

Influence of fecundity on recruitment variability of marine fish

G. Mertz and R.A. Myers

Abstract: It has often been contended that the strong variability of recruitment in marine fish populations is a consequence of their large fecundities. To test this proposal, a simple linear relationship is derived linking the standard deviation of log-recruitment for a species to its log-fecundity, and a specific prediction of the slope coefficient is provided. This result is tested using all available data for major marine fish stocks. We found that the derived relationship approximately predicts the ratio of recruitment variability to log-fecundity for the centroid of the cluster of data points, but the scatter about the centroid is so great that no significant relationship exists between recruitment variability and log-fecundity.

Résumé : On a souvent soutenu que la forte variabilité du recrutement des populations de poissons marins était une conséquence de leur grande fécondité. Pour vérifier cette hypothèse, nous avons établi une relation linéaire simple qui lie l'écart-type du logarithme du recrutement pour une espèce au logarithme de sa fécondité, et nous donnons une prédiction spécifique du coefficient de la pente. Nous testons ce résultat avec toutes les données disponibles sur les principaux stocks de poissons marins. Nous avons trouvé que la relation dérivée prédit approximativement le taux de variabilité du recrutement par rapport au logarithme de la fécondité pour le centroïde de la grappe de données ponctuelles, mais la dispersion autour du centroïde est si grande qu'il n'existe aucune relation significative entre la variabilité du recrutement et le logarithme de la fécondité.

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Introduction

Much of fisheries science has revolved around the recruitment problem, that of discerning the factors underlying the large variations in year-class strength. It is commonly held (e.g., Houde 1987; Sale 1990; Pepin and Myers 1991; Koslow 1992) that the strong recruitment variability in marine fish is a consequence of high fecundity, or, equivalently, high total mortality from egg to recruit.

In this paper we formulate a simple equation linking recruitment variability of a species to its fecundity. This equation contains one empirical constant, relating variability of mortality to mean mortality (Bradford 1992), and it makes specific predictions of the slope of a scatter plot of the standard deviation of log-recruitment ($\sigma_{\ln R}$) versus the logarithm of fecundity. The prediction of this equation is compared with results from regressions of $\sigma_{\ln R}$ on log-fecundity, for all available marine fish species and for various taxonomic categories.

Data and methods

The data on recruitment variability were taken from the data base described in Myers et al. (1995). Briefly, Myers et al. (1995) attempted to compile all available data on spawner abundance and recruitment for marine, anadromous, and freshwater species. Spawning stock biomass and recruitment were estimated from dedicated research vessel surveys and by sequential population analysis (SPA) of

commercial catch-at-age data. SPA techniques include virtual population analysis (Gulland 1965), cohort analysis (Pope 1972), and related methods that reconstruct population size from catch-at-age data (Deriso et al. 1985, 1989; Gavaris 1988; Megrey 1989). Although the focus is on populations that are strictly marine, to extend the range of fecundity we include anadromous species for which reliable data are available. (We do not examine freshwater species because our analysis relies on a regression (Bradford 1992) that did not include freshwater populations.) We only had one set of data for an elasmobranch, spiny dogfish (*Squalus acanthias*), which had a much lower fecundity than any other species examined. The estimate of recruitment for this population was based upon research vessel estimates that may overestimate the recruitment variability (Silva 1993); we should not put too much weight on this estimate. See Myers and Barrowman (1996) for a listing of the individual stocks used in the analysis.

Two estimates of recruitment variability were examined: the standard deviation of log-transformed recruitment estimates, and the standard deviations of log residuals from a Ricker spawner recruitment function. Maximum likelihood was used to estimate the parameters of the spawner recruitment function under the assumption that the variability in recruitment for any spawner abundance was log-normally distributed (see Myers et al. (1995) for details). Similar estimates of the variability were obtained if alternative spawner recruitment functions were used.

Fecundity estimates were obtained from literature reviews, e.g., Scott and Scott (1988) and Knijn et al. (1993). We estimated the mean fecundity per year for reproductive individuals. If several batches of eggs are matured throughout the year, we attempted to estimate the sum over the year.

Formulation and analysis

The goal of this section is to obtain a testable relationship between recruitment variability and fecundity or some function of it.

The variability of a quantity is conveniently represented by its coefficient of variation. For recruitment, which tends to have a highly skewed distribution (Myers et al. 1995), it may

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G. Mertz¹ and R.A. Myers. Science Branch, Department of Fisheries and Oceans, Northwest Atlantic Fisheries Centre, P.O. Box 5667, St. John's, NF A1C 5X1, Canada.

