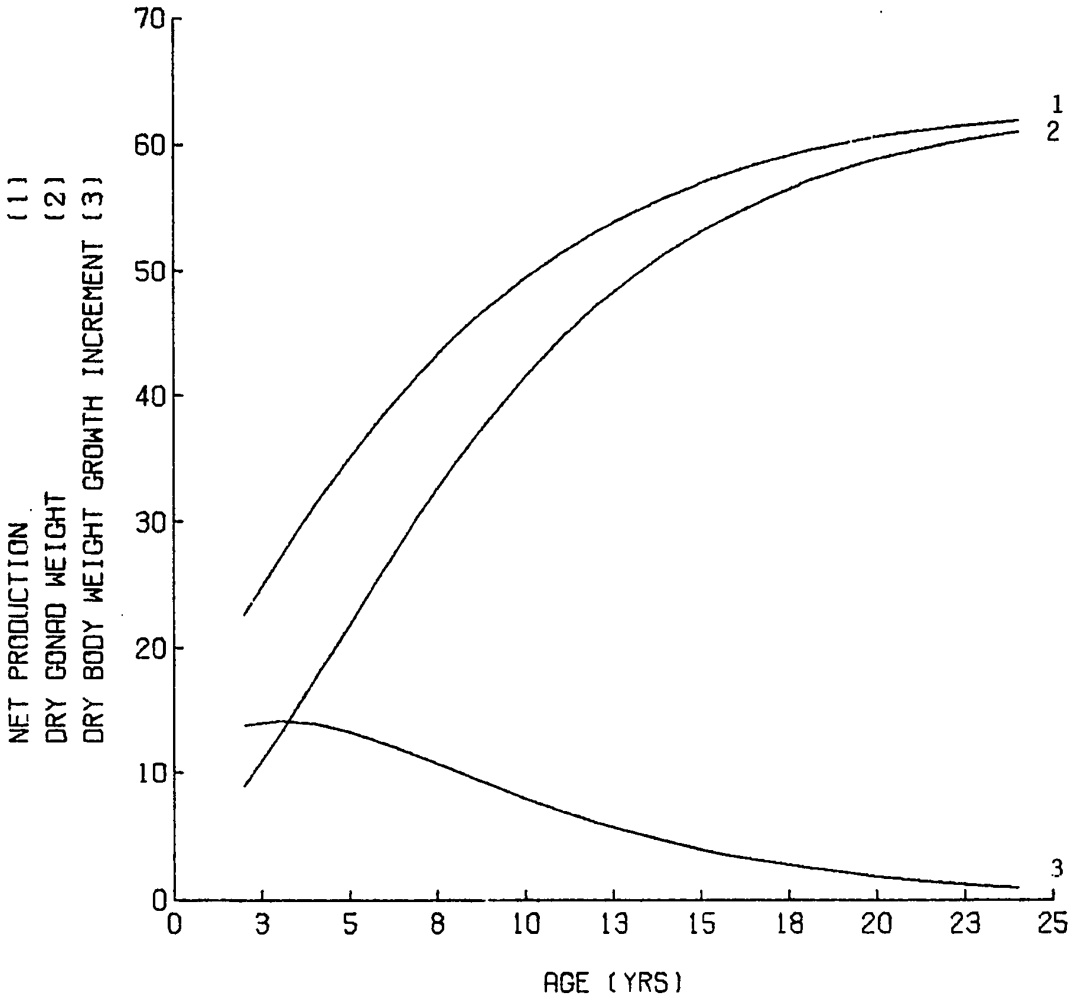


Fig. 30. Net production (in g, 1 = 2 + 3), dry gonad weight (2) and dry body weight growth increment (3) versus age for English sole.

Table 33. Age and length specific gonad and somatic growth increments for English sole.

Age	L	DGwgt	DBwgt	DBwgt	Net Production	Gonad: % NP
2	294 mm	8.87 g	41.52 g	13.77 g	22.64 g	.392
3	324	12.94	55.54	14.14	27.08	.478
4	349	17.34	69.60	13.89	31.23	.555
5	370	21.85	83.18	13.23	35.08	.623
6	388	26.30	95.96	12.29	38.59	.682
7	403	30.56	107.72	11.22	41.78	.731
8	416	34.54	118.38	10.10	44.64	.774
9	427	38.19	127.92	8.98	47.17	.810
10	436	41.50	136.37	7.92	49.42	.840
11	443	44.44	143.79	6.93	51.37	.865
12	450	47.06	150.26	6.03	53.09	.886
13	455	49.35	155.88	5.22	54.57	.904
14	460	51.35	160.73	4.50	55.85	.919
15	464	53.09	164.91	3.87	56.96	.932
16	467	54.59	168.49	3.31	57.90	.943
17	470	55.89	171.56	2.83	58.72	.952
18	472	57.00	174.18	2.42	59.42	.959
19	474	57.95	176.42	2.06	60.01	.966
20	476	58.76	178.32	1.75	60.51	.971
21	477	59.45	179.94	1.49	60.94	.976
22	478	60.04	181.31	1.26	61.30	.979
23	479	60.54	182.48	1.07	61.61	.983
24	480	60.97	183.46	.91	61.88	.985

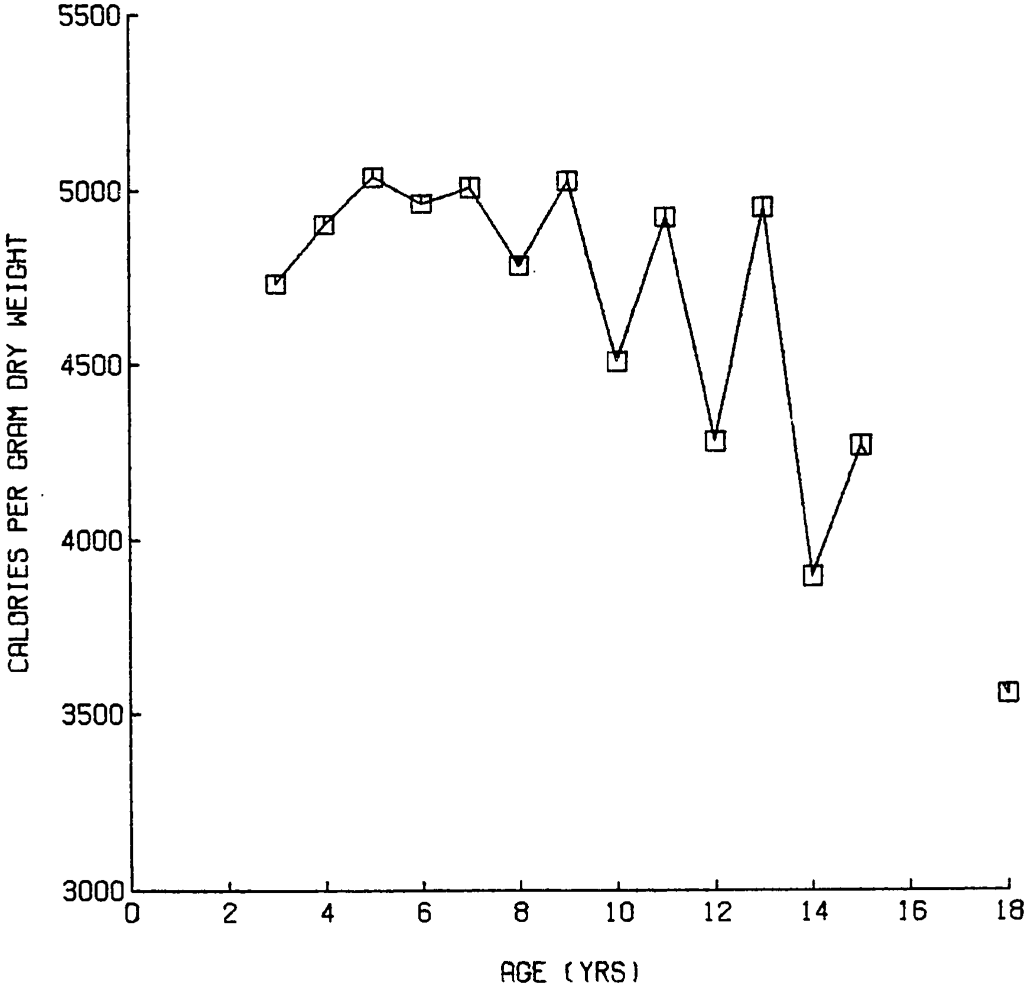


Fig. 31. Body calorie content versus age plot for ripe English sole.

age-class (Figure 32). Trends in other body constituents only became evident after the data were aggregated into 4 size-classes or age ranges (Tables 34 and 35).

One probable reason why the expected age-dependent trends were not more evident was that I was unable to obtain many truly old fish. In the absence of fishing and assuming a constant natural mortality rate of .26, about 4% of the fish in a sample should be 12 years of age or older. However, despite sorting through literally tons of fish and specifically looking for large individuals, only seven 12+ fish were collected during the spawning season and 3 of those were spent. This obviously is a consequence of the fact that English sole in this area have been fished heavily for decades. As a result, old fish are simply no longer part of the population.

Comparison of the condition of the oldest fish in the sample with those that are presumably in peak condition (5-year-olds, for example) confirm that the expected size and age trends in condition do occur. The average condition index of 5-year-olds was .270 (N = 24, S = .0499) compared to a value of .214 (n = 7, S = .0488) for 12+ fish. These values are statistically different ($P \leq .01$).

Similar comparisons of the body calorie data for age 5 and 12+ fish also show significant differences (5039 vs. 4215 cal/g dw, $P \leq .001$). These results suggest that despite the considerable variability within age-classes (noted in the previous section) English sole do show a trend of reduced condition with age.

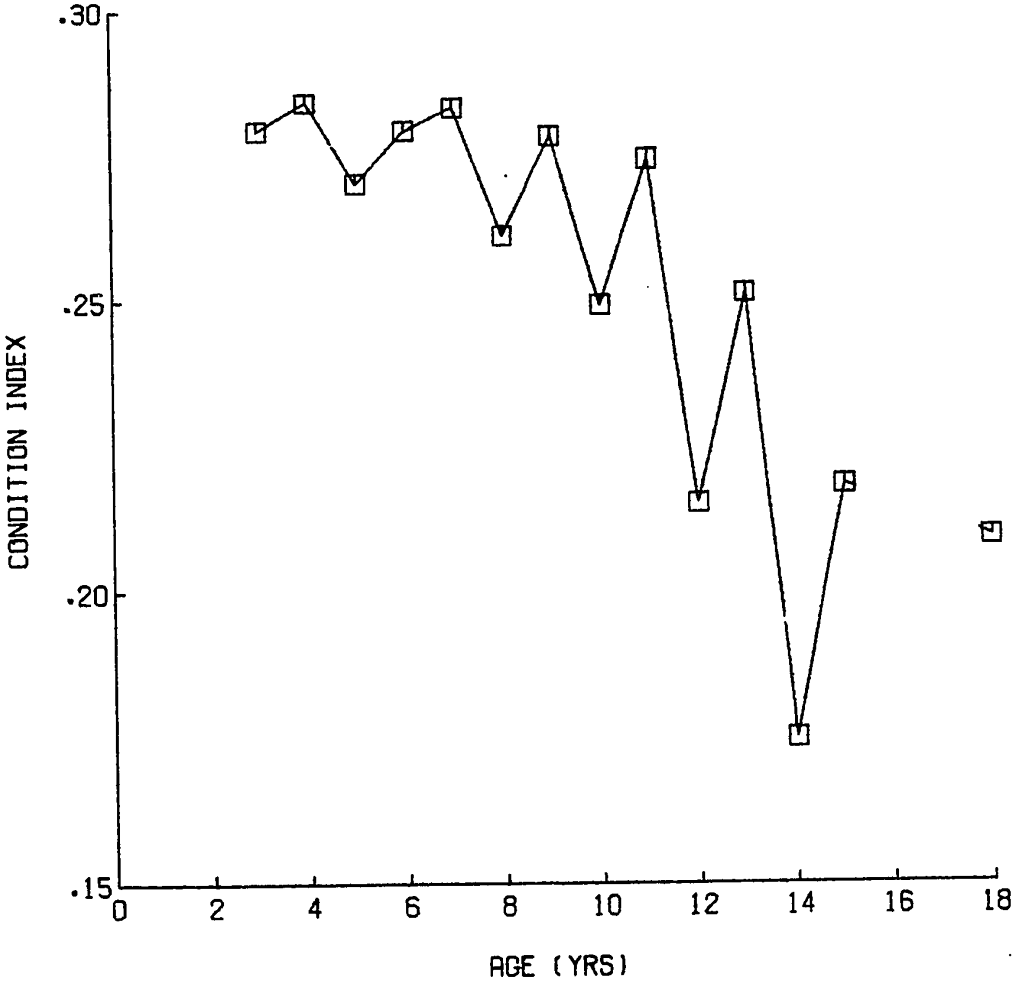


Fig. 32. Condition index [(Dry Bwgt/Lgth$^{3.308}$) x 10^{6}] versus age plot for ripe English sole.

Table 34. Average body constituent composition for four length classes of English sole. P is probability associated with ANOVA F-test of between group means.

Parameter	Length class				
	≤350 mm	350-400	400-450	>450	p
BCAL (cal/g dw)	4864	5005	4914	4658	.050
BDRY (%)	21.0	22.1	21.7	21.1	.277
BASH (%)	15.8	14.3	14.2	16.2	.023
BLP (%)	14.0	16.7	15.2	13.3	.232
BPR (%)	67.6	66.3	68.4	68.9	.098

Table 35. Average body constituent composition for four age classes of English sole. P is probability associated with ANOVA F-test of between group means. Lines show significant differences between means as determined by SNK multiple range test.

	Age class				
Parameter	≤4	5-8	9-12	>12	p
BCAL (cal/g dw)	4859	4978	4752	4165	.000
BDRY (%)	21.9	21.8	21.2	18.3	.019
BASH (%)	15.4	14.3	15.9	18.3	.001
BLP (%)	14.1	16.1	14.0	7.1	.022
BPR (%)	68.1	67.2	67.7	72.4	.085

One complicating feature of the data is the suggestion that size- or age-dependent trends are probably not monotonic. That is, young/ small fish seem to be qualitatively less well off than fish that are just a bit older (Figure 31, Tables 34 and 35). Additional support for this conclusion was found in the limited sample of ripe fish taken during the 1983 spawning season which contained only small to mid-size fish. Seventeen fish were analyzed from the 1983 samples ranging in size from 275-391 mm. Only 2 were greater than 370 mm, the estimated size of a 5-year-old (these fish were not aged). Consideration of the data shows that water and ash content decreased with body weight (BDRY r = .627, p = .007; BASH r = .596, p = .012) while body calorie content was significantly higher in larger fish (BCAL r = .726, p = .001). Each of these relationships suggests that the physical condition of the smallest fish is less than that of fish that are in the small- to mid-size range.

The smaller fish were probably spawning for the first time. It is apparent that the early recruits are either more adversely affected by or less prepared for their spawning activity. Fish in these younger age groups are in a phase of their life history where somatic growth is of primary importance. Fat accumulation as an energy storage product is of secondary importance. The younger fish that do spawn may be those that are at least marginal in terms of their accumulated fat stores, whereas other members of the cohort are not. However, the combined stress of gonad development and the fall/winter fast is apparently excessive relative to fish that are older and more prepared for seasonal energy demands.

Roff (1982) has suggested that one of the mechanisms that determines age of first reproduction in flatfishes is a physiological lower limit which sets the bounds on early reproduction. Consideration of the English sole data suggests that the limiting factor may be the ability of young fish to grow and accumulate sufficient lipid reserves to meet the demands of reproduction. Those that spawn too early could be selected against because of the associated increase in mortality rates.

The second complicating factor in the data is the suggestion of a biannual cycle in body condition. If allowances are made for the youngest ages, the data show that both body calorie content and condition alternate from high to low through at least 4 1/2 complete cycles (Figures 31 and 32). However, this result must be considered an unlikely coincidence since it is difficult to conceive of any mechanism that would result in such a pattern. Biannual cycles are not unusual, but are generally the result of an alternating pattern between years (e.g., pink salmon). In this case however, the suggestion is that within a year all even aged fish cycle in unison and out of phase with odd aged fish. In order for this to occur, it would be necessary that each cohort become fixed into the cycle and maintained in phase throughout its lifetime. It is more reasonable to believe that the observed pattern has occurred by chance. The observed fluctuations, therefore, are best viewed as part of the inherent variability between age-groups.

Herring show an even greater increase in relative gonad weight than English sole. The exponent of the gonad weight-length function (B =

4.353) was significantly higher than that of the body weight-length function ($B = -2.796$, $Z = 4.660$, $p < .001$).

The body calorie content data of the 1982 fish strongly suggest that larger fish are increasingly depleted (Figure 33). The estimated calorie content values for fish that were 150 and 250 mm in length are 6063 and 5371 cal/g dw, respectively. Water content as indicated by the estimates of percent dry matter showed a weak but significant increasing trend with size ($r = -.339$, $p < .10$, $n = 25$) again suggesting a decline in body condition.

