Indirect estimates of natural mortality rate for arrowtooth flounder (*Atheresthes stomias*) and darkblotched rockfish (*Sebastes crameri*)

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Indirect estimates of instantaneous natural mortality rate (M) are widely used in stock assessment and fisheries management. They are essentially a form of meta-analysis, in which prior information on M and key life history parameters from a variety of stocks is used to estimate M for the stock in question.

In this study we report indirect estimates of M for arrowtooth flounder (*Atheresthes stomias*) and darkblotched rockfish (*Sebastes crameri*) obtained by the methods described in Gunderson (1997), and a modification of Pauly's method (1980), and compare them with estimates previously derived by Hoenig's (1983) method. Pauly's original method was based on the correlation of M with von Bertalanffy growth parameters (K and L_∞) and temperature. The modification we used was indicated by a number of reviews of Pauly's data (Charnov, 1993; Pascual and Iribarne, 1993; Jensen, 1996) and relies only on the correlation between M and K. The high correlation between these variables has been observed in a number of taxa and is the basis for the M–K "invariant" used widely in life history theory (Beverton, 1992; Charnov, 1993).

Gunderson's method is based on the high correlation between reproductive effort and natural mortality rate and has a well-established basis in experimental ecology and life history theory (Reznick, 1996). Increases in reproductive effort often come at a cost, and trade-offs between reproductive effort and adult growth or survival have been reported in a wide range of field studies and manipulation experiments (Roff, 1992; Stearns, 1992). Gunderson (1997) found a linear relationship (r^2=0.75) between M and reproductive effort as measured by the gonadosomatic index (GSI=ovary weight/somatic body weight) for 28 stocks of fish, and theoretical analysis (Charnov et al., 2001; Charnov, 2002) has shown that this equation can be a predictable result when maximizing the lifetime production of young.

Pascual and Iribarne (1993) noted that one shortcoming of indirect methods of estimating natural mortality is that no variance estimate is usually associated with the predicted value of M. In this study, we used the delta method (Seber, 1982) to derive estimates of the variance of predicted values of M using Gunderson's technique and Jensen's (1996) modification of Pauly's technique. In the case of the method developed by Hoenig, where natural mortality is estimated from longevity, no comparable variance estimator could be obtained because the results depend on the sample size used to estimate longevity (Hoenig, 1983).

Materials and methods

Data on darkblotched rockfish were collected in 1986 and 1987 during research surveys conducted off the Oregon coast (43°10′–45°50′) aboard commercial groundfish and shrimp trawlers. Fish were weighed to the nearest gram, and fork length was measured to the nearest millimeter. Gonads were removed and weighed to the nearest 0.01 g. Gonad color, size, and structure were recorded for each specimen, and macroscopic observations were made at sea for the presence of fertilized eggs, eyed larvae, and residual larvae in the ovaries. Gonads were preserved in 10% phosphate-buffered formalin and histological analysis was conducted later in the laboratory for selected specimens. It was assumed that the ovaries collected during November–January were fully mature because oocyte fertilization occurs during December–February (Nichol, 1990). Only mature females (36.7 cm or greater) classified as being in the "vitellogenesis" stage (Nichol and Pikitch, 1994) during November–January (n=28) were used to estimate the parameters for the length–ovary-weight relationship, and fish collected during August–November were added when estimating the length–somatic-weight relationship (total n=86).

Data on arrowtooth flounder were collected from research trawls made during September 1993 on Portlock Bank near the eastern end of Kodiak Island, Alaska (Zimmermann, 1997). Fish (less stomach contents) were weighed (+/–2 g) and fork length (cm)

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was obtained. Gonads were assigned a macroscopic maturity stage based on external appearance, and were removed and preserved in 10% formalin buffered with sodium acetate. Gonads were subsequently removed from formalin, weighed (+/–0.001 g) in the laboratory, and classified histologically to maturity stage. Only mature females (47 cm and greater) with ovaries in the "migratory nucleus" stage (Zimmermann, 1997) were used in estimating the length–ovary-weight relation (n=19), and fish in the "late vitellogenesis" stage were added when estimating the length–somatic-weight relation (total n=59).