¹ Author to whom all correspondence should be addressed.
e-mail: mertz@athena.nwafc.nf.ca

be appropriate to log-transform the data. The standard deviation of the log-transformed recruitment ($\sigma_{\ln R}$) may then be employed as a gauge of recruitment variability (Pepin and Myers 1991; Myers 1991). In developing the relationship between recruitment variability and variability of mortality we will briefly discuss the relationship between $\sigma_{\ln R}$ and the coefficient of variation for recruitment (CV_R).

We can write recruitment as

$$(1) \quad R(t) = E(t) \exp(-C_1(t) + C_2(t) + \dots + C_4(t)),$$

where t refers to a specific year, E is the total number of eggs produced, and C_i is the cumulative mortality in stage i , and for definiteness we have specified four stages (egg, early larval, late larval, and juvenile).

Let $C_i(t) = \bar{C}_i + \Delta C_i(t)$, and $\ln E(t) = \overline{\ln E} + \Delta \ln E(t)$. Then,

$$(2) \quad \ln R(t) = \overline{\ln R} + \Delta \ln E - \Sigma \Delta C_i(t),$$

where

$$(3) \quad \overline{\ln R} = \overline{\ln E} - \Sigma \bar{C}_i = \ln(E_* \exp(-\Sigma \bar{C}_i)),$$

and where E_* is the geometric mean egg production. It is now easily shown that

$$(4) \quad \sigma_{\ln R} = \overline{(\ln R - \overline{\ln R})^2}^{1/2} = \overline{(\Delta \ln E - \Sigma \Delta C_i)^2}^{1/2}.$$

Note that, in general, we cannot write the mean of the squared sum as a sum of mean squares in (4) because there are likely to be correlations among some of the terms ΔE , ΔC_i (e.g., high larval survival might correspond to high juvenile mortality; Myers and Cadigan 1993a, 1993b).

If there are no correlations in mortality between stages, then (4) may be simplified to

$$(5) \quad \sigma_{\ln R}^2 = \sigma_{\ln E}^2 + \sigma_{c1}^2 + \dots + \sigma_{c4}^2,$$

where $\sigma_{\ln E}$ is the standard deviation of log-transformed egg production and σ_{c1} is the standard deviation of mortality in stage 1, and similarly for the other stages. Relation (5) equates the variance in log-recruitment to the sum of the mortality variances plus the variance in log-transformed egg production. It is apparent from (4) and (5) that there is a very simple relationship between the recruitment variability index $\sigma_{\ln R}$ and the variability of the mortalities.

Heretofore, we have not specified the distribution for R . With the assumption that R is described by a log-normal distribution, a reasonable premise (Fogarty 1993a, 1993b), we can immediately write down, on the basis of the well-known properties of the log-normal distribution, the expression for CV_R :

$$(6) \quad CV_R = (\exp(\sigma_{\ln R}^2) - 1)^{1/2}.$$

For $\sigma_{\ln R} = 0.5$ we find from (6) that $CV_R = 0.53$ and for $\sigma_{\ln R} = 1.0$ we have $CV_R = 1.31$. Thus, it is apparent that for $CV_R \leq 1$, the two indices CV_R and $\sigma_{\ln R}$ are almost equivalent measures of recruitment variability. In the empirical treatment to follow we will find that the bulk of $\sigma_{\ln R}$ values for different fish stocks lie in the range of 0.3 to 1.0, so that there is, in general, no substantive difference between the magnitudes of these two indices. We will adopt $\sigma_{\ln R}$ as our working index, because of its more direct relation to variability of mortality ((4) and (5)).

As noted in the Data and methods section, we will work with recruitment series from which the stock (egg production)

contribution to variability has been removed. Therefore, it is appropriate to neglect the $\Delta \ln E$ term in (4), and our working equation becomes

$$(7) \quad \sigma_{\ln R} = ((\Sigma \Delta C_i)^2)^{1/2}.$$

Fecundity versus variability of mortality

If the CV for total mortality prior to recruitment is close to constant across fish stocks and species, this will imply that very fecund fish will suffer higher recruitment variability. To test this posit (a constant CV for total mortality) we require an expression for total mortality that will permit its calculation from data at hand.

Toward this goal, we must introduce the equilibrium relationship between recruits and spawners. First, let R_* be the geometric mean recruitment, then, from (3),

$$(8) \quad E_*/R_* = \exp(\Sigma \bar{C}_i).$$

We assume that R_* can be taken to represent the equilibrium recruitment, so that

$$(9) \quad R_* = ((1 - l)/\gamma)S_*,$$

where S_* represents the equilibrium number of spawners, l is the annual survival fraction for spawners, and γ is the number of spawners per recruit. With $E_* = (S_*/2)F$, where F is the fecundity, then using (8) and (9), we have

$$(10) \quad \Sigma \bar{C}_i = \ln \left(\frac{\gamma}{2(1-l)} F \right) = \ln F + \ln \left(\frac{\gamma}{2(1-l)} \right).$$

This equation allows the calculation of the total mean mortality from generally available information for a fish species. The final term in (10) varies from about -0.2 to 0.7, depending on species, whereas the $\ln F$ term ranges from about 1 (sharks) to about 16 (some gadoids). For our analysis, the range of $\Sigma \bar{C}_i$ is the most important consideration and since the term $\ln(0.5\gamma/(1-l))$ has little influence on it, it is permissible to drop this term in (10).