Analysis of the 1984 body calorie content data indicated a weak and barely significant ($p = .055$) decline with size (Figure 33) but as will be discussed in the next section, it appears that all of the 1984 fish were depleted relative to those examined in 1982.

Characteristics of the herring gonads also changed with size. The dry weight of individual eggs was related to length by the function

$$\mathrm{DEwgt} = .01385 + .00081\ (\mathrm{Lgth}) \qquad r = .611 \qquad p = .000 \qquad n = 101$$

indicating that egg weight increased by 60% over the size range from 150-250 mm. Gonad calorie content also increased with size.

$$\mathrm{GCAL} = 5389.4 + 1.329\ (\mathrm{Lgth}) \qquad r = .594 \qquad p = .002 \qquad n = 25$$

although the predicted increase over the above mentioned size range was only about 130 cal/g dw.

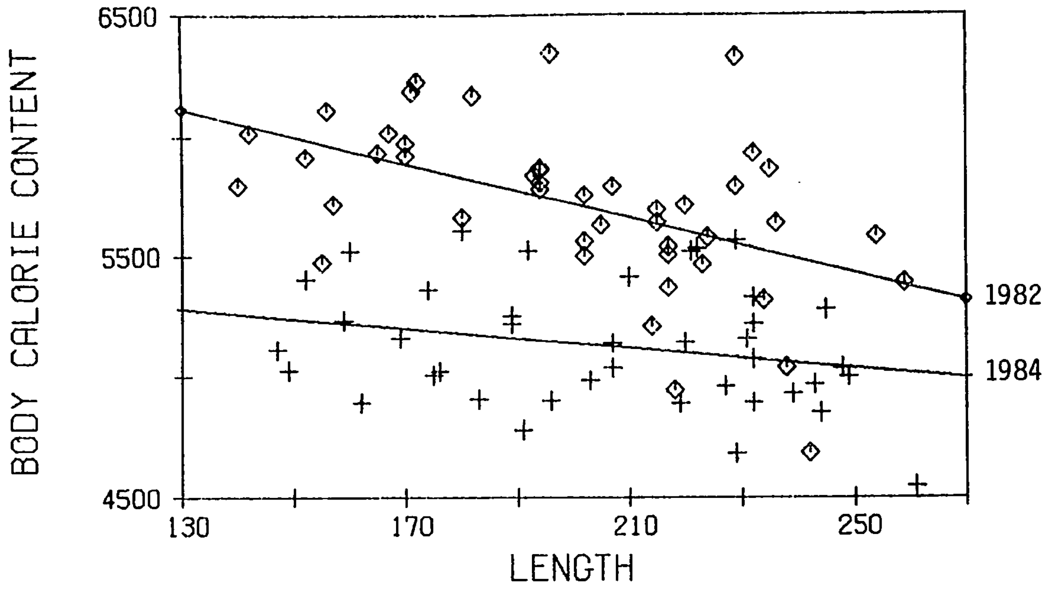


Fig. 33. Body calorie content versus length (mm) for herring sampled in 1982 and 1984.

Discussion

One of the reasons for the analysis of size- and age-dependent differences was the concern that size effects could obscure potential differences between species in the interspecific WGSI versus M analysis. It is important that we compare the relative reproductive effort estimates for fish that are in comparable phases of their life histories. I chose to use average size of a mature female as the size selection criterion 1) because it could be applied objectively and 2) because it had biological meaning in that it incorporated both the age of maturity and the natural mortality rate estimates. The selection criterion is intuitively appealing, but there is no way to determine whether it leads to the selection of fish that are comparable in terms of all appropriate life history characters. It is possible however to evaluate the potential error by examining how much the reproductive effort indices vary with size for different species.

What is of concern is how much the gonad-somatic tissue indices could vary over a reasonable size range. The reproductive effort indices were calculated by inserting a selected length value into gonad weight-length and body weight-length functions and calculating a ratio. The change in reproductive effort with length therefore depends on the relative magnitude of the exponents of these power functions. If the exponents are equal, reproductive effort does not change with size. If the gonad weight-length exponent is larger, then relative reproductive effort increases with size.

Comparison of the estimated exponents for some of the species considered during this study (Table 36) indicate that for dogfish and English sole, errors in size selection will not appreciably affect the estimates whereas for herring they could. For English sole the estimated WGSI values for the 380-400 mm size range (selected representative size ± 10 cm) is .164-.169. The WGSI values for a 20 mm size range of herring (209 ± 10 cm) however are .227-.265. Herring probably represent an extreme case (i.e., the exponents are very different) but the results do suggest that representative sizes should not be selected arbitrarily and could have some effect on the estimates.

A second reason for considering size-dependent effects was to evaluate the presumed mechanistic link between reproductive effort, somatic depletion and size or age, and to consider whether some measure of reproductive effort or condition might serve as a scaling parameter for estimating size-dependent mortality rates. Both the English sole and herring data confirm the suggestion that older/larger fish are in poorer condition and that there is a coincidental increase in relative reproductive effort. However, correlation does not establish causation. It is still appropriate to consider whether reproductive effort is the cause of reduced body condition via the mechanism of somatic depletion.

The results of the previous section clearly demonstrate that the fish with the highest reproductive effort were those in peak condition. The feeding experiments of Tyler and Dunn (1976) also showed that the fish that ate more were more fecund and in better condition. Their results were confirmed in the field when they found that fish in better

Table 36. Gonad weight-length and body weight-length exponents of selected species.

	Gwgt	Bwgt
Dogfish	3.197	3.016
English sole	3.941	3.294
Cod	3.718	2.833
Herring	4.452	2.844

condition also had higher reproductive effort, just as was the case for English sole. Similar observations have been made by Hirshfield (1980) and by Bagenal (1957a) who stated that "there is no evidence of the more fecund fish being in poorer condition."

A clarification of some terminology may be of some value at this point. The supposition is that reproductive effort is related to somatic depletion. This is in fact a matter of definition. Somatic depletion is a seasonal phenomenon experienced by all mature fish whereby somatic energy is transferred to the gonad and used for maintenance during gonad development. Most fish are at the bottom of their annual condition cycles after spawning and are, therefore, presumed to be most susceptible to the proximate causes of mortality. In this sense, reproduction leads to somatic depletion and increased mortality. But somatic depletion is something that occurs in all spawning fish and does not necessarily reflect the comparative well being of different fish.

The pertinent measures of a fishes' susceptibility to mortality are measures of physical condition such as condition indices, proximate composition or calorie content. It is apparent from the results of the analysis that body condition does decline with age. However, whether these averaged trends are directly related to reproductive activity is unclear. It is possible that, on the average, older fish do utilize a greater relative proportion of all somatic energy during gonad development. But it also may be that the effects are less direct. Perhaps the decline in condition of older fish is the result of the cumulative effects of years of reproductive activity or other senescent phenomena that are not adequately understood.

One of my original objectives in this section was to consider whether measures of reproductive effort could be used to scale age dependent estimates of M. A prerequisite of this approach was that I be able to demonstrate the causal relationship between reproductive effort and condition, which I have been unable to do. However, it may be unimportant whether physical condition and reproductive effort are causally related. My own data clearly show that condition does decline with age. If we assume that reduced condition leads to higher mortality, then measures of condition rather than reproductive effort could be used to scale age-specific mortality rates for a given species or stock. This then brings us back to the critical assumption: is physical condition directly related to mortality? It certainly has intuitive appeal and is a pervasive suggestion in the literature.

Roff (1982) provides a good review of the relationship between physical condition and potential mortality. He concludes that stress due to starvation or depletion undoubtedly increases a fishes' susceptibility to disease, predation, and adverse environmental stresses. Starved fish selectively utilize myotomal muscle which is used for burst activity and high speed cruising. Fish in poor condition would therefore be more susceptible to predation. Parasite infections lead to increased sluggishness, impaired swimming ability, increased respiration, weight loss, and death. Sublethal affects are likely to be more severe when the additional stresses of starvation and reproductive activity are introduced. Reproduction itself brings fishes into closer proximity and therefore provides an opportunity for the transmission of parasites and disease.

Unusual environmental circumstances have led to mass mortalities. Roff (1982) refers to examples where large numbers of fish have died following severe cold spells in the North Sea, Norway, Newfoundland, Maine, and Florida involving a wide variety of marine species. Fish in poor condition will be less able to adjust to physiological stresses of this type. Shulman (1960) reviewed a large volume of Russian literature which demonstrates that low fat content in fish leads to higher winter mortality. Hirshfield's (1980) laboratory studies on medaka show that the best predictors of mortality in spawning fish was weight loss and the proportion of consumed energy allocated to reproduction. This work demonstrates that fish in poor condition die at a higher rate.

I have now suggested that both reproductive effort and condition could be used as predictors of M but at different scales of application; reproductive effort at the interspecific level and condition at the intraspecific level. Reproductive effort has value as an interspecific predictor of mortality as has been shown by the significant correlation between M and WGSI. At this level the presumed mechanism linking reproductive effort and condition (i.e., reproductive effort - somatic depletion) may be less important. Adult fish die for reasons other than those associated with physical condition. Predators obviously will take advantage of weaker fish, but predation mortality occurs throughout the year and regardless of condition.

Life history strategies involve a number of coevolved traits. It is therefore difficult to conclude that any one trait is the result of another. However, at the level of interspecific comparison, reproductive effort may be more a result of a given mortality schedule than a cause. That is, short-lived fish have evolved higher reproductive rates because predation mortality is high. Price (1974) advocated this point of view. However, it was rejected by Calow (1979) who argued that it did not provide an evolutionary reason for long-lived fish to have reduced reproductive effort. The problem with Calow's reasoning, however, is the presumption that one mechanism must explain all phenomena. Short-lived fish have few opportunities to reproduce successfully. Reproductive effort is therefore high despite the fact that individuals become partially debilitated and incur additional risk of mortality. High proportional allocation of surplus energy to reproduction would be selected for.

Longer-lived fish are more likely to have multiple spawning opportunities. As a result, it is prudent for these fish to reduce their effort enough to avoid substantial reproduction related mortality. High allocation to reproduction is therefore selected against.

I should also mention here that there are probably other important determinants of life history strategies. For example, Murphy (1968) suggested that juvenile mortality, and the variance thereof, might be a critical factor dictating reproductive schedules and mortality rates. In fact, the relative importance of different mechanisms probably varies from one species or taxonomic group to the next. However, whatever the mechanism, there is enough empirical evidence and theoretical rationale to justify the supposition that reproductive effort can be used as an interspecific predictor of natural mortality.

The second suggestion was that measures of condition be used as indicators of intraspecific mortality. Gonad somatic indices are probably not very precise indicators of reproductive effort. Hirshfield and Tinkle (1975) and Tinkle and Hadley (1975) argue on theoretical grounds that a preferred measure of reproduction would be the proportion of consumed energy allocated to reproductive activity. Unfortunately, consumption cannot be routinely measured. As a result, such measures do not offer a practical option for analysis. Fortunately, at the interspecific level, gonad somatic indices seemed to be adequate even if not ideal.

At the intraspecific level all adult fish have essentially the same mortality potential. For example, fish of similar size can all be eaten by the same suite of predators. The primary difference between fish is, therefore relative condition. Fish in poor condition are more likely to die from disease or predation than well fed fish. The original suggestion was that reproductive effort was inversely related to condition and therefore directly related to mortality. Results of previous analyses indicate that there is a coincidental increase in relative reproduction effort, and a decrease in condition with size and age. However, my work on English sole which compares fish of similar size and age, and that of Tyler and Dunn (1976) and Hirshfield (1980) suggest that GSI is more likely to be positively associated with condition than inversely as theory would suggest. At the very least this positive association within size and age groups will tend to obscure any empirical definition of the size-dependent relation between reproductive effort and condition (something I found when analyzing the data which had not been aggregated in some way).

An alternative approach is to use measures of condition directly. Condition can be determined relatively easily. Since somatic depletion is the mechanistic link which presumably relates reproduction to mortality, I suggest that the functional form of the relation between age and mortality might best be found in measures of condition. A practical way to determine age-dependent mortality rates may therefore be to scale existing estimates of M by a function defined by the changing relation between age and average condition.

CHAPTER 3.

MONITORING BETWEEN-YEAR DIFFERENCES IN GROWTH AND REPRODUCTION

Introduction

Consideration of the general topic of variability in growth and reproduction has provided a unifying theme for much of my dissertation research. As a result of this broad analysis I have come to the conclusion that between-year differences in growth, reproduction, and other biological parameters could be used in a monitoring context to provide insight into how changes in biological circumstances affect the abundance and production characteristics of commercial fish stocks. In this last chapter I therefore outline a practical method for monitoring interannual variability and discuss the benefits that would accrue from it's use.

It is generally recognized that food abundance is one of the important regulators of population size and structures--others being predation, disease, competition, and environmental phenomena. Fisheries biologists, therefore, have long been interested in developing measures of primary and secondary production that could be related to the interannual variability and long-term trends in fish stock production and abundance. Unfortunately, routine monitoring of the food supply in the ocean is impractical because of the spatial and temporal complexities of the environment, and the costs of sampling. As a result, fisheries biologists have little specific information on how and when food may act to regulate fish populations.

Large-scale fluctuations in stock abundance occur in response to detectable perturbations such as overfishing, short-term oceanographic disruptions like El Niño, or long-term changes in climatic cycles such as those noted by Cushing (1982). During these occurrences, changes in stock abundance and/or growth characteristics are often presumed to be related to food supply. However, the magnitude and extent of the effects are usually poorly understood.

Other large-scale fluctuations in fish stocks occur that are not coincident with notable events. Sometimes the changes are gradual, such as the current decreasing trend in the Strait of Georgia herring stock abundance, and sometimes the fluctuations are quite precipitous, such as those noted for a number of stocks in the Bering Sea and Gulf of Alaska during recent years (e.g., king crab, Pacific cod, pollock). Unfortunately, we can rarely explain why these shifts in abundance occur. An understanding of the net production dynamics of a stock both prior to and during such an event would be of considerable value in determining the relative importance of food as a causative factor.

Although it is not possible to sample the environment directly, it may be possible to monitor the relative food supply by analyzing the foraging success or net production of the fish. The strategy would be to allow the fish to sample the environment, and then use some particular measures of growth, reproductive effort and condition as comparative indicators of foraging success. By defining the range of variability in these net production parameters (and other biological indicators) during periods of stock stability, biologists would be in a position to interpret the role of relative food abundance both within the "steady state" and during periods of significant stock fluctuations.

The program for monitoring between-year production differences was developed as a way to measure the effects of changes in relative food abundance. It is legitimate to suggest that between-year difference in production may be related to fluctuations in temperature, or some other environmental or biological variable, but any debate about specific causes is premature until we begin to accumulate these measures of between-year variability.

I have outlined the rationale and methodology for the monitoring program using the context of relative food abundance. This was done partly because it provides a convenient framework for explaining the ideas, and partly because my own speculative bias is that fluctuations in relative food abundance are important. However, my primary concern is to convey that between-year differences can be measured, and that the associated costs are small relative to the potential benefits.

I have three objectives relating to the following discussion of the monitoring program. The first is to describe a methodology for monitoring interannual variability in the relative food abundance of commercial fishes. The second objective is to evaluate two important questions. If these measures of interannual variability are to be of any value, it is necessary to establish 1) that between-year differences in the production parameters can be measured, and 2) that the differences have biological meaning. The final objective is to demonstrate how these production indicators could be used in conjunction with other biological information to analyze how and why changes occur in the size, structure and growth characteristics of populations. This is done by applying the concepts of the monitoring program to a time series of herring data.

Monitoring Interannual Variability

Any monitoring program will require a long-term commitment. It is therefore essential that the necessary information be simple and inexpensive to obtain.

Most of the required information could be derived from a size stratified sample of ripe female fish. It would be necessary to measure the length, gonad weight and somatic body weight (gonad removed and gut emptied) of each fish in the sample. It would also be desirable to determine the water content of the gonad and somatic tissues of a subsample of these fish (see below). The final information requirement would be the average size-at-age of the youngest one or two age-classes that are adequately sampled by the catch.

The production indicators that will be most sensitive to changes in food abundance concern measures of relative reproductive effort and condition in adults, and somatic growth in the young. Juvenile fish put all of their available energy into somatic growth. It is therefore logical to focus attention on growth indicators (i.e., size-at-age) in young fish. Adults on the other hand, put an increasing proportion of their net surplus energy into reproduction. As an example, consideration of the generalized growth pattern and energy distribution of English sole (Fig. 30) demonstrates that even relatively young adults put 70 to 80% of their available net production energy into gonad development. Reproduction and condition in older fish would therefore be more sensitive indicators of production than those dealing with somatic growth.

