A Method to Estimate the Stock–Recruitment Relationship of Shrimps

DANIEL PAULY
International Center for Living Aquatic Resources Management
MCC Post Office Box 1501, Makati, Metro Manila, Philippines

Abstract

A procedure is proposed by which recruit numbers and parental biomass of shrimp stocks can be derived, given a series of catch-per-effort data and estimates of a few ancillary variables. In the Gulf of Thailand, shrimp recruitment decreased with decreasing egg production, but increased with decreasing total (mainly fish) standing stock. The net result of these counteracting effects was an overall increase in shrimp recruitment, attributable to a greatly reduced prerecruit mortality.

Although shrimp stocks throughout the world support highly profitable fisheries, little is known of the biology of the various species that support these fisheries, with the possible exception of the Penaeus species of the northern Gulf of Mexico. Least is known about the population dynamics of tropical penaeid shrimps that greatly contribute to the economy of many developing countries.

Of the various factors that determine the yield of a fishery, recruitment certainly is the most evasive (Marr 1976). This is true particularly in the case of shrimps, the stock-recruitment relationships of which appear rarely to have been established.

The present contribution is an attempt to identify the stock-recruitment relationship of a commercially exploited stock of penaeid shrimps, and is based mainly on catch/effort data from the Gulf of Thailand demersal trawl fishery. The analysis is preliminary and relies heavily on a set of assumptions that were necessary to extract any information from the crude data presently available.

Methods

Data for the Thai Fishery

The mean total catch per effort of the Thai Research Trawler R/V Pramong 2 for the years 1963 to 1972, the total effort exerted by the commercial fishery, and the overall fishing mortality for the Thai portion of the Gulf of Thailand inshore waters (<50m depth) are summarized in Table 1. The total catch per effort (c/ef) and effort figures (ef) are from Ritragsa (1976) and from Boonyubol and Hongskul (1978), respectively. The estimates of fishing mortality (F) stem from Pauly (1980) and were obtained by means of the swept-area method (Gulland 1969) and the reduction of mean size of six species of fish in the years 1963 to 1972, both methods providing similar estimates of F (Pauly 1980). Total annual yield in weight (Y) was obtained through the relationship

\[ Y = (c/ef)\cdot ef. \]

The yield values so obtained were multiplied by 1.6 to account for the different mesh sizes used by the research and the commercial trawlers in the Gulf of Thailand (4-cm and about 2.5-cm stretched mesh, respectively) as suggested by Boonyubol and Hongskul (1978).

The total annual yield figures were used to obtain estimates of mean total standing stock size (B) for each year:

\[ B = \frac{Y}{F}. \]

These values (Table 1) will be used in the subsequent analysis as an index of the biomass of all potential shrimp predators and competitors, as they consist overwhelmingly of fishes and other animals (including the shrimps themselves) that at some part of their life history feed on or compete for food with larval or adult shrimps.
14 PAULY

From Pauly (1980), based on catch-per-effort data in Ritragsa (1976) and effort and other data in Boonyubol and Hongskul (1978).

**Biology of Penaeid Shrimps**

Published growth and natural mortality \((M)\) estimates for penaeid shrimps are quite scarce. Of the three species listed in Table 2, I have selected *Penaeus indicus* to represent the "typical" Gulf of Thailand shrimp, both because it is the smallest and because it is the only one that actually occurs in the Gulf of Thailand.

If a value of 0.75 is assumed for the ratio between length at first maturity \((L_m)\) and asymptotic length \((L_\infty)\) (Cushing 1966), estimated age at first maturity \((t_m)\) is 0.372 years when the growth parameters of *P. indicus* in Table 2 and a condition factor of \(100W/L_\infty^3 = 0.8\) are used for the computations. The fecundity of average size mature female shrimps of several species was used to derive relative fecundity (number of eggs/g body weight). The available data provide a mean relative fecundity of 15.9 (Table 3).