The hypothesis that the CV for total mortality is constant across species can be expressed as $((\Sigma \Delta C_i)^2)^{1/2} / (\Sigma \bar{C}_i) = \text{const}$, or, using (7) and (10),

$$(11) \quad \sigma_{\ln R} = \text{const} \times \ln F.$$

The constant in (11) can be obtained from simple calculations using data on the mean and variance of natural mortality compiled by Bradford (1992). The predictions of (11), with the constant specified, can be readily tested with available fishery data.

Bradford's analysis

Bradford (1992) compiled, from the literature, daily mortality rates and their interannual variances for the egg, larval, and juvenile stages for a wide variety of marine fish. From this amalgamation of daily mortality (M) data, Bradford regressed its interannual variance (σ_m^2) on \bar{M} and obtained a highly significant fit, holding across both stages and species: $\ln(\sigma_m^2) = 2.231 \ln \bar{M} - 1.893$ ($r^2 = 0.90$; $p < 0.0001$). Equivalently, we have $\sigma_m = 0.39 M^{1.12}$.

For a given stage, if we assume that \bar{M} does not change from the beginning to the end of the stage, then $\bar{C} = \bar{M} \times t_s$ (t_s is the stage duration) and, correspondingly, $\sigma_c = \sigma_m \times t_s$. It follows that

Table 1. List of species used in the analysis, with fecundity per year, median standard deviation of log-recruitment, mean standard deviation of log Ricker residuals, and the number of stocks constituting the species.

	Fecundity (thousands)	Median SD	Mean Ricker SD	Number of stocks
Clupeiformes				
Clupeidae				
<i>Brevoortia patromus</i> (Gulf menhaden)	335.0	0.45	0.42	1
<i>Brevoortia tyrannus</i> (Atlantic menhaden)	335.0	0.56	0.62	1
<i>Clupea harengus</i> (herring)	142.0	0.80	0.74	41
<i>Sardinops sagax</i> (sardine)	200.0	0.71	0.68	5
Engraulidae				
<i>Engraulis capensis</i> (S.A. anchovy)	25.0	0.32	0.32	1
<i>Engraulis mordax</i> (northern anchovy)	25.0	0.83	0.84	1
<i>Engraulis ringens</i> (Peruvian anchoveta)	25.0	1.12	0.79	1
Gadiformes				
Gadidae				
<i>Gadus macrocephalus</i> (Pacific cod)	1200.0	0.86	0.88	3
<i>Gadus morhua</i> (cod)	2000.0	0.57	0.55	25
<i>Melanogrammus aeglefinus</i> (haddock)	700.0	1.06	1.08	14
<i>Merlangius merlangus</i> (whiting)	400.0	0.54	0.51	5
<i>Merluccius bilinearis</i> (silver hake)	700.0	1.05	0.71	3
<i>Merluccius gayi</i> (Peruvian hake)	200.0	0.24	0.18	3
<i>Merluccius productus</i> (Pacific hake)	79.0	1.12	1.13	1
<i>Micromesistius poutassou</i> (blue whiting)	200.0	0.40	0.38	2
<i>Pollachius virens</i> (pollock or saithe)	225.0	0.47	0.41	6
<i>Theragra chalcogramma</i> (walleye pollock)	600.0	0.54	0.48	5
<i>Trisopterus esmarkii</i> (Norway pout)	38.7	0.67	0.65	1
<i>Urophycis tenuis</i> (white hake)	9500.0	0.38	0.32	1
Lophiiformes				
Lophiidae				
<i>Lophius piscatorius</i> (monkfish)	1320.0	0.56	0.44	1
Perciformes				
Ammodytidae				
<i>Ammodytes marinus</i> (sandeel)	15.0	0.72	0.73	4
Carangidae				
<i>Trachurus trachurus</i> (horse mackerel)	364.0	0.99	0.93	2
Scombridae				
<i>Scomber japonicus</i> (chub mackerel)	1000.0	1.31	1.37	2
<i>Scomber scombrus</i> (mackerel)	400.0	0.93	0.91	2
Pleuronectiformes				
Pleuronectidae				
<i>Eopsetta jordani</i> (petrale sole)	800.0	0.61	0.68	1
<i>Hippoglossoides platessoides</i> (American plaice)	400.0	0.31	0.32	4
<i>Hippoglossus stenolepis</i> (Pacific halibut)	2500.0	0.37	0.36	1
<i>Lepidopsetta bilineata</i> (rock sole)	850.0	0.76	0.77	1
<i>Limanda ferruginae</i> (yellowtail flounder)	1500.0	0.82	0.65	3
<i>Pleuronectes platessa</i> (plaice)	80.0	0.46	0.42	8
<i>Reinhardtius hippoglossoides</i> (Greenland halibut)	165.0	0.15	0.15	2
Soleidae				
<i>Solea vulgaris</i> (sole)	350.0	0.56	0.43	7
Salmoniformes				
Osmeridae				
<i>Mallotus villosus</i> (capelin)	40.0	0.48	0.49	3
Salmonidae				
<i>Oncorhynchus gorbuscha</i> (pink salmon)	1.5	1.026	1.073	23
<i>Oncorhynchus keta</i> (chum salmon)	3.6	0.501	0.521	9
<i>Oncorhynchus mykiss</i> (steelhead trout)	4.5	0.449	0.371	3
<i>Oncorhynchus nerka</i> (sockeye salmon)	3.6	0.597	0.631	33
<i>Salmo salar</i> (Atlantic salmon)	8.3	0.320	0.345	15