A fresh-weight to formalin-weight conversion equation for gonads was obtained by collecting 22 females during a research cruise conducted during late October and early November 1999 off Oregon and northern California. Gonads for these specimens were weighed fresh at sea (+/– 2 g) and again after being stored for 1–4 months in 10% formalin buffered with sodium bicarbonate (+/–0.001 g). Fresh ovary weights for these specimens ranged from 2 to 500 g. The equation for conversion of fresh weight to formalin weight obtained by linear regression was

$$\textit{Fresh weight} = 1.04305\ (\textit{formalin weight}) + 1.82277 \qquad (P<0.001)$$

and was used to correct all arrowtooth flounder ovary weights to fresh weights.

The length–somatic-weight (where somatic weight=total weight minus gonad weight) and length–ovary-weight relationships for both species followed allometric ($y=aX^b$) relationships and were fitted by using nonlinear regression (EXCEL SOLVER, Microsoft Corp., 1998). The relation of length to GSI (gonadosomatic index=ovary weight/somatic weight) was fitted to an allometric relationship because the ratio of two allometric relationships will also be an allometric relationship. The length-GSI relationship was then used to predict the GSI for a mature female of average size in the population.

The average size of a mature darkblotched rockfish was estimated to be 42.7 cm, based on the size composition of females greater than 36.5 cm (the size at 50% maturity, Nichol and Pikitch, 1994) during the 1977 NMFS trienniel trawl survey (Rogers[1]). There is no directed fishery for arrrowtooth flounder, and they have been exploited only lightly. As a result, the average size of a mature (47 cm or greater; Zimmermann, 1997) arrowtooth flounder was estimated to be 55.5 cm, based on the size composition in the 1999 NMFS trawl survey, which covered their entire size range with a single gear type (Brown[2]).

The instantaneous rate of natural mortality was estimated from the equation M=1.79 GSI developed by Gunderson (1997). The variance of this estimate was estimated using the delta method to obtain

$$\mathrm{Var}(\hat{M}) = \mathrm{Var}(\hat{k}\,\hat{GSI}) = (\hat{GSI})^2\,\mathrm{Var}(\hat{k}) + \hat{k}^2\,\mathrm{Var}(\hat{GSI}),$$

$$\mathrm{Var}(\hat{GSI}) = \left[ef(\overline{L}_m)^{f-1}\right]^2 \mathrm{Var}(\overline{L}_m) + (\overline{L}_m^{2f})\mathrm{Var}(e)$$

$$+\left[e\,\overline{L}_m^f \ln(\overline{L}_m)\right]^2 \mathrm{Var}(f) + (2\overline{L}_m^f)\left[e\overline{L}_m^f \ln(\overline{L}_m)\,\mathrm{Cov}(e,f)\right];$$

$$\mathrm{Var}(\hat{k}) = \frac{s^2}{\sum (GSI_i - \overline{GSI})^2} \quad \text{(Draper and Smith, 1981) = 0.03389)}$$

where L_m = mean length of a mature female in the unexploited population;

e,f = coefficients in the length-GSI relationship (GSI=eL^f);

s^2 = residual mean square from GSI-M regression equation (Gunderson, 1997);

$\hat{GSI}$ = mean value of GSI used to predict M in this study;

$\overline{GSI}$ = mean value of GSI in regression sample (Gunderson, 1997);

GSI_i = GSI value for i^{th} species in the regression sample; and

$\hat{k}$ = constant from the GSI-M regression = 1.79.

The Var (e), Var (f), and Cov (e,f) terms in Var ($\hat{GSI}$) were estimated from the variance-covariance matrix of a nonlinear regression algorithm for the length-GSI relationship by using S-PLUS (Venables and Ripley, 1997). The Var($\overline{L}_m$) term was estimated from the length-frequency data used to estimate $\overline{L}_m$.