The ageing of fish which is required to determine size-at-age, can be a difficult and time-consuming task. However, the job is greatly simplified if we are only interested in aging young fish. In most cases, comparison of size-frequency modes would probably be sufficient for the analysis of between-year differences in early somatic growth. Information concerning the size-at-age of older fish should not be ignored if it is available. However, estimating the average size of older fish is expensive, and therefore an impractical expectation for the purposes of routine monitoring.

The careful selection of females with fully-developed gonads is a critical requirement of the monitoring program. The selection of ripe fish is important because both the body and gonad undergo dynamic seasonal fluctuations in length-specific weight. Careful selection procedures will minimize unnecessary variability in the estimates of reproductive effort and condition.

Since the selection of fish with fully-developed gonads is so important, it is worthwhile to consider how that can best be done. Fish that are ripe and running, or that have hydrated eggs, are readily identifiable by visual inspection. However, there are two problems with using fish with hydrated eggs. First, eggs may be lost during handling. If there is any doubt about shedding, that individual should be excluded from the sample. Second, as will be discussed below, the process of hydration involves the active uptake of large quantities of water. If the water content of gonad tissues is not going to be determined, then it may be desirable to also exclude all gonads with appreciable hydration. One would thereby avoid the increased variability in gonad weight estimates associated with varying degree of hydration.

If the presence of hydration is excluded as a visual cue, then the identification of ripe fish becomes more subjective, and problems associated with inter-observer variability become a concern. This will be more of a problem with some species than others, depending on how distinct the characteristics are that differentiate developing fish from ripe ones. Some additional control can be maintained by minimizing the number of people (preferably those with some experience in staging gonads) that do the actual selection.

One practical method that can greatly increase the objectivity of the selection process is the use of an egg sizing device. The best indicator of development stage is egg diameter. It is possible to determine if the eggs within a gonad have reached a given diameter by using a piece of Nitex mesh of the appropriate size. The mesh is glued to a glove and worn on the back of the hand. After a few eggs are smeared across the Nitex, one looks to see if a single egg fills each mesh. Depending on the egg size this can sometimes be done with the unaided eye. In some cases a small hand lens may be necessary. However, the procedure is quick and applicable to field situations.

Determinations of the appropriate egg size (i.e., that which is fully developed) for a given species can be done by obtaining fish that contain some hydrated eggs. The hydration confirms that the gonads are fully developed. It is then necessary to measure the diameter of a sample of unhydrated eggs using an ocular micrometer. As an example, I determined that the diameter of fully developed, but unhydrated eggs of English sole and Pacific cod were approximately .55 and .73 mm, respectively.

There is one additional step in the processing of fish that could greatly increase the precision of the estimated production indicators. This would involve the determination of the water content of gonad and somatic tissues for at least a portion of the monitoring sample.

The water content of gonads changes considerably during egg development. In English sole, for example, percent dry matter increases with egg diameter until development is nearly complete at a size of .50-.55 mm (Fig. 25a). Percent dry matter decreases sharply once the process of hydration begins. This increase in water content during hydration can greatly effect the wet weight of a gonad. For example, an increase in gonad water content from 66 to 76% (.34 to .24 dry matter) would result in a 42% increase in the wet weight of the gonad. Since the process of hydration probably occurs over a period of several hours to a few days, variations in water content of the gonads could obscure real interannual differences.

Water content of somatic tissues is also important since it changes depending on the relative condition of the fish. As energy stores are used, they are replaced by water. As a result, wet weight data may tend to mask real differences in the length specific weight or condition of the fish. The dry weight analysis would eliminate the associated variability.

The proper procedure for analyzing somatic tissue water content involves grinding of whole fish and subsampling the homogenate. This is an unrealistic expectation for the purposes of routine monitoring. A practical alternative would be to use a standardized sample of muscle tissue excised from a particular point on the body.

There are three factors that should be considered in deciding whether a particular species and stock is appropriate for inclusion in the monitoring program. The first is the reproductive habit. Since reproductive effort would be estimated by gonad weight it is appropriate to include only those species that spawn a single batch of eggs per year.

The second consideration is cost. It is unlikely that there would be new money allocated for this program once the initial development period has been completed, particularly given the need for a long-term commitment. The objective is therefore to incorporate the monitoring program into existing management related sampling efforts with the direct participation of agency personnel. The required samples would already be available either from the management surveys or the commercial catch (i.e., no requirements for additional boat time or personnel). The only additional costs and time requirements would therefore be those associated with the selection of ripe females and the relatively simple processing of samples (much of which could be done at a later date as time permits).

A final consideration is the availability of additional biological information. Species selection already requires the existence of an ongoing management program, so some ancillary information will automatically be provided. However, the ability to interpret correctly stock responses to changing circumstances will be directly proportional to the quality of additional information concerning stock biomass, size-at-age of both young and old fish, the age frequency distribution, maturity indicators, mortality rates, environmental parameters and so on. For the time being, it would therefore be more appropriate to concentrate on the more intensively managed stock.

Some particular stocks that fit all of the above criteria include many of the localized herring stocks of the Pacific west coast, Puget Sound hake, and Gulf of Alaska pollock. Other species that could be considered where the necessary management structures are in place include Pacific cod, dogfish, sablefish, Pacific ocean perch and other rockfishes, flatfishes or salmonids.

It is important to emphasize at this point that the sampling objectives of the monitoring program are designed to quantify between-year differences in production. I have focused on these production indicators because they are important, and because they can not usually be estimated from the data of typical management related sampling programs. However, the production indicators are not meant to be used alone. Instead, the analysis of interannual variability should include consideration of all other biological information that may be available. Data collection focuses on the estimation of production indicators, but the analysis must seek to explain all available information.

Materials and Methods

The data used in considering whether between-year differences are measurable include samples of herring, Pacific cod and dogfish. The herring data include my own 1982 and 1984 samples from the Strait of Georgia. The samples of Pacific cod were also taken from the Strait of Georgia fishery in 1983 and 1985. The fish collected in 1984 were not considered because of an inadequate sample size and size distribution. Data from cod taken off the west coast of Vancouver Island and in Hecate Strait in 1976 were also available providing an opportunity to analyze location differences within a given year. The Canadian data were not compared to the more recent Gulf of Georgia samples. The dogfish samples used in the analysis were those which I collected in 1983 and 1984.

The time series of herring data was provided by the Washington State Department of Fisheries. These data, which also pertain to the Strait of Georgia herring stock, include biomass estimates collected since 1973 and biological data collected from 1976 to 1984. During the WDF trawl surveys length, weight, sex, age and development stage are recorded. These data differ from my own primarily in that gonad and somatic body weights are not recorded directly. The two herring data sets therefore are not directly comparable but the WDF data can be analyzed independently for between-year differences and long-term trends.

A note of definition will be useful at this point. I will refer to fish from the 1984 herring sample as the post-El Niño fish. Although they were collected during the spring and summer of 1984, their seasonal growth and energy storage occurred during the late spring and summer of 1983 when the effects of El Niño were most pronounced. The post-El Niño fish therefore provide a convenient marker for analyzing between-year differences in relative foraging success.

Results

Analysis of the Gulf of Georgia cod data indicates that there were no between year differences in gonad weight. However, the relative body weight of fish taken in 1983 was 8% higher than in 1985 (Table 37). Comparison of the 1976 Canadian data suggests that relative body weights were equivalent, but that the Vancouver Island fish had substantially larger gonads (30-77%) than those taken in Hecate Strait (Table 37).

Comparative analysis of the dogfish data shows that gonad weights were equivalent, but that relative body weight was 8% lower in 1984 (Table 38). There is no data available on the between year differences in the body constituents of either cod or dogfish.

A comparative analysis of the body weight-length and gonad weight-length regression for the Strait of Georgia herring sampled in 1982 and 1984 demonstrates that small differences in measures of the net

Table 37. Estimated coefficients for the gonad weight-length and body weight-length functions (wgt = $aLgth^b$) for Pacific cod by year and location. P_1 and P_2 are probabilities associated with the partial F-tests for entry of intercept and slope terms (in that order) into the log-linear regression models. Also shown are fitted values for fish of three representative lengths.

Location/year	a	b	length class			P_1	P_2	n
Strait of Georgia			600	700	800			
Gwgt 1983/85	1.7745×10^{-8}	3.718	379	672	1103	.874	.380	27/111
Bwgt 1983	3.4448×10^{-5}	2.833	2557	3957	5776	.000	.215	56
Bwgt 1985	3.1824×10^{-5}	2.833	2362	3655	5336			146
Vancouver Island and Hecate Strait								
Gwgt V.I. 1976	1.5794×10^{-8}	3.766	458	819	1354	.000	.027	32
Gwgt H.S. 1976	8.6927×10^{-6}	2.737	349	532	767			43
Bwgt VI/HS 1976	6.1343×10^{-6}	3.086	2297	3696	5581	.452	.047	32/4

Table 38. Estimated coefficients for the gonad weight-length and body weight-length functions (wgt = $aLgth^b$) for dogfish by year. P_1 and P_2 are probabilities associated with the partial F-tests for entry of intercept and slope terms (in that order) into the log-linear regression models. Also shown are fitted values for fish of three representative lengths.

Year		a	b	Length class			P_1	P_2	n
Dogfish				950	1050	1150			
Gwgt	1983/84	8.8771×10^{-8}	3.197	294	405	541	.256	.165	46/201
Bwgt	1983	3.8508×10^{-6}	3.016	3684	4983	6556	.000	.854	78
	1984	3.5599×10^{-6}	3.016	3406	4606	6060			201

production parameters are detectable. The covariance analysis indicates that the gonad weight of a 200 mm fish was 12.4% higher in 1984. The statistical probability associated with this measured difference between intercepts was 0.001. The body weight of a 200 mm fish decreased by 4.8% in 1984. In this case, the probability of the associated t-test was much less than 0.001 (Table 39).

These results indicate that the 1984 herring had higher gonad weights and lower body weights relative to those considered in 1982. Additional analysis of the body constituent data confirms that the 1984 fish were in comparatively poor condition. As noted earlier, body calorie content of the 1982 fish showed a substantial decline with size. The results of the caloric analysis of the 1984 fish was very different. The size trend was barely significant (p = .055) and the observed levels were substantially lower overall (Figure 33).

Additional calorie determinations were done on 10 large fish taken in 1985, 8 of which were greater than 220 mm in length. The average calorie content of these fish was 5349 cal/g dw, which is comparable to the expected value for the larger fish taken in 1982 and greater than the average value of all fish taken in 1984 (Table 40). This again suggests that the 1984 fish were severely depleted compared to those collected in 1982 or 1985.

The body water and ash content data also indicate a depleted condition in 1984. These parameters do not show size trends but a between year comparison of the mean values demonstrate that there are significant between-year differences (Table 40).

Table 39. Estimated coefficients for the gonad weight-length and body weight-length functions ($wgt = aLgth^b$) for Pacific herring by year. P_1 and P_2 are probabilities associated with the partial F-tests for entry of intercept and slope terms (in that order) into the log-linear regression models. Also shown are fitted values of gonad weights for fish of three representative lengths.

Year		a	b	Length class			P_1	P_2	n
Pacific Herring				150	200	250			
Gwgt	1982	1.3329X10-9	4.452	6.5	23.4	63.2	.001	.464	87
	1984	1.4965X10-9	4.452	7.3	26.3	70.9			149
Bwgt	1982	2.6955X10-5	2.844	41.6	94.4	178.0	.000	.226	87
	1984	2.5694X10-5	2.844	39.7	89.9	169.7			149

Table 40. Mean of the body tissue characteristics of Pacific herring samples from different years. P is probability from t-test for differences between means (1985 Bcal data not included in analysis).

	1982	1984	1985	p
BCAL (cal/g dw)	5752	5126	5349	.000
BDRY	.279	.240	-	.000
BASH	.091	.116	-	.000

The WDF data also support the contention that the production characteristics of the 1984 fish were different from those of 1982. Gonad weights were not measured directly, but could be estimated from the difference in total weight of ripe (stage 5) and recovering (stage 8) female fish. Weight-length regressions were therefore calculated for both stages in both years (Table 41). The calculated gonad weights for fish of representative lengths showed that (except for the smallest length-classes) reproductive effort was substantially higher in 1984 (Table 44) than in 1982.

Results of the comparative analysis of spent body weights (stage 8) of fish from 1982 and 1984 WDF samples differed from those of my own data. The regression lines were different and both the slope and intercept terms were significant. However, the magnitude of the estimated differences were relatively small (1.4 g at the extremes of the size range).

Despite this discrepancy between my data and that of WDF concerning condition, additional considerations clearly show that the growth rates of fish sampled in 1984 (the annual growth increment of these fish occurred during the 1983 El Niño year) were significantly lower than in any other year in the time series. In 1984, the observed length of 2-year-old fish was the lowest in the nine year time series (Table 42). The growth rates of older fish were also lower than in previous years. These were estimated by taking the difference between present length at age (in April-May) and the length of fish that were a year younger in the previous year (Table 43). The observed linear

Table 41. Estimated coefficients for the body weight-length functions (Bwgt = aLgth^b) for stage 5 and 8 Pacific herring for 1976-84. Also shown are fitted values for three representative size classes.

	Year	a	b	150	200	250
Stage 5	76	6.4387E-6	3.175	52.2	130.2	264.4
	77	1.1526E-5	3.059	52.3	126.0	249.4
	78	7.8175E-6	3.130	50.6	124.5	250.4
	79	1.3185E-5	3.035	53.0	127.0	249.9
	80	1.5271E-5	2.997	50.8	120.2	234.7
	81	1.7462E-5	2.967	50.0	117.3	227.4
	82	1.2116E-5	3.041	50.2	120.4	237.4
	83	6.6278E-6	3.158	49.4	122.5	247.8
	84	5.0472E-6	3.210	48.8	122.8	251.4
Stage 8	76	1.7265E-5	2.947	44.7	104.3	201.4
	77	1.6097E-5	2.952	42.8	100.0	193.2
	78	1.5632E-5	2.957	43.9	102.7	198.7
	79	1.0607E-5	3.032	41.9	100.2	197.2
	80	1.9578E-4	2.459	43.8	89.9	153.9
	81	2.2412E-5	2.871	39.7	90.6	172.0
	82	1.1418E-5	3.007	39.8	94.6	185.1
	83	2.0710E-5	2.893	40.8	93.7	178.7
	84	1.7610E-5	2.927	41.2	95.7	183.9

Table 42. Average length (mm) at age for female Pacific herring for years 1976-84 (Stages 4, 5 and 8 combined).

Year	2	3	4	5	6	7	8	9	10
1976	161.8	180.5	210.2	225.1	239.9	240.9	249.3	248.5	
77	162.6	190.2	202.6	221.8	231.7	243.0	250.7	248.1	252.8
78	164.7	189.4	203.2	217.4	230.1	238.9	251.2	253.6	256.5
79	169.5	189.9	208.2	219.0	233.3	243.8	250.6	257.4	260.7
80	170.5	191.0	212.3	224.6	235.2	243.6	253.1	257.3	258.0
81	167.5	197.1	208.6	227.9	236.9	243.2	243.1	252.9	259.3
82	170.0	195.7	214.7	225.0	240.2	244.5	251.5	257.0	
83	166.5	196.6	214.5	228.7	236.1	241.6	246.1	253.9	
84	161.4	190.6	209.5	225.5	233.3	239.6	251.5	249.7	

Table 43. Annual linear growth increment (mm) for Pacific herring for different ages in years 1976-84. The first entry (28.4) refers to fish that were 3 years old when sampled during the spring of 1977.

Year	Age 2-3	3-4	4-5	5-6	6-7
76-77	28.4	22.1	11.6	6.6	3.1
77-78	26.8	13.0	14.8	8.3	7.2
78-79	25.2	18.8	15.8	15.9	13.7
79-80	21.5	22.4	16.4	16.2	10.3
80-81	26.6	17.6	15.6	12.3	8.0
81-82	28.2	17.6	16.4	12.3	7.6
82-83	26.6	18.8	14.0	11.1	1.4
83-84	24.1	12.9	11.0	4.6	3.5

Table 44. Estimated gonad weights (three representative size classes) and gonad somatic indices (200 mm fish) for Pacific herring from 1976-84.

Year	150	200	250	200
76	7.5	25.9	63.0	.248
77	9.5	26.0	56.2	.260
78	6.7	21.8	51.7	.212
79	11.1	26.8	52.7	.268
80	7.0	30.3	80.8	.337
81	10.3	26.7	55.4	.295
82	10.4	25.8	52.3	.273
83	8.6	28.8	69.1	.307
84	7.6	27.1	67.9	.283

growth increment of 3-year-olds was the second lowest on record and that of the 4, 5 and 6-year-olds were the lowest in the nine year time series. So, although the WDF data do not reflect the changes in condition suggested in the analysis of my data, it is clear that the growth characteristics of the fish sampled during 1984 were very different from previous years.