Table 1 (concluded).

	Fecundity (thousands)	Median SD	Mean Ricker SD	Number of stocks
Scorpaeniformes				
Scorpaenidae				
<i>Sebastes entomelas</i> (widow rockfish)	477.5	0.83	0.81	1
<i>Sebastes</i> sp. (redfish)	17.5	0.66	0.55	8
Squaliformes				
Squalidae				
<i>Squalus acanthias</i> (spiny dogfish)	0.003	0.97	0.74	1

$$(12) \quad \sigma_c = 0.39 \bar{M}^{0.12} \bar{C}.$$

Table 1 of Bradford (1992) reveals that across stages and major fish species, \bar{M} ranges typically from 0.01 to 0.1 day⁻¹, and correspondingly, the factor $\bar{M}^{0.12}$ ranges from 0.58 to 0.76. Clearly, little information is lost by replacing $\bar{M}^{0.12}$ with 0.7 and then writing $\sigma_c \approx 0.3 \bar{C}$. Since Bradford's regression is valid across stages we can be more specific and write $\sigma_{ci} \approx 0.3 \bar{C}_i$, where the index i indicates a specific stage. Mertz and Myers (1995) found that the slope coefficient in this equation is likely to be inflated by error in the estimation of mortality from field abundance data. Their analysis suggested that 0.2, rather than 0.3, is appropriate for the proportionality constant, and thus

$$(13) \quad \sigma_{ci} \approx 0.2 \bar{C}_i.$$

Final formulation

Equation (13) can be substituted into (5), permitting an explicit relation between $\sigma_{\ln R}$ and $\ln F$ to be derived. However, (5) is insufficiently general, since it permits no density dependence. Instead, we will apply the more general (7), after specifying a density dependence that enters through mortality in the juvenile stage. Myers and Cadigan (1993a) established the plausibility of density-dependent juvenile mortality for groundfish populations. In their model

$$(14) \quad \Delta C_4 = \alpha \Delta N_3 + \epsilon,$$

where ΔC_4 is the juvenile mortality minus its mean, α represents the strength of density dependence, N_3 is the abundance late in the larval stage, and ϵ represents the portion of juvenile mortality not associated with density dependence.

From (7) and (14) one can easily show (Mertz and Myers 1995) that

$$(15) \quad \sigma_{\ln R}^2 = (1 - 2\alpha)((\sigma_{c1})^2 + (\sigma_{c2})^2 + (\sigma_{c3})^2) + (\sigma_{c4})^2.$$

Myers and Cadigan (1993a) have shown that cod populations are subject to strong density dependence, $\alpha \approx 0.5$. This will be one limit considered here, the other being $\alpha \approx 0$.

For strong density dependence, (15) gives $\sigma_{\ln R} = \sigma_{c4}$. Using (13), we have $\sigma_{\ln R} = 0.2 \bar{C}_4$. From Bradford's (1992) analysis, it is reasonable to treat \bar{C}_4 as constituting about one quarter of mean total mortality (all four stages make an appreciable contribution to total mortality). It follows that $\sigma_{\ln R} \approx 0.25 \times 0.2 \times \sum \bar{C}_i$ and thus, using (10),

$$(16) \quad \sigma_{\ln R} \approx 0.05 \ln F$$

(recall that we have concluded that it is permissible to drop the final term in (10)).

