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Is recruitment related to spawning stock in penaeid shrimp fisheries?

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The relationship between spawning stock and recruitment in penaeid shrimp fisheries has been questioned because they exhibit unique characteristics with respect to population dynamics and fisheries. This study used meta-analyses to test the null hypothesis that recruitment is a series of random, independent events based on the penaeid shrimp stocks found in published sources. Both the derivative hypothesis test and Granger causality test rejected the null hypothesis. Thus, recruitment is related to spawner abundance. Shrimp populations should be managed so as to maintain sufficient spawning stock abundance to yield high recruitment.

Key words: shrimp, recruitment, stock-recruitment relationship, meta-analysis, hypothesis test.

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Introduction

There have been some clear examples of spawning stock recruitment relationship (SRR) and recruitment overfishing in penaeid shrimp fisheries over the last decade (Penn and Caputi, 1986; Penn *et al.*, 1995; Gracia, 1996). However, there is no published test of the null hypothesis that recruitment is independent of spawning stock in penaeid shrimp fisheries. If a general test cannot reject the null hypothesis, then it is highly probable that the individual SRRs are merely some of the small percentage of cases that would arise by chance. The relationship between recruitment and spawning stock in fisheries has been a fundamental subject of many studies. Rejecting the null hypothesis leads to management strategies of preserving spawning stock abundance (Ricker, 1954; Beverton and Holt, 1957; Cushing, 1971; Tyler, 1992; Iles, 1994; Myers and Barrowman, 1996; Francis, 1997; Myers, 1997). In contrast, accepting the null hypothesis means, "periods of recruitment appear to be environmentally induced and unavoidable" (Gilbert, 1997), implying there is no need to set spawning stock threshold to keep the stock sustainable (Koslow *et al.*, 1987; Wooster and Baily, 1989). This paper conducted two meta-analyses to test the null hypothesis based on the data derived from a thorough literature search for published studies on SRR of penaeid shrimp fisheries.

Materials and Methods

The meta-dataset

A literature search of spawning stock and recruitment data for shrimp stocks found 21 sets of time series data. Of these, three series (Boddeke, 1989; Hannah, 1993) were eliminated because they did not belong to penaeid species; one series (Penn and Caputi, 1986) was excluded because it overlapped with other time series; and four series (Gracia, 1983, Gracia, 1996) were not included because either the time series information was not available, or the time series was not consecutive. This left 13 series for analysis (Fig. 1), among which few statistically significant SRRs were established (Table 1). *Penaeus semisulcatus* of Kuwait and *Penaeus orientalis* of China were included twice because of incompatible time periods and different measures used for both spawning stock and recruitment.

Spawning stock (S) means either the number of spawners, or the number of eggs, or in most cases, some index of spawner abundance derived from catch per unit of effort of research vessels. Recruitment (R) is defined as the individual number of shrimp or a relative index. For shrimp fisheries, accurate commercial catch-at-age data are not available in most cases, and abundance of spawning stock and recruitment is represented most