**Stock-Recruitment Model**

Ritragsa (1976) gives shrimp catch-per-effort data obtained by R/V Pramong 2 in 1963 and 1966 through 1972 (Table 4); these data are affected by the difference between the mesh sizes of the research and commercial trawlers. Here, however, an adjustment better than the constant 1:1.6 ratio that had to be used for the total stock could be used, as given by the relationship

\[
k = \frac{1}{Z} + \frac{3 \exp(-Kt_1)}{Z + K} + \frac{3 \exp(-2Kt_1)}{Z + 2K} + \frac{\exp(-3Kt_1)}{Z + 3K}
\]

\[
Z = M + F = \text{total mortality};
\]  
\[
r_1 = \left( t_{c(3.5)} - t_0 \right);
\]  
\[
r_2 = \left( t_{c(6)} - t_0 \right);
\]  
\[
r_3 = \left( t_{c(4)} - t_{c(3.5)} \right);
\]  
\[
M = \text{mean age at first capture of shrimps caught with 2.5-cm meshes};
\]  
\[
t_{c(4)} = \text{mean age at first capture of shrimps caught with 4-cm meshes};
\]

**Table 1.—Basic data for the Gulf of Thailand demersal trawl fishery.**

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Catch per effort (kg/hour)</td>
<td>*</td>
<td>248</td>
<td>131</td>
<td>151</td>
<td>106</td>
<td>103</td>
<td>97.4</td>
<td>66.3</td>
<td>63.1</td>
</tr>
<tr>
<td>Effort (10^6 trawling hours)</td>
<td>0.096</td>
<td>2.078</td>
<td>2.800</td>
<td>5.500</td>
<td>5.600</td>
<td>5.800</td>
<td>6.200</td>
<td>7.188</td>
<td></td>
</tr>
<tr>
<td>Total demersal standing stock (10^3 tonnes)</td>
<td>1,978</td>
<td>1,264</td>
<td>681</td>
<td>592</td>
<td>545</td>
<td>550</td>
<td>502</td>
<td>345</td>
<td>325</td>
</tr>
</tbody>
</table>

*From Pauly (1980), based on catch-per-effort data in Ritragsa (1976) and effort and other data in Boonyubol and Hongskul (1978).*

**Table 2.—Growth and mortality parameters of selected stocks of penaeid shrimps.** *W* is the asymptotic weight, and K and \(t_0\) are constants (expressed on a yearly basis) of the von Bertalanffy growth equation. M (exponential coefficient of natural mortality) also is expressed on an annual basis.

<table>
<thead>
<tr>
<th>Species</th>
<th>(W_\infty)</th>
<th>(K)</th>
<th>(t_0)</th>
<th>M</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Penaeus plebejus</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>♀ and ♂</td>
<td>50</td>
<td>4.16</td>
<td>-0.35</td>
<td>2.6</td>
<td>Clark and Kirkwood (1979)</td>
</tr>
<tr>
<td><em>Penaeus duorarm</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>♀</td>
<td>80</td>
<td>2.04</td>
<td>-0.25</td>
<td>1.86</td>
<td>Garcia (1975a, 1975b)</td>
</tr>
<tr>
<td>♂</td>
<td>30</td>
<td>3.56</td>
<td>-0.26</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Penaeus indicus</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>♀</td>
<td>27.8</td>
<td>4.13</td>
<td>0.10</td>
<td>2.40</td>
<td>Marcille (1978)</td>
</tr>
<tr>
<td>♂</td>
<td>11.9</td>
<td>4.48</td>
<td>0.01</td>
<td></td>
<td></td>
</tr>
<tr>
<td>♀ and ♂</td>
<td>~20</td>
<td>~4.3</td>
<td>~0.05</td>
<td>2.4</td>
<td></td>
</tr>
</tbody>
</table>
TABLE 3.—Estimation of mean relative fecundity (eggs/gram body weight) in penaeid shrimps. Intercept values in parentheses are based on an assumed value of 3 for the slopes (isometric growth).