For the opposite extreme of no density dependence, $\alpha = 0$, we can use (13) and (15) to write

$$(17) \quad \sigma_{\ln R} \approx 0.2 (\bar{C}_1 2 + \dots + \bar{C}_4 2)^{1/2}.$$

Assuming again that there are four stages of roughly equal importance, we can write $((\bar{C}_1 2 + \dots + \bar{C}_4 2)^{1/2}) \approx (1/2)((\bar{C}_1 + \dots + \bar{C}_4))$. Thus, $\sigma_{\ln R} \approx 0.1 \sum \bar{C}_i$, and with (10) we have

$$(18) \quad \sigma_{\ln R} \approx 0.10 \ln F.$$

Thus, the coefficient relating $\sigma_{\ln R}$ and $\ln F$ is about twice as large in the case of no density dependence as it is for the case of strong density dependence.

Finally, to summarize the results of this analysis, we have

$$(19) \quad \sigma_{\ln R} = (0.05 \text{ to } 0.10) \times \ln F.$$

In the next section we will compare the predictions of (19) with data-based regressions.

Results

Empirical test of (19)

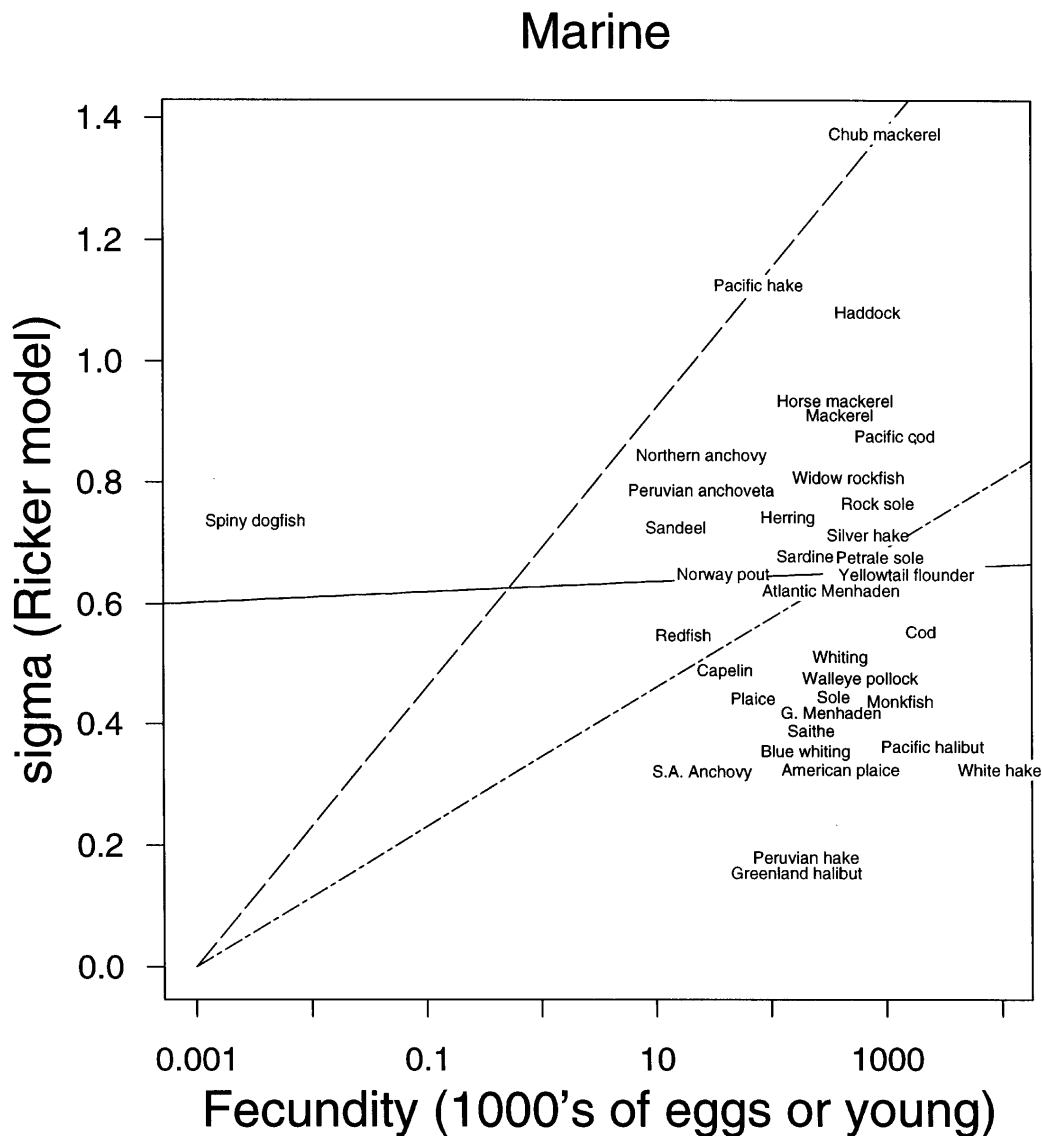
In Figs. 1–3 we have presented scatter plots of $\sigma_{\ln R}$ versus log-fecundity using all available marine species (Table 1) including three ovoviviparous species (in Fig. 1 only), one of which has very low fecundity, spiny dogfish. The parameters for the regressions of $\sigma_{\ln R}$ on $\ln F$ are reported in the figure captions. Note that the ordinate is shown in log to the base 10 form, while the slopes given for the linear regressions are based on $\sigma_{\ln R}$ versus the natural log of fecundity.