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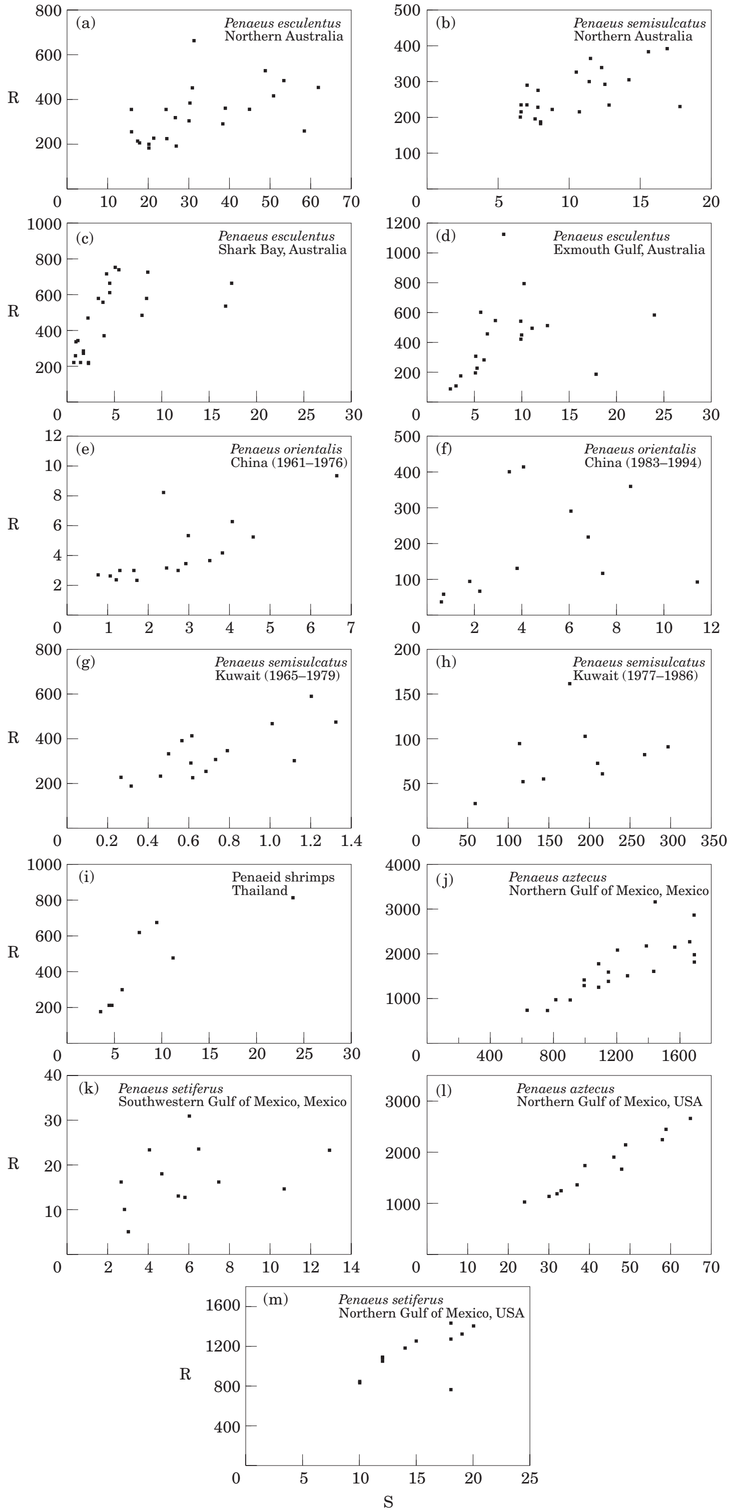

Figure 1. Stock-recruitment diagrams for 13 penaeid shrimp stocks (for units see Table 1).

Table 1. Test statistics of the penaeid shrimp species used for the meta-analysis.

Series no.	Stock	Area	Measure (R/S)	Median slope	Granger test $p_i(S \Rightarrow R)$	Granger test $p_i(R \Rightarrow S)$	SRRs	Source
1	*Penaeus esculentus*	Northern Australia	c.p.u.e.[2]	–	0.022	0.004	$r^2=0.23$, p=?[3]	Wang & Die, 1996
2	*Penaeus semisulcatus*	Northern Australia	c.p.u.e.	–	0.075	0.681	$r^2=0.52$, p=?[3]	Wang & Die, 1996
3	*Penaeus esculentus*	Shark Bay, Australia	c.p.u.e. (research)	+	0.000	0.629	$r^2=0.50$, $p<0.01$	Penn *et al.*, 1995
4	*Penaeus esculentus*	Exmouth Gulf, Australia	c.p.u.e. (research)	+	0.087	0.358	Not fitted[4]	Penn *et al.*, 1995
5	*Penaeus orientalis*	China (1961–1976)	Number	+	0.014	0.061	$r^2=0.32$, $p=0.02$	Ye, 1984
6	*Penaeus orientalis*	China (1983–1994)	Number/c.p.u.e.	+	0.001	0.506	$r^2=0.51$, $p<0.01$	Deng *et al.*, 1996
7	*Penaeus semisulcatus*	Kuwait (1965–1979)	Number/c.p.u.e. (single fleet)	–	0.076	0.103	Not fitted	Morgan & Garcia, 1982
8	*Penaeus semisulcatus*	Kuwait (1977–1986)	Number/c.p.u.e.	+	0.218	0.683	$r^2=0.25$, $p=0.14$	Morgan, 1989
9	Penaeid shrimps	Thailand	Number/egg	+	0.002	0.482	Not fitted	Pauly, 1982
10	*Penaeus aztecus*	Northern Gulf of Mexico	Number	+	0.010	0.568	Not fitted	Garcia, 1983
11	*Penaeus setiferus*[1]	Southwestern Gulf of Mexico	Number	+	0.368	0.588	$r^2=0.25$, $0.1<p<0.2$	Gracia, 1991
12	*Penaeus aztecus*	Northern Gulf of Mexico, USA	c.p.u.e.	+	0.012	0.424	Not fitted	Rothschild & Brunenmeister, 1984
13	*Penaeus setiferus*	Northern Gulf of Mexico, USA	c.p.u.e.	+	0.107	0.535	Not fitted	Rothschild & Brunenmeister, 1984