Consideration of the entire WDF time series places the 1982 and 1984 data into a broader perspective. The stock biomass has declined steadily since 1973 while the number of individuals in the population has fluctuated without an apparent trend (Fig. 34). The fishing pressure was relatively heavy during the first few years of the fishery with 29 and 36% of the spawning biomass taken in 1974 and 1975, respectively. For the next 5 years the catch was lower and relatively constant in the range of 16-19% (Fig. 34). Except for a small (6%) catch in 1982, fishing has been closed since the 1980 fishery. Nevertheless, the stock has continued to decline.

During this period of decline a number of the important biological characteristics of the stock underwent significant changes, and 1980 seems to have been an important year of transition. I will argue that the stock has declined because of the combined effects of fishing, poor year-class strength and an increase in the rate of natural mortality. The observed changes in age-at-maturity and juvenile growth rates are interpreted as density-dependent responses to declining biomass. However, additional observations concerning relative condition and reproductive effort suggest that there has been a shift in the entire suite

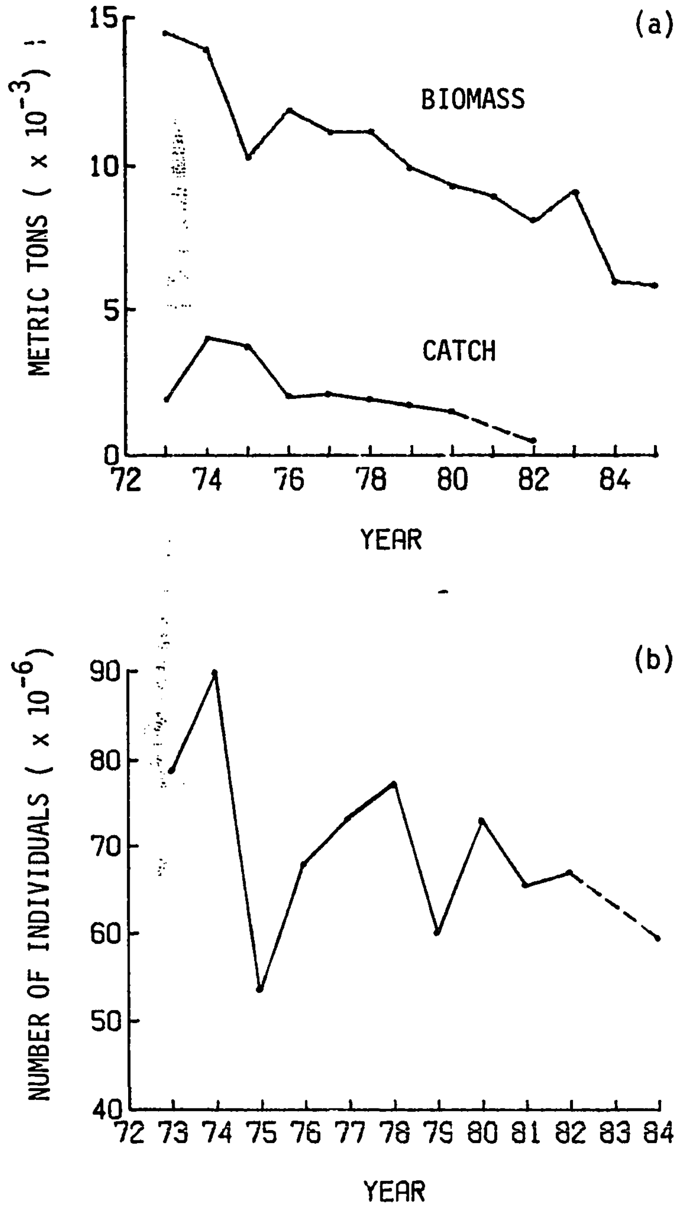


Fig. 34. Population trends in Washington State Strait of Georgia Pacific herring (a - biomass and catch; b - individuals).

of life history characteristics with an increasing emphasis on reproduction at the expense of physical condition. Finally, I will suggest that there are mechanisms which will tend to prevent the stock from returning to its previous condition.

In 1980 several characteristics of the stock underwent pronounced change. The frequency of 2-year-olds in the catch serves as an indicator of age-of-maturity. Before 1980 there were few mature 2-year-olds. Since 1980 the frequency has been variable but certainly higher than in previous years, suggesting a decrease in the age of maturity (Fig. 35a).

We can get an indication of juvenile growth rates by looking at the average length of 2-year-olds. The average length increased gradually, peaking in 1980, and has remained higher since (except for the 1984 post-El Niño fish, Fig. 35b, Table 42).

There has also been a decline in the condition of the fish (as indicated by the comparison of length-specific weight). The weights of 200 mm spent fish were determined for each year from individually calculated length-weight regression lines (i.e., separate slope and intercept terms). The results suggest that there was a sharp transition to reduced physical condition beginning in 1980 (Fig. 36a, Table 41).

Reproductive effort has increased in recent years. The average estimated gonad weight of a 200 mm fish before 1980 was 25.1 g; since 1981 it has been 27.7 g ($t = 2.208$ $p < .05$). However, this comparison

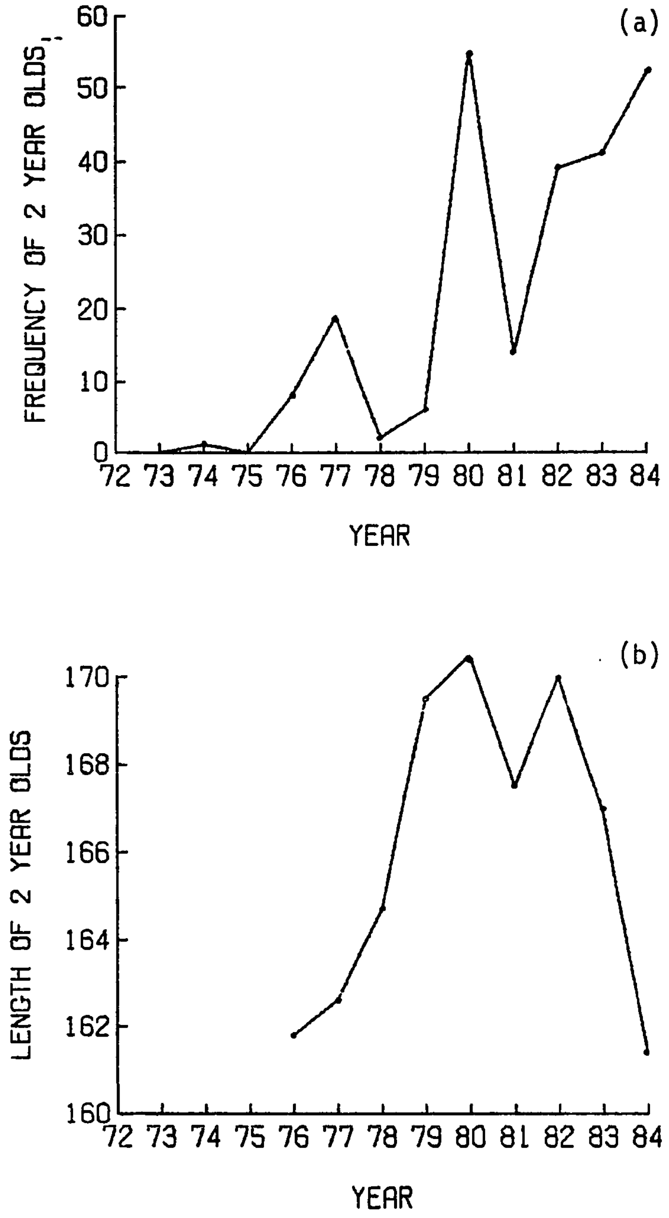


Fig. 35. Two-year-old fish as a proportion of total number of spawning herring (a) and average length of two-year-old herring (b).

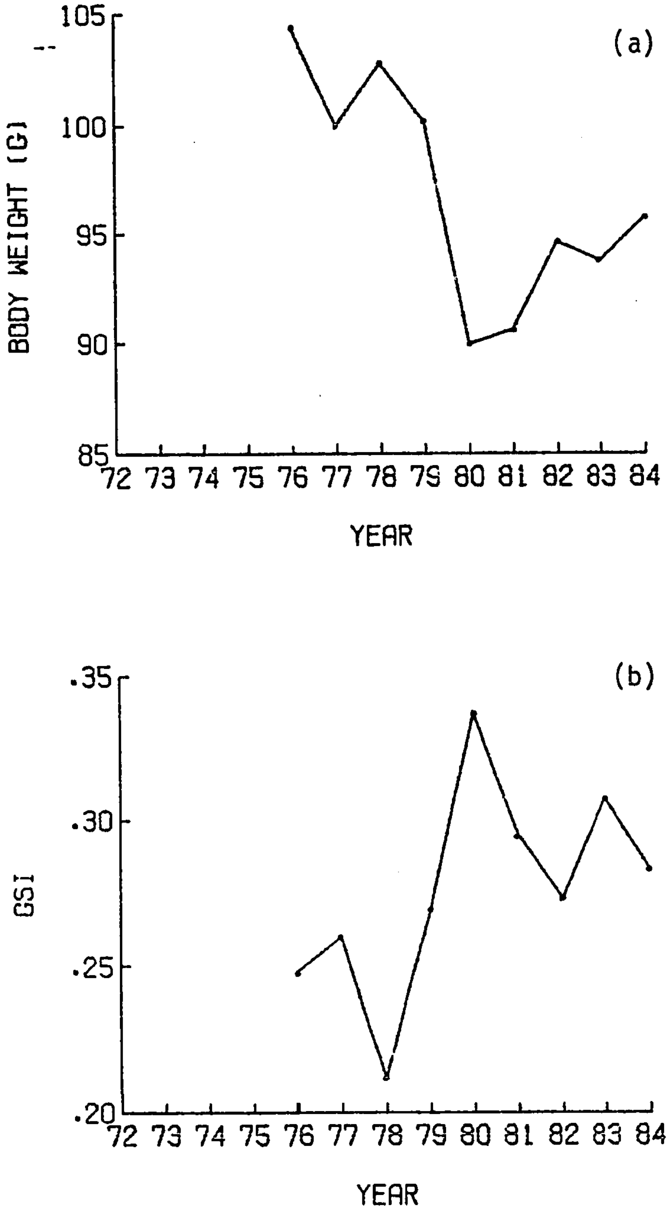


Fig. 36. Condition (a), shown as estimated somatic body weight of a stage 8 200-mm fish, and gonad somatic index (b) of herring plotted versus year.

does not account for the fact that fish in later years were lighter in weight. A comparison of gonad somatic indices for 200 mm fish therefore shows an even greater shift in relative reproductive effort for fish of a given length ($\bar{x} = .247$ vs $\bar{x} = .299$, Fig. 36b, Table 44).

Finally, there is good indication that there has been an increase in the rate of natural mortality. Total mortality rates for the 67-80 cohorts were estimated by fitting regression coefficients to log abundance versus age data in Table 45 [$\ln N_t = a - Z(t)$]. The average instantaneous fishing mortality rate was also estimated for each cohort. Age-specific abundance (N) and catch (C) data were available for each year (Tables 45 and 46). Natural mortality during the brief fishing season can be ignored, so the average F for each cohort was determined using the equation

$$F = -[\sum_{i=1}^{n} \ln(1-\frac{C_i}{N_i})]/n$$

where n was the number of available age specific abundance estimates for a given cohort. The natural mortality rate for each cohort was estimated by subtracting F from Z (Table 47, Figure 37).

The results of this analysis suggest that there may be 2 problems with the mortality estimates for some of the first cohorts in the data set. The natural mortality estimates for the 1969 and 1970 cohorts were unrealistically low (.03 and .02). Such values could be the result of immigration or problems with abundance estimates during the early years of the survey.

Table 45. Number of Pacific herring by age (x 10^{-6}) in years 1973-84.

Year	2	3	4	5	6	7	8
1973	.2	11.0	32.8	21.0	12.7	2.5	.6
74	.6	25.4	15.1	25.3	15.6	6.3	1.1
75	.1	15.5	6.2	9.4	13.3	7.4	1.9
76	5.5	13.0	19.7	9.0	10.4	11.1	3.9
77	14.0	19.0	4.8	8.8	5.9	8.0	7.7
78	1.2	48.4	17.2	5.8	5.5	3.3	3.4
79	3.8	7.8	24.0	9.3	3.4	3.8	1.4
80	40.2	6.4	5.1	10.8	7.8	2.1	1.5
81	8.9	32.3	7.7	4.8	8.0	2.3	.4
82	26.3	15.8	18.7	5.8	2.4	1.7	.4
83	--	15.5	10.4	13.1	3.0	.8	1.2
84	31.0	8.0	6.8	6.4	5.2	1.2	.4

Table 46. Catch of Pacific herring by age (x 10^{-6}) in years 1973-84.

Year	-3	4	5	6	7	8
1973	1.05	4.98	3.37	1.62	.33	.06
1974	1.30	3.52	9.05	6.63	2.66	.33
1975	2.91	2.19	4.31	6.09	3.01	.76
1976	.99	3.32	1.87	2.08	2.11	.68
1977	1.42	.61	2.59	1.81	2.18	1.75
1978	4.97	2.66	1.34	1.53	.84	.82
1979	1.27	4.45	2.10	1.01	.91	.39
1980	1.04	1.74	1.82	.97	.34	.15
1981	.00	.00	.00	.00	.00	.00
1982	.76	.41	.15	.13	.05	.02
1983	.00	.00	.00	.00	.00	.00
1984	.00	.00	.00	.00	.00	.00

Table 47. Estimated mortality rate for Pacific herring -- cohorts 1967-78.

Cohort	Z	$\bar{F}$	M
1967	.950	.398	.584
68	.580	.366	.214
69	.372	.339	.033
70	.314	.297	.017
71	.616	.284	.332
72	.600	.241	.359
73	.583	.169	.414
74	.729	.111	.618
75	.764	.089	.675
76	.603	.107	.496
77	.624	.041	.583
78	.584	.005	.579
79	.452	.017	.435
80	.824	.000	.824

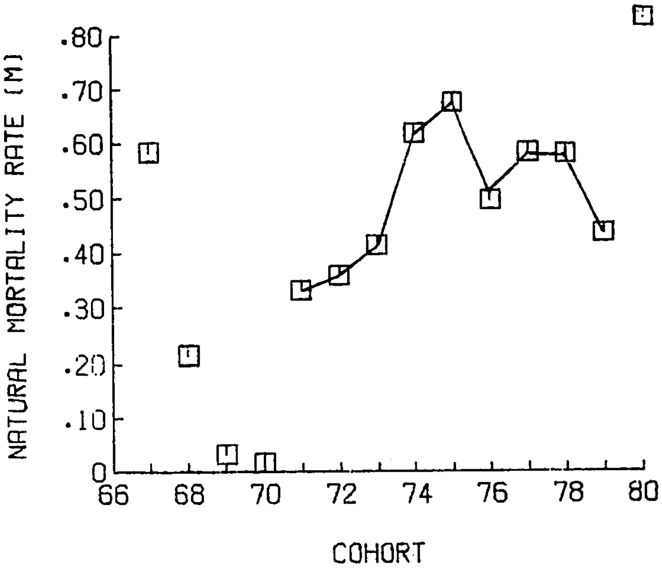


Fig. 37. Estimated natural mortality rate for each cohort of the Washington State Strait of Georgia herring. Points not connected by lines were excluded from the time trend analysis (see text).

The second problem is associated with the bias of age dependent mortality. The average natural mortality rates for ages 3-7 show a generally increasing trend (.33, .14, .22, .48 and .69) (Trumble, pers. communication). Tester (1955) also showed that mortality was age dependent for a herring stock from west Vancouver Island. The estimated M values for the 1967 cohort in particular may be high because only fish that were 6, 7 and 8 years old were available for analysis. Because of this age bias problem and the improbability of the M values for the 1969 and 1970 cohorts, the 67-70 cohort mortality estimates were excluded from the analysis of time dependent trends. The M values for the 1980 cohort was also excluded for the present since it was based on the abundance estimates of only 2 age classes. The 1980 cohort will be reincorporated into the analysis as future survey results become available.

The conclusion of this mortality analysis is that M has gone up from an average of .37 for the 71-73 cohorts to .56 for the 74-79 cohorts (Table 47, Figure 37). The difference between these average values is statistically significant ($P < .01$). I do not mean to imply that mortality has gone from one stable value to another but it is clear that M has increased in recent years. It is also pertinent to note that total mortality has been variable, but without apparent trend for the 71-79 cohorts (those which are considered reliable, Table 47). The decline in fishing mortality was compensated for by an increase in natural mortality.