In Fig. 1 we have included (broken lines) the lines specified by the two slopes given in (19). A linear regression of $\sigma_{\ln R}$ on $\ln F$ (solid line) does not yield a significant correlation, and the resulting slope does not accord with (19).

In Fig. 2 we have removed ovoviviparous species (to eliminate spiny dogfish) and added a number of salmon species for which reliable data were available. Bradford's (1992) regression, which was used to derive the relationship between $\sigma_{\ln R}$ and $\ln F$, was based on data that included salmon populations. The inclusion of salmon species gives fairly uniform coverage over nearly four orders of magnitude in fecundity, yet there is still no indication of a significant relationship between $\sigma_{\ln R}$ and $\ln F$.

If we look at the data on the basis of orders (Fig. 3), we see that there are again no consistent relationships. In no case is the slope of $\sigma_{\ln R}$ versus $\ln F$ significantly different from zero, although for pelagic species the regression approaches statistical significance and the slope and intercept have reasonable values. We repeated the analysis eliminating stocks with less than 15 years of recruitment data; again there were no significant relationships (data not shown).

Fig. 1. Scatter plot, based on all available marine fish species, of the standard deviation of the natural log of the Ricker residuals of recruitment versus fecundity on a log (to the base 10) scale. For each species the entered label represents the mean for all available stocks constituting the species. The solid line represents the least squares fit to the data that may be expressed, in terms of $\ln F$, as $\sigma_{\ln R} = a \ln F + b$, where $a = 0.004$, $b = 0.602$ ($r^2 = 0\%$, $p = 0.822$). The broken lines represent (19), $\sigma_{\ln R} = (0.05 \text{ to } 0.10) \ln F$.



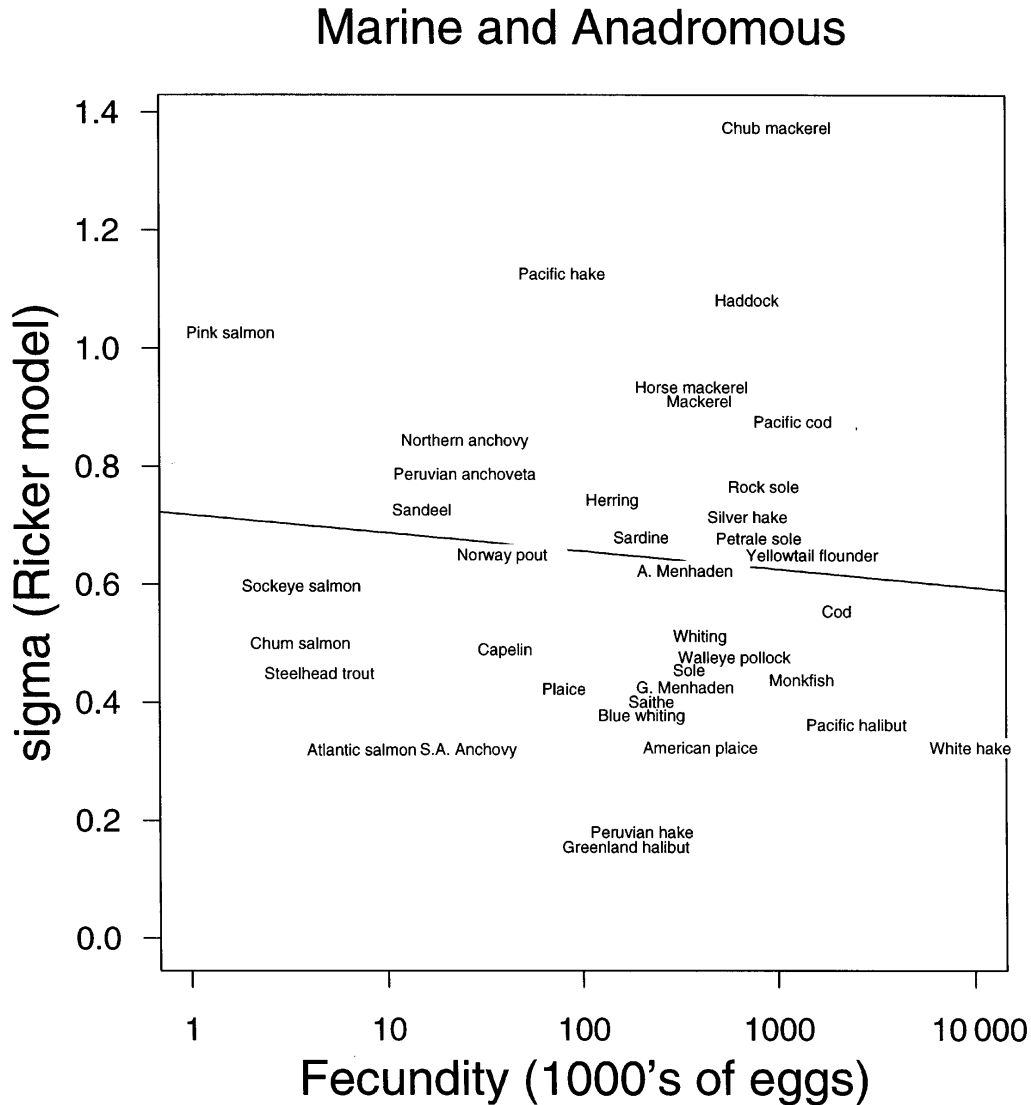
We tested the robustness of our conclusions by considering various sources of bias in the estimates of recruitment variability. When recruitment is estimated from SPA, aging errors will cause the estimate of the variability to be negatively biased (Bradford 1991; Myers and Cadigan 1993a). Since aging errors nearly always increase with age (Bradford 1991), we considered only those populations in which the first age used in the SPA was less than 2, which should minimize this effect; the results still showed no relationship between recruitment variability and fecundity (Fig. 3f). When recruitment is estimated from research surveys, the estimate will be positively biased unless estimation methods are used to separate out the estimation error variance. When we considered the previous analyses using only research vessel series or SPA, we still could see no effect.