Indirect estimates of M were also obtained using a modification of Pauly's (1980) method. Jensen (1996) showed that in terms of either the standard error or proportion of variation in predicted M, the simple linear regression of M on the von Bertalanffy growth parameter K is as good as a multiple linear regression model that includes asymptotic size and temperature. The correlation between M and K is a predictable result from life history theory when optimizing the trade-off between survival and fecundity (Jensen, 1996), and has been shown to occur in a wide variety of invertebrate and vertebrate groups (Beverton, 1992; Charnov, 1993).

Pauly's (1980) data for 175 stocks of fish were used to estimate the coefficient ($\hat{g}$=1.598; r^2=0.72) in the equation $M=\hat{g}K$. Estimates of K were obtained by fitting age-length data (sexes combined) for 3930 darkblotched rockfish and 706 arrowtooth flounder to the Von Bertalanffy growth model (Ricker, 1975) by using a nonlinear regression algorithm in AD Model Builder (Fornier, 2001;Wilderbuer[3]). The variance of the estimates was estimated with the delta method to be

$$\mathrm{Var}(M) = \hat{g}^2\mathrm{Var}(K) + K^2\mathrm{Var}(\hat{g}).$$

The Var(K) term was estimated by using AD Model Builder, and Var($\hat{g}$) was estimated by using Pauly's data, and the same method used above to estimate Var($\hat{k}$) (Draper and Smith, 1981).

[1] Rogers, J. B. 2001. Personal commun. Northwest Fisheries Science Center, 2030 SE Marine Science Dr., Newport OR 97365.

[2] Brown, E. S. 2002. Personal commun. Alaska Fisheries Science Center, 7600 Sand Point Way NE, Seattle, WA 98115.

[3] Wilderbuer, T. K. 2002. Personal commun. Alaska Fisheries Science Center, 7600 Sand Point Way NE, Seattle, WA 98115.

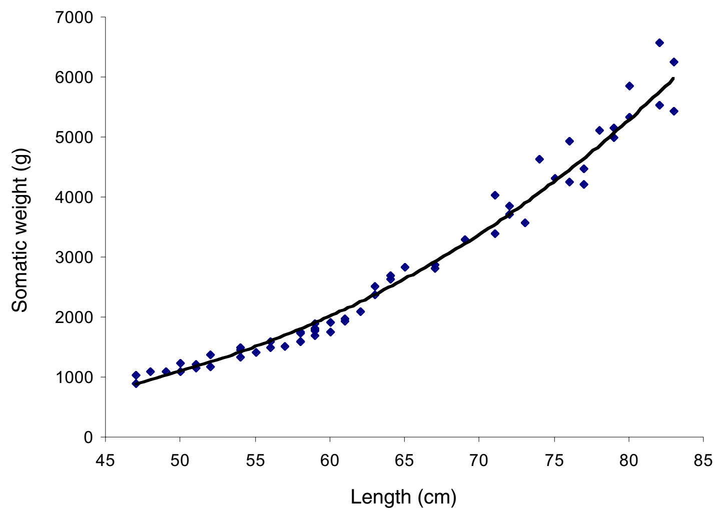

Figure 1

Length–somatic-weight relationship for arrowtooth flounder (*Atheresthes stomias*).

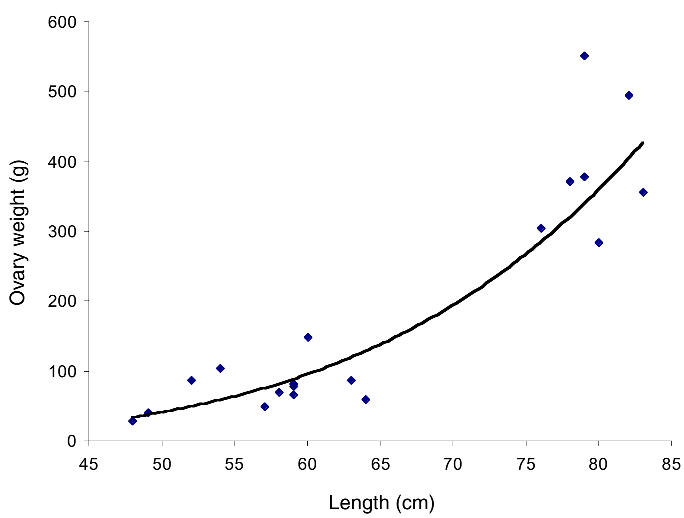

Figure 2

Length–ovary-weight relationship for arrowtooth flounder (*Atheresthes stomias*).