<table>
<thead>
<tr>
<th>Species</th>
<th>Length/fecundity relationship intercept (for total length in mm)</th>
<th>Length/fecundity relationship slope (for total length in mm)</th>
<th>Absolute fecundity of 5-g female (10^9 eggs)</th>
<th>Relative fecundity (10^9 eggs/g)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Penaeus setiferus</em></td>
<td>-0.7721</td>
<td>3</td>
<td>99.5</td>
<td>19.9</td>
</tr>
<tr>
<td><em>Metapenaeus dobsoni</em></td>
<td>-0.7175</td>
<td>2.847</td>
<td>5</td>
<td>12.2</td>
</tr>
<tr>
<td><em>Parapenaeopsis stylifera</em></td>
<td>-1.575</td>
<td>3.344</td>
<td>77.4</td>
<td>15.5</td>
</tr>
<tr>
<td>Mean</td>
<td></td>
<td></td>
<td></td>
<td>15.9</td>
</tr>
</tbody>
</table>


K, t₀ = parameters of the von Bertalanffy growth equation;

k = multiplicative factor that converts the catch rates obtained with larger meshes to the catch rates that are obtained with smaller meshes.

This equation is a simplified version of Equation (7) in Hempel and Sarhage (1959).

Finally, the values of the two ages at first capture (t(<sub>2</sub>) and t(<sub>4</sub>) were obtained indirectly from the relationship

L<sub>c</sub> = (S.F.)<sub>mesh size</sub> (4)

(Jones 1976), where L<sub>c</sub> is the mean length at first capture and S.F. the selection factor for shrimps, the value of L<sub>c</sub> being converted to an age estimate by means of the values of K and t₀ given in Table 2 and a value of L<sub>c</sub> = 13.6 based on a condition factor of 0.8 (see above).

A value of 1.5 was used for the selection factor because S.F. values for shrimps seem to range from 0.4 (Aoyama 1973) to 3.5 (Simpson and Perez 1975) and because values of about 1.5 correspond to the S.F. of the bulkiest fishes of the South China Sea area (Sinoda et al. 1979). The value of S.F. = 1.5 for shrimps resulted in t(<sub>2</sub>) = 0.125 and t(<sub>4</sub>) = 0.186 year, respectively.

The growth parameters of Table 3 in conjunction with the F values of Table 1 allow for calculation of yield-per-recruit (Y/R) values by means of the relationship

\[
\frac{Y}{R} = FW\left[\frac{1 - \exp(-Z\lambda)}{Z} - 3\exp(-K\lambda)\left[1 - \exp(-(Z + K)\lambda)\right]\right] \frac{Z + K}{Z + 2K} \left[1 - \exp(-(Z + 3K)\lambda)\right] \frac{Z + 3K}{Z + 3K}
\]

TABLE 4.—Data for the identification of a stock–recruitment relationship in Gulf of Thailand shrimp stocks.

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Research catch per effort of penaeid shrimps (kg/hour)&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.567</td>
<td>0.269</td>
<td>0.116</td>
<td>0.090</td>
<td>0.112</td>
<td>0.147</td>
<td>0.260</td>
<td>0.218</td>
<td></td>
</tr>
<tr>
<td>Gear-conversion factor k</td>
<td>1.014</td>
<td>1.015</td>
<td>1.019</td>
<td>1.022</td>
<td>1.024</td>
<td>1.024</td>
<td>1.025</td>
<td>1.034</td>
<td>1.038</td>
</tr>
<tr>
<td>Commercial catch/effort (kg/hour)</td>
<td>0.576</td>
<td>0.274</td>
<td>0.119</td>
<td>0.092</td>
<td>0.115</td>
<td>0.151</td>
<td>0.269</td>
<td>0.266</td>
<td></td>
</tr>
<tr>
<td>Catch (10&lt;sup&gt;3&lt;/sup&gt; tonnes)</td>
<td>402</td>
<td>569</td>
<td>333</td>
<td>322</td>
<td>414</td>
<td>574</td>
<td>1,668</td>
<td>1,624</td>
<td></td>
</tr>
<tr>
<td>Yield per recruit (g)</td>
<td>0.499</td>
<td>1.256</td>
<td>1.579</td>
<td>1.840</td>
<td>1.872</td>
<td>1.983</td>
<td>2.486</td>
<td>2.627</td>
<td></td>
</tr>
<tr>
<td>Recruits (10&lt;sup&gt;3&lt;/sup&gt;)</td>
<td>1,000&lt;sup&gt;b&lt;/sup&gt;</td>
<td>807</td>
<td>475</td>
<td>211</td>
<td>175</td>
<td>221</td>
<td>297</td>
<td>671</td>
<td>618</td>
</tr>
<tr>
<td>Standing stock (tonnes)</td>
<td>2,664&lt;sup&gt;c&lt;/sup&gt;</td>
<td>1,827</td>
<td>889</td>
<td>383</td>
<td>295</td>
<td>370</td>
<td>486</td>
<td>869</td>
<td>728</td>
</tr>
<tr>
<td>Adult stock conversion factor m</td>
<td>0.842</td>
<td>0.824</td>
<td>0.791</td>
<td>0.772</td>
<td>0.754</td>
<td>0.732</td>
<td>0.747</td>
<td>0.687</td>
<td>0.662</td>
</tr>
<tr>
<td>Adult stock (tonnes)</td>
<td>2,243</td>
<td>1,505</td>
<td>705</td>
<td>296</td>
<td>222</td>
<td>278</td>
<td>363</td>
<td>597</td>
<td>492</td>
</tr>
<tr>
<td>Annual egg production (10&lt;sup&gt;6&lt;/sup&gt;)</td>
<td>35.5</td>
<td>7.52</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Daily mortality (%) of prerecruits</td>
<td>5.57</td>
<td>5.15</td>
<td>6.68</td>
<td>6.57</td>
<td>6.36</td>
<td>6.29</td>
<td>5.63</td>
<td>5.36</td>
<td></td>
</tr>
</tbody>
</table>