Other mortality estimates are similar to those reported here for the earlier cohorts (i.e., before the transition). Schweigert and Hourston (1980) estimated an M = .36 for Barkley Sound herring. Trumble (pers. communication, PFMC, 1982)) derived an estimate of .40 for the Strait of Georgia herring stock using an earlier version of the data set used in my analysis. When I applied similar analysis techniques to a comparable data set I derived identical results. However, my current analysis differs from Trumble's original work in two ways. First, I had 3 years of additional data, and second, I analyzed the data using a perspective which emphasized between-year differences. Instead of trying to calculate an average annual mortality rate, I was looking for trends in M that could be related to the observed changes in other life history parameters. Comparison of these earlier estimates with my own results again show that current natural mortality rates are higher than they were in previous years.

Discussion

In order to evaluate the significance of the proposed measures of between-year differences in production, it is necessary to demonstrate that even small interannual effects are detectable and biologically meaningful. Analysis of the cod, dogfish and herring data all show that differences in both relative gonad weight and body weight can be detected with a high degree of statistical significance even though the magnitude of the differences may only be on the order of 5 or 10%.

Other authors have also shown that between-year differences are detectable. Bagenal (1957a) considered 3 years of plaice (*Pleuronectes* platessa) data and 2 years of data for Long Rough Dab (Hippoglossoides platessoides). The plaice data showed that there were significant differences in size-specific fecundity and body condition, and that the two were positively associated. Between-year effects were not detected for Dab.

Hourston et al. (1981) analyzed herring data taken in 1974 and 1978 for 10 different stocks located along the British Columbia coast. Covariance analysis was used to determine whether fecundity varied between years within each of the 10 stocks. The independent variables used were length, weight, age and combinations thereof. When length was used as an independent variable, between-year differences were detected in 6 out of the 10 stocks. When all 3 independent variables were included, 7 of the stocks showed significant differences in the intercept terms.

A recent analysis (Reish et al. 1985) of the growth characteristics of Atlantic menhaden (Brevoortia tyrannus) showed that the coefficients of the length-weight function varied with stock abundance. Although the analysis did not explicitly compare between year difference, it is clear that the growth characteristics of fish do change.

The literature that discusses density-dependent phenomena also provides numerous examples where changes in growth characteristics are either presumed or shown to be related to changes in relative food abundance. Ware (1985) showed that the weights of 6-year-old herring off the coast of British Columbia have increased by as much as 72% from 1949 to 1962. Burd's (1985) review of the North Sea herring stocks indicated that the average length of 4-year-olds has varied over a range of 4 cm. In both cases growth rates were related to stock abundance. Burd is even more specific in attributing some of the effect to measured changes in Calanus abundance.

Pacific halibut may provide the most dramatic example of changed growth rates. Schmitt and Skud (1978) showed that the size-at-age has increased by 126% coincident with long term changes in abundance. Similar effects have been noted for Gulf of St. Lawrence herring (Winters 1976), menhaden (Reish et al. 1985), American plaice (Pitt 1975), North Sea sole (DeVeen 1976),and North Sea haddock (Jones 1983), just to name a few.

The point of this review is to demonstrate that changes in growth characteristics of fish are commonly observed and are at least partially related to food abundance. In some cases (e.g., halibut) the effects can be quite dramatic. However, as shown above, even very small between-year differences in growth and reproduction can be routinely measured with a high degree of statistical significance. I submit that these too can be interpreted as the result of changes in relative food abundance.

Iles (1984) has taken a different view concerning the factors which regulate herring production. He suggests that seasonal feeding and growth cycles are controlled by endogenous cycles in hormonal activity which are adapted to average annual seasonal conditions. The hormonal cycles, therefore, effectively decouple herring production from environmental control with the result that competition for food is not a major ecological factor for herring once they have passed an acknowledged but unspecified density-dependent stage. He notes as supporting evidence for this conclusion that the fish appear to stop feeding while food abundance is still high. However, his suggestion is contrary to much of the evidence cited above.

Ware (1985) has also taken a somewhat different view of herring production characteristics. I have suggested that both growth and reproduction will vary significantly between years. Ware defines surplus energy as the sum of the somatic growth increment and reproductive output. He has found that surplus energy varies significantly between years, that reproduction is tightly correlated with body weight, and that the relationship between gonad weight and body weight does not vary between management units or years. Based on these observations he concludes that "between year and age variation in surplus energy must appear as differences in growth, and that ovary weight is not affected to a significant extent by interannual and regional variations in environmental conditions or stock abundance." The point that comes out of this is that gonad weight is unaffected by variations in environmental factors or stock abundance (see for example Haist and Stocker 1985). However, if the growth increment is reduced, because of an El Niño for example, then the fish will be smaller and the reproductive effort, which is proportional to weight, will have been adversely affected. Reproductive effort is affected by changes in relative food abundance.

There is a further procedural problem with Ware's (1985) method of analysis. Gonad weight is defined as a power function of total body weight. But the gonad makes up 20-30% of the total weight. It is, therefore, not surprising that the observed correlations between gonad and body weight are so high. If gonad weight were related to somatic weight as suggested by Bagenal (1967) and Wootten (1979), I suspect that Ware would have found significant between year and location differences in reproductive effort. In fact, Hourston et al. (1981) analyzed a portion of the same data set used by Ware and showed significant between year differences in the fecundity-weight relationship for 7 out of the 10 stocks considered.

In evaluating the significance of the proposed measures of between-year differences in production it is also necessary to show that the differences are biologically meaningful. Ware (1985) and Reish et al. (1985) have both concluded that such differences are not very significant from a biological standpoint. However, the scale of variation in production differences is a continuum. During periods of relative stability, variations may be small in magnitude even though clearly measurable. As shown above, larger scale events can change production rates dramatically. The question, therefore, becomes at what point do we begin to pay attention to these observed differences. It is my contention that all measurable changes in production rates occur for a reason. If we continue to ignore these differences, our ability to interpret and anticipate larger scale events will continue to be rather limited.

The fact that fish were sampled in 1984, immediately after the El Niño year provides a convenient marker for analyzing the biological significance of between-year differences. It is clear that fishes in the lower latitudes were severely affected by El Niño as were some of the salmonid stocks taken off the coasts of Oregon and Washington (Wooster and Fluharty 1985). Oceanographic effects and anomolous species distributions were noted well up into the Gulf of Alaska. But specific measures of the production characteristics of a pelagic planktivore such as herring have not been reported as far north as the Washington and British Columbia coasts, which are the presumed summer feeding grounds of the Strait of Georgia herring stocks (PFMC, 1982).

Comparison of the fish taken in 1982 and 1984 show that the 1984 fish were in a depleted condition. The length-specific weight of a 200 mm fish in 1984 was lower by 4.8% (Table 39). Other condition indicators also provide strong evidence that the post-El Niño fish were severely depleted. The calorie content of these fish was much lower, while the water and ash content were significantly higher (Table 40).

Growth rates were also much lower. The length of the 2-year-olds in 1984 was the lowest in the time series. The growth rates of the older age-classes were also uniformly low. Haist and Stocker (1985) found that the surplus energy of different age-classes of mature fish fluctuated in parallel indicating that they were all equally affected by changing conditions. This was again the case in 1984. The relative reproductive effort of fish taken in 1984 was higher than that of 1982. This effect was evident in my samples as well as those of WDF.

Higher reproductive effort in what were presumably stressed fish was somewhat unexpected, but must be interpreted in terms of the life history strategy of the species. It appears that herring respond to food limiting conditions by increasing reproductive effort at the expense of somatic growth and physical condition. A similar result was suggested in the earlier section concerning the comparison of similar individuals where an inverse association between reproductive effort and condition was indicated. This was in direct contrast to the result found for English sole where reproductive effort and condition were positively related. Others have discussed the strategic options of energy allocation when faced with food limiting conditions (Tyler and Dunn 1976; Roff 1982). Of the species considered, only three-spined stickleback (Wootten 1977) and now perhaps herring seem to sacrifice physical condition to maintain reproductive effort during periods of food limiting conditions.

In examining the WDF time series data, it is evident that 1984 was not unequivocally the worst year in the 9 year time series. The growth rates were lowest (2nd lowest for 3-year-olds) but there were other years where condition was lower and reproductive effort was higher. For fish collected in 1980, for example, condition was quite low (Table 41) and relative reproductive effort high (Table 44). However, size of the 2-year-olds in 1980 (Table 42) as well as 1979-80 growth increments for the 4-, 5- and 6-year-olds were the highest on record (Table 43), again showing that the production characteristics of different age-classes within years vary in parallel (Haist and Stocker 1985). The reasons for this apparent contradiction are not clear at this point. However, as will be discussed below, the life history of this stock is undergoing some rather dramatic changes. The observed inconsistencies may be related to this apparent instability.

Some of the more obvious changes that have occurred in the Strait of Georgia herring stock over recent years are the decline in biomass, increase in size of age 2 fish, and earlier age of maturity. These circumstances are typically interpreted as a juvenile density-dependent growth response and have been noted for a number of other stocks and species (Iles 1967: Lett and Kohler 1976; Hubold 1978; Ware 1980; Anthony and Fogarty 1985; Haist and Stocker 1985).

One apparent enigma is the fact that, although the biomass has declined steadily, the total number of individuals has been variable but without apparent trend (Fig. 34). This implies that the number of young individuals in the spawning stocks is actually increasing. This probably results from the fact that fish are recruiting earlier and as a result, there are more of them. That is, each cohort is subjected to the mortality factors for a lesser period of time before recruiting to the mature stock.

The data also indicate that beginning in 1980, spent fish have been in reduced condition and have had higher relative reproductive effort (Tables 41 and 44, Figs. 36a and 36b). These observations, coupled with the reduced age of maturity and increased growth rate, suggest that there has been a significant change in the entire complex of life history parameters. Herring show changes in both the size- and age-at-maturity, although of the two the age reduction is the more significant change. The age-at-maturity has declined by at least a year. However, despite the fact that juvenile growth rates are higher, newly recruited fish are still much smaller than they were in previous years. It is clear that there has been a marked change in the emphasis of energy allocation from early growth to higher relative reproductive effort at an early age.

Natural mortality is another important life history parameter and it too has changed in recent years. The mortality rate increased sharply beginning with the 1974 cohort, which first appeared in the fishery in 1977. Higher mortality has continued to affect all subsequent cohorts. The reason for the increased rate is unclear.

A consideration of the timing of events suggests some partial explanations for the changes which have affected the herring stock. By combining the mortality and biomass figures (mortality was lagged ahead 3 years in order to approximate the age of entry for each cohort into the fishery, i.e., 1974 cohort plotted in 1977) we can see that the initial decrease in biomass apparently preceded the increase in natural mortality (Fig. 38). From 1973 to 1977 fishing pressure, particularly in 1974 and 1975, probably contributed to the decline in biomass. From 1977 to 1980 both fishing and the increase in M would have affected the stock. (It is worth noting that managers at the time had no way of knowing that mortality rate had increased, and were permitting exploitation at a rate of 20% or less, which even now is considered a reasonable if not conservative harvest rate.) After 1980 the fishery was closed. Nevertheless, the biomass has continued to decline suggesting that the mortality rate may still be at an elevated level.

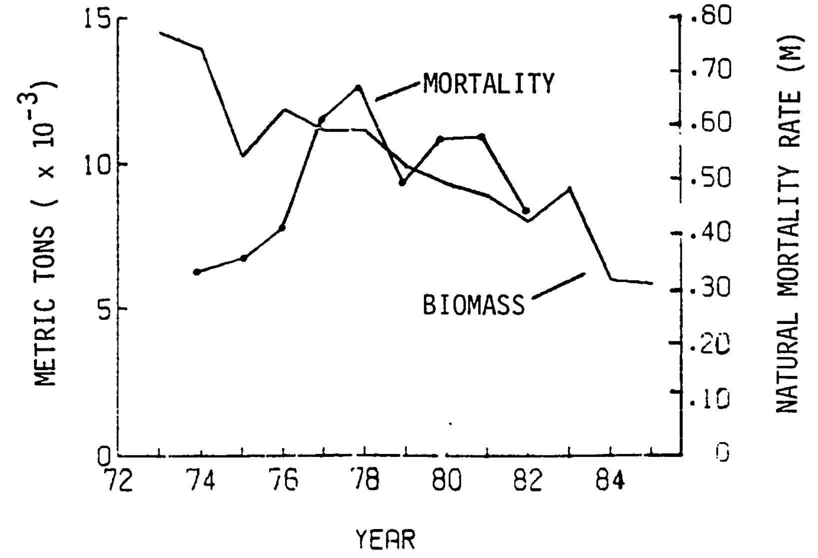


Fig. 38. Recent trends in stock biomass of Strait of Georgia herring and the cohort specific rate of natural mortality (M lagged ahead 3 years).

Year-class phenomena are an important feature of the biology of pelagic fish and their relevance has yet to be discussed. It is often the case that the majority of the biomass of a stock is supported by a few periodic year-classes. These strong year-classes presumably occur as a result of the fortuitous occurrence of a combination of biotic and abiotic factors during critical periods of the early life history. The Strait of Georgia herring had good year-classes in 1969, 1975 and 1978, but none since, and this too must be considered an important factor in the continuing decline in biomass.

There is also sufficient evidence to suggest that fluctuations in adult mortality may be an important driving force affecting stock abundance. My data provide empirical evidence that mortality rate and biomass are inversely related, although this time series in itself is not sufficient to warrant strong conclusions. There is, however, a much longer time series pertaining to the herring stocks from the west coast of British Columbia. Haist (pers. communication) used a modeling approach to analyze fluctuations in biomass and found that the unexplained variance was reduced considerably when she incorporated a depensatory functional relationship between natural mortality and stock abundance.

The usual alternative view is that mortality is constant. It is possible for biomass to decline as it has without invoking the changed mortality rate mechanism. In the absence of good recruitment, biomass will decline as the last strong cohorts age out of the population. If recruitment continues to be bad, fewer recruits will make an ever smaller contribution to the declining biomass. However, in the case of herring it appears that the increase in mortality rate has been an important force affecting stock biomass. I think it is still proper to view year-class fluctuations as the principal determinant of stock abundance. However, consideration of the possibility that mortality rates are also fluctuating will give a more realistic view of the factors which control stock biomass.

A schematic diagram can be used to summarize how the Strait of Georgia herring stock has changed in recent years, and to suggest two feedback mechanisms which may tend to inhibit the stocks return to previous condition (Fig. 39). The combined influences of declining biomass and increased mortality have led to higher juvenile growth rates, earlier maturity and increased reproductive effort. Higher reproductive effort leads to reduced physical condition in herring, which, as was discussed earlier in this dissertation, is related to higher mortality. These results suggest that the changed relationships between biological parameters and mortality may be self-perpetuating.

The combined events of declining biomass and increased mortality have also led to a reduction in population fecundity and a compressed age-structure (i.e., fewer old fish). Because older fish spawn larger eggs earlier in the season, there are now fewer eggs spread over a smaller proportion of the time/space continuum. This reduces the probability that the strong year-classes needed to reverse the continuing trend of declining biomass will occur.

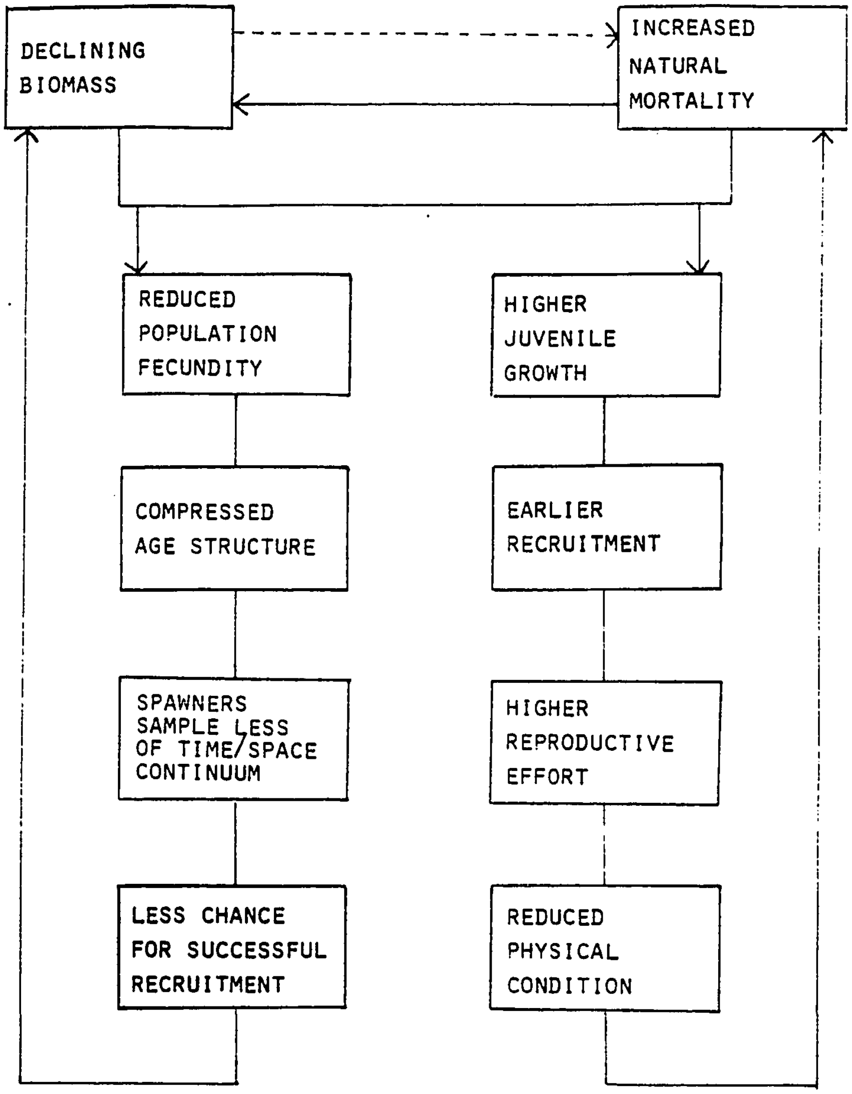


Fig. 39. Schematic flow diagram showing recent sequence of events affecting Washington State Strait of Georgia herring.