Results

The length–somatic-weight and length–ovary-weight data for arrowtooth flounder (Figs. 1 and 2) and darkblotched rockfish (Figs. 3 and 4) both conformed to allometric relationships. Length–somatic-weight data for both species conformed closely to the model fitted to them (r^2=0.90–0.98, Table 1). The data for the length–ovary-weight relationship conformed to the fitted line reasonably well for arrowtooth flounder (r^2=0.85) and only moderately well for darkblotched rockfish (r^2=0.65). Although sample sizes for ovary weight data were low for both species (n=19–28), the histological classifications available for arrowtooth flounder helped to assure that all fish collected were fully mature and to minimize the scatter about the length–ovary-weight relationship. The scatter about the length-GSI relationships for both species (Figs. 5 and 6) was relatively high (r^2=0.32 for arrowtooth and 0.36 for darkblotched rockfish). The GSI estimates for both species were at the lower end of the distribution of the GSI and M values used to develop the original predictive relationship (Fig. 7).

Indirect estimates of the instantaneous rate of natural mortality were estimated to be M = 0.08 for arrowtooth flounder with the gonadosomatic index and 0.11 with the growth coefficient K (Table 1). Corresponding estimates for darkblotched rockfish differed more substantially (M=0.11 with the gonadosomatic index and 0.30 with K). Precision for the estimates of M was higher for the estimates based on K (CV=5 to 12%) than for those based on the gonadosomatic index (CV=17%).

Table 1

Estimates of instantaneous natural mortality rate (M) using the gonadosomatic index (GSI), von Bertalanffy growth coefficient (K), and maximum age. Allometric coefficients are shown for length–ovary-weight ($y=aL^b$), length–somatic-weight ($y=cL^d$), and length-GSI ($y=eL^f$) relationships. CI = approximate 95% confidence interval.

	Arrowtooth flounder	Darkblotched rockfish
Mean length (cm)	55.5	42.7
a	0.000000591	1.33E-09
b	4.62	6.57
r^2	0.85	0.65
n	19	28
c	0.0022	0.0322
d	3.35	2.82
r^2	0.98	0.90
n	59	86
e	0.000422	0.00000154
f	1.16	2.82
r^2	0.32	0.36
n	19	28
GSI	0.045	0.0598
VAR (GSI)	0.0000344	0.0000705
M (Gunderson)	0.081	0.107
VAR (M)	0.00018	0.00035
SE (M)	0.0134	0.0186
CI	0.054–0.108	0.07–0.144
K	0.0701	0.1852
Var (K)	0.000060	0.0000085
M (Jensen)	0.112	0.296
Var (M)	0.000175	0.000175
SE (M)	0.0132	0.0132
CI	0.09–0.14	0.27–0.32
Max. age (yr)	23	105
M (Hoenig)	0.18	0.05

Discussion

An estimate of Z=0.18 was previously obtained for arrowtooth flounder by using Hoenig's (1983) relationship between total instantaneous mortality rate (Z) and maximum age in 84 stocks of fish, and an estimated maximum age of 23 years (Turnock et al.[4]). Because this stock has been exploited only lightly, it was assumed that the resulting estimate of Z was equivalent to M. The resulting estimate was somewhat higher than the value obtained from reproductive effort (M=0.08) or K (M=0.11) and outside the approximate 95% confidence limits (±2SE) for both estimates (Table 1).

A range of maximum ages (60 to 105 years) was previously used to obtain estimates of Z (assumed to be approximately equal to M) = 0.025–0.05 for darkblotched rockfish based on Hoenig's method, due to uncertainties in age determination (Rogers et al.[5]). An estimate of M=0.05 provided the best fit to a population dynamics model, although it is somewhat lower than the estimate of M=0.11 obtained in this study with the gonadosomatic index and substantially lower than the estimate of M=0.30 with the growth coefficient K. The estimate obtained with Hoenig's method was once again outside the approximate 95% confidence limits for the other indirect estimates.