<sup>a</sup> Recalculated from Tables 5–13 in Ritragsa (1976).

<sup>b</sup> Estimated from Fig. 1.

<sup>c</sup> Estimated by extrapolating to F = 0 the natural logarithm of the 1965 and 1966 standing stock values plotted against the corresponding values of fishing mortality.
of Beverton and Holt (1957), where \( Z \) and \( T_t \) are defined as in Equation (3), and where \( \lambda = t_A - t_c(2.5) \), \( \lambda \) itself being "the maximum age of significant contribution to the fishery" (Ricker 1975) or more simply, the longevity of the shrimps.

Under an assumption that the oldest shrimps reach about 95% of their asymptotic length (Beverton 1963), \( t_A \) can be estimated from the rearranged version of the von Bertalanffy growth equation:

\[
\log_e \left( 1 - \frac{L_u}{L_u - 0.95} \right) = \frac{t_A - t_c(2.5)}{-K} + t_u,
\]

which provides values of \( t_A = 0.75 \) and \( \lambda = 0.625 \), used in conjunction with Equation (5).

With the yield-per-recruit values obtained from Equation (5), the approximate number of recruits produced for each year \( (R) \) was estimated from the relationship

\[
R = \frac{Y}{(Y/R)}.
\]

The use of this expression to estimate recruitment appears justified because \( \lambda \) being rather small (0.625 year), a cohort of shrimps will make a significant contribution for only a short period of time (slightly more than \( \frac{1}{2} \) year), during which \( F \) can be assumed constant, although this approach would not be appropriate in the case of long-lived fish (the annual yield of which is the sum of partial yields from a large number of cohorts). The numbers of recruits estimated by means of Equation (7) are given for each year in Table 5.

Estimation of the stock-recruitment relationship requires a measure of the adult stock, or better, the quantity of eggs produced annually. In the present case, the adult stock is that proportion \( (B_w) \) equal to or older than mean age at first maturity, \( t_m = 0.372 \) year. The proportionality constant \( m \) is approximated by

\[
m = \exp(-Zr_1) \left[ 1 - \frac{3 \exp(-Kt_A) - 3 \exp(-2Kt_A) + 3 \exp(-3Kt_A)}{Z + 3K} \right] - \frac{\exp(-3Kt_A)}{Z + 3K}.
\]

The values of \( m \) computed by Equation (8) are given in Table 4, along with the derived estimate of adult biomass. Annual egg production was then obtained by directly multiplying adult biomass by mean relative fecundity (Table 2); underlying assumptions are that the female stock makes up half of the adult stock, and that spawning occurs twice a year.