[1]Gracia (1996) separated the most and second abundant cohorts of the southwestern Gulf of Mexico shrimp (*Penaeus setiferus*) and studied their stock–recruitment relationships. Unfortunately, the data sets he used are not consecutive and cannot be used in this analysis.
[2]All c.p.u.e. indices are calculated from commercial catch data except those indicated.
[3]No p-value was provided in the source paper.
[4]No simple SRR was fitted, but a SRR with spawning stock and rainfall in January and February as independent variables was established.

often by relative abundance index, catch per unit of effort (Table 1).

The methods

There are some different methods to test the null hypothesis that recruitment is independent of spawning stock. Iles (1994) carried out tests by fitting models to individual flatfish stocks. Myers and Barrowman (1996) used non-parametric, meta-analytical methods. Gilbert (1997) developed different test statistics that he claimed could reduce the time series effects on estimates of relationships between S and R. As mentioned above, the time-series effect is an important source for biases in SRR of penaeid shrimp fisheries. Therefore, this study first conducted Gilbert's test (Gilbert, 1997) and then applied the Granger causality test (Granger, 1969; Sims, 1972) to the same data used for Gilbert's test. The causality test has two advantages. First, it can address the autocorrelation problem in recruitment, which is believed to create very difficult statistical problems (Myers, 1997) and to be the source of biases in the estimates of the model parameters of stock-recruitment relationship (Walters, 1985; Caputi, 1988). Second, it can find the feedback causality from recruitment to spawning stock, which is a unique feature of penaeid shrimp fisheries.

Hypothesis test based on derivatives

Suppose R is a function of S of either the Ricker (1954) or Beverton-Holt (1957) kind, its derivative (the slope of the function) would be positive, except perhaps at high S-values. Estimates of the derivative are obtained by taking the ratios of the first differences of the time series, $\Delta R/\Delta S$. Under the null hypothesis $\Delta R/\Delta S$ would scatter randomly around zero. For each stock, the median of $\Delta R/\Delta S$ is used as the intermediate statistic to reduce the negative impact of error on the power of the test. Here, the number of stocks with positive median slopes is counted (Table 1). Under the null hypothesis (with random error) the intermediate statistic, median slope for a stock, would vary around zero. Values would tend to be near zero, and on average, half would be above zero, i.e. $\pi=0.5$ (Gilbert, 1997). Significance levels were then obtained from the binomial distribution to test the null hypothesis against the model.

Hypothesis test of Granger causality

The unique features of penaeid shrimp do not only make the stock-recruitment relationship very obscure, but also make spawning stock a function of recruitment that same year (Garcia, 1983; Caputi, 1988). A great difficulty arises when the spawning stock and recruitment data of this kind are fitted to a traditional SRR model (Walters and Ludwig, 1981; Walters, 1985). The failure to fit SRR leads to doubts about the causal function of spawning stock to recruitment. One way to address the relationship between R and S is to test causality between these two variables, using the method proposed by Granger (1969) and popularized by Sims (1972). Testing causality, in the Granger sense, involving using F-tests to test whether lagged information on spawning stock S provides any statistically significant information about recruitment R in the presence of lagged R. If not, then "S does not Granger-cause R".

There are many ways to implement a test of Granger causality. A simple approach uses the auto-regressive specification of a bivariate vector auto-regression. Assume a particular auto-regressive lag length J, and estimate the following unrestricted equations by ordinary least squares (OLS):

$$R_t = c_1 + \sum_{j=1}^{J} \alpha_j R_{t-j} + \sum_{j=1}^{J} \beta_j S_{t-j} + u_t, \tag{1}$$

where c_1, α_j and β_j are parameters and u_t is a white-noise random error. If some β_j is not zero, then S_t is causing R_t. The null hypothesis is:

$$H_0: \beta_1 = \beta_2 = \ldots = \beta_J = 0.$$

Conducting F-test of the null hypothesis by estimating the following restricted equation also by OLS:

$$R_t = c_0 + \sum_{j=1}^{J} \gamma_j R_{t-j} + e_t, \tag{2}$$

where c_0 and γ_j are parameters and e_t is a white-noise random error.

Compare their respective sum of squared residuals:

$$RSS_1 = \sum_{t=1}^{T} \hat{u}_t^2 \qquad RSS_0 = \sum_{t=1}^{T} \hat{e}_t^2,$$

where T is the number of observations. If the test statistic:

$$S_1 = \frac{(RSS_0 - RSS_1)}{RSS_1/(T-2J-1)} \sim F(J, T-2J-1) \tag{3}$$

is greater than the specific critical value, then reject the null hypothesis that S does not Granger-cause R. For penaeid shrimp, biological evidence of a one-year life span in the fishery shows that spawning stock of this year may significantly affect next year's recruitment. Therefore, J of the above equations is simply 1 in the case of penaeid shrimp.

Separate analysis on each set of the 13 shrimp-stock data tested the same scientific hypothesis that recruitment is independent of spawning stock. Each of these tests furnished a probability value for the particular outcome, assuming the hypothesis to be correct. The probability for a specific stock may be low enough to reject the null hypothesis or high enough to accept the null hypothesis. A difficulty then arises to establish statistical significance of all the data sets as a whole. Fisher (1954, section 21.1) developed a technique for combining the outcomes of several experiments to obtain an overall significant test for a given hypothesis. In this study, results are combined across populations instead of experiments. That is, the time series of each population is treated as a realization of a natural experiment, and the results across populations are combined.

Suppose p_i is the probability value for i-th daa set, and $\ln p_i$ is distributed as $-1/2\chi^2_{[2]}$. By twice evaluating the negative natural logarithm of each probability and totalling these values, a total was obtained that can be looked up for 2k degrees of freedom (k = the number of separate tests and probabilities), there being two degrees of freedom for each probability value looked up. The resulting $-2\ln\Sigma p_i$ with $\chi^2_{[2k]}$ is then compared. If the overall probability was larger than a $\chi^2_{[2k]}$ at a specified significance level, the test was concluded to be significant at this specified level and the null hypothesis was rejected (Sokal and Rohlf, 1981).

The feedback test

The equation of causality test given above implies that S_t causes R_t, provided that β_j in Equation (1) is not zero. Penaeid shrimp only live for one year in the fishery. Those shrimp that survive to the end of a fishing season become spawning stock (Garcia, 1983; Walters, 1985). If the survival rate is ρ_t, which is a function of fishing mortality, in year t, the relation between spawning stock and recruitment can be written: $S_t = \rho_t R_t$ (Garcia, 1983; Caputi, 1993; Penn *et al.*, 1995). To test this possible instantaneous causality, of R_t causing S_t, Equations (1) and (2) were changed as follows (Granger, 1969; Sims, 1972):

$$S_t = c_1 + \sum_{j=1}^{J} \alpha_j S_{t-j} + \beta_0 R_t + u_t \qquad (4)$$

and

$$S_t = c_0 + \sum_{j=1}^{J} \gamma_j S_{t-j} + e_t \qquad (5)$$

The null hypothesis is that recruitment has no effects on the spawning stock of the same year:

$H_0{:}\beta_0 = 0$

R_t causes S_t, provided that β_0 is not zero. The test statistic of Equation (3) was also used in this test. If both events, S_t causing R_t and R_t causing S_t, occur, there is said to be a feedback relationship between S_t and R_t (Granger, 1969).

Results and discussion

The results of the hypothesis test based on the derivative of R with respect to S are shown in Table 1. Ten of the 13 stocks have positive median slopes. The probability of at least the observed number of slopes exceeding zero under the null hypothesis was calculated to be p = 0.011 from the binomial distribution. The null hypothesis that recruitment is independent of spawning stock can be rejected. Two data sets for *P. semisulcatus* of Kuwait and for *P. orientalis* of China were included because the sets covered different time periods and used different measures for reporting spawning stock and recruitment. Had only one data set for each stock been analyzed, reducing the number of stocks from 13 to 11, the null hypothesis would still have been rejected at the 5% significance level (p = 0.033).

If the stock had a dome-shaped stock-recruitment relationship, with observations occurring on both sides of the dome, ΔR/ΔS would have had both positive and negative values. In such cases, the derivative test may then falsely fail to reject the null hypothesis. To address this potential problem, the test was conducted after censoring the data. All the S and R data sets were firstly fitted to Ricker's model, R = Sexp(a − bS) as the stock-recruitment curves for penaeid shrimp are most likely to be dome-shaped (Garcia, 1983; Gulland and Rothschild, 1984). For those stocks for which the fitted Ricker model had a maximum within the range of the S data, ΔR/ΔS was negative to the right of the maximum, and those observations were excluded. Walters (1985) drew attention to an important source of bias present in the estimates of the parameters for stock-recruitment relationship fitted using the usual regression technique, therefore, a non-linear procedure was used when fitting the Ricker model.

Time-series effects bias estimates of relationships between S and R when they are treated as independent observations (Walters, 1985). Time-series effects can also cause hypothesis tests on time-series data of S and R to be potentially misleading (Gilbert, 1997). Such time-series bias is present in all SRRs based on natural variation in spawning stock, and the bias is great in a species with a one-year life cycle like the penaeid shrimp. Walters and Ludwig (1981) and Walters (1985) noted that the combined effect of measurement error and time-series bias was to make recruitment appear to be independent of spawning stock. This could partially be the reason why many previous studies were unable to show SRR for prawns (Garcia, 1983; Caputi, 1988). The test used in this study was based on estimates of a derivative of R with respect to S and avoided this time-series difficulty (Gilbert, 1997).

The derivative hypothesis test (Gilbert, 1997) has been criticized by Myers (1997) for its inefficiency when the year-to-year changes in the size of the spawner biomass were relatively small (i.e. median $|\Delta S/S| < 1$). The median $|\Delta S/S|$ for all the stocks in this study was calculated and were found to be less than 1. However, the result still rejects the hypothesis, suggesting that the effect of the spawning stocks on recruitment might be even stronger than indicated by this test.

Table 1 also lists the details of individual causality test for each stock. A total of seven of the 13 stocks have a probability value (p_i) lower than 0.05. The overall test value of $-2\ln\Sigma p_i$ is 107.89, much greater than $\chi^2_{0.001[26]} = 54.05$. The hypothesis that recruitment is independent of spawning stock can therefore be rejected. If only one data set of *P. semisulcatus* in Kuwait (Morgan and Garcia, 1982) and *P. orientalis* in China (Ye, 1984) was included, the value of $-2\ln\Sigma p_i$ was reduced to 96.99, still much higher than $\chi^2_{0.001[22]} = 48.27$. Rejection of the null hypothesis was highly significant. Thus, it would seem that the spawning stock value in the previous year helps to explain the variation in recruitment.

The feedback-causality test statistics of all the species used are also listed in Table 1. Only one stock has a probability value of less than 0.05. The overall test statistic is 33.69, lower than $\chi^2_{0.10[26]} = 35.56$. This result cannot reject the hypothesis that spawning stock is not determined by recruitment of the same year. Although spawning stock is associated with the survival of recruits of the same year, the feedback is not statistically significant. This is not surprising, because the survival (S_t) is greatly determined by the fishing mortality coefficient. Most shrimp fisheries around the world are fully exploited and have very low survival rates (Garcia, 1983; Gulland and Rothschild, 1984). The failure to reject the null hypothesis indicates that fishing effort plays a more significant role in controlling spawning stock than recruitment.

The above causality test is relative to the set of data used. If relevant data had not been included in this set, then spurious causality could arise. For instance, if the set used was assumed to consist only of the two variables, $D = (R_t, S_t)$, but, in fact, there was a third series X_t which was causing both within the enlarged set, $D' = (R_t, S_t, X_t)$, then for the original set D, spurius causality between R_t and S_t may be found (Granger, 1969). This is similar to spurious correlation and partial correlation between sets of data that arise when some other statistical variable of importance has not been included. In fisheries, there is an argument that variation in recruitment is induced by environment (Cushing, 1971, 1996; Klima, 1989). Given that X_t is the environmental variable that has a significant effect on recruitment R_t, if the argument holds, then environment induces recruitment, i.e. X_t causes R_t. In penaeid shrimp fisheries, although S_t is the survival of R_t, R_t as proved by the above feedback test does not deterministically cause S_t. Thus, X_t does not cause both R_t and S_t. The causality between spawning stock and recruitment is unlikely here to be spurious. The causality tests assumes linearity (Granger, 1969; Ashley *et al.*, 1980). For the stocks, data of which could be fitted to the Ricker SRR, the observations to the right of the maximum R were excluded, with the Gilbert test. In fact, Garcia (1983) found that linear relationships between spawning stock and recruitment were often observed for penaeids.

The null hypothesis that each year's recruitment is an independent event was rejected in both the tests, suggesting that spawning stock abundance cannot be ignored in the management of shrimp fisheries. Effective measures must be taken to maintain sufficient spawner abundance to prevent recruitment overfishing. However, there are probably few situation in nature in which variation in one variable is wholly caused by another. The identification of the causality relationship between spawning stock and recruitment does not exclude possible effects of environmental variables on recruitment.

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References

Ashley, R., Granger, C. W. J., and Schmalensee, R. 1980. Adverting and aggregate consumption: an analysis of causality. Econometrica, 48: 1149–1167.

Boddeke, R. 1989. Management of the brown shrimp (*Crangon crangon*) stock in Dutch coastal waters. *In* Marine invertebrate fisheries: their assessment and management, pp. 35–62. Ed. by J. F. Caddy. J. Wiley & Sons, New York. 752 pp.

Beverton, R. J. H., and Holt, S. J. 1957. On the dynamics of exploited fish populations. Fisheries Investment Series 2, Vol. 19 U.K. Ministry of Agriculture and Fisheries, London. 533 pp.

Caputi, N. 1988. Factors affecting the time series bias in stock-recruitment relationships and the interaction between time series and measurement error bias. Canadian Journal of Fisheries and Aquatic Science, 45: 178–184.

Caputi, N. 1993. Aspects of spawner-recruit relationships, with particular reference to crustacean stocks; a review. Aust. J. Mar. Freshwater Res., 44: 589–607.

Cushing, D. H. 1971. The dependence of recruitment on parent stock in different groups of fishes. J. Cons. Int. Explor. Mer., 33: 340–362.

Cushing, D. H. 1996. Toward a science of recruitment in fish populations. Excellence in Ecology 7. Ecology Institute, Germany. 175 pp.

Deng, J., Zhu, J., and Ren, R. 1996. A study on dynamics of stock recruitment relationship of penaeid shrimp in the Pohai sea. J. Fish. Sci. China, 3: 20–26.

Fisher 1954. Statistical methods for research workers. 12th edit. Oliver & Boyd, Edinburgh. 356 pp.

Francis, R. I. I. C. 1997. Comment: how should fisheries scientists and managers react to uncertainty about stock-recruitment relationships? Can. J. Fish. Aquat. Sci., 54: 982–983.

Garcia, S. 1983. The stock-recruitment relationship in shrimps: reality or artifacts and misinterpretations? Oceanogr. Trop., 18: 25–48.

Gilbert, D. J. 1997. Towards a new recruitment paradigm for fish stocks. Can. J. Fish. Aquat. Sci., 54: 969–977.

Gracia, A. 1991. Spawning stock-recruitment relationships of white shrimp in the southwestern Gulf of Mexico. Transactions of the American Fisheries Society, 120: 519–527.

Gracia, A. 1996. White shrimp (*Penaeus setiferus*) recruitment overfishing. Mar. Freshwater Res., 47: 59–65.

Granger, C. W. J. 1969. Investigating causal relations by econometric models and cross-spectral methods. Econometrica, 37: 424–438.

Gulland, J. A., and Rothschild, B. R. 1984. Penaeid shrimps – their biology and management. Fishing News Books Limited, England. 308 pp.

Hannah, R. W. 1993. Influence of environmental variation and spawning stock levels on recruitment of ocean shrimp (*Pandalus jordani*). Can. J. Fish. Aquat. Sci., 50: 612–622.

Iles, T. C. 1994. A review of stock-recruitment relationships with reference to flatfish populations. Netherlands Journal of Sea Research, 32(3/4): 399–420.

Klima, E. 1989. Approaches to research and management of US fisheries for penaeid shrimp in the Gulf of Mexico. *In* Marine invertebrate fisheries: their assessment and management, pp. 87–113. Ed. by J. F. Caddy. John Wiley & Sons, New York. 752 pp.

Koslow, J. A., Thompson, K. R., and Silvert, W. 1987. Recruitment to northwest Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) stocks: influence of stock size and climate. Can. J. Fish. Aquat. Sci., 44: 26–39.

Morgan, G. R. 1989. Separating environmental and fisheries effects in the recruitment of Gulf shrimp. Kuwait Bulletin of Marine Science, 10: 51–59.

Morgan, G. R., and Garcia, S. 1982. The relationship between stock and recruitment in the shrimp stocks of Kuwait and Saudi Arabia. Oceaogr. Trop., 17: 133–137.

Myers, R. A. 1997. Comment and reanalysis: paradigms for recruitment studies. Can. J. Fish. Aquat. Sci., 54: 978–981.

Myers, R. A., and Barrowman, N. J. 1996. Is fish recruitment related to spawner abundance? Fishery Bulletin, 94: 707–724.

Pauly, D. 1982. A method to estimate the stock-recruitment relationship of shrimps. Transactions of the American Fisheries Society, 111: 13–20.

Penn, J. W., and Caputi, N. 1986. Spawning stock-recruitment relationships and environmental influences on the tiger prawn (*Penaeus esculentus*) fishery in Exmouth Gulf, Western Australia. Aust. J. Mar. Freshwater Res., 37: 491–505.

Penn, J. W., Caputi, N., and Hall, N. G. 1995. Stock-recruitment relationships for the tiger prawn (*Penaeus esculentus*) stocks in Western Australia. ICES mar. Sci. Symp., 199: 320–333.

Ricker, W. E. 1954. Stock and recruitment. J. Fish. Res. Bd. Can., 11: 559–623.

Rothschild, B. J., and Brunemeister, S. L. 1984. The dynamics and management of shrimp in the northern Gulf of Mexico. *In* Penaeid shrimps – their biology and management, pp. 145–172. Ed. by J. A. Gulland, and B. J. Rothschild. Fishing News Book Limited, England. 308 pp.

Sims, C. 1972. Money, income and causality. American Economic Review, 62: 540–552.

Sokal, R. R., and Rohlf, F. J. 1981. Biometry – the principles and practice of statistics in biological research. 2nd edit. W. H. Freeman and Company, New York. 859 pp.

Tyler, A. V. 1992. A context for recruitment correlations: why marine fisheries biologists should still look for them. Fisheries Oceanography, 1: 97–107.

Walters, C. J. 1985. Bias in the estimation of functional relationship from time series data. Can. J. Fish. Aquat. Sci, 42: 147–149.

Walters, C. J., and Collie, J. S. 1988. Is research on environmental factors useful to fisheries management? Can. J. Fish. Aquat. Sci., 45: 1848–1854.

Walters, C. J., and Ludwig, D. 1981. Effects of measurement errors on the assessment of stock-recruitment relationships. Can. J. Fish. Aquat. Sci., 38: 704–710.

Wang, Y., and Die, D. 1996. Stock-recruitment relationships of the tiger prawns (*Penaeus esculentus* and *Penaeus semisulcatus*) in the Australian northern prawn fishery. Mar. Freshwater Res., 47: 87–95.

Wooster, W. S., and Bailey, K. M. 1989. Recruitment marine fishes revisited. *In* Effects of ocean variability on recruitment and an evaluation of parameters used in stock assessment models, pp. 153–159. Ed. by R. J. Beamish, and G. A. McFarlane. Can. Spec. Publ. Fish. Aquat. Sci. 108.

Ye, C. 1984. The prawn (*Penaeuus orientalis*) in Pohai sea and their fishery. *In* Penaeid shrimps – their biology and management, pp. 49–60. Ed. by J. A. Gulland, and B. J. Rothschild. Fishing News Book Limited, England. 308 pp.