

The stock-recruitment relationship in shrimps : reality or artefacts and misinterpretations ? ⁽¹⁾

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ABSTRACT

After a detailed review of the information available on stock-recruitment relationships and environmentally-driven variations of abundance in shrimps, the impact of this variability on the apparent shape of the SRR is examined. The existence of a strong autocorrelation in yearly data is stressed and it is concluded that the presently-available relationships do not demonstrate that the recruitment of shrimps is a function of stock size.

Examination of the particular cases when "seasonal" relationships have been established with monthly data shows that despite a certain similarity in shape they should not be interpreted as SRR sensu stricto and a three-dimensional interpretation is proposed instead.

The other possible sources of error and bias are finally examined and the consequences of the above findings on management strategies are briefly discussed.

KEY WORDS : Population dynamics -- Recruitment -- Fishery --- Management -- Environmental factors -- Statistical models -- Literature reviews -- Shrimp.

RÉSUMÉ

LA RELATION STOCK-RECRUTEMENT CHEZ LES CREVETTES : RÉALITÉ OU ARTEFACTS ET MÉPRISES ?

L'information disponible sur les relations stock-recrutement (RSR) chez les crevettes est examinée de manière détaillée, en particulier en ce qui concerne la qualité et la pertinence des indicateurs utilisés ainsi que l'interprétation des observations. Il apparaît que dans la majorité des cas la RSR pourrait être matérialisée par une droite passant par l'origine, ce qui a été interprété par divers auteurs comme la preuve que la pêche affectait directement le recrutement.

Remettant cette interprétation en question, l'auteur rappelle que les crevettes sont des animaux à vie courte dont les stocks, composés le plus souvent d'une seule classe d'âge annuelle, sont caractérisés par des variations inter-annuelles de recrutement et d'abondance en relation avec l'environnement (dont l'effet sur la survie des phases estuariennes du cycle vital est important). Il rappelle que ces variations d'abondance, tout comme celle de l'hydro-climat, sont le plus souvent autocorrélées. Dans ces conditions, le modèle traditionnel et déterministe de la RSR devrait être remplacé par un modèle dérivé mais différent qui, au lieu de considérer l'effet de l'environnement sur la relation comme un « bruit », l'intégrerait de manière explicite.

L'auteur montre, en outre, que lorsque l'on considère qu'il n'existe pas pour un stock donné une seule RSR mais une famille de relations correspondant à différents états de l'environnement, les variations autocorrélées de ce dernier conduisent à l'observation de pseudo-RSR linéaires quand la mortalité par pêche varie peu.

Examinant plus particulièrement le cas des RSR « saisonnières » -- établies sur une base de temps inférieure à l'année, pour des cohortes mensuelles par exemple -- l'auteur conclut que les mêmes artefacts peuvent conduire aux

(1) This topic has been shortly addressed by the author in a note on "Environmental Aspects of Penaeid Shrimp Biology and Dynamics", a paper presented at the Workshop on the Scientific Basis for the Management of Penaeid Shrimp. Key West, Florida, 18-24 November 1981.

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mêmes mauvaises interprétations. Il indique que les relations ne peuvent être interprétées que comme les relations entre un stock reproducteur donné à un moment donné de l'année (caractérisé par un ensemble propre de paramètres climatiques) et le recrutement qui en découle. Le phénomène représenté par une RSR « saisonnière » quand seuls S et R sont considérés ne matérialise pas la réaction du recrutement (R) à des variations du stock (S) dues à la pêche mais il est le résultat d'une adaptation ontogénétique complexe de la population à un environnement aux caractéristiques saisonnièrement oscillantes.

Au cours de la discussion qui suit l'exposé de cette théorie, l'auteur examine les autres sources possibles de biais ou d'artéfact dans les RSR chez les crevettes et conclut que la non prise en compte de l'exploitation des pré-recrues et de ses éventuelles variations est une très sérieuse source potentielle de biais pouvant conduire à l'observation de RSR linéaires passant par l'origine.

L'auteur conclut que l'existence de RSR sensu stricto chez les crevettes reste encore à démontrer en prenant en compte beaucoup plus de données, à de nombreux niveaux d'effort, de manière à définir la forme exacte de la relation, et en utilisant une approche multivariable.

En matière d'aménagement il souligne que les questions essentielles concernent : l'identification des facteurs influant sur le recrutement, la quantification des effets respectifs de la pêche et des autres facteurs, et les possibilités réelles de contrôle ou de prédiction des différents facteurs pertinents (parfois non réversibles dans le cas de certaines dégradations littorales) par les organismes chargés de l'aménagement.

MOTS-CLÉS : Dynamique population — Recrutement — Gestion stock — Facteur abiotique — Modèle statistique — Revue bibliographique — Crevette.

1. INTRODUCTION

The problem of the shape of the stock-recruitment relationship (SRR) (1) in marine animals has been the subject of a large number of papers in the last decade following the earlier classics of BEVERTON and HOLT, and RICKER.

In the particular case of crustaceans, the literature has been very sparse up to 1980. This lack of information was underlined by HANCOCK (1973; 1979). In the particular case of penaeid shrimp, NEAL (1975) recognized that no relationship had been identified in the Gulf of Mexico and summarized the assumptions that had emerged:

(a) because of the high fecundity of shrimp a relatively small population of spawners is required to maintain stock levels;

(b) the fishery is operating somewhere on the flat part of the (asymptotic) curve so that environmental fluctuations rather than changes in spawner abundance are the primary cause of stock fluctuations;

(c) overfishing is unlikely because fishing becomes unprofitable at levels of abundance which are still on the flat part of the curve.

These assumptions were apparently considered still valid when establishing the Fishery Management Plan for the U.S. shrimp fishery in the Gulf of Mexico (GMFMC, 1981). In their review of the biology

and dynamics of penaeids GARCIA and LE RESTE (1981) noted that there were no published indications showing with certainty that recruitment had been affected by fishing. They also noted that according to BAKUN and PARRISH (1981), if nurseries have limited and relatively constant biological capacity, the Beverton and Holt-type relationship is the most likely one. They stated that "for practical purposes, however, if there is no clear relationship between the stock and the recruitment within a range of reasonable levels of exploitation, such relationship can be wholly neglected and recruitment can be considered to depend on environment only". This conclusion, even if not clearly expressed, underlies the elaboration of the numerous predictive models for shrimps based on a relationship between annual production and environmental parameters (rainfall, temperature, river outflow, estuarine habitat, etc.) extensively reviewed by GARCIA and LE RESTE.

More recently at the Workshop on the Scientific Basis for the Management of Penaeid Shrimp, organized by NOAA/NMFS (Key West, Florida, 18-24 November 1981) there were a number of papers presented dealing with the subject.

The purpose of the present paper is to examine the recent information on stock-recruitment of shrimps in the context of the well-documented existence of important variations in recruitment and stock size caused by environmental factors.

(1) Throughout the text SRR stands for stock-recruitment relationships, $R = f(S)$, while the symmetric function $S = f(R)$ is called replacement line.

Section 2 of the document provides a review of the available evidence on SRR and on the existence of natural or man-induced environmentally-driven changes in stock size of shrimps.

In section 3 the theoretical and practical implications of the existence of important variations in recruitment not directly related to stock size (and level of fishing) on the traditional SRR concept are examined. Attention is drawn to the existence of strong serial correlation in the data and the consequent production of "apparent" stock and recruitment trajectories, sometimes resembling SR relationships but which could be interpreted as artefacts.

In Section 4, the published SRR are re-examined in the light of the aforementioned phenomena and particular attention is paid to the "seasonal" SRR's. It is tentatively demonstrated that all SRR's published can indeed be artefacts or misinterpretations and that the possible existence of SRR in shrimp has still to be demonstrated. Finally, after reviewing the other possible sources of error and bias the consequences in terms of management are given.

2. REVIEW OF THE AVAILABLE INFORMATION

In order to present the elements of a discussion we shall summarize here the available information on published SRR's and natural variations of stock size and recruitment.

2.1. Stock-recruitment relationships

Two types of observations are available for penaeids suggesting either a quasi-linear relationship between stock and recruitment within the range of observed values or no relationship at all. The first type of observations have been found in: ROTHSCHILD and PARRACK (1981), BRUNNENMEISTER (1981) and PARRACK (1981) in the Gulf of Mexico; YE (1981) in the Yellow Sea; MORGAN and GARCIA (1982) in Kuwait. The second type of information was given by KIRKWOOD (1981) in Australia and NICHOLS (1981) in the Gulf of Mexico.

In addition, BODDEKE (1982) found a Beverton and Holt-type of relationship for the Caridean brown shrimp *Crangon crangon* populations of four

geographical areas along the coast of the Netherlands and Belgium.

In a very thorough analysis of catch and effort statistics of the Gulf of Mexico penaeid shrimp fisheries BRUNNENMEISTER (1981) examined the relationship between the yearly catch per unit of effort in year $n+1$ and the calculated number of survivors available during the main spawning season in year n , for both *Penaeus setiferus* and *P. aztecus* and found significant correlations (Figure 1). According to the author this suggests that "the abundance in any year is related to the degree of exploitation and stock size in the previous one", and ROTHSCHILD and PARRACK (1981) considered this was a stock-recruitment relationship, the cpue in year $n+1$ being taken as an index of recruitment. However, it must be noted that the number of survivors available for spawning in year n and the average abundance in year $n+1$ both depend on the level of effort exerted in the respective years considered. Therefore a substantial part of the correlation observed by BRUNNENMEISTER may be due to the strong serial correlation generally observed in a time series of annual effort levels.

After a virtual population analysis using the Gulf of Mexico brown shrimp *Penaeus aztecus*, fishery data base PARRACK (1981) proposed an interesting set of SRR's established on a seasonal (monthly cohort) basis. The biomass of 8 months and older age group available every month was used as a measure of the spawning stock. The estimated biomass of the smaller size group in the catch is taken as a measure of monthly recruitments. The relationships have been established between the spawning stock estimated for a given month and the recruits three months later (1), by grouping the data by birth (spawning) month in order to "partition out as much environmentally-caused variations as possible". According to PARRACK, the data shows that spawner-recruit relations (2) do exist (Figure 2). These relations are nearly linear and their slope changes seasonally: the steepest slopes are observed for winter and early spring spawned cohorts (December-March) while the smallest ones are found for the summer spawned ones (July-August). Intermediate slopes are observed for spring (April-May) and autumn (October-November) spawning.