The (natural) mortality, in percent per day, of the shrimp prerecruits, finally was estimated from the relationship

\[
\% \text{ mortality/day} = 1 - \left\{ \exp(\log_e(\text{recruits/eggs}) / t_c(2.5)) \right\},
\]

with \( t_c(2.5) = 45.7 \) days. The percent mortality

<table>
<thead>
<tr>
<th>Year</th>
<th>Annual shrimp egg production( a ) (10^6 eggs)</th>
<th>Biomass of predators and competitors( a ) (10^6 tonnes)</th>
<th>Annual shrimp recruitment( a ) (10^6 recruits)</th>
<th>Predicted recruitment( a ) (10^6 recruits)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Virgin stock</td>
<td>35.7</td>
<td>1,978</td>
<td>1,006</td>
<td>590</td>
</tr>
<tr>
<td>1963</td>
<td>23.9</td>
<td>1,264</td>
<td>807</td>
<td>950</td>
</tr>
<tr>
<td>1966</td>
<td>11.2</td>
<td>681</td>
<td>475</td>
<td>526</td>
</tr>
<tr>
<td>1967</td>
<td>4.71</td>
<td>592</td>
<td>211</td>
<td>218</td>
</tr>
<tr>
<td>1968</td>
<td>3.53</td>
<td>345</td>
<td>175</td>
<td>166</td>
</tr>
<tr>
<td>1969</td>
<td>4.42</td>
<td>530</td>
<td>221</td>
<td>219</td>
</tr>
<tr>
<td>1970</td>
<td>5.77</td>
<td>502</td>
<td>297</td>
<td>306</td>
</tr>
<tr>
<td>1971</td>
<td>4.49</td>
<td>345</td>
<td>671</td>
<td>622</td>
</tr>
<tr>
<td>1972</td>
<td>7.66</td>
<td>325</td>
<td>618</td>
<td>563</td>
</tr>
</tbody>
</table>

\( a \) From Table 4. \( a \) From Table 1. \( a \) From Equation (10).
values so obtained may be found in Table 4, along with the estimated annual egg production.

Results

Table 5 summarizes the results obtained (annual shrimp egg production, biomass of predators and competitors, and annual shrimp recruitment), as computed with the methods described above.

From these data, three relationships were drawn or estimated.

(1) There was no direct stock–recruitment relationship for penaeid shrimps in the Gulf of Thailand (Fig. 1). Recruitment at first diminished from a relatively high value in 1963 (and presumably in the virgin stock as well), then increased again in the early 1970s.

(2) However, there has been a strong dependence of prerecruit mortality on the biomass of predators and competitors (Fig. 2), with high mortality in the early 1960s and reduced mortality in the early 1970s.

(3) Annual shrimp recruitment \( R \) is related to annual shrimp egg production \( P \) and the biomass of predators and competitors \( B \) by

\[
\log_{10} R = 3.440 + 1.126 \log_{10} P - 0.6708 \log_{10} B, \tag{10}
\]

which has a multiple correlation coefficient of 0.996. Equation (10) also can be written

\[
R = 10^{3.440 + 1.126 P^{1.126} B^{-0.6708}}, \tag{11}
\]

where \( R \) is viewed as proportional to a power of parental biomass or egg number (as in Cushing 1971) and inversely proportional to a power of the biomass of predators and competitors.

Discussion

We know that fish eat shrimps and that many small demersal fish feed on organisms also consumed by shrimps (Tiews et al. 1972; Tiews et al. 1973). Thus, generally speaking, fishes are both the predators and the competitors of shrimps, while both fishes and shrimps are "prey" of a demersal fishery.

The demersal fishery, by offsetting the natural balance between shrimps and fishes, can indirectly increase the survival of shrimps by removing their predators and competitors (Fig. 2). This is probably what happened in the Gulf of Thailand where the standing stock of shrimps, along with that of other invertebrates (crabs, squids, cuttlefish) and some fishes such as conger eels (Muraenidae spp.) and flatfish (Bothidae, Pleuronectidae, Soleidae, Psettodidae) stayed more or less constant, or even increased, as the total standing stock decreased (Pauly 1979). Such interactions explain why plotting shrimp recruitment against egg pro-
duction and the total demersal standing stock removes such a large fraction (>0.99) of the variance in recruitment. Conversely, the high value of this fraction suggests that recruitment in the Gulf of Thailand shrimp stocks is determined solely by biological and fishery-induced changes in biomass and species composition, and not, as in temperate waters, predominantly by fluctuations in the abiotic environment.