The original objective of the monitoring program was to use indicators of foraging success to distinguish the importance of food as a regulator of stock abundance and production. Consideration of the post El Niño fish demonstrates that it is possible to measure biologically meaningful differences in production parameters that are related to relative food abundance. It is also clear from the time series analysis that important trends in production and other biological parameters can be detected. At this point it is not possible to interpret what role food availability may have had in effecting this long-term change of the herring stock. Higher relative food abundance may have affected growth rates. However, there is no indication that changes in food availability were responsible for the long-term decline in biomass. It seems sufficient to suggest that the observed decline in biomass resulted from the combined effects of successive poor year classes, the increase in natural mortality and fishing pressure.

Our ability to explain such events will improve as we gain more experience with additional case histories and longer time series. In particular, more information is needed on the variability of parameter estimates during times of relative stability. It is difficult to interpret the herring data because the entire time series is characterized by instability, leaving no normal time frame for comparison. Meaningful analysis of time series data will also depend on an understanding of species-specific strategies of response to various perturbations. It is apparent, for example, that herring respond to food limiting conditions by increasing relative reproductive effort at the expense of physical condition. This is in contrast to English sole for which condition and reproductive effort are directly related.

The monitoring program, as originally conceived, depends on some particular measures of growth, reproductive effort and condition. The parameters (relative reproductive effort, somatic condition and juvenile growth) and protocol were specified because they provide objective measures of the important components of production that are generally not adequately quantified during routine management related sampling programs. However, I do not mean to imply that these production indicators are to be used independently. Instead, all information that is available from the existing program should be considered, including biomass, maturity indicators, incremental growth data, abundance-at-age, and environmental data. As was the case in the herring example, none of the observed indicators by themselves convincingly demonstrated that the stock had been seriously affected. However, all parameters taken together were consistent in indicating that there has been a major transition in the life history of this stock.

The conceptual strategy of the monitoring program is to define the range of variability in the parameter estimates during periods of stock stability so that biologists will be in a position to interpret the role of relative food abundance when significant stock fluctuations do occur. This strategy would allow us to analyze the importance of food both within the "steady state" and during periods of departure from the norm.

Quantification of net production characteristics during times of relative stability would serve to define parameter bounds that will be used for comparison during times when stocks are undergoing significant changes. However, the monitoring programs would be more than just a tool for analyzing the causes of major shifts in stock abundance. One of the important short-term benefits of a monitoring program would simply be that it would enable us to learn more about the biology of these animals that just has not been apparent in the past. In particular, we will be able to view how the fish respond to any changes in their biological circumstance. As we gain a better understanding of these species-specific responses we will be able to use the entire array of biological parameters as an early warning system for the detection of potential problems. When a significant biological change is first observed, the cause, whether it be the beginning of a long-term event or simply random variation, may not be immediately apparent. However, detection of the signal will permit managers to adjust near-term exploitation strategies and place biologists in a better position to observe and analyze the change as it occurs instead of merely documenting and then trying to explain the event after the fact.

Finally, the program will lead to a different view of some of these important biological parameters. Fisheries biologists are increasingly moving away from the concept of stability. Recruitment and biomass, for example, are no longer treated as constants. The monitorng program offers another step in that same direction. The suggestion is that mortality rates, growth parameters, the age-at-maturity, reroductive effort, and other biological parameters vary through time in response to changes in environmental and biological circumstances. The monitoring program provides the perspective that will permit us to quantify the variability in parameter estimates, as well as the interrelationships among these important life history parameters.

SUMMARY

The first objective of my research was to evaluate the feasibility of using measures of reproductive effort as a predictor of the natural mortality rate. The observed correlation coefficient relating M to the wet gonad somatic index (WGSI) was $r = .831$ ($n = 15$, $p = .001$). For most species estimates of reproductive effort can be obtained in a single spawning season, thereby providing a quick preliminary estimate of the rate of natural mortality.

The traditional methods for estimating M require either tagging or the aging of fish, techniques which are costly, time-consuming and sometimes impossible. Other correlative models used to predict M utilize estimates of one or both of the growth parameters L_∞ and K. However, these parameters also are estimated from tagging or aging data and therefore are of limited value relative to methods of direct estimation.

Copper rockfish were one of the species included in the analysis of reproductive effort. At least some species within the genus _Sebastes_ are viviparous. It was therefore necessary, as part of the assessment of reproductive effort, to quantify the maternal energy contribution made to embryos during gestation. I estimated that 11.5% of the energy consumed by embryos during gestation was contributed by the mother, but concluded that the null hypothesis of no maternal contribution could not be rejected because of the variance and potential biases of the estimate. As a result maternal energy contribution was not incorporated into the estimate of reproductive effort for copper rockfish.

Northern anchovy were also to be included in the reproductive effort-mortality analysis. Anchovy are multiple batch spawners. A critical number in estimating their reproductive effort is therefore the number of egg batches spawned per year. Histological examination and frequency analysis of the adult spawning stock suggests that anchovy may spawn 20 or more times per year. However, my own energetics analysis indicates that this is probably not feasible. Because of the uncertainty concerning this critical parameter anchovy were excluded from the analysis.

A second objective of my research was to consider the general topic of the variability in growth and reproduction of fish. Three levels of analysis were covered, including: 1) seasonal energy cycles, 2) variability between fish of similar size and age, and 3) changes in growth and reproduction with size and age.

English sole were the subject of study concerning seasonal energy cycles. Results of the analysis showed that the expected net growth increment of a fish of representative size was 15.5 mm and 12 g dw. However, the seasonal fluctuations in body weight were much larger. The representative fish gained 74 g dw during the spring and summer, but subsequently lost 62 g dw during the 5 months from October to March.

Coincident with the decline in weight was an increase in gonad weight. Thirty-two percent of the lost body mass was accounted for by the increase in gonad mass. Consideration of the fate of the individual proximate constituents showed that 52.7% of the lost body protein, 45%

of the lost body ash, and 5.3% of lost lipids can be accounted for by the gains during gonad development.

One practical implication of English sole analysis was that a consideration of seasonal cycles in body condition could lead to substantial increases in yield without any detrimental impact on the stock. Because seasonal weight loss is almost all recoverable muscle tissue, the yield from an individual fish taken in October could be as much as twice that of the same fish taken the following March.

Consideration of the variability between fish of similar size and age provided insight into the strategies of energy allocation for growth and reproduction. My analysis suggested that the reproductive strategies of English sole, dogfish and perhaps cod are different from that of herring. The English sole data in particular showed that there was a strong positive correlation between relative reproductive effort and several different measures of physical condition. Additional analysis showed that fish of a given length that are in better condition and that have larger gonads are younger than those that are apparently less well off. Based on these observations I concluded that much of the variability between fish of similar size results from inherited dissimilarities in individual abilities to obtain and process food.

Consideration of the herring data suggested that the above explanation may not be universally sufficient or applicable to all species. There is some indication that condition and reproductive effort in herring are inversely related. This suggested that herring may have a trade-off strategy for allocating energy between growth and reproduction which is different from that of the other species considered. Although herring must also have inherited dissimilarities it is apparent that there are additional factors which contribute to the observed variability between fish of similar size and age.

There were two reasons for considering the changing relationship between reproductive effort and size and age. One concern was that size effects could obscure potential differences between species in the interspecific WGSI vs. M analysis. My conclusion was that there was some potential for error and that representative sizes for each species should not be selected arbitrarily. The use of the average size of a mature female selection criterion is appropriate because it can be applied objectively and because it has biological meaning.

The second reason for analyzing how reproductive effort changes with size and age was to consider whether some measure of reproductive effort or condition could be used as a scaling parameter for estimating intraspecific size dependent mortality rates. This suggestion was derived from the assumption that reproductive effort and mortality are linked via the mechanism of somatic depletion. Although there was a coincidental inverse relationship between reproductive effort and condition with size and age it was not possible to show that the two were causally related in an inverse way. In fact, the analysis of fish of similar size and age showed a strong positive correlation between reproductive effort and condition and at the very least this would tend to obscure any direct empirical estimates of size-dependent trends. Physical condition, however, is easy to measure and can be directly related to mortality. I therefore suggested that a practical way for estimating how mortality changes with age may be to scale existing estimates of M using a function defined by the changing relation between age and average condition.

The herring data provided the focus for the final topic concerning between-year differences in growth and reproduction. Consideration of my own samples from 1982 and 1984 (the post-El Niño fish) showed that the El Niño fish had a 12.4% higher rate of relative reproductive effort but that physically they were extremely depleted. The calorie content of the body tissues of the 1984 fish, for example, was substantially lower for all size classes than in 1982 or 1985.

The effect of El Niño on the 1984 fish was also reflected by the time series analysis of WDF data. The average length of the 2-year-olds in 1984 was the lowest recorded during the 9-year time series. The annual growth increments for the 4-, 5- and 6-year-olds were also the lowest on record.

Further consideration of the WDF data showed that the biomass of the stock has declined steadily from 14,500 tons in 1973 to less than 6,000 tons in 1985. The decline has continued despite the fact that the stock has not been fished since 1980 (except for a minor catch in 1982). It was also apparent that there was a sudden shift in a number of the life history characteristics of this stock and that 1980 was an important year of transition. The age-at-maturity and length-specific weight (i.e., condition) declined while the average size of 2-year-olds and relative reproductive effort increased. A significant change in the natural mortality rate was also observed.

The sequence of events suggests that the combined effects of fishing, increased mortality and poor recruitment are responsible for the decline in the herring stock, and that some feedback mechanisms may be operating that will inhibit stock recovery.

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APPENDIX A

Introduction

Boehlert and Yoklavich (1984) reported that female Sebastes melanops (black rockfish) contributed a significant amount of maternal energy to developing embryos during gestation (matrotrophic viviparity). The objective of this report is to present new information on the reproductive biology of Sebastes caurinus. In particular we present the results of an assessment of the maternal energetic contribution made by Sebastes caurinus to embryos during gestation. This study, together with previous work on the black rockfish, suggests that the degree of matrotrophy varies widely within the genus Sebastes.

Materials and Methods

The reproductive habits of Sebastes caurinus (copper rockfish) are similar to those of other members of the Sebastes genus (Moser 1967). Mating and insemination occurs in January and February, but the internal fertilization of eggs does not begin until early March (Washington et al. 1978). Gestation of developing embryos lasts about six weeks. The spawning of well-developed (first-feeding) pelagic larvae takes place from mid-April to mid-May (DeLacy et al. 1964).

The approach used for estimating the maternal energy contribution during gestation was to take the difference between the energy lost per embryo, and the energy consumed per embryo, from the time of fertilization to birth. Energy lost was determined as the difference between the energy content per individual at the beginning (fertilized egg stage) and end of gestation. Energy consumed was estimated from a derived relationship between respiration rate (ul 0_2/embryo/hr) and embryonic age. The respiration function was then integrated and evaluated over the length of the gestation period, and converted to energy units using an oxycaloric equivalent.

Twelve of the fish used for the analysis of embryonic development and respiration rate were collected near Bainbridge Island, Washington, on 20 and 27 February 1983 using gill nets. Three additional females were taken with gill nets and hook and line gear during 1984. Supplementary data on the relationships between development stage, embryo dry weight and caloric content were obtained from fish taken by spearfishing in 1984.

The live fish were immediately transferred to the National Marine Fisheries Service lab at Manchester, WA, where each fish received a prophylactic shot of an antibiotic and was marked with a spaghetti tag. The fish were held in 1.2 m circular tanks and in floating net pens which were approximately 2.4 x 2.4 x 3.0 m in size. No more than two fish were placed in a single circular tank. Two concrete blocks were placed in each tank as artificial substrate. The tanks were supplied with unfiltered flow-through seawater at ambient temperature. The temperature in the tanks increased from 9.1 to 11.5°C during the period when the respiration estimates were made. The fish were given a constant supply of live herring and/or live shore crabs. Food items did occasionally disappear from the enclosures, but total consumption was minimal.

I anticipated that there might be problems with mortality and premature abortion due to the stress of capture and subsequent handling. During 1983 the fish were therefore divided into 2 groups. Four of the fish held in the tanks were used for the observation of early larval development (group 1). Each of these fish did in fact die or abort before the embryos developed fully. Eight fish (group 2) were held in the net pens and left undisturbed initially. This second group of fish was used for observing later development and estimating the length of full term gestation. Six of the eight fish eventually spawned full term larvae. The 3 fish taken live in 1984 also completed reproductive development.

Embryos from the fish in group 1, and later group 2, were sampled at approximately weekly intervals to monitor the progress of development. The embryos were extracted by catheterization with a flexible polyethylene tube. The outside diameters of the catheters used were either 1.90 or 2.42 mm depending on the size of the fish and stage of development. The tubing and gonopore were swabbed with alcohol before the catheter was inserted into the gonadal opening. The tubing was attached to a pipette and the embryos extracted using suction applied by mouth. In order to minimize stress, the fish were catheterized quickly and without anesthetic using the method described by Stahl-Johnson (1984).

The embryos were categorized as to developmental stage using a 13-stage index developed by Stahl-Johnson (1984) for copper rockfish. During later development some embryos were found to have intermediate characteristics and were assigned a fractional stage designation (i.e., 11.5 for embryos with descriptive characteristics between stages 11 and

12). This was necessary because of the need to estimate the relation between stage and embryonic age as closely as possible.

Samples of embryos extracted from different fish at various stages of development were retained for estimating dry weight. Dry weights were determined by counting between 100 and 200 embryos, placing them in preweighed aluminum foil pans, and drying to a constant weight at 80°C. The pans were then reweighed to the nearest .01 mg.

The respiration rate per embryo was measured using a Gilson differential respirometer and standard manometric techniques, employing a methodology similar to that of Boehlert and Yoklavich (1984). Extracted embryos were extruded into an isotonic saline solution (325 mOsM/kg, Forster and Hong 1958; Boehlert and Yoklavich 1984), and quickly sorted with a pipette to insure that only undamaged embryos were used. The embryos were then placed in 15 ml respiration flasks containing the same saline solution, attached to the manometers, and allowed to equilibrate for 1 hr before starting the respiration observations. Once the embryos began to develop eye pigmentation the reaction flasks were wrapped in dark plastic to exclude light. Comparative light-dark respiration experiments showed that earlier embryos were not light sensitive. The temperature was always held at 9.1°C and runs were generally done in triplicate. Run times ranged between 3 and 10 hrs depending on the observed rate of oxygen consumption. After each run, the embryos were counted, placed in foil pans and used along with additional samples for dry weight analysis.

Caloric content of whole gonad tissue containing embryos of known age were determined using a Parr Instruments adiabatic bomb calorimeter. The caloric content of whole gonads is probably not exactly the same as that of the embryos within, since the integumentary and connective tissue does have a slightly different energy content (mean for spent gonads = 5,725 cal/g, n = 4). However, the spent gonad weight was only about 8% of the whole gonad weight at the time of fertilization. Any correction would therefore be small relative to the predominant effects of declining caloric content (see below).