Although none of the data on somatic and ovary weights were collected with the specific aim of estimating natural mortality, they served to provide a reasonable estimate of M for arrowtooth flounder and a first approximation of this parameter for darkblotched rockfish. More detailed histological data on the ovaries used in the darkblotched rockfish analysis would have improved the reliability of this estimate and a larger sample size of mature ovaries for both species would have been preferable.

The estimates of M derived from the growth coefficient K (Table 1) were obtained by using age-length data for sexes combined because most of the original data (Pauly, 1980) was in this format. However, because of sexual dimorphism in growth, estimates of M would have differed if males and females had been treated as separate "stocks" as was done for 33 of the observations in Pauly's database. Sexual dimorphism was substantial for arrowtooth flounder, where K was 0.194 (corresponding to an estimated M=0.31) for males and 0.065 (M=0.10) for females and was less pronounced in darkblotched rockfish, where K was 0.211 (M=0.34) for males and 0.164 (M=0.26) for females. Averaging these sex-specific estimates would not change

[4] Turnock, B. J., T. K. Wilderbuer, and E. S. Brown. 1999. Arrowtooth flounder. *In* Stock assessment and fishery evaluation report for the groundfish resources of the Gulf of Alaska, p. 226–253. North Pacific Fishery Management Council, Anchorage, AK.

[5] Rogers, J. B., R. D. Methot, T. L. Builder, K. Piner, and M. Wilkins. 2000. Status of the darkblotched rockfish (*Sebastes crameri*) resource in 2000. *In* Stock assessment and fishery evaluation: appendix to the status of the Pacific Coast groundfish fishery through 2000 and recommended acceptable biological catches for 2001, 71 p. Pacific Fishery Management Council, Portland, OR.

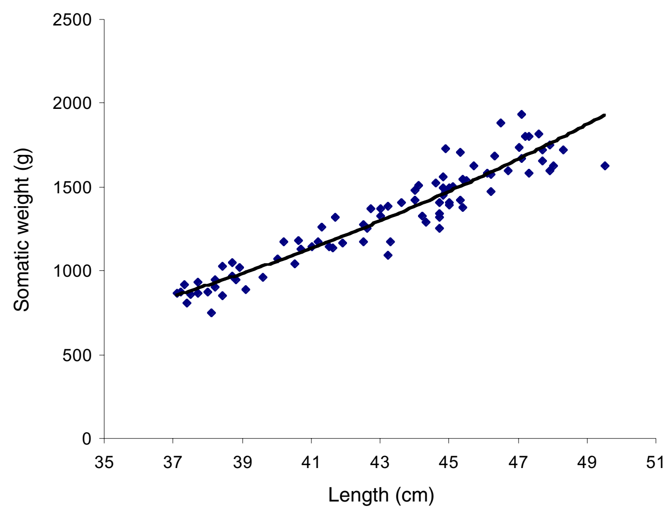

Figure 3

Length–somatic-weight relationship for darkblotched rockfish (*Sebastes crameri*).

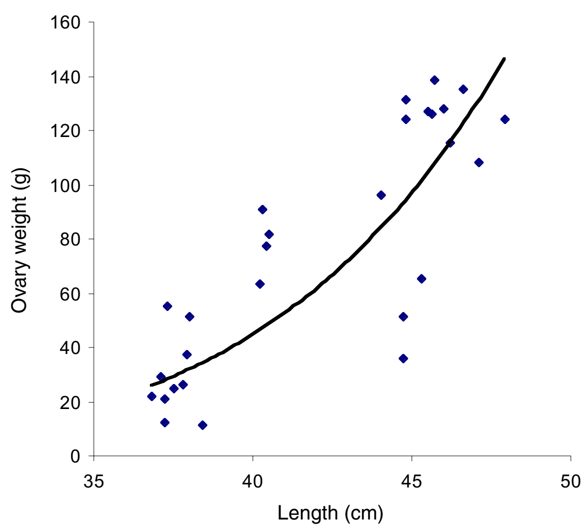

Figure 4

Length–ovary-weight relationship for darkblotched rockfish (*Sebastes crameri*).

the darkblotched estimate of M appreciably from what was obtained by pooling the age-length data to estimate a common K, but the estimate for arrowtooth flounder would increase from 0.11 to 0.21.