Baranov (1927), cited in Ricker (1975), stated that “a fishery, by thinning out a fish population, itself creates the production by which it is maintained.” As it appears, “thinning out a fish population” also has the effect of reducing the predation and food competition affecting the shrimp stocks associated with these fishes. This can result, eventually, in an increase of the shrimp component in the catch, granted that the parental (shrimp) population is itself not too badly reduced.

The method outlined here to derive a stock-recruitment relationship from catch-per-effort data, estimates of $F$, and growth and natural mortality parameters, is still tentative. However, it appears to generate, among other things, a classical “Ricker curve” when used in combination with other data—for example, in the case of the false trevally *Lactarius lactarius* from the Gulf of Thailand (Pauly 1980). Another type of stock-recruitment relationship, a dependence of recruitment on predator and competitor biomass only, was generated by applying the method to data on the Indian halibut *Psettodes erumei*, also in the Gulf of Thailand (Pauly 1980). Thus, the method has generated three different types of stock-recruitment relationships, possibly corresponding...
Table 6.—Biological predictors of recruitment in selected tropical fish and crustacean stocks.

<table>
<thead>
<tr>
<th>Predictor variable(s)</th>
<th>Taxa</th>
<th>Life-history strategy</th>
<th>Remarks</th>
</tr>
</thead>
<tbody>
<tr>
<td>Adult stock size</td>
<td><em>Lactarius lactarius</em>&lt;sup&gt;a&lt;/sup&gt; (Pisces, Lactariidae)</td>
<td><em>K</em>-strategy</td>
<td>Corresponds to a typical Ricker curve (see Ricker 1975)</td>
</tr>
<tr>
<td>Adult stock size and biomass of predators and competitors</td>
<td><em>Penaeid shrimps</em>&lt;sup&gt;b&lt;/sup&gt; (Crustacea, Penaeidae)</td>
<td>Intermediate strategy</td>
<td>Intertidal vegetation area may be considered as an additional predictor of shrimp recruitment (Martosubroto and Naamin 1977; Turner 1977).</td>
</tr>
<tr>
<td>Biomass of predators and competitors</td>
<td><em>Psittoides crumen</em>&lt;sup&gt;b&lt;/sup&gt; (Pisces, Psittodidae)</td>
<td><em>r</em>-strategy</td>
<td>The relationship obviously does not hold for extremely low levels of adult stock.</td>
</tr>
</tbody>
</table>

<sup>a</sup> As defined in Pianka (1970).
<sup>b</sup> Pauly (1980).
<sup>c</sup> Present paper.

to three different ecological strategies (Table 6). Because it does not always generate the same type of stock–recruitment relationship, this method seems to lack inherent bias.

A drawback of the method—when taxa larger than species are considered—is the need to use "representative" organisms with "representative" values of growth and mortality parameters. Because such representative organisms do not really exist, all estimates of yield-per-recruit, recruit number, egg production, et cetera will be biased to an unknown extent. I have performed, therefore, all calculations with parameter values that are as realistic as possible in order to assess the appropriateness of some numerical results. For example, the values of 7.52 to 5.36% deaths per day for shrimp prerecruits (Fig. 2) appear reasonable, as they are within the range of the mortality values reported from fish larvae in different areas of the world (Dahlberg 1979). Still, more will have to be done with this type of approach in order to assess its overall applicability, particularly with regards to the approximations involved in Equation (7) and to the use of a linear regression model Equation (10), the assumptions of which (normality, zero mean, homoskedasticity, and non-autoregression; see Kmenta 1971) may be met only partially.

Acknowledgment
I thank Jay Maclean for his assistance with the revision of the original manuscript.

References


GARCIA, S. 1975a. Biologie de *Penaeus duorarum no- tialis* en Côte d'Ivoire V—nouvelles études de la croissance. Centre de Recherches Oceanogra-