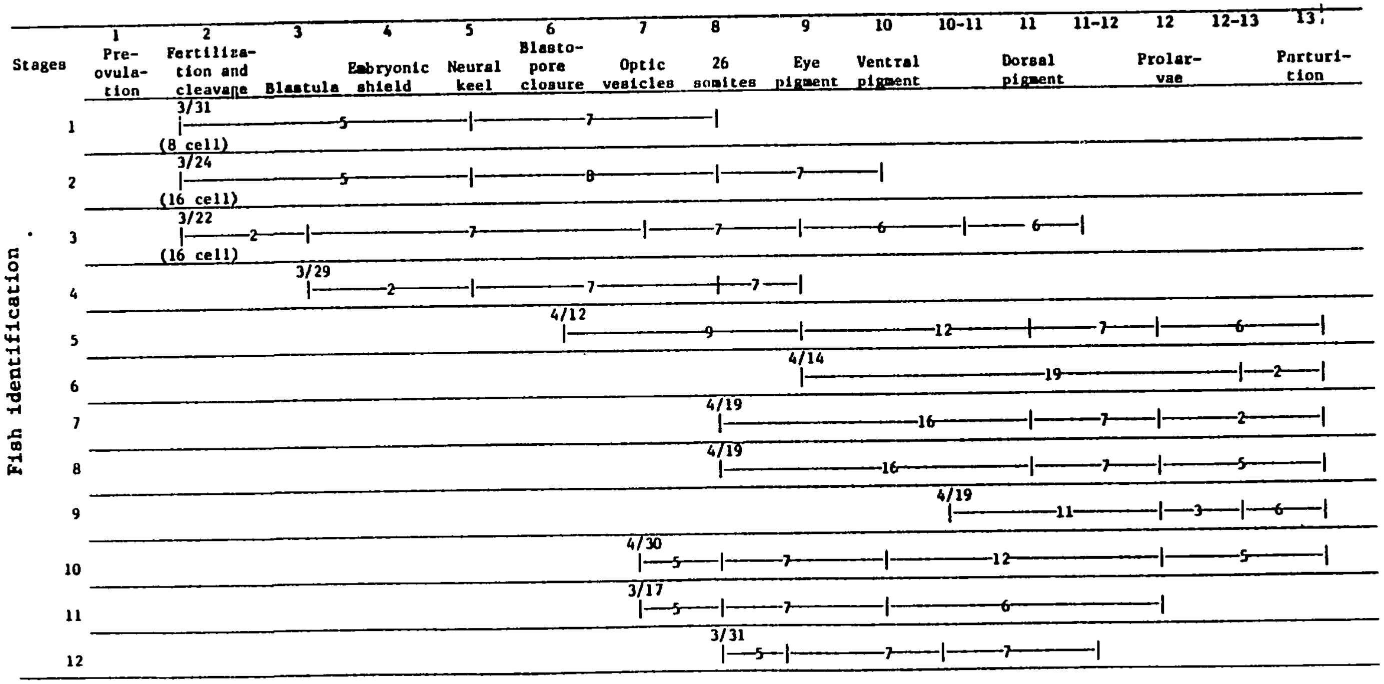
Results

Embryo staging data were used to estimate the length of the gestation period and the age of embryos at each stage. A total of 50 stage observations were made on 12 different fish (Table A.1) during the embryonic development study of 1983. These data were supplemented when necessary with 21 stage observations of 8 fish made by Stahl-Johnson (1984).

To estimate the length of the gestation period, it was necessary to sum a number of estimates of stage duration. The data permitted the grouping of the data into 2 stage intervals: stages 2-8 and 8-13. Stage 2 begins with fertilization and stage 13 ends at birth.

The earliest observations after fertilization were of 8- and 16-celled embryos (Stage 2). The fish identified as 1 and 2 took 5 days to reach stage 5 (Table A.1). Stahl-Johnson (1984) observed the ovulation and fertilization of one fish and a 4-celled stage of another. Both of these fish took 6 days to reach stage 5. I therefore estimated

Table A.1. Stage duration observations from *in vivo* sampling of copper rockfish embryos (stages after Stahl-Johnson (1984)).



that it took 1 day to develop from fertilization to an early cleavage stage. --

Fishes 1-4 provided a mean estimate of development time from early cleavage up to stage 8 of 12.5 days (Table A.2). The estimated length of stage interval 2-8 is therefore 13.5 days. The average development time of stage interval 8-13 was estimated, using later term fish (numbers 5-10), to be 27.8 days (Table A.2). The estimated total gestation period was therefore 41.3 days. Application of this same method to Stahl-Johnson's data yielded an estimate of 41.7 days. As a result, an average value of 41.5 days was used as the best estimate of gestation length.

The staging data were also used to estimate the age of embryos of a given stage relative to the time of fertilization. In order to calculate the respiration rate-age relation, each stage for which a respiration observation existed had to be assigned an age. My own data were combined with that of Stahl-Johnson to provide these more detailed embryonic age estimates (Table A.3). The sum of the individual stage duration observations provided a second estimate of gestation length of 42.8 days. As indicated above, the former value (41.5 days) is preferred because it has a lower theoretical variance.

The functional relationship between oxygen consumption (R, ul 0_2/embryo/hr) and age (days) was determined using 20 respiration rate observations for 12 different development stages (Figure A.1, Table A.4). The function

Table A.2. Estimates of stage interval duration for determining gestation length.

Stage interval	Fish I.D.	Duration (days)	Average duration
Fertilization-early cleavage		1 day*	1 day
Early cleavage - 8	1	12	
	2	13	
	3	14	
	4	11	12.5 days
8-13	5	31	
	6	27	
	7	25	
	8	28	
	9	32	
	10	34	27.8 days
		Total	41.3 days

*See text

Table A.3. Estimates of stage interval duration. Brackets in the left column group stage intervals for which the greatest number of observations exist. Brackets in the right column subdivide the interval as needed to provide the necessary age-stage estimates.

Stage interval	Observed duration (days)		Average duration (days)	
	Dygert	Stahl		
1-2			1	
2-3	2	2	2	
3-5	2	4	3	
5-6	7,7,8	8	7.5	1
6-8				6.5
8-9	5,7	6	6	
9-10	6,7		6.5	2
10-10.5				4.5
10.5-11	11		11	4
11-11.5				4
1.5-12				3
12-12.5	2,5,5,6,9	8	5.83	3.83
12.5-13				2
		Total	42.83	

Table A.4. Embryonic respiration rate observation by stage and age.

Stage	Fish I.D.	Estimated age (days)	Embryo dry weight (mg)	ul O_2/ embryo/hr	n	s
3	3	3	.150	.0191	2	.0018
5	1	6	.157	.0143	2	.0066
5	4	6	.181	.0221	3	.0094
6	5	7	.143	.0125	2	.0019
8	11	13.5	.167	.0395	3	.0140
8	4	13.5	.141	.0267	3	.0023
9	3	19.5	.128	.0310	2	.0072
9	12	19.5	.121	.0377	3	.0107
9	5	19.5	.125	.0292	6	.0077
10	11	21.5	.133	.0585	3	.0040
10	2	21.5	.120	.0595	3	.0038
10.5	12	26	.131	.0562	2	.0161
10.5	3	26	.132	.0652	3	.0080
11	3	30	.146	.1183	3	.0151
11.5	12	34	.122	.1828	5	.0126
12	8	37	.125	.2877	3	.0327
12	7	37	.130	.2947	3	.0069
12.5	9	40.83	.114	.2787	3	.0141
13	6	42.83	.121	.3414	3	.0206
13	8	42.83	.115	.2786	3	.0225

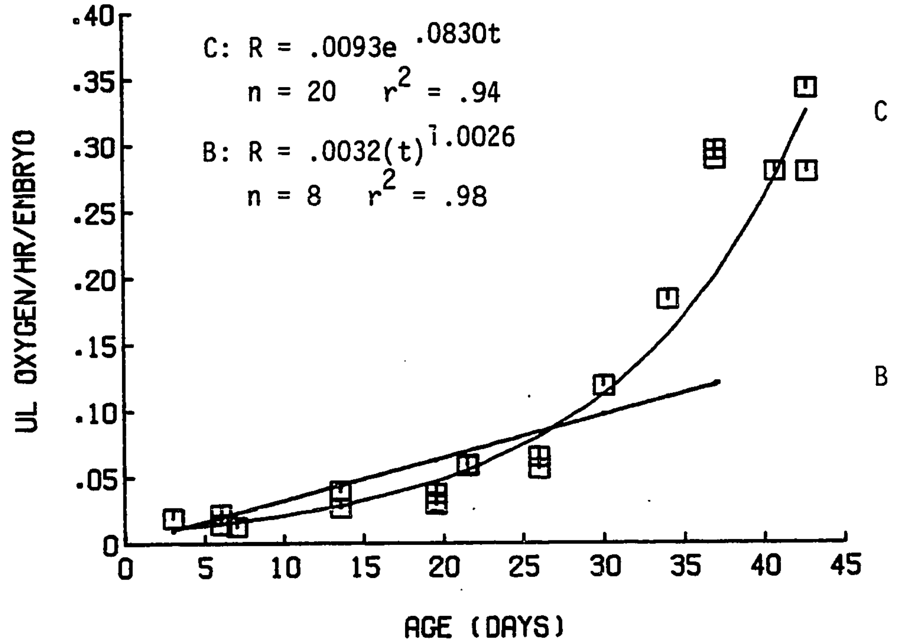


Fig. A.1. Oxygen consumption rate of copper (C) and black (B) rockfish (Boehlert and Yoklavich 1984) shown as a function of embryo age. Points plotted for copper rockfish only.

$$R = .0093e^{.08305t},$$

was then integrated, evaluated over the gestation length of 41.5 days, and multiplied by 24 hr/day. The result (81.68 ul O_2/embryo) was converted to .408 calories consumed per embryo using the oxycaloric equivalent of .005 calories/ul O_2 (Lasker 1962; Boehlert and Yoklavich 1984).

To estimate the number of calories lost per embryo during gestation it was necessary to account for the decline in both weight and caloric content. The weights of ova at fertilization (.160 mg) and (embryos at) birth (.127 mg) were estimated from age-weight regression function (Figure 10) which utilized all available data from the two-year study. The decline in caloric content was best described by a quadratic equation (Figure 14). The estimated caloric content of gonads at fertilization and birth were 6,554 and 5,419 cal/g dry weight, respectively. The estimated caloric loss per embryo was therefore estimated to be .361 calories (Table 19).

	Dry weight (mg)	Calorie content per g dry wt	Calorie content per individual
Fertilization	.160	6,554	1.049
Birth	.127	5,419	0.688
			0.361

The difference between the energy consumed (.408 cal/embryo) and energy lost (.361 cal/embryo) during gestation indicates that .047 calories/embryo, or 11.5% of the energy utilized during gestation, is contributed by the mother after fertilization.

Discussion

The estimate of 11.5% suggests that copper rockfish make a minor maternal contribution of energy during embryonic development. However, a consideration of the precision of the estimates used in obtaining this figure leads to the conclusion that we cannot reject a null hypothesis of no maternal contribution. One result of this finding was that the estimate of maternal contribution was not included in the calculation of the reproductive effort of copper rockfish in Chapter 1. A manipulation of the values within the 95% confidence intervals of the embryo weight-at-age relationship, for example, includes an equivalence between the estimates of energy consumption and loss. It is also possible that larval activity may have been artificially elevated over _in utero_ conditions. To the degree that it exists, such bias would lead to an overestimate of both oxygen consumption and maternal contribution. However, because of the similarity in methodology employed, our results can be compared directly with those of Boehlert and Yoklavich (1984) who found a substantially greater (70 vs. 12%) maternal contribution for black rockfish. Their conclusion concerning the maternal contribution in black rockfish was confirmed with additional histological data which demonstrated the active uptake of nutrients (Boehlert and Yoklavich 1984).

The development of black rockfish embryos differed from that of copper rockfish in that blacks lost proportionally less weight during gestation. Black rockfish embryos lost .0043 mg or 6.1% of their initial weight (.071 mg) whereas copper rockfish lost .033 mg or 20.6% of their weight at fertilization (.160 mg). This differential weight loss was the predominant factor responsible for the difference in the estimates of maternal contribution.

There were also some major differences in the respiration data. Integration of the respiration curves led to estimates of 54.67 and 81.68 ul O_2/embryo for black and copper rockfish, respectively. However, it is important to note that the functional form of the curves was different (Fig. A-1). The results for black rockfish were nearly linear (ul O_2/embryo/hr = $.0032t^{1.0026}$), whereas a steeply rising exponential function fitted our data. However, the respiration data presented by Boehlert and Yoklavich only included observations for the first 27 days of the 37-day gestation period. Inspection of Figure A-1 with this in mind suggests that they may have missed the dominant inflection point in the respiration data and therefore underestimated total oxygen consumption per embryo. Recent comparable work on Sebastes schlegeli has shown an exponential increase in the respiration function (Boehlert, pers. communication) similar to that found for copper rockfish. If the total respiration of black rockfish is underestimated, then the maternal energy contribution estimate may be even greater than previously reported.

Boehlert and Yoklavich (1984) described a trend in the evolutionary development of the subfamily Sebastinae toward an increasing maternal commitment to the progeny. More primitive genera probably spawned eggs shortly after fertilization (Barsukov 1981). Members of the genus Helicolenus retain eggs for longer periods of time but the length of this period varies between species (Graham 1939; Kreft 1961).

Species within the genus Sebastes are more advanced and release fully developed larvae. Direct examination of the embryonic energetics of copper and black rockfish has shown that matrotrophic viviparity does exist within Sebastes, but that there is considerable variability in the magnitude of the maternal contribution during gestation.

APPENDIX B

Introduction

The principal parameter of concern in my analysis of the reproductive effort of anchovy (see Chapter 1) is the number of batches of eggs spawned per year. Hunter and Leong (1981) report that female anchovies of average size spawn every 7 to 10 days during the peak spawning months (February to mid-April) and about 20 times per year in total. A more recent analysis considered the age dependence of reproductive effort (Anon. 1984). This work suggests that 1, 2, 3 and 4 year old fish spawn 6.8, 15.2, 22.8, and 31.9 times per year with a peak spawning frequency of 4-5 days for the older fish.

These estimates of spawning activity are based on observed frequencies of post ovulatory follicles (Hunter and Leong 1981) and hydrated eggs (Anon. 1984) from samples of adult fish. However, the adults are not uniformly distributed. There is apparently an onshore-offshore gradient and a latitudinal gradient (Picquelle and Hewitt 1983) in the size distribution of fish. In addition it appears that the composition of individuals within schools is very dynamic and changes on a daily basis in relation to spawning activity (Hunter and Goldberg 1980). Because of difficulties associated with sampling from such a non-random distribution, it is possible that the spawning frequency and spawnings per year estimates are biased.

I considered the problem from an energetics point of view. The question is, can these fish maintain the suggested rates of reproduction given their energy stores and available food. Hunter and Leong (1981) presented a brief energetics analysis and concluded that an average daily feeding rate of about 4% wet body weight/day would be sufficient to meet the energy needs of the fish. The problem with their analysis is that it was based on annual averages. However, neither the available food or the demands for energy are evenly distributed through time. Instead of using annual averages, it is therefore more appropriate to consider 1) whether the energy stores and available food are sufficient to meet the daily requirements associated with high rates of spawning activity, and if so 2) whether those rates of energy expenditure could be maintained long enough to support 20-30 spawnings per year.

Consideration of Parameter Estimates

There are numerous parameter estimates required in an energetics analysis of this type. Most of the estimates have been adequately defined and will be used (and referenced) without comment or review. Three critical parameters which have not been adequately specified are conversion efficiency, respiration rate, and daily consumption rate. Before I outline the analysis I will therefore review the best available information pertaining to these parameters.

Conversion efficiency (production/consumption) is itself dependent on ration and activity level. Hunter and Leong (1981) observed a conversion efficiency of 12.8% during feeding and growth experiments. These fish were receiving a very high ration and, as a result, grew at abnormally high rates. Under such conditions conversion efficiencies are typically low.

Boggs (unpubl. ms.) estimated conversion efficiencies for northern anchovy ranging from 0 to 38% depending on feeding rate and exercise regime. An efficiency of 12.8 percent is almost certainly too low and 38% is unreasonably high. Brett and Groves (1979) suggested that a 20% conversion efficiency is a reasonable average value for carnivorous fish and will therefore be used during this analysis, although other values will also be tabulated.

The biggest unknown in determining an average daily respiration rate is activity level in the natural environment. Estimates of either routine (unforced spontaneous activity of unfed fish) or standard (zero activity) metabolism provide minimum requirement estimates for daily caloric consumption. Boggs (unpub. MS) calculated standard respiration rates for northern anchovy by extrapolation from exercise treatments. He fit his observations of oxygen consumption to a weight specific function

$$Q_0 = 20.9 \ m^{-0.2} \ \text{cal/g wet/day}$$

where m is wet mass (g). His results suggest that fish weighing 10 and 25 g require 13.2 and 11.0 cal/g/day, respectively. These values are slightly higher than the routine metabolic rates estimated for northern anchovy by Leong (9.7 cal/g wet/day; unpublished data), and Kaupp (11.9 cal/g wet/day; unpublished data). Brett and Groves (1979) report comparable standard rates (9.3 cal/g wet/day) for 100 g sockeye salmon held at 15°C.

Boggs also conducted experiments with starved anchovy held at 17°C and exercised for 12 hrs per day at rates of 8.7 and 21 cm/sec. The observed respiration rates were 17.6 and 28.2 cal/g/day, respectively. Lasker (1970) estimated that sardines respired an equivalent of 33.6 cal/g/day if one assumes that they spend half of their time feeding or actively swimming and the other half cruising at some minimum rate. Similar estimates of caloric consumption rates were made for sardine and anchovy (25 and 29 cal/g/day, respectively) swimming at 8-10 cm/sec (Lasker, unpublished data).