Discussion

The foregoing analysis has shown that there is no significant relationship between $\sigma_{\ln R}$ and $\ln F$, regardless of how the data are partitioned taxonomically. (19), and its weaker form, (11), which does not specify the slope, are both rejected by the data analysis. However, the area enclosed in Fig. 1 by the limiting slopes of (19) does encompass the centroid of the cluster of data points. This suggests that (19) approximately predicts, for the centroid of the data, the correct ratio of $\sigma_{\ln R}$ to $\ln F$. This provides some substantiation for Bradford's (1992) relation between variability of mortality and mean mortality, (12), with the correction applied by Mertz and Myers (1995).

The extreme scatter evident in Fig. 1 appears not to be consistent with the tight relationship, obtained by Bradford (1992), between variability of mortality and mean mortality.

Fig. 2. As in Fig. 1, but with the addition of salmon data (note that the ovoviviparous species have been removed), and omitting the line representing (19). For each species the entered label represents the mean for all available stocks constituting the species and the bars signify the upper and lower quintiles. The solid line (the least squares fit) is given by $\sigma_{\ln R} = 0.005 \ln F + 0.591$ ($r^2 = 0\%$, $p = 0.826$).

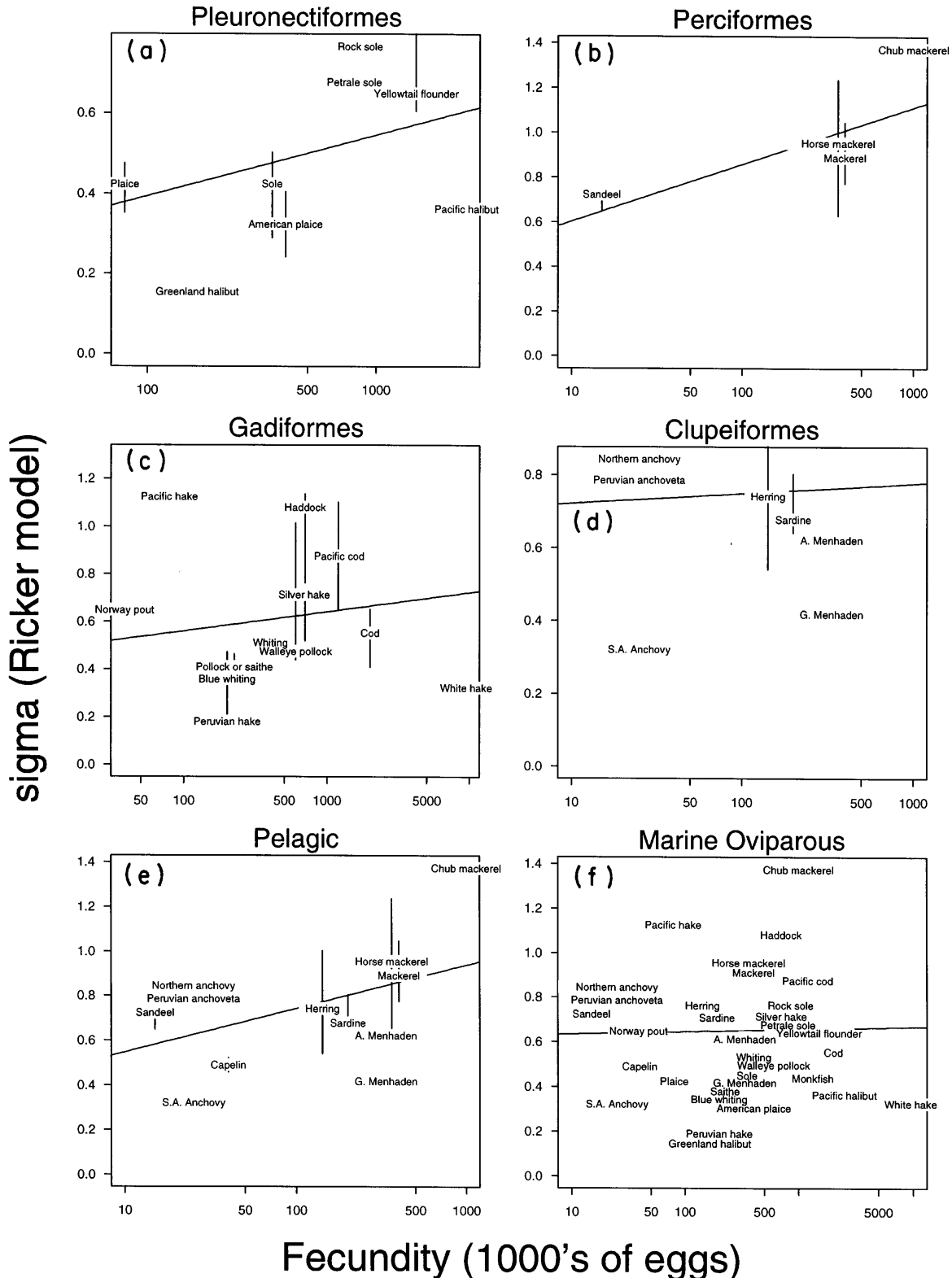


However, the gap between the two broken lines in Fig. 1 suggests that about one half the scatter can be accounted for by stock to stock differences in the strength of density dependence (α). Conceivably, the influence of density dependence could be even greater, since we somewhat arbitrarily limited α to being less than 0.5. Moreover, Bradford's relation was based on the log-transformed variances and means of mortality; obtaining a relation between recruitment variability and fecundity requires the untransformed version of the relation, (12), which is certain to have a much lower r^2 . Additionally, derivation of the relationship between recruitment variability and fecundity requires summing over four stages, so that the imprecision of the variability-mean relationship for each stage becomes compounded in the final result. These factors will account, at least in part, for the scatter apparent in Fig. 1.