All indirect methods of estimating M rely on the correlation established in their basic data set (28 fish stocks for Gunderson, 175 for Pauly, and 84 for Hoenig). As a result these methods are subject to bias in the estimates of M, K, maximum age, and reproductive effort in the original correlation data, and in the estimates of these parameters being used to extrapolate the correlations to new species. Although Pauly's database is the most extensive (in terms of the number of stocks available), age determination and stock assessment methods have improved in the years since it was initially compiled, and estimates of M have tended to decline. An updated database would probably reduce the estimates of M based on K.

The estimate of maximum age required by Hoenig's method assumes that the age determination technique being employed is unbiased. Validating this assumption is of-

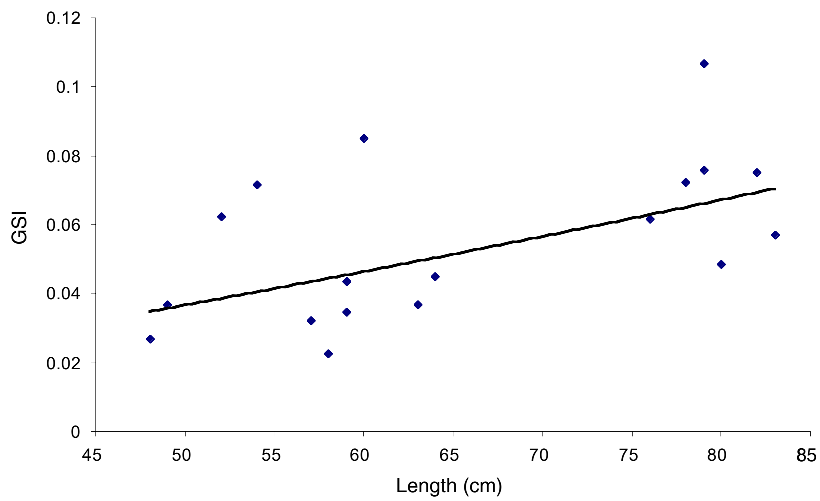

Figure 5

Length-gonadosomatic index (GSI) relationship for arrowtooth flounder (*Atheresthes stomias*).

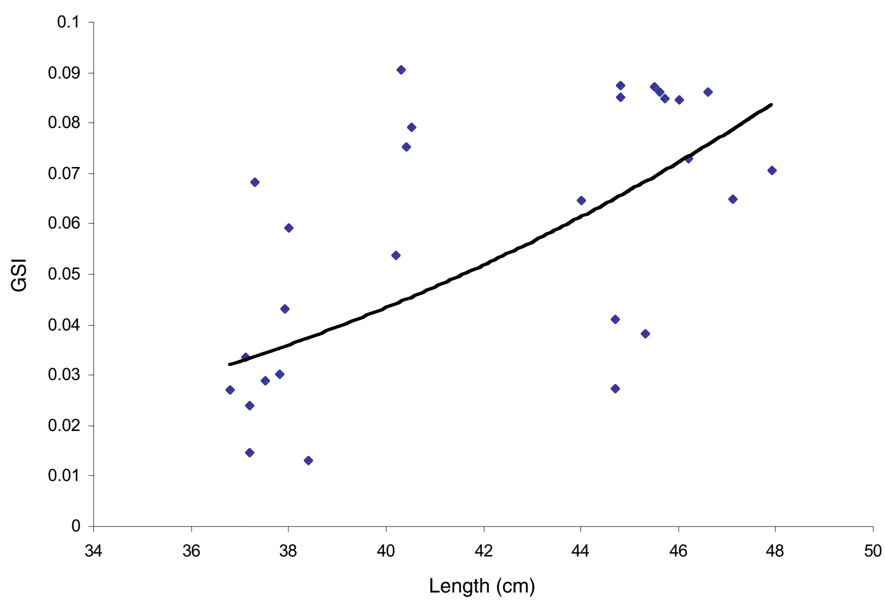

Figure 6

Length-gonadosomatic index (GSI) relationship for darkblotched rockfish (*Sebastes crameri*).