There are few measures of the natural activity of anchovy in the ocean. Holliday (1977) tracked a school of fish thought to be anchovy for 40 minutes and found it to be moving at a relatively uniform rate of 45 cm/sec. Koslow (1980) noted that one of the criteria used for identifying an actively feeding school of anchovy was that it be moving at a rate of 10-40 cm/sec. Brett and Solmie (1982) estimated that the average swimming speed of herring acclimated to conditions in large net pen enclosures was 25-35 cm/sec.

Although fish in the wild are probably not actively feeding for 12 hrs per day, they are trying to forestall a potential energy deficit and therefore must be feeding for at least part of each day. The fact that fish probably have food in their stomachs much of the time suggests that respiration rates will almost always be greater than the quoted routine levels, since digestion activity will elevate metabolism. Anchovy are also involved in what must be energy intensive (i.e., highly active) spawning behavior for at least several hours every few days and are changing their patterns of distribution relative to other fish in the interim. These observations all suggest that consumption estimates from Boggs' exercise regimes probably are reasonable and may even be conservative. Ten cal/g/day must therefore be considered as an absolute minimum requirement and 24 cal/g/day was judged to be a reasonable, but by no means upper, estimate of the probable daily respiratory requirements.

There is no information concerning the natural feeding rates of northern anchovy. Laboratory work suggests that anchovy have the capacity to eat at least 5% of their own weight within one hr when presented natural food in a small tank (Boggs, pers. communication). These fish may be able to ingest such a ration twice a day, depending on their digestion rate (Sirotenio and Danileusky 1977). Anchovy clearly have a very high feeding potential, but field observations on the Black Sea anchovy Engraulis encrasicholus suggest that typical rations are often much lower. Sirotenio and Danileusky (1977) estimated feeding rates of 1.5 - 3.7% body weight/day, and Mikhman and Tamanovich (1977) observed a rate of 3.4% for the same species when feeding on zooplankton.

Zooplankton are the principle food of adult northern anchovy (Koslow 1980). However, the seasonal peak of zooplankton abundance does not occur until June (Smith and Eppley 1982) while the peak time of spawning activity occurs from early February to mid-April. This mismatch between food availability and spawning activity must be compensated for to some degree by the energy stores laid down during the previous summer.

Energy reserves built up during the previous summer are depleted during the spawning season. Lipids are the principle energy storage product (although, see discussion below concerning protein as a potential energy store) but gonads are only 18% lipid (Hunter and Leong 1981). Since lipids cannot be routinely converted to protein (Iles 1984), the often discussed concept of seasonal energy translocation is inappropriate. Instead, the lipid reserves are probably used primarily for respiration, thus permitting all assimilated energy to be channeled into gonad development. However, it is important to note that given the current scenario, fish must eat enough during the spawning season to meet the protein demands of their reproduction. For heuristic purposes, I have therefore divided the spawning season into 2 segments. As long as lipid reserves are available, the daily feeding requirement will be determined by assimilation rather than conversion efficiency. That is, since lipids can be used to meet the metabolic demands, all assimilated food can be converted to gonad production. Boggs (unpub. ms.) reported that northern anchovy lose a relatively constant 30% of consumption to egestion, excretion and SDA. I have therefore assumed that 70% of the consumed ration can be converted to tissue growth. Once the lipid reserves are gone, both metabolic and production costs must be met by feeding, in which case it is appropriate to use a conversion efficiency of around 20%.

Results

Before the daily feeding requirements can be outlined, it is necessary to estimate the size of the energy reserves (Table B.1) and the calorie content of a batch of eggs (Table B.2). Hunter and Leong (1981) determined that fat free dry weight can be related to length using a power function and that lipid content at the beginning and end of the spawning season is a fixed proportion (41 and 15%, respectively) of this weight. The difference between lipid content at the start and end of spawning defines the energy reserves. The implicit assumption is that protein content remains unchanged. Fecundity was calculated using a linear function of wet weight (see Table B.2).

A convenient result of the energetics formulation used here is that daily consumption requirement can be expressed as a direct proportion of weight. This follows from the fact that fecundity, which defines the energy demand, is estimated as a linear function of weight, and that the conversion efficiencies are considered to be independent of size. As a result consumption can be expressed as percent body weight per day. No additional corrections for size or age differences are required. The consumption requirements of all fish therefore can be conveniently tabulated since they depend only on assumptions concerning spawning frequency and conversion efficiency (see Fig. B.1, Table B.3 and B.4).

As long as the energy stores last, daily feeding requirements are estimated to be between 1.6 and 4.1% (Table B.4). A critical question then is how long the energy reserves be expected to last. Given the

Table B.1. Methods for estimating the quantity of available energy storage products (lipids) for some representative sizes of northern anchovy. Lengths used are the average of 2 successive length at age estimates (Spratt 1975).

Age	Length	Fat free(1) Dry weight	Lipid weight (2) At 41%	At 15%	Lipid loss (g) during spawning	Caloric(3) equivalent
1+	102	D = 1.78	F = 1.24	.31	.93	8581
2	118	2.84	1.97	.50	1.47	13564
3	129	3.78	2.63	.67	1.96	18085
4	140	4.90	3.41	.87	2.54	23437
5	150	6.11	4.25	1.08	3.17	29250

(1) Equation 2, Hunter and Leong 1981

(2) 15%: $F = \frac{.15D}{.85}$, 41%: $F = \frac{.41D}{.59}$

(3) 9227 cal/g (Hunter and Leong 1981)

Table B.2. Estimates of batch fecundity and suggested annual reproductive energy expenditures of northern anchovy.

Age	Wet(1) weight (g)	Batch(2) fecundity	Egg(3) batch weight (mg)	Egg(4) batch calories	Batches/(5) year	Calories spawned/ year
1	9.76	5308	160	871	6.8	5922
2	15.56	8649	260	1419	15.2	21567
3	20.70	11610	350	1905	22.8	43423
4	26.83	15141	456	2484	31.9	79232
5	33.45	18954	571	3109	31.9	99186

(1)Equation 1 using 15% lipid (F) (Hunter and Leong 1981).
(2)Fecundity = -313.4+576 (wet weight) (Hunter and Leong, pers. comm.).
(3)1 egg = .0301 mg (Hunter and Leong 1981).
(4)Ovaries = 5450 cal/g (Hunter and Leong 1981).
(5)Anon. (1984).

Table B.3. Sample of the method used for calculating daily consumption requirements for northern anchovy. (see Table B.4 and Figure B.1.)

Age: 4+
Length: 140 mm
Wet weight: 26.83 g
Fecundity: 15141 eggs = 2484 cal
Spawning frequency: 7 days
Conversion efficiency: .20

$$2484\ \text{cal}/7\ \text{days} = \frac{355\ \text{cal/day}}{.20} = \frac{1774\ \text{cal consumed/day}}{5252\ \text{cal/gdw copepods}} = \frac{.338\ \text{gdw/day}}{.153\ \text{gdw/gww}}$$

$$= 2.208\ \text{gww/day}$$

$$\frac{2.208\ \text{gww/day}}{26.83\ \text{gww}} = 8.2\%/\text{day}$$

Table B.4. Daily consumption requirement (% wet body weight/day) for different spawning frequencies (days between successive spawning) and conversion efficiences for northern anchovy. (See Table B.3 for method of estimation).

Efficiency		Spawning frequency			
		4	5	7	10
	.1	28.8	23.0	16.5	11.5
Assumed production efficiency -	.2	14.4	11.5	8.2	5.8
	.3	9.6	7.7	5.5	3.8
	.4	7.2	5.8	4.1	2.9
	.5	5.8	4.6	3.3	2.3
	.6	4.8	3.8	2.7	1.9
Assumed assimilation efficiency -	.7	4.1	3.3	2.4	1.6
	.8	3.6	2.9	2.1	1.4
	.9	3.2	2.6	1.8	1.3

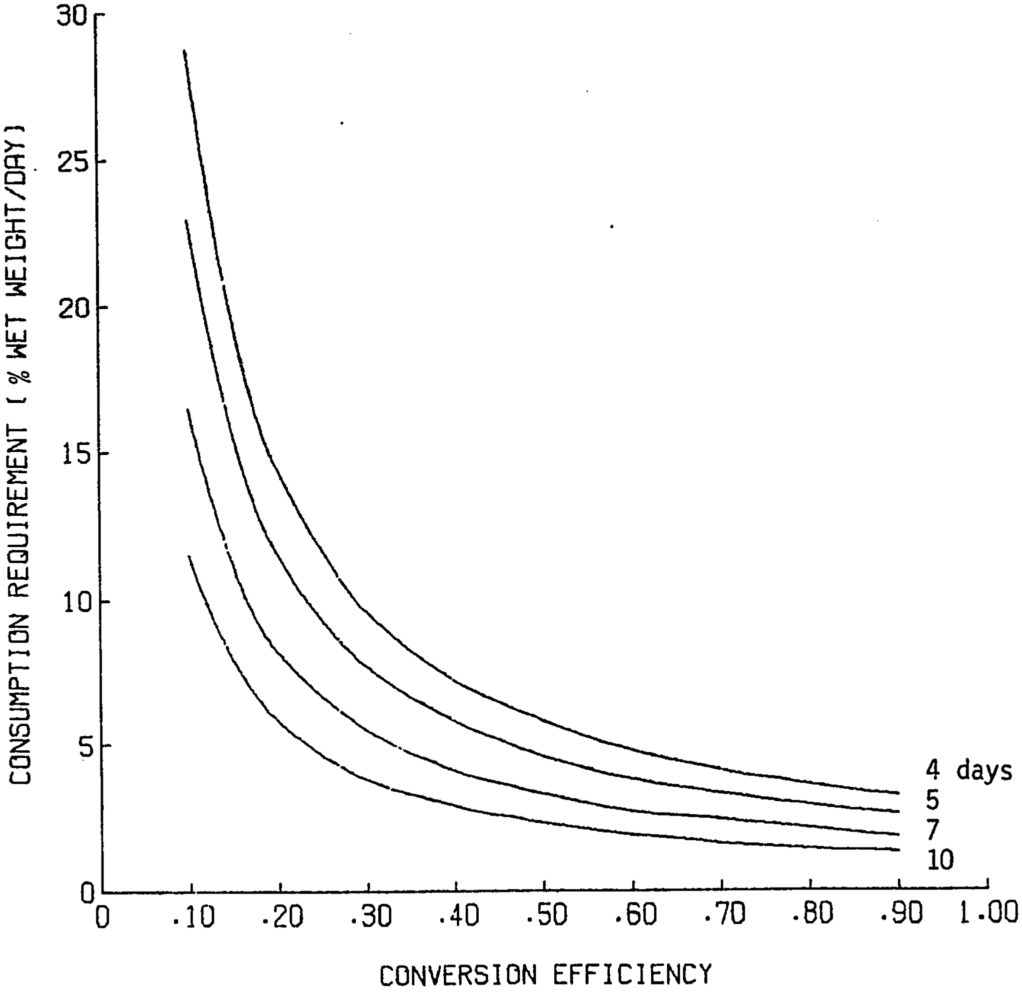


Fig. B.1. Daily consumption requirements (% wet body weight/day) for different spawning frequencies (4, 5, 7 and 10 days between successive spawnings) and conversion efficiencies (.10-.90) for northern anchovy. (See Table B.3 for method of estimation.)

methods of calculation (Table B.5), this too is independent of size since both the magnitude of the lipid stores and the respiration rate (expressed as cal/g/day) are directly proportional to weight. For respiration rates of 10 and 24 cal/g/day, the lipids can be expected to last 87 and 36 days, respectively.

Discussion

The results of this analysis are necessarily inconclusive simply because of the number of unknowns. I believe it is safe to conclude that anchovy can spawn 6-10 times per year. Thirty-two times per year seems far less plausible since it would require that one accept the most favorable estimates of all assumptions.

To accomplish the first 20 of the 32 spawnings at a frequency of every 5th day would require 100 days. The lipid reserves would last 87 days at most, (assuming only sustained routine metabolism throughout, i.e., 10 cal/g/day) if the fish could feed at an average rate of 3.3% per day. Once the lipid reserves were exhausted the required feeding rate would jump to 11.5%. Twelve additional spawnings would have to be spread out during the remainder of the year. Obviously, if fish can feed at an average rate greater than 3.3% per day throughout the spawning season, lipid store depletion would be forestalled.

Given the available data, I believe that 24 cal/g/day is a more reasonable estimate of the respiration rate and, if so, it calls into question the ability of the average fish to spawn even 20 times per year. The lipid reserves would only last on the order of 36 days. Even at a spawning frequency of 4 days (which would require a daily

Table B.5. Method for calculating the length of time that energy stores will last for northern anchovy for two different daily respiration rates (10 and 24 cal/g/day) demonstrating that the outcome is independent of size.

Age	Wet weight (g)	Lipid[1] stores (cal)	Daily respiration requirement (10 cal/g/day)	Daily respiration requirement (24 cal/g/day)	Length of time at 10 cal/ g/day	Length of time at 24 cal/ g/day
1	9.76	8529 = a	97.6 = b	234.2 = b	a/b =87.4	36.4
5	33.45	29250	334.5	802.8	87.4	36.4

[1] See Table B.1.

feeding rate of 4.1%), fish could release only 9 batches of eggs before the lipid stores would be depleted. Thereafter, the feeding rates required to maintain spawning frequency rates of even 7-10 days are 6-8% body weight/day.

One further point that needs to be made is that the analysis has yet to include provisions for somatic growth. It is probably reasonable to assume that there is no growth during the peak months of the spawning season (February - mid-April). Collins and Spratt (1969) indicate that ring formation on otoliths occurs during late spring and that by June 1, nearly all otoliths have newly completed rings. It is probable, therefore, that growth rates begin to increase in late April and May, and that the change in growth rate is related to the decrease in spawning frequency.

The continued presence of small quantities of eggs and larvae in the environment through the summer indicates that fish do continue to spawn. However, the frequency of spawning must be greatly reduced since there are significant demands for somatic growth and energy store accumulation. The annual somatic growth increment is a decreasing proportion of size, but in absolute terms is actually relatively constant. That is, net growth is about 6.0 g wet weight per year for all ages (see Table B.2). The approximate gain in calories per year can be calculated by comparing the weight gain of fish that are at the end of their spawning cycles in subsequent years. The water and calorie content of spent fish are 79% and 4894 cal/g (.85 x 4129 + .15 x 9227 = 4894), respectively (Hunter and Leong 1981). The annual net caloric growth increment is therefore about 6166 cal (6.0 g ww x .21 g dw/g ww x 4894 cal/g dw = 6166 cal). Although the above calculations account for net growth, energy stores that will be needed for spawning the following year must also be accumulated. These are a constant proportion of size and range in magnitude from about 8500 cal to 29000 cal depending on the age of the fish (Table B.1). This growth must be accumulated using a 20% conversion efficiency and most of the production probably occurs during a 5-month growing season (June-October). If one averages this growth over 150 days, the daily feeding requirements just for meeting the growth demands are still on the order 5% body weight/day. Feeding conditions are presumably better during the summer and apparently fish can routinely feed at this rate. But spawning in the summer must depend on the frequency of encounter of unusually rich feeding conditions. However, the point is, that once tissue growth begins, the spawning frequency will necessarily be greatly reduced.

The number of spawnings per year is critical to my estimates of the annual reproductive effort of anchovy. Because the above analysis suggests that current estimates of number of spawnings per year may be unrealistic, I have excluded this point from the correlation analysis relating mortality to reproductive effort. If the point were to be included, it would be an outlier. The plot (Figure 15) suggests that reproductive effort was overestimated by a factor of about 2, (assuming 20 spawnings per year).

One of the implicit assumptions of the analysis of Hunter and Leong (1981) and thus this analysis is that protein (as indexed by fat-free dry weight) is constant and therefore does not play a role as an energy storage product. This may in fact be erroneous and an inclusion of protein in the analysis could make some of the suggested spawning rates more plausible. Apparently there are no data available that can be used to address the question of protein utilization (Hunter pers. comm.). However, it would be fairly easy to conduct the analysis by determining the proximate composition of size stratified samples of fish taken before and after the peak spawning season.

Obtaining estimates of respiration rates of fish in a natural setting will continue to be a problem. However, estimates of daily feeding rates during different times of the year could be obtained using routine methods of gut content and digestion rate analysis. Such estimates would be of considerable value in conducting a more refined energetics analysis of potential annual reproductive output.

A final parameter that may be of some importance in this analysis is the dry weight-wet weight conversion for food items. Hunter and Leong (1981) have used a value of .153 which is apparently appropriate for copepods. Boggs (unpub. MS) quotes an estimate of .21 for euphasiids. The use of a higher dry-wet conversion factor could lead to a significantly lower estimated daily consumption requirement (see Table B.4). Better definition of the diet composition and the appropriate conversions would therefore be of considerable value.

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