Our study appreciably subtracts from the plausibility of the

often-proposed general relationship between variability of reproductive success and fecundity. Figures 1, 2, and 3 do not suggest a relationship between $\sigma_{\ln R}$ and $\ln F$. In particular, the data in Fig. 2 span almost four orders of magnitude in fecundity ($1.5 \times 10^3 \leq F \leq 9.5 \times 10^6$), which represents more than half the logarithmic range from very fecund fish ($F \approx 10^7$) to large (low fecundity) mammals ($F \approx 1$). The absence of a relationship over this range is forceful evidence against a general relationship between the variability of reproductive success and fecundity. Unfortunately, there are few data for species having very low fecundities, although Beddington and Basson (1994) have recently reported a stock-recruit analysis for red deer on the Isle of Rhum. They state, "It is amusing to note that the level of variation around the recruitment relationship seems to be at least in line with that observed for fish species." This lends some corroboration to our interpretation of the data.

Fig. 3. As in Fig. 2. For pleuronectiformes, $\sigma_{\ln R} = 0.066 \ln F - 0.364$ ($r^2 = 10.7\%$, $p = 0.111$). For gadiformes, $\sigma_{\ln R} = 0.035 \ln F + 0.155$ ($r^2 = 1.1\%$, $p = 0.419$). For pelagic species, $\sigma_{\ln R} = 0.085 \ln F - 0.235$ ($r^2 = 5.1\%$, $p = 0.097$). For perciformes, $\sigma_{\ln R} = 0.111 \ln F - 0.415$ ($r^2 = 24.1\%$, $p = 0.18$). For clupeiformes, $\sigma_{\ln R} = 0.012 \ln F + 0.612$ ($r^2 = 0\%$, $p = 0.90$). For marine oviparous species, those shown are those for which the first age in the sequential population analysis was less than 2 (error bars have been suppressed for graphical clarity). The regression line is $\sigma_{\ln R} = -0.005 \ln F + 0.702$ ($r^2 = 0\%$, $p = 0.857$).



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