The concept of monthly SRR's is attractive because it would allow opportunity for recognizing the existence of both continuous spawning and

(1) Assuming therefore that the age at recruitment (3 months), the duration of the stay in the nursery and the growth in the pre-recruit phase are fixed, and that seasonal variations do not exist.

(2) But the author points out that the analyses do not prove any cause-effect relationship.

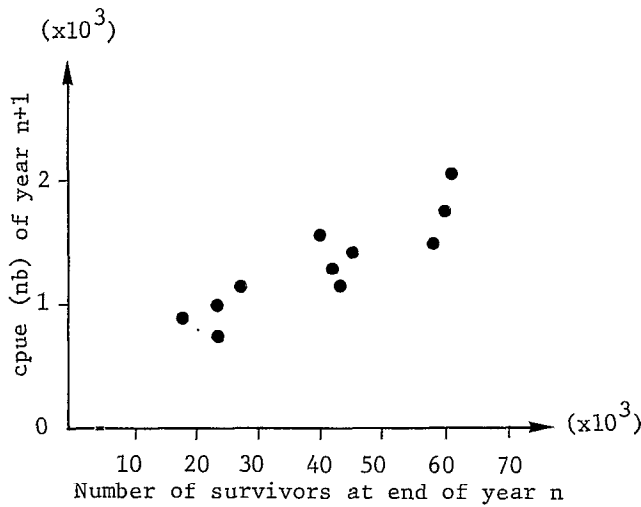


FIG. 1. — Stock-recruitment relationship for *Penaeus aztecus* from BRUNNENMEISTER (1981).
Relation stock-recrutement chez *Penaeus aztecus*, d'après BRUNNENMEISTER (1981).

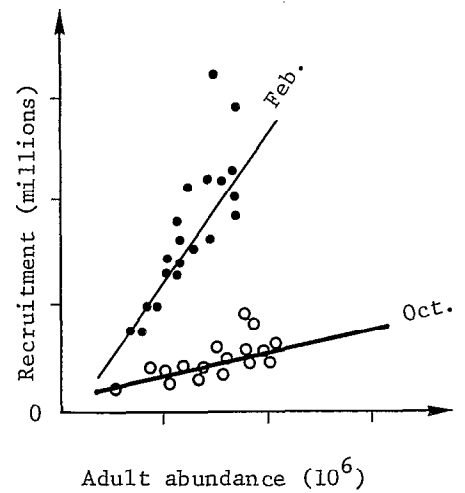


FIG. 2. — Seasonal stock-recruitment relationship for *Penaeus aztecus* (from PARRACK, 1981). The lines drawn by eye have been added.
Relation saisonnière stock-recrutement chez *Penaeus aztecus* (d'après PARRACK, 1981). Les droites d'ajustement "à l'œil" ont été surajoutées.

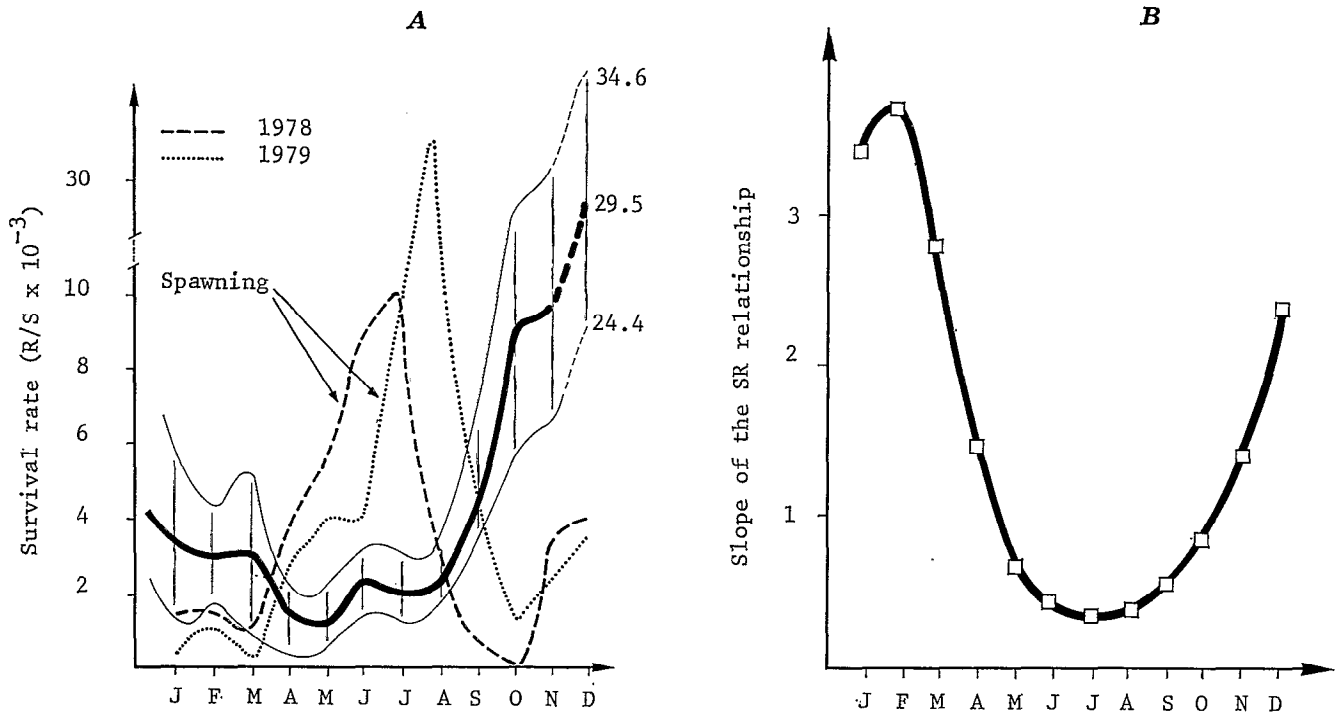


FIG. 3. — A: variations of survival rate between the egg and recrutement (average 1970-75). Data from BODDEKE and BECKER (1979). The dotted lines show the spawning cycle in 1978 and 1979 (from BODDEKE, 1982). B: changes in the slope of the apparent linear stock-recruitment relationship in *P. aztecus* (data from PARRACK, 1981).

A: variations du taux de survie — de l'œuf aux recrues — (moyenne 1970-75). Données d'après BODDEKE and BECKER (1979). Les lignes pointillées indiquent le cycle de ponte en 1978 et 1979 (d'après BODDEKE, 1982). B: évolution annuelle de la pente de la droite représentant la relation apparente stock-recrutement chez *P. aztecus* (données d'après PARRACK, 1981).

a very short generation time, and therefore provide more data points (than when working with annual data) and compensate for the shortness of most of the available time series. However, the interpretation of the results of such analyses is not straightforward:

(a) The seasonality observed in the slopes of the relationships could indeed reflect the expected natural seasonal variations in survival from the egg to recruitment. The available knowledge on the combined effects of temperature and salinity on larval survival (FORD and ST. AMANT, 1971, ZEIN ELDIN and GRIFFITH, 1969) indicates that the worse conditions (and likely lowest survival rates) are met in winter and early spring. This does not seem to fit with PARRACK's results where the lowest survivals apparently occur in summer and autumn. It must be noted that BODDEKE and BECKER (1979) also found an apparent seasonal pattern in larval survival to recruitment for *Crangon crangon* using a totally different approach (Figure 3).

(b) The observed seasonality may also be, at least partly, artificially produced by the introduction into the model of inappropriate assumptions. The age at recruitment for instance has been fixed at 3 months for all cohorts while seasonal changes in size and age at recruitment occur in many fisheries (1). This would introduce a distortion in the observed relationships. BODDEKE and BECKER (1979) also pointed out this possibility.

(c) The most potentially-serious problem however lies in the estimation of the spawning stock abundance. In PARRACK's work, the abundance of all individuals of 8 months and older is taken as a spawning stock for each month. However, the spawning activity is highly seasonal in this species, despite the fact that there are always some females (especially the big ones) spawning even in winter. RENFRO and BRUSHER (M.S.) have indicated that spawning activity of *P. aztecus* is maximum in spring and autumn and minimum in summer and winter. Moreover, when spawning starts after a winter resting period, most of the adults are supposed to spawn, but immediately after part of the adult population is not available anymore for spawning for some time (this is shown by the seasonal pattern of abundance of spent individuals). We must therefore conclude that only a seasonally-variable part of the age 8+ adult stock spawns effectively each month, and this would indeed also

create apparent seasonal patterns in the relationships when not taken into account.

As a conclusion, it can be said that Parrack's seasonal approach of SRR is a potentially-powerful tool for analysis of the phenomenon, but that the fit between the simplifying assumption and the biological facts (concerning especially the seasonal stability of the age at recruitment, the overwintering problem, and the seasonal pattern of spawning activity) may need some improvements before definite conclusions can be drawn. However, the type of relation observed by PARRACK for the main cohort, recruited in April-June at 3 months and therefore spawned in January-March (see Figure 2 for the February cohort as an example), could probably be the least biased one because it corresponds to the main spawning period. In addition, it is felt that the potential biases which may have been introduced are unlikely to be responsible for the fact that correlation between stock and recruitment in this case is best represented by a positive linear relationship. BODDEKE and BECKER (1979) also have analyzed on a monthly basis the SRR of the North Sea brown shrimp *Crangon crangon* which is also a coastal, short-lived species with a protracted spawning season. They analyzed the ratio between the calculated abundance of ripe eggs (2) (S) laid in a given month and the number of recruits (R) at 52 mm total length four months later, from 1970 to 1975. Their data show an apparent seasonal pattern in survival rate (Figure 3) but the authors pointed out that some of the higher values may be biased and retained an average value of $R/S = 2.55 \times 10^{-3}$ for the January-September period.

BODDEKE (1982) used the same type of data from 1977-80 to establish conventional SRR relating the stock size in March-April, May and June to the recruitment four months later (July to October). The four curves given in (Figure 4) correspond to four different areas with different potentials. According to the author the 4 asymptotes indicate the (recruitment) "levels on which the different stocks reach their maximum size" and the nursery grounds area is the limiting factor. However, the limited data contain a clear upward trend (Figure 5) and the possibility of occurrence of even higher recruitment sizes (and higher asymptotes) in the future, cannot be totally rejected.

The question of the significance of these sorts of curves obtained by a combination of monthly data points will be particularly examined later on.

(1) Some overwintering of the autumn spawned larvae have even been suggested for that species (TEMPLE and FISCHER, 1967; COOK and LINDNER, 1970).

(2) In *Crangon crangon* eggs are carried out by the female until hatched. Only ripe eggs were used for recruitment calculations.

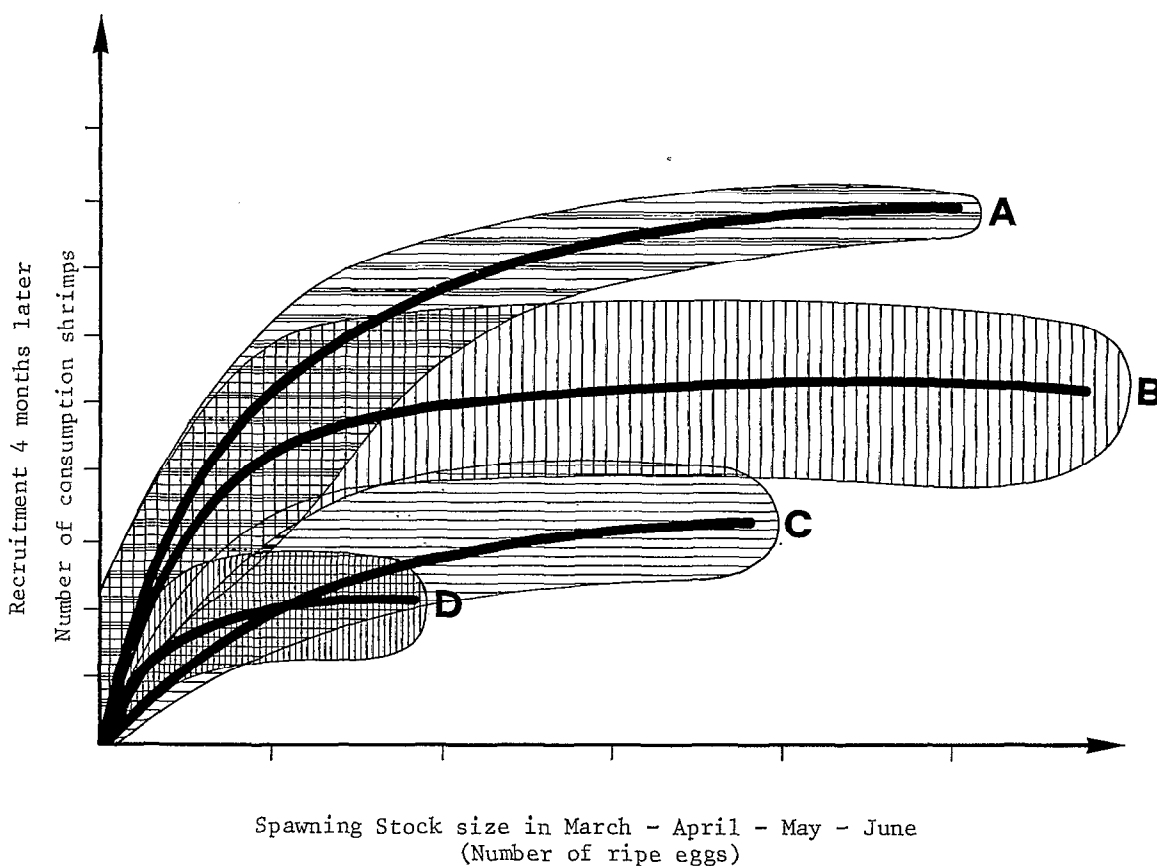


FIG. 4. — Apparent stock-recruitment relationship for *Crangon crangon* in four different sectors of the coast of Belgium and Netherlands (modified from BODDEKE, 1982). A = northern, B = northwestern, C = western, D = southwestern.

Relation apparente stock-recrutement chez Crangon crangon dans quatre secteurs des côtes Belges et Hollandaises (modifiée d'après BODDECKE, 1982). A = secteur nord, B = secteur nord-ouest, C = secteur ouest, D = secteur sud-ouest.

ROTHSCHILD and PARRACK (1981) also found a SRR for *P. aztecus* and *P. setiferus* in the Gulf of Mexico using different measures of stock and recruitment sizes. They showed that when the yearly catch per unit of effort (in weight) in year n is taken as an index of average spawning stock size, and the highest monthly catch per unit of effort in numbers for year $n+1$ as an index of the subsequent recruitment, only a weak relationship (if any) could be found for *P. setiferus*, but a strong one was observed for *P. aztecus* (Figure 6). The relationship has not been fitted but appears to be quasi-linear within the data range (as in Parrack's results which were obtained with a different type of data). They concluded that "the practical management implications are clear: recruitment is affected by stock size and stock size is affected by effort as demonstrated by the production models", and that "it is possible, given the relationships, to get

stock sizes each year to give optimal recruitment over a series of years."

It should however be noted that during the period of observation (1965-1975) fishing mortality seems to have been constant (PARRACK, 1981) despite an increase in fishing effort (BRUNNENMEISTER, 1981), and that even though there is a recruitment decrease between 1965 and 1975, the overall trend (1960-1979) is upward as indicated in Figure 7. The absence of a good SRR for *P. setiferus* is confirmed by NICHOLS (1981). His analysis on an extensive data base for the period 1960-1979) by cohort analysis shows that important fluctuations of stock size from year to year occur, and that these fluctuations are not well related to changes in effort level but are very well related to changes in recruitment of the year before. No SRR is discernible within the range of the data. In addition, NICHOLS states that the important reduction in

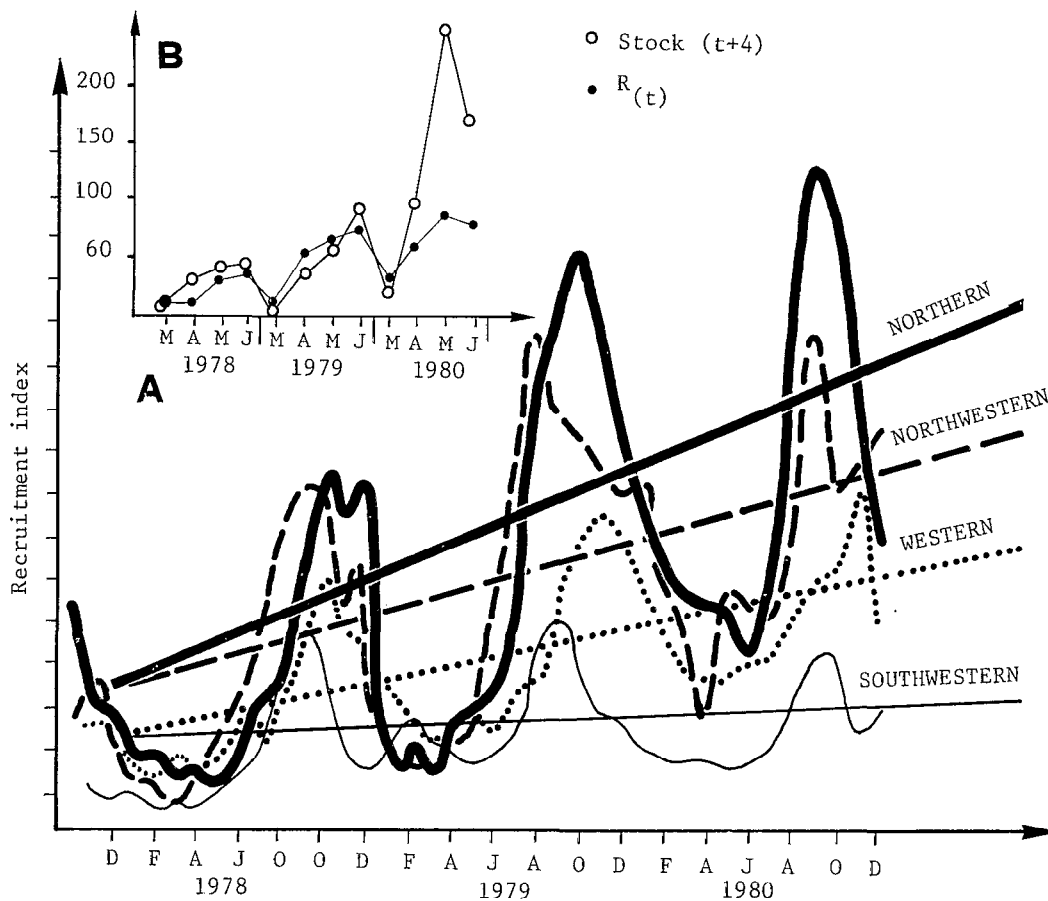


FIG. 5. — A: trends in monthly recruitment for *Crangon crangon*. B: trends in spawning stock-size (at time t) and recruitment (at time $t+4$) in the data used in Figure 4 (modified from BODDEKE, 1982).

A: *tendances du recrutement mensuel chez Crangon crangon*. B: *tendances du stock pondeur (au temps t), et du recrutement (au temps $t+4$), dans les données utilisées pour la figure 4 (modifié d'après BODDEKE, 1982).*

annual catch levels between 1939-1946 (75×10^6 lbs.) and 1960-1978 ($13-48 \times 10^6$ lbs.) cannot satisfactorily be explained by the effect of fishing with a smooth SRR, and that a more complicated function with two successive inflexion points would be necessary.

Another set of data on penaeids is given by PAULY (*in press*) which proposes a methodology usable for producing SRR's when catch per unit of effort series and a few ancillary variables are available. The spawning stock size in year n is estimated by the theoretical number of eggs available for spawning, calculated from Bm_n —the biomass of mature stock—, and the fecundity relationship. Bm_n is calculated as a variable portion of the total exploited biomass B_n (by using an equation involving Z , K ,

t_0 , size at first capture, size at first maturity). B_n is simply estimated by the ratio between the yearly catch Y_n and fishing mortality F_n , i.e. ($B_n = Y_n/F_n$). The recruitment which produced the stock of the year and on which the catch was taken is calculated simply by $R_n = Y_n/(Y/R)_n$ because the bulk of the catch in any year is obtained on the present year class. The relationship between stock and recruitment can then be analyzed and Pauly applied this methodology to the Gulf of Thailand shrimp stocks (1). The author states that "there is no direct stock-recruitment relationship" but taking into account the usual variability which characterizes this type of phenomenon it could be said that the apparent relationship established

(1) All species combined, using the biological parameters of *P. indicus* as representative of the "average" shrimp.

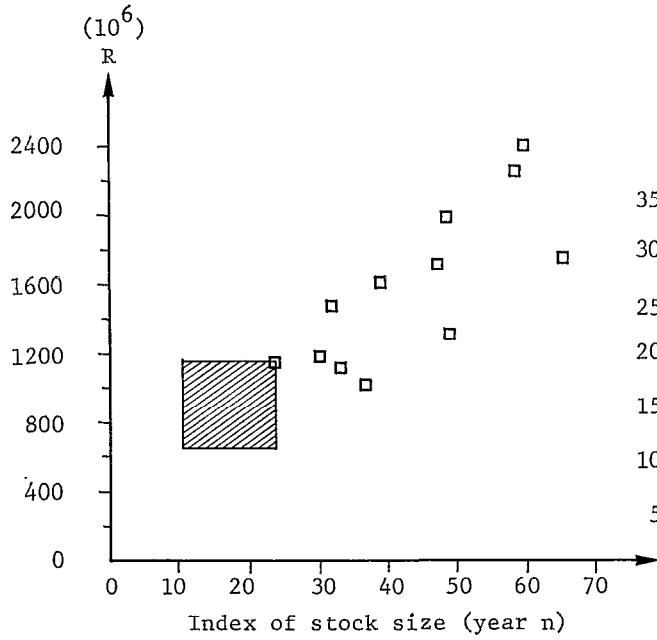


FIG. 6. — Stock-recruitment relationship for *P. aztecus*. The shaded area represents the data range for the white shrimp *P. setiferus* (data from ROTHSCHILD and PARRACK, 1981).

Relation stock-recrutement chez *P. aztecus*. La surface hachurée représente l'ensemble des données de la crevette blanche *P. setiferus* (données d'après ROTHSCHILD and PARRACK, 1981).

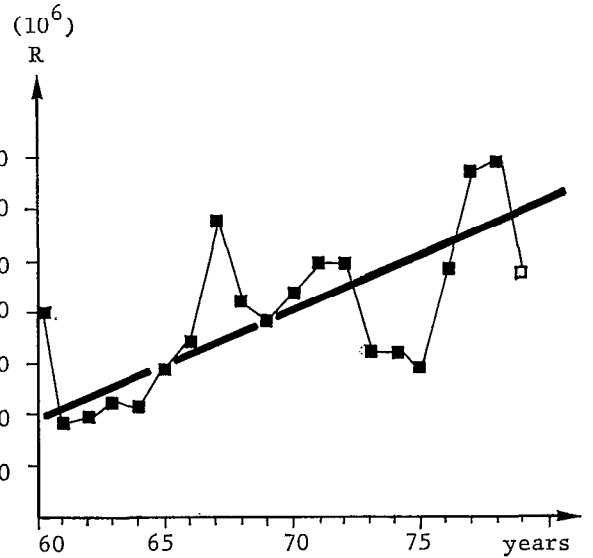


FIG. 7. — Trends in recruitment of *P. aztecus* (data from PARRACK, 1981).

Tendances du recrutement de *P. aztecus* (données d'après PARRACK, 1981).

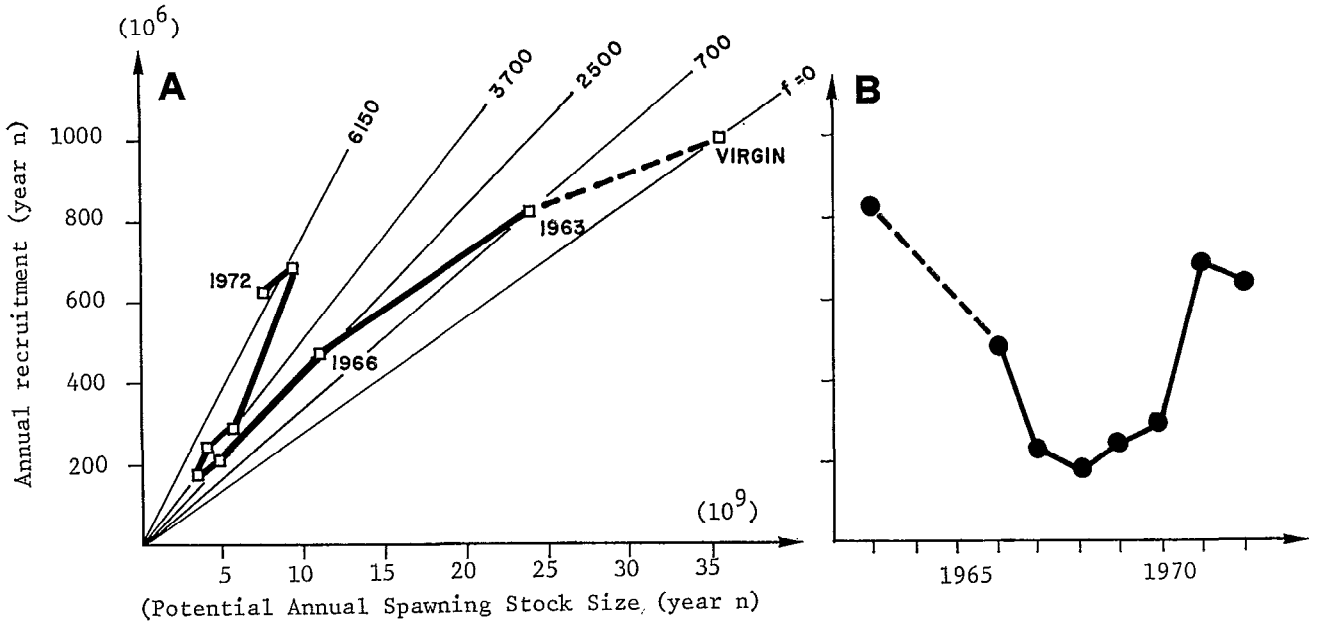


FIG. 8. — A: apparent stock-recruitment relationship for the shrimps of the Gulf of Thailand. The lines passing through the origin represent the $S = f(R)$ functions for various levels of effort (from $f = 0$ to $f = 6150$). B: trends in recruitment in the same data set (data from PAULY, *in press*).

A: relation apparente stock-recrutement chez les crevettes du golfe du Siam. Les lignes passant par l'origine représentent les fonctions $S = f(R)$ pour divers niveaux d'effort de pêche (de $f = 0$ à $f = 6150$). B: tendances du recrutement pour le même ensemble de données (données d'après PAULY, *in press*).

by the author is not worse than any other (see Figure 8).

However, the main problem when interpreting the 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* (1), confounding the usual SRR (where $R_{n+1} = f(S_n)$, involving density-dependent larval survival), and the replacement function $S_n = f(R_n)$, which slope is affected by F . In addition it is clear that the plot of $Y_n/(Y/R)_n$ on 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.

YE (1981) presented an analysis of the intensive *Penaeus orientalis* fishery in the Pohai Sea (North China). The resource undertakes important seasonal migrations between wintering and spawning grounds and the fishery can therefore be divided into two phases. The author used the total annual catch in

numbers from one year class as an index of recruitment (2) and the catch in number from the spring fishery (just before spawning) as an index of parental stock size. It is interesting to note that in this particular case the level of effort does not appear to have any effect on stock size within the range of available data. On the contrary the year-to-year variations in annual catches and catch rates closely follow the variations in recruitment. As a consequence the annual catch is indeed a good index of recruitment—as shown in Figure 9—by comparing the trends in annual catch and in juvenile abundance experimental indexes. The observed SRR is shown in Figure 10, and was fitted by YE with a RICKER and a BEVERTON and HOLT curve.

MORGAN and GARCIA (1982) also found for *Penaeus semisulcalus* in Kuwait a quasi-linear relationship between stock size in biological (3) year n —as measured by the average cpue in weight—and recruitment in year $(n+1)$ —calculated by dividing the annual catch Y_{n+1} by the yield per recruit

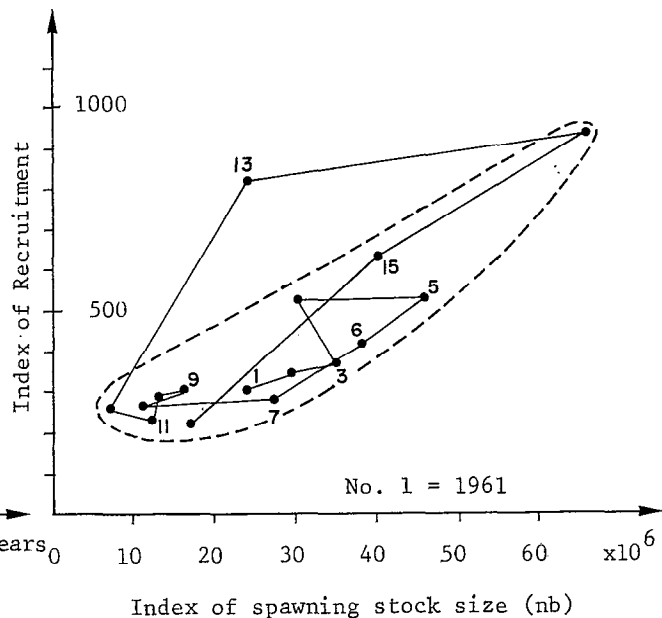
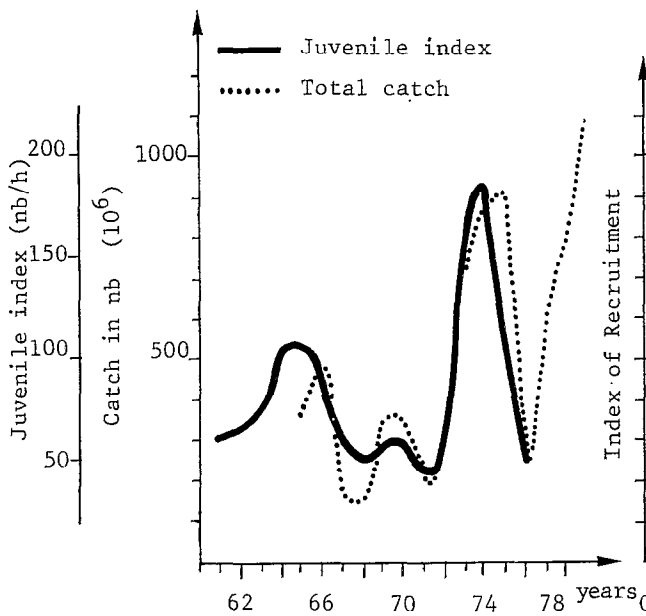


FIG. 9. — Comparison between trends in recruitment and total catch in *P. orientalis* (from YE, 1981).

Comparaison entre tendances du recrutement et total des prises chez *P. orientalis* (d'après YE, 1981).

FIG. 10. — Stock-recruitment relationship for *P. orientalis* (modified from YE, 1981).

Relation stock-recruelement chez *P. orientalis* (modifié d'après YE, 1981).

(1) On the hypothesis that equilibrium is reached within the year.

(2) After showing that the year to year variations in catches and catch rates are the same for the main fishery (the autumn one) in a shorter series of data.

(3) A biological year is a twelve months period starting at recruitment of the main cohort.

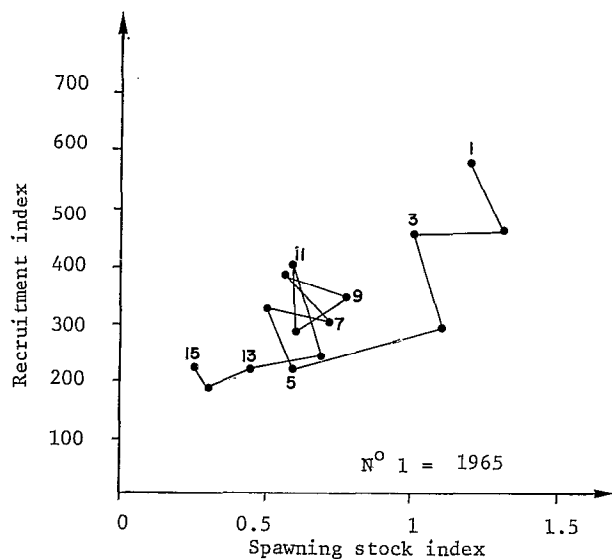


FIG. 11. — Apparent stock-recruitment relationship for *P. semisulcatus* in Kuwait (from MORGAN and GARCIA, 1982).

Relation stock-recrutement apparente des P. semisulcatus du Koweït (d'après MORGAN and GARCIA, 1982).

$(Y/R)_{n+1}$, (Figure 11). The statistical bias introduced by Pauly's approach should be largely avoided by introducing a lag time of one year in the correlation despite the existence of some unavoidable serial correlation in the effort series. The reality of the observed trends in recruitment have been confirmed by two other indexes likely to be much less affected by this phenomenon: the catch rate in weight for the first month of the fishing season immediately following the entry of the recruits in the fishery, and the average annual catch rate within periods of stable effort. However, when interpreting the results, the authors noticed that variations in stock size were not well related to fishing effort changes and that a high variability in stock size was observed for periods of stable effort. They suggested that, in their case, the observed stock-recruitment relationship might be an artefact produced by a driving force other than stock size and fishing effort (e.g. environment).

PENN (1981) analyzed the relationship between stock resilience to fishing (as shown by decline of yields) and catchability (related to schooling behaviour), assuming that the "level of catchability will be reflected in the degree to which spawning stocks and therefore recruitment can be reduced by fishing." He proposes a classification of shrimp stocks in groups of respectively low, medium and high catchability (for highly schooling species), and

suggests that the decreases in annual yield observed in some stocks of medium and high catchability may be an indication that recruitment has been affected by fishing. It must be noted however that in the case of *P. semisulcatus* of Kuwait and *P. merguensis* of Australia different interpretations have also been proposed recently by MORGAN and GARCIA (1982) and KIRKWOOD (1981) respectively involving the action of environmental factors. The last author indicates that in spite of the recent reduction in annual yields in the heavily fished *P. merguensis* stocks of Australia, no evidence of recruitment overfishing can be obtained when the effect of rainfall on annual catches is removed. In the case of *P. setiferus* of the Gulf of Mexico the long term decrease in recruitment does not seem to be questionable, but could be explained by fishing only assuming a peculiar stock-recruitment curve with two inflexion points (NICHOLS, 1981), or alternatively assuming that the changes imposed to the Mississippi outflow year after year have reduced the potential of the estuaries of that region for that species, in the same way as the potential for *Crangon crangon* recruitment in the Netherlands and Belgium has been reduced by the action of man (BODDEKE, 1982).

However PENN (personal communication) confirmed that the drastic reduction in annual yields of *P. esculentus* in Shark Bay and Exmouth Gulf (Australia), since 1980 and 1981 respectively, are certainly due to the decimation of the main spring spawning by unusually high levels of effort. These last observations may indicate that there indeed is a level of effort above which recruitment problems are met. In addition, owing to the quality of the data available it must be recognized that none of the interpretations given above for these species is fully safe. The idea of a possible link between catchability and resilience put forward by PENN is interesting and the question remains open.

As a conclusion to this section it can be said that a number of papers reviewed present some potential sources of bias in the estimations of the recruitment levels, either because of the methodology used (e.g. recruitment indexes not independent of fishing effort, introduction of statistical spuriousness in the correlations), or the possible misfit between some working hypothesis and the real life cycle of shrimps when seasonal SRR's are established.

In most papers, a significant relationship could well be fitted by a straight line passing through the origin, except in Boddeke's paper where the *apparent* relationships are definitely of a BEVERTON and HOLT type. The following sections will tend to demonstrate that they can be artefacts or misinterpretations.

2.2. Inter-annual variations in shrimp stock-size

It has long been recognized that the penaeid and caridean shrimp catches vary from year to year. A great part of these variations can be directly related to the environmental variations, and the literature on these resources is full of attempts to establish predictive models using sunspot activity, temperature, rainfall, river outflow, nursery area, etc. as the independent variable. Examples are given by GARCIA and LE RESTE (1981), STAPLES, DALL and VANCE (1981) for Australia (1), TURNER and CONDREY (1981) and BROWDER and MOORE (1981) for the Gulf of Mexico. An annotated short list of possible effects of environment on larval survival in penaeids is given by GARCIA and LE RESTE and good experimental and field observations are given by ZEIN ELDRIN and ALDRICH (1965; 1969) and by FORD and ST. AMANT (1971), respectively.

ZEIN ELDRIN and ALDRICH demonstrated the combined negative effect of low salinity and low temperature on survival of shrimp postlarvae and on cohort abundance. FORD and ST. AMANT have clearly shown the importance of the matching between the date of arrival of the main larval cohorts in the estuaries and the start of the spring warming phase on cohort success, and indicated there was no direct relationship between larval abundance indexes and recruitment success. BERRY and BAXTER (1969) who undertook most extensive work on the relationship between postlarval abundance and commercial catches noted the absence of useful correlation (2) (p. 786). On the contrary, the relations are good when juvenile abundance indexes and catches are considered by the same authors, by YOKEL (1969) and BARRET and GILLESPIE (1975).

In the case of *Crangon crangon* the effects on stock size of predation after the postlarval stage

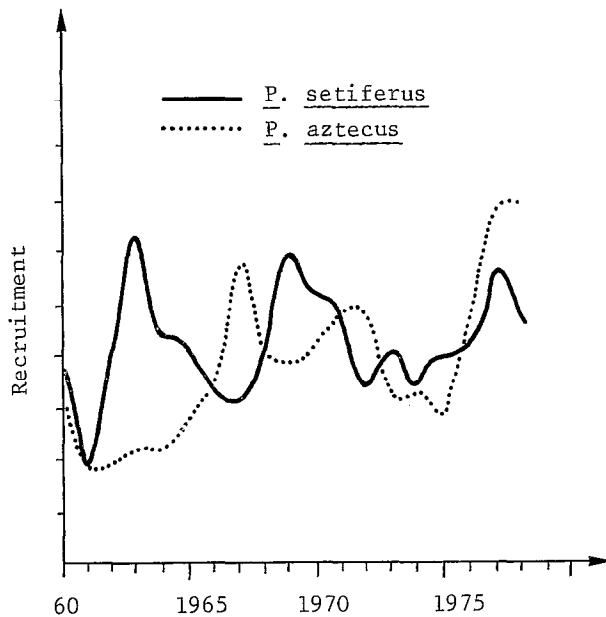


FIG. 12. -- Trends in recruitment indexes for *P. setiferus* (from NICHOLS, 1981) and *P. aztecus* (from PARRACK, 1981) in the Gulf of Mexico.

Tendances des indices de recrutement chez *P. setiferus* (d'après NICHOLS, 1981) et *P. aztecus* (d'après PARRACK, 1981) dans le Golfe du Mexique.

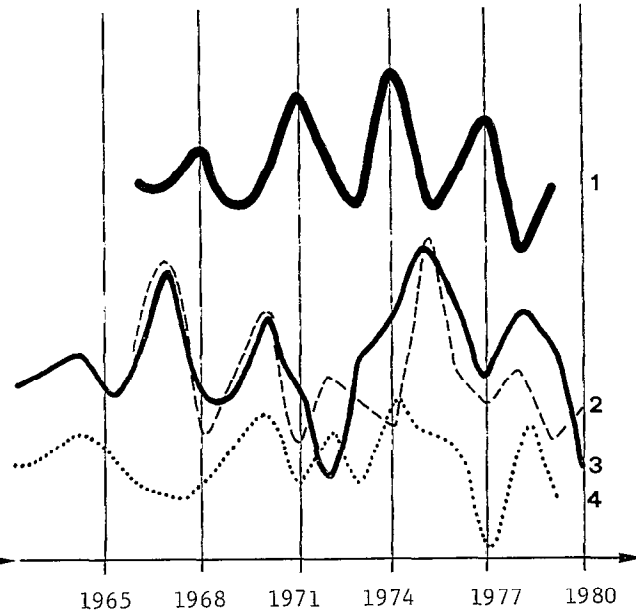


FIG. 13. -- Trends in the residuals of the relationship between catch and effort (approximate data graphically extracted from Figures given in PENN, 1981). 1: *P. merguensis* (Gulf of Carpentaria); 2: *P. esculentus* (Exmouth Bay); 3: *P. esculentus* (Shark Bay); 4: *P. latisulcatus* (Shark Bay).

Tendances des valeurs résiduelles de la relation prise/effort (données approchées tirées des figures de PENN, 1981). 1: *P. merguensis* (Golfe de Carpentarie); 2: *P. esculentus* (Baie d'Exmouth); 3: *P. esculentus* (Baie Shark); 4: *P. latisulcatus* (Baie Shark).

(1) This particular paper shows a good relationship between rainfall at recruitment and annual yields. It points therefore towards environmentally-driven changes in catchability or age at migration (and first capture?).

(2) According to the authors the correlation might possibly be strengthened by improving the sampling efficiency.

has been reached is well documented (TIEWS, 1965, REDANT, 1980), as well as the seasonal and inter-annual changes in predation (TIEWS and SCHUMACHER, 1982; BODDEKE, 1982). These results indicate that an important regulation of recruitment occurs between the postlarval stage and recruitment.

BROWDER and MOORE (1981) pointed out that the survival of juveniles in penaeid shrimps in estuaries is related to the degree of matching two favourable types of habitat: a dynamic (water mass) and a static one (bottom, depth area, fixed vegetation). They showed that the degree of matching varies from year to year through changes affecting the dynamic habitat (rainfall), or the static one (action of man, reclamation, erosion, subsidence). A further indication that recruitment may be largely governed by the environment is given by the fact that species having divergent ecological preferences show, in the same area, contrasting year-to-year variations in abundance, while similar species in different areas seem to follow similar patterns. FORD and ST. AMANT (1971) point out that "when white shrimp production is low, brown shrimp production increases, appearing to compensate for the annual crop." While this could come from changes in target species by the fishery, Figure 12 shows that the recruitment estimates for the two species indeed follow reversed cycles, at least up to 1975.

A first graphical examination (1) of the residuals of the catch/effort relationships given by PENN (1981) for different Australian species (Figure 13) shows that the year-to-year variations are very much the same for *P. esculentus* in two different areas: Shark Bay and Exmouth Gulf (12 points on 15 points are in agreement). It also shows that the "bad" years for this species in the two areas considered correspond to "good" years for *P. merguensis* in the Gulf of Carpentaria. GARCIA and LE RESTE (1981) also pointed out that the long-term oscillations (1930-1960) of *Penaeus setiferus* catches in Texas and Louisiana were very similar, and MORGAN and GARCIA (1982) demonstrated that recruitment trends of *P. semisulcatus* in Kuwait and Saudi Arabia were identical.

The effect of environment changes on production are therefore a key characteristic of shrimp stocks. These changes are most probably related to changes in recruitment (2). They may be more or less periodic when linked to natural fluctuations of the environment but they can also appear as trends if related

to modifications of the environment by man: EHRARDT *et al.* (1981), indicate that in the State of Sonora (Mexico) the white shrimp (*P. vannamei*) has been replaced by the blue shrimp (*P. stylirostris*) after modifications of drainage for agricultural purposes. DOI *et al.* (1973), showed the decrease in *P. japonicus* production under progressive land reclamation in Japan. MORGAN and GARCIA (1982) showed a long-term decreasing trend in the recruitment of *Penaeus semisulcatus* in Kuwait and Saudi Arabia (Figure 8) which was not well related to changes in effort, and could be the result of the very intensive land reclamation which occurred in some of the main bays. BODDEKE (1982) indicates that the brown shrimp production has experienced a considerable decrease in the western Wadden Sea after the closure of the Zuiderzee in 1931.

The effect of environment on stock size of shrimp stocks are so important that environmental parameters have even been included into production models in order to improve the year-to-year forecast (GRIFFIN, LACEWELL and NICHOLS, 1976; GRIFFIN and BEATIE, 1978; TURNER and CONDREY, 1981).

3. THE EFFECT OF ENVIRONMENTALLY-DRIVEN RECRUITMENT CHANGES IN THE STOCK-RECRUITMENT CONCEPT

3.1. The traditional SRR concept

It is generally agreed that there must be some regulatory mechanisms enhancing the reproductive capacity of a stock when its biomass is approaching 0, and reducing reproductive success when biomasses reach very high levels (LARKIN, 1973). Relationships between the spawning stock and the recruitment may be described by a wide family of curves. The exact shape of the curve is most often difficult to define with any statistical accuracy because of the high variability generally observed. Some hypotheses on the main mechanism underlying larval survival may therefore be necessary in order to prejudge which type of curve might be adequate (i.e. cannibalism of young by adults, or limiting food and habitat, RICKER, 1975, p. 281).

Figure 14 summarizes the general understanding. An arbitrary SRR curve $R = f(S)$ is given, as well as a family of replacement lines $S = f(R)$ corresponding to different levels of exploitation (see

(1) PENN gives graphs showing the catch-effort data points. The line passing through these points (equivalent of an empirical production model) has been drawn by eye and the vertical distances of the data points to the line measured graphically. These results must therefore be one considered as very preliminary.

(2) But a recent paper by STAPLES, DALL and VANCE (1981) showing good correlations between shrimp production and rainfall during the migration/recruitment process indicates that an effect of rainfall on availability/catchability is also possible.

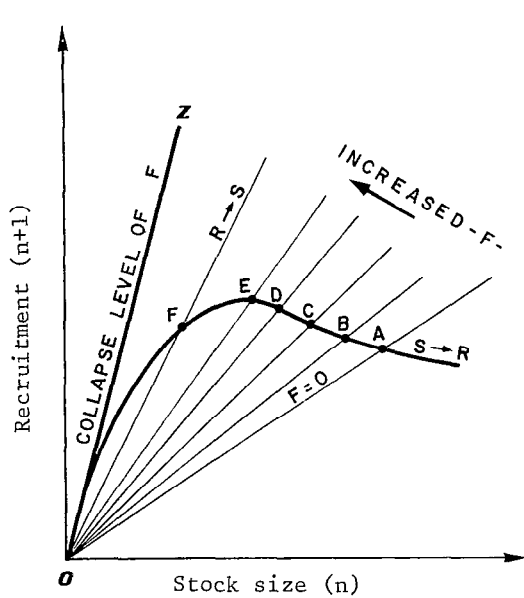


FIG. 14. — A theoretical stock-recruitment curve showing the different "equilibrium" situations corresponding to various levels of fishing (deterministic approach).

Courbe stock-recrutement théorique indiquant les différentes situations d'équilibre qui correspondent à divers niveaux de pêche (approche déterministe).

RICKER, 1975, p. 284). The line OA corresponds to the unexploited stock; the line OZ, tangent to the $R = f(S)$ curve at the origin, corresponds to the exploitation level beyond which the stock would collapse because the number of recruits produced will be insufficient to cover the density-independent mortality (GARROD, 1973). In a deterministic approach, it is generally assumed that the stock reaches some sort of "equilibrium" at each level of fishing at the intersection between the $R = f(S)$ curve and the $S = f(R)$ line (points A to E). Ideally, when the fishery develops and stock size consequently decreases, a series of "equilibrium" situations would be detected, progressively showing the shape of the stock-recruitment curve. The phenomenon is assumed to be reversible when effort is reduced for management purposes.

In this traditional concept the effect of environment variability on larval survival is neglected and it is assumed that it will "only" somewhat blur the relationship (1).

In case the environmental effects are recognized as very important, i.e., they cannot be neglected

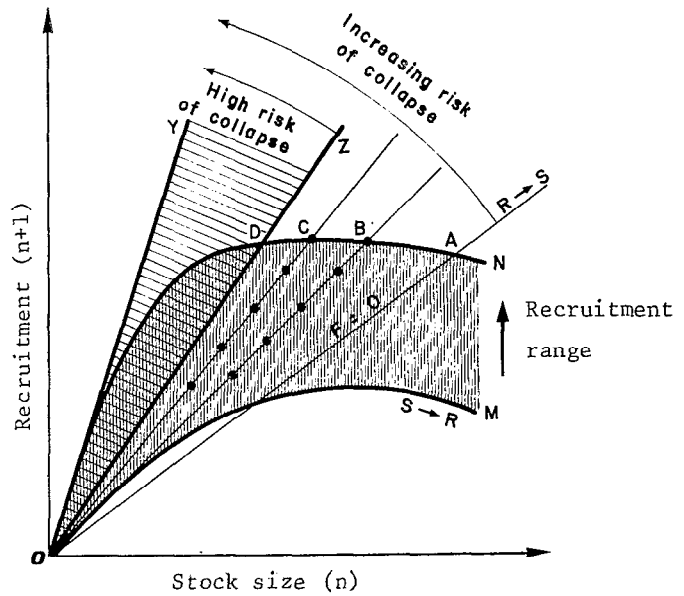


FIG. 15. — A theoretical stock-recruitment model when natural variability is taken into account.

Modèle théorique de stock-recrutement intégrant la variabilité naturelle.

anymore, then it must also be recognized that a given stock may produce a range of recruitments depending on the environmental conditions. The $R = f(S)$ curve therefore becomes $R = f(S, E)$ surface, where E stands for a set of environmental variables (see Figure 15).

If we assume that the environmental variability has little effect on the slope of the replacement line, it can be seen from the figure that under a given level of exploitation, the stock will not find an "equilibrium point" (e.g. A to D) but will move across the SRR surface, along the replacement line (e.g. OB or OC), which will become an "equilibrium line" when F is stable.

Similarly, the line OZ in Figure 14 should be replaced by a surface YOZ limited by the tangents to the upper and lower envelopes to the SRR surface. This surface delimits the ranges of F where the risk of collapse is extremely high, but it must be noted that a limited risk exists even at much lower levels of effort and increases with the fishing pressure (see LAUREC, FONTENEAU and CHAMPAGNAT, 1980, for simulation analysis of this problem).

When the environmentally-driven changes in larval survival become largely dominant as compared to stock size the usefulness of the concept of

(1) The SRR line is taken as representing the informative "signal" while the environmental variability is considered as a "noise" in the relationship.

“collapse level of effort” is limited to the determination of the level beyond which the risk of collapse becomes unacceptable. On the other hand, the analysis of the environmental “noise” itself becomes essential for long or short-term prediction purposes, the time-scale of the projections that can be made depending on the time-scale of the environmental parameters considered.

3.2. The existence of a serial correlation

It should be remembered that a penaeid shrimp stock contains essentially one year class. The recruitment generally has seasonal peaks, even if some recruitment occurs throughout the year. A typical shrimp fishery intensively exploits the main group of recruits (3 months old), following it all throughout the year, and leaving very few survivors (8 months and older) for spawning. In this case the annual average stock size, the size of the spawning stock, and the annual catch are much more strongly related to the recruitment of the year than in the case of a multi-age resource. Their adjustment to any change of yearly fishing effort will be “instantaneous” e.g. when the yearly time interval is considered, the stock is in “permanent equilibrium”.

As a consequence, when the level of effort changes rather slowly or is stabilized (as in fully-developed fisheries) the stock size in year n (B_n), will follow very closely the year-to-year variations of the recruitment (R_n) (1). These variations are generally not random but serially-correlated (as the environmental changes also are), and the plot of R_n against B_{n-1} will produce a spurious positive relationship, no matter what the true SR relationship is.

This problem, which could explain at least partly the apparent linear relationships observed for penaeids (cf. Section 2) was raised by MORGAN and GARCIA (1982) and discussed by GARCIA (1981).

3.3 The apparent trajectories observed.

The relationship reviewed in Section 2.1 can now be discussed in light of the above considerations. When the effect of environment on recruitment is more important than the effect of limited changes in fishing mortality, the concept of an “average” stock-recruitment line around which some “noise” occurs is not the most useful one, and one might consider that there are in fact a family of SRR lines, corresponding to different sets of environmental conditions. This is certainly true of recruits on a

seasonal basis (a given number of eggs will produce different numbers of recruits according to the period of the year when they are laid), and also on a year-to-year basis. The fact that an environmental variable has to be introduced in production models (cf. Section 2.2.), leading in fact to a family of production curves for the same resource, is the same as saying that there is not one stock-recruitment curve but a family of them (if it is assumed that the effect of year-to-year changes in environment on yield-per-recruit is negligible).

GARCIA (1981) showed the similarity between these two problems and pointed out that in both cases the limited number of data points obtained from fishery data (catch and effort, or stock and recruitment) will describe the trajectory of the stock not along a single curve (production model or SRR line) but across a surface. He indicated that in a more or less stabilized fishery, and because of the short time needed in order to reach the equilibrium, the apparent $R_{n+1} = f(S_n)$ plotted relationship will in fact be very close to the $S_n = f(R_n)$ one (the replacement line for a given exploitation rate), especially when the year-to-year environmentally-driven changes in recruitment are small (see Figure 16). The

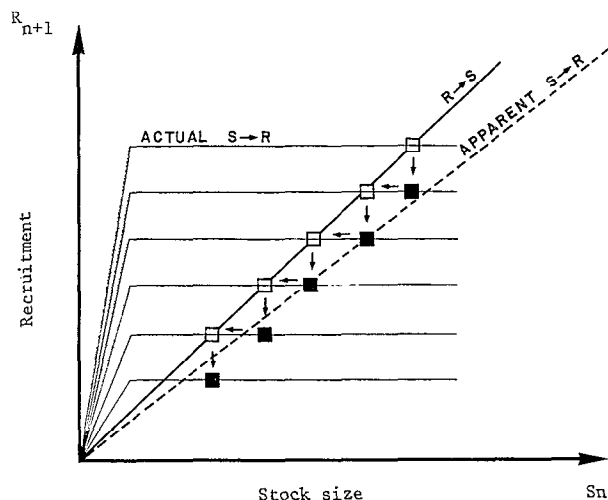


Fig. 16. — Hypothetical trajectory of the S/R data points across a stock-recruitment surface (materialized by a family of curves) when F is constant and the survival rate decreases from year to year for environmental reasons.

Trajectoire hypothétique des points représentatifs des données S/R à travers une surface de stock-recrutement (matérialisée par une famille de courbes) quand F est constant et que le taux de survie décroît d'année en année par dégradation de l'environnement.

(1) It is much less the case with multi-age stock structures and progressive recruitment.

serial correlation and cyclic recruitment levels will be shown by some ranking of the data points along the *apparent* SRR line.

If changes in fishing effort and natural factors occur together, the data points will describe a more complex trajectory: the "SRR" curve given in Figure 8, obtained by PAULY (*in press*), and which has been said earlier to be in fact a $S_n = f(R_n)$ plot (cf. Section 2) may be an example. The original figure has been modified by adding the lines joining the origin to groups of points corresponding to comparable effort levels and representing therefore the theoretical "replacement lines" for the various levels of effort. It can then be understood why the decrease in recruitment from 1963 to 1968 and its following increase, corresponding to different levels of effort, gave different trajectories on the apparent SRR plot. Another example of the similarity between SRR and replacement plot in penaeid shrimps can be worked out by using the data given by YE (1981). The author gives a correct SRR relationship (Figure 10). We have plotted for comparison, in Figure 17, the relationship between R_n and S_n (or replacement plot). The comparison

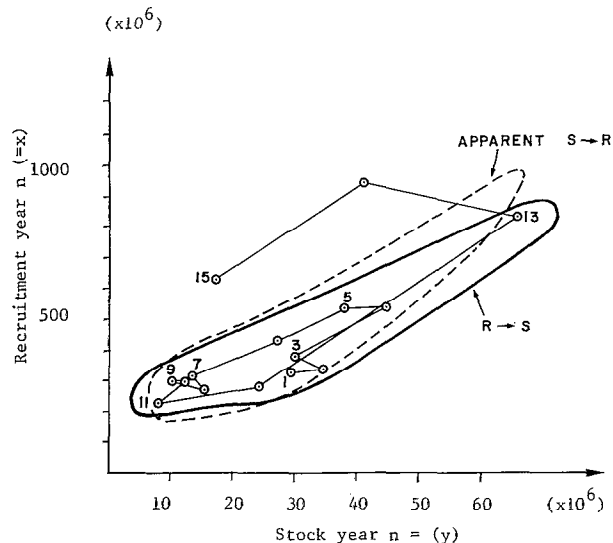


FIG. 17. — Relation between the recruitment in year n and the progeny spawning stock in year $n+1$ (from YE, 1981). (The X and Y axis have been interchanged to facilitate the comparison with Figure 10).

Relation entre le recrutement dans l'année n et le stock pondéral qui en est issu dans l'année $n+1$ (d'après YE, 1981). (Les axes X et Y ont été échangés l'un pour l'autre en vue de faciliter la comparaison avec la figure 10).

(1) Provided the catch statistics are not grossly erroneous.

of the two figures when they are superimposed shows that the positive relationships are nearly the same and that the apparent SRR (assuming density-dependent larval mortalities) is in fact an image of the replacement function (related to fishing mortality). The same could apply to the results obtained by ROTHSCHILD and PARRACK, 1981 (Figure 6) because the annual recruitment level has fluctuated (with a possible slight upward trend), while F stayed between 0.13 and 0.17 from 1960 to 1977 (according to PARRACK 1981). The seasonal linear SRR's given by PARRACK (1981) are interesting despite their limitations (cf. Section 2), because the steepest slopes obtained are observed for the main cohorts which are also the most-intensively fished ones. In fact, the seasonal changes in slope he observed seem to reproduce the seasonal changes in F , which is what one would expect if they were in fact replacement lines.

The lack of any good apparent SRR for *P. setiferus* (ROTHSCHILD and PARRACK, 1981; NICHOLS, 1981) however, raises a puzzling problem. The Gulf of Mexico white shrimp underwent important changes in abundance between 1930 and 1960 (GUNTER and EDWARDS, 1969) and is likely to be rather sensitive to environmental changes and, as a consequence, likely to produce the same type of positive relationship. The solution could be looked for in Nichols' methodology. For instance, important biases may have been introduced in the cohort analysis by using an average age-length key for males and females when decomposing catches into cohorts. However, the parameters used by ROTHSCHILD and PARRACK (1981), when analyzing the stock-recruitment pattern of this species, are much less subject to bias and still no good relationship is apparent.

Another explanation may be found in the fact that the range of the stock sizes and recruitment data for that shrimp is much more limited than for brown shrimp *P. aztecus*. This range is indicated for comparison in Figure 6 together with the brown shrimp data expressed in the same units. The data for *P. setiferus* is more or less in line with the trend detected for brown shrimp but corresponds to relatively smaller abundances, and the relative limitation of the data range becomes obvious when it is noted that the white shrimp recruitments may have been about 4 times higher in the past (1939-1946) in order to account for the very high catches reported at that time (1) (NICHOLS, 1981). In this case, there may have been a trend in recruitment (tentatively indicated by the trend in catches),

and the plot referred to above would represent a small portion of the whole relationship where the variability (of a magnitude similar to the one observed on brown shrimps) can easily mask any possible trend.

3.4. SRR : reality or artefact and misinterpretations

3.4.1. REALITY?

It has been shown that the correlations observed between stock and recruitment of shrimp were quasi-linear (except for Boddeke's work on *Crangon crangon* which is examined later on). In theory, the stock-recruitment relationship cannot be linear within the whole range of possible stock sizes, or there would not be any possibility of stabilization of the stock biomass at some positive level (the only intersection between linear $R_{n+1} = f(S_n)$ and $S_n = f(R_n)$ functions, and therefore equilibrium point for the stocks, being the origin of the plot).

Because of the variability existing in all the data sets, the observed relationships could also be taken as slightly curved downwards. However, the vertical distances between the curve and the replacement lines—which are an estimate of the surplus recruitment and therefore an estimate of the resilience of the adult stock size to external perturbations by fishing and natural causes—would be so small that it would be highly unlikely that the shrimp stocks could have maintained themselves for such a long time.

It can of course be argued that the observations refer to the ascending limb of the left-hand part of the SRR when fishing is so hard that recruitment becomes proportional to stock size and tends to zero. In this case it would be necessary to believe that these stocks are presently very intensively exploited by fishing and severely depleted, up to a level close to the collapse situation. However, PARRACK (1981) found for brown shrimp that the values of F oscillated only between 0.13 and 0.17/month in the period of observation, when $M = 0.15$ /month. These results do not indicate "excessive" fishing effort and the overall recruitment may have even increased with time despite increasing levels of effort (Figure 7).

In Kuwait also the linear-relationship observed by MORGAN and GARCIA (1982) do not refer to a biologically-overexploited fishery, and the decrease in recruitment occurs at a (more or less) constant level of effort close to the F_{MSY} level. On the other hand no relationship could be found for the banana

prawn, *P. merguensis*, in the Gulf of Carpentaria, when the effect of environment is extracted (KIRKWOOD, 1981) despite the fact that the yearly exploitation rate exerted is among the highest ever measured (78 to 85 percent according to LUCAS, KIRKWOOD and SOMMERS, 1979).

The case of *P. setiferus* is even more striking because NICHOLS (1981) found exploitation rates of 15 to 25 percent only between 1960 and 1978, a period during which the overall recruitment seems to be much smaller than it probably used to be in the earlier years of the fishery.

There is therefore no convincing evidence that the positive, quasi-linear relationships between stock and recruitment observed up to now are related to excessively-high levels of fishing and could be taken as the left ascending limb of the usually-assumed relationships. The existence of a SRR which would really be nearly linear over the whole range of possible stock sizes cannot be taken as compatible with the stability demonstrated by these resources which are among the oldest marine species (according to BURUKOWSKY, 1970); *Penaeus* species already existed during the cretaceous period.

3.4.2. ARTEFACTS AND MISINTERPRETATIONS.

The "apparent" stock-recruitment relationships obtained might thus be artefacts (1) or need to be interpreted in completely different terms. This argument has been tentatively substantiated in the present paper.

A great number of papers have demonstrated (cf. Section 2) that:

(a) An important regulation of recruitment occurs in the estuaries between the postlarval and the migrating juvenile stages of penaeid shrimps in relation to environmental factors such as temperature and salinity combinations.

(b) In penaeid and caridean shrimp fisheries the annual production is strongly correlated with climatic factors (rainfall, temperature, river outflow, estuarine areas), and the fit of production models in some penaeid stocks has been greatly improved by the addition of environmental variables.

(c) The changes exerted by man on the nursery areas of penaeid and caridean shrimps have in the past had drastic effects on annual production.

(1) In the sense that despite having a "familiar" shape, they are not the result of the same phenomena (effect of fishing on stock size and subsequent recruitment), and cannot be interpreted in the same way in terms of management.

(d) Seasonal and year-to-year changes of caridean shrimps abundance are related to changes in natural mortality due to predation (BODDEKE, 1982; TIEWS and SCHUMACHER, 1982).

It should therefore be concluded that for some shrimp stocks the effect of the environment on recruitment may be at least as important, if not more so, than the effect of fishing, the natural variability of annual production differing probably from stock to stock (cf. GARCIA and LE RESTE, 1981, Page 119, for references).

When this variability is high, the SRR line should be better-defined by a SRR surface across which the stock will "move" as an immediate response to the levels of both the (environmentally-driven) recruitment and fishing effort.

The short-lived nature of shrimp stocks (recruited at 3 months, reaching adulthood at 8 months, and having a generation time of 1 year) introduces a direct linear relationship between the size of the recruitment in year n (R_n) and the size of the subsequent adult stock (S_n , in the same year). As a consequence the existence of an environmentally-driven serial correlation in recruitment oscillations would therefore lead to the existence of a serial correlation in stock sizes, and to the production of a spurious positive relationship between S_n and R_{n+1} (justifying the word artefact).

The two seasonal stock recruitment approaches which have been found in the literature and are described in this paper (PARRACK, 1981; BODDEKE, 1982) are worth a separate comment. The relationship is established between the spawning stock size (spawners biomass or overall fecundity) and the recruitment 3 or 4 months later. This procedure is a major step towards better understanding of the production mechanisms in short-lived species but raises some problems concerning the actual significance of the relationships obtained, as compared to the traditional stock-recruitment approach based on yearly data.

The seasonal relationship has been established between the spawning stock in a given month, say April, and the subsequent recruitment in July when a series of years is available, exploiting the year-to-year variability in stock size in order to identify the relationship characterizing a month (cf. PARRACK, 1981). This approach is a refinement of the traditional method because seasonal patterns in recruitment survival and fishing mortality may be accounted for but has the same limitations as

described above (possible confusion between the SRR and the replacement functions).

The relationships have also been established between a series of successive monthly spawning stock sizes (e.g. March, April, May and June), and the subsequent recruitments 4 months later (BODDEKE, 1982). In this case, the data contains a strong serial correlation because of the existence of natural seasonal variations of recruitment (cf. Figure 5) which induce seasonal variations in stock sizes (1). Relating the two variables with a time lag will always produce a relationship which apparent shape will largely depend on the time lag used. Assuming that the proper lag is known (and constant), Figure 18 shows on a three-dimensional diagram the trajectories of stock sizes and subsequent recruitment during the year and the projection of this trajectory on the stock-recruitment plan. It can be said that the shape of the "apparent" stock-recruitment plot (implicitly assumed to be a density-dependent function) is in fact given by superimposing monthly independent SR areas (2) which position on the diagram depends both on fecundity level and survival to recruitment. The survival of a given monthly cohort may also be density-dependent but it is largely governed by the seasonal environmental conditions. This means that each exponential type of curve established by BODDEKE for each geographical area considered cannot be interpreted as general relationships showing the effect of stock size on recruitment but as a mixture of relationships between a given stock *in a given month* (with its own environmental conditions) and the subsequent recruitment. In other words the phenomenon represented by the "seasonal" SRR when only the R and S axes are used is not the response of the recruitment to changes in stock size (by fishing), but the result of the complex ontogenetic adaptation of the population to a seasonally-oscillating environment.

In this sense, the curves drawn by BODDEKE (1982) give an interesting summary of the recruitment survival strategy (3) followed by the population, especially when expanded in a block diagram as in Figure 18, but they do not predict global recruitment changes resulting from changes imposed on the population size by fishing.

Because of the existence of long-term variations of annual overall level of recruitment and abundance in shrimps the exact shape of the curve and the position of an eventual asymptote will however be defined only when a long time series becomes

(1) In addition, Figures 5A and 5B show the existence of a long-term trend in the time series used by BODDEKE.

(2) The exact shape of these SR areas is not important for the reasoning.

(3) At seasonal level it is also useful to calculate the monthly values of the ratio R/S given by BODDEKE and BECKER (1979), Figure 3A.

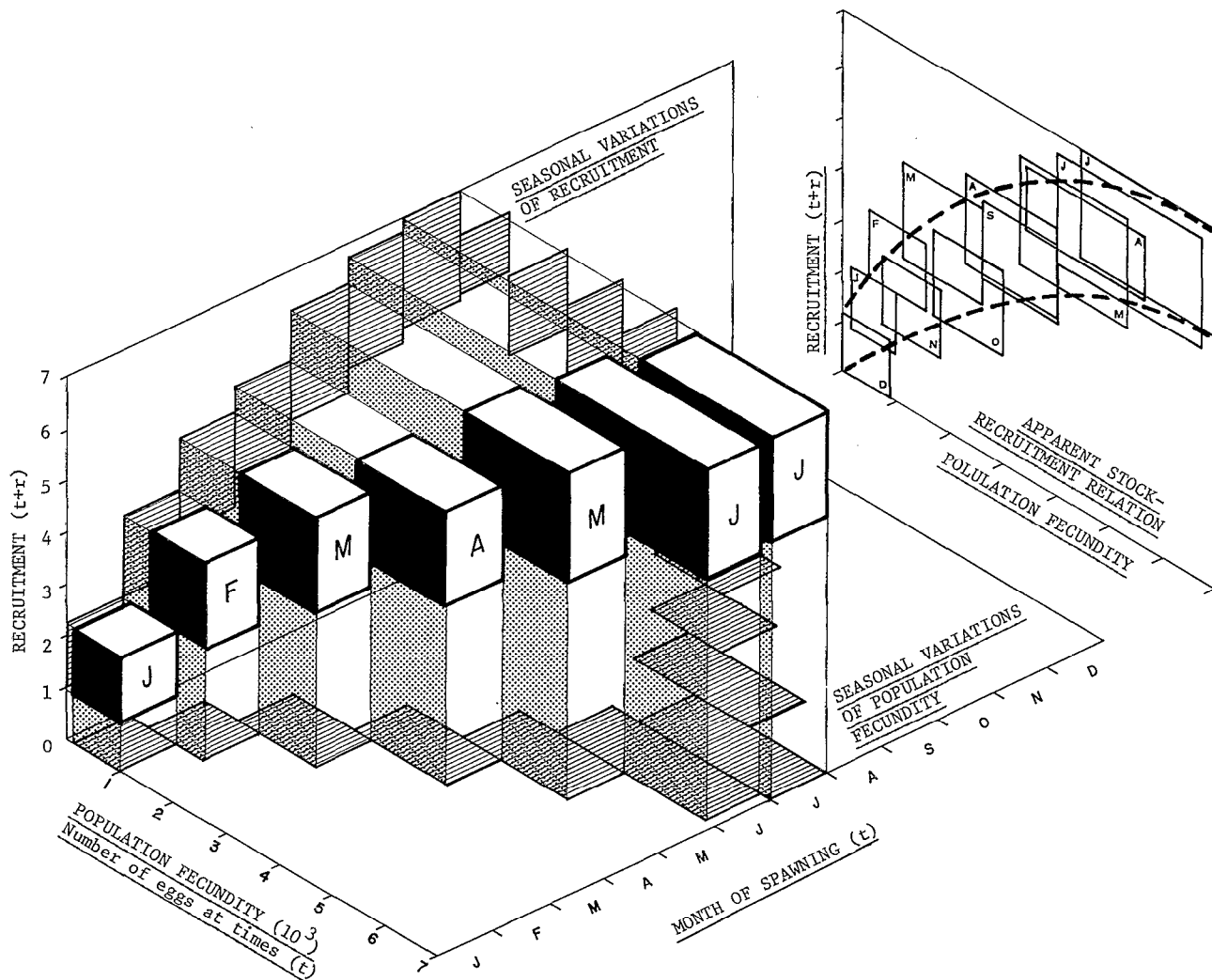


FIG. 18. — Seasonal patterns of spawning stock-sizes (time t) and recruitment ($t+r$) and apparent stock-recruitment relationship.
Modèles saisonniers des stocks pondéