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Prerecruit Mortality in Gulf of Thailand Shrimp Stocks

Pauly's (1982) procedure to estimate the stock-recruitment relationship of a shrimp stock offered a remarkably clear explanation of the dependency of prerecruit mortality on the density of the exploited stock of all fish and crustaceans in the Gulf of Thailand. The purpose of this Comment is to demonstrate that there is no evidence that recruitment is density-dependent as claimed. Although the methods quoted and the procedure are correct in principle, the use of data resulted in estimates of recruits R , egg numbers P , and total biomass of the exploited multispecies stock B that are functionally interdependent. All estimates depend highly on instantaneous fishing mortality F of the combined multispecies stocks. When the variables are expressed as functions of F , the apparent shrimp mortality rates derived by Pauly can be predicted closely without any data from the shrimp stock itself. In the following demonstration, symbols follow Pauly (1982) unless otherwise indicated, and his numerical values are used.

The decline of B , reflecting the original catch-per-effort (c/f) data, clearly depends on fishing effort. The upwardly concave relationship between c/f and F suggests the Gulland-Fox exponential version of the Graham logistic curve (Ricker 1975); indeed, 90% of the variance of $\log_e(c/f)$ is explained by F , which was derived independently from length frequencies by Pauly (1980). Equation (1) was derived from the geometric-mean regression, as recommended by Ricker:

$$\log_e(c/f) = a_0 - b_0F; \quad (1)$$

$$a_0 = 5.43;$$

$$b_0 = 0.656.$$

Therefore,

$$B = Y/F = 1.6(c/f)/q$$

$$= c \exp(a_0 - b_0F); \quad (2)$$

Y = total multispecies yield;

1.6 = mesh-size correction factor (Pauly 1982);

q = overall catchability (0.31 as in Pauly 1980);
 $c = 1.6/q = 5.16$.

The number of shrimp eggs produced per year P is the product of fecundity per unit biomass E , the total biomass of fished stock B , and a correction factor for adult biomass (Pauly's m). The latter is a function of fishing mortality, for which Pauly used the multispecies estimate F , and is controlled almost entirely by the first exponential term in Pauly's equation (8). Consequently, a simpler expression, which explains 99% of the variance of $\log_e(m)$, can be derived to describe Pauly's data:

$$\log_e(m) = a_1 - b_1F; \quad (3)$$

$$a_1 = 0.846;$$

$$b_1 = 0.108.$$

Therefore,

$$P = E \exp(a_1 - b_1F)(Y_s/F_s); \quad (4)$$

F_s = instantaneous fishing mortality of the shrimp stock;

Y_s = shrimp yield as estimated by Pauly (1982);

$E = 15.9$ eggs/g (Pauly 1982).

Finally, the number of recruits R is given by

$$R = \frac{Y_s}{(Y/R)} = \frac{Y_s}{F_s} \left(W_\infty \left| \frac{1 - \exp(-Z\lambda)}{Z} \right. \right.$$

$$\left. - \frac{3 \exp(-Kr_1)(1 - \exp[-(Z + K)\lambda])}{Z + K} \right.$$

$$\left. + \frac{3 \exp(-2Kr_1)(1 - \exp[-(Z + 2K)\lambda])}{Z + 2K} \right.$$

$$\left. - \frac{\exp(-3Kr_1)(1 - \exp[-(Z + 3K)\lambda])}{Z + 3K} \right| \Big)^{-1}; \quad (5)$$

(Y/R) = yield per recruit for the shrimp stock;

$Z = F_s + M$;

M = natural mortality; and other symbols are as defined in Pauly (1982).

The percentage daily mortality of prerecruits D is

$$D = \{1 - [\exp \log_e(R/P)/t_c]\} 100; \quad (6)$$

t_c = mean age at first capture.

Equation (9) in Pauly (1982) is the same, but for a typographical error, as equation (6) here. Therefore, D is a function of R/P because t_c is constant. Division of equation (5) by equation (4) expresses this ratio as a function of F_s and F , because the shrimp yield Y , cancels out. Pauly's error was to assume that the overall fishing mortality F could be substituted for that of the shrimp stock only (F_s). By this assumption, R/P or D are functions of F and hence of the whole multispecies biomass B (by substitution in equation 2) and, therefore, can be predicted by B . Values of D generated by the function of B are very similar to Pauly's, illustrating that apparent prerecruit mortality can be predicted independently of any variables pertaining to the shrimp stock itself:

B Pauly (1982)	D	
	Pauly (1982)	This Comment
1,264	7.15	7.46
681	6.68	6.59
592	6.57	6.40
545	6.36	6.29
530	6.34	6.25
502	6.29	6.17
343	5.63	5.67
325	5.36	5.60

The monotonic decrease of the apparent R/P as B increases is independent of shrimp yield when $F = F_s$, and the biologically plausible density-dependent effect(s) cannot be demonstrated. Conversely, the environmental explanation suggested by Martosubroto and Naamin (1977) and Turner (1977), work acknowledged by Pauly, does account for some of the yield variability in shrimp stocks.

This Comment is not intended to detract from the usefulness of Pauly's procedure, if it is used correctly, and I hope this and similar multispecies approaches will be used and developed in the future.

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I accept Bayley's Comment that use of the same fishing-mortality values for the shrimp stock F_s and the total demersal stock F in the Gulf of Thailand leads to the absurd situation of being able to predict shrimp mortality without shrimp data—I have little choice, given the elegance of his demonstration.

Bayley correctly notes that setting $F_s = F$ was an error as well as an assumption. It was an error in the sense that it allowed yields to cancel out when his equations (4) and (5) are combined. As an assumption, on the other hand, the equality seemed justified because trawlers catch shrimp and fish concurrently in the Gulf of Thailand.

Garcia (1983) also wrote on this problem:

However, the main problem when interpreting [Pauly's] results lies in the fact that the relationship has been established between the number of eggs potentially produced in year n and the recruitment in the same year [emphasis in the original] In addition, it is clear that the plot of $Y_n/(Y/R)_n$ and Y_n/F_n is a plot of one function of Y_n against another function of Y_n , both involving F_n as a variable. This can generate a strong positive correlation purely as a statistical artefact.

The reason I used the F_s values of the same year to generate both P and R values is that most Gulf of Thailand shrimps have extremely short life spans, the bulk of the cohort going through the fishery in less than 6 months. This has the result that given a constant F_s within a year, one can, indeed, conceive of the same F_s values affecting two successive shrimp generations. However, as shown by Bayley, this does lead to statistical artefacts. The question now is: Where do we go from here?

Both Bayley's and Garcia's criticisms can be accommodated in a rather straight-forward manner because the problem can be resolved if mortalities of successive years (F_n, F_{n+1}) are used. The result of such reanalysis (based on Table 4 of Pauly 1982) is a trajectory (Fig. 1) similar to that of Fig. 1 of the original paper: initial decrease of recruitment with reduction in a parental stock, followed by an increase. Similarly (Fig. 2), there remains a significant reduction of prerecruit mortality of shrimps with decreasing fish biomass, as in Fig. 2 of the original paper (although the fit—which is not an artefact any more—is not nearly as good as it was).

Thus, as acknowledged by Bayley, the method I suggested is useful—when used correctly.

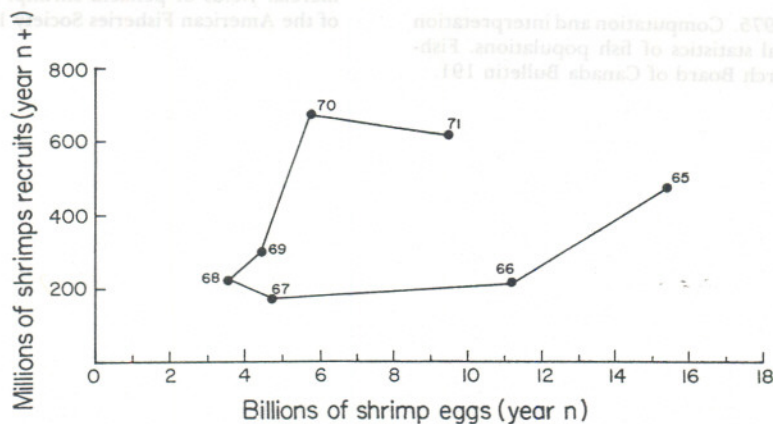


FIGURE 1.—Trajectory of egg production and subsequent recruitment of Gulf of Thailand shrimps, 1965–1972. (Based on Table 4 in Pauly 1982, with egg production for 1965 interpolated between 1963 and 1966.)

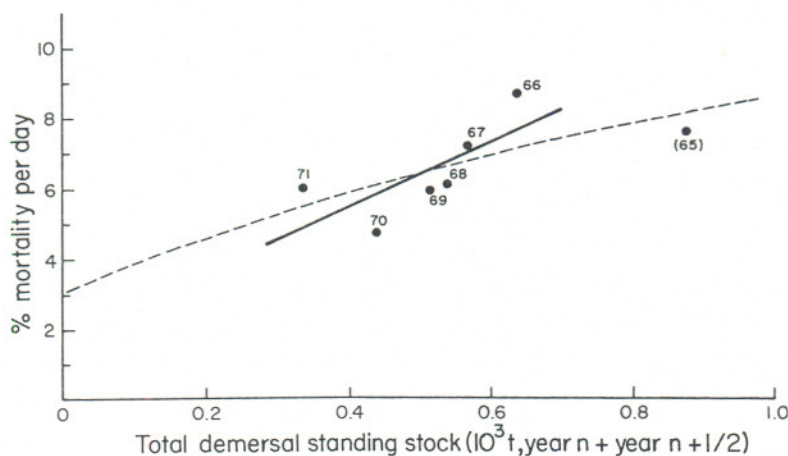


FIGURE 2.—Relationship between percent daily mortality of shrimp prerecruits and the biomass of shrimp predators and competitors in the Gulf of Thailand. The solid line is a linear regression that excludes the interpolated point for 1965, and has a slope significantly different from zero ($P < 0.05$). The broken line, which includes 1965, has an asymptote at 13.2%.

Moreover, it does lead, in the case investigated here, to a demonstration of “biologically plausible density-dependent effects.”

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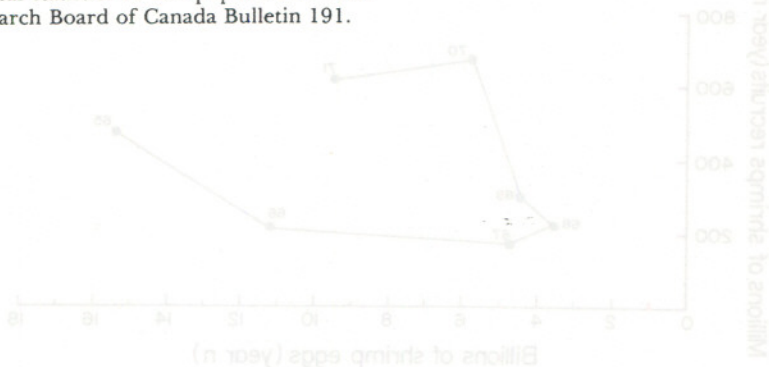


FIGURE 1.—Trends of egg production and subsequent recruitment of Gulf of Thailand shrimp, 1982-1992. (Based on Table 4 in Pauly 1982, with egg production for 1982 interpolated between 1981 and 1983.)

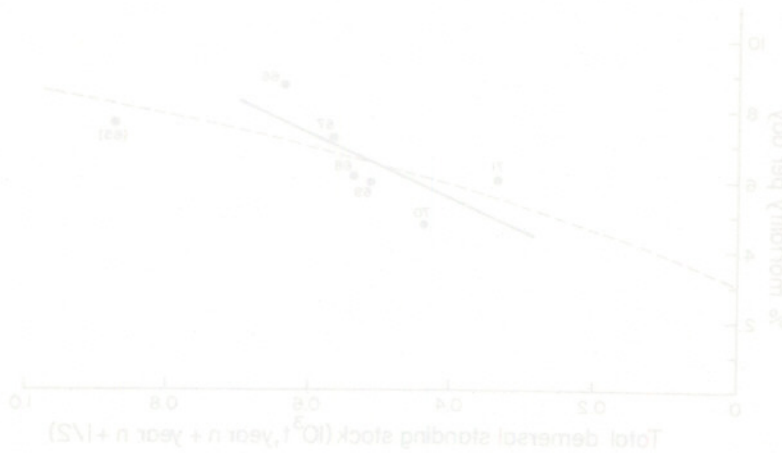


FIGURE 2.—Relationship between present daily mortality of shrimp (presently and the biomass of shrimp predators and competitors in the Gulf of Thailand). The solid line is a linear regression that excludes the interpolated point for 1982, and has a slope significantly different from zero ($P < 0.05$). The broken line, which includes 1982, has an equation of $Y = 13.2X$.

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MOREOVER, it does lead, in the case investigated here, to a demonstration of "biologically plausible density-dependent effects."
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