ten difficult for the older, more difficult-to-age individuals but can be accomplished by using a variety of techniques ranging from marking to analysis of radioactive isotopes (Lai et al., 1996). The estimate of longevity is also dependent on sample size and previous fishing history. Hoenig (1983) showed that maximum age tends to increase slowly with increasing sample size after about 200 individuals have been examined, but longevity has probably declined from historical levels because of fishing, particularly in the case of the darkblotched rockfish. A small sample size for age determination, underaging, and previous exploitation would all result in an overestimate of M with Hoenig's method and might explain some of the difference between the estimate of arrowtooth flounder mortality based on reproductive effort or K (M=0.08–0.11) and the previous estimate (M=0.18).

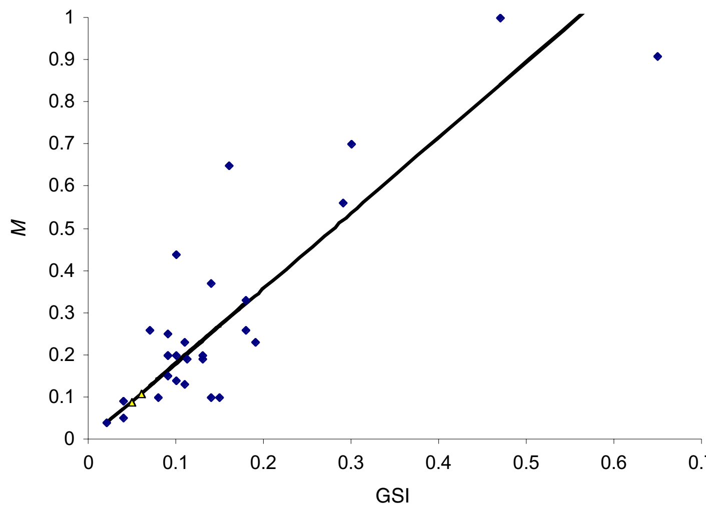

Figure 7

Location of arrowtooth flounder *Atheresthes stomias*) and darkblotched rockfish (*Sebastes crameri*) (open triangles) in relation to the data set for gonadosomatic index (GSI) and natural mortality rate (M) used to obtain the predictive relation between them (Gunderson, 1997).

In the case of darkblotched rockfish, the estimate of mortality based on reproductive effort (M=0.11) was actually higher than the estimate based on longevity (M=0.05), and neither undersampling nor underaging would explain the differences. Overestimation of the gonadosomatic index (and the estimated M) by using macroscopic rather than histological criteria to classify maturation stage may explain the higher estimate but seems less likely than underestimating it because several oocyte size classes that might be included in the "vitellogenesis" stage are not fully developed. Underestimation of the mean length of a mature female could also lead to an estimate of GSI (and M) that is too low, but estimates of GSI are relatively insensitive to length. For darkblotched rockfish, the mean length of a mature female would have to be 32.4 cm (below the size at maturity) in order for M to equal 0.05.

Indirect estimates of M offer access to a meta-analysis that can be used to explore consistency of natural mortality estimates with prior knowledge on a variety of stocks and put these estimates in the broader context of life history theory. The use of several alternative indirect techniques can minimize bias in stock assessment and expose any misconceptions or errors regarding reproductive biology or age determination at an early stage in a stock assessment program.

Bias is clearly a more important problem than precision when using indirect methods to estimate M. Each of the methods used in our study has a firm basis in life history theory (the M–K and M–GSI "invariants") or population dynamics (Z≈1/maximum age), and when derived from a database for a large number of species, they can be relatively precise (CV=5–17% for the estimates made in this paper). Nevertheless, many of the original data points on which these relationships are based have become outdated as improved methods of age determination and stock assessment have come into wide usage and ignoring these outdated data points can lead to significant bias when using them to estimate M. Indirect methods are widely used, and it is important that the databases from which they are derived be continually updated and expanded as new information becomes available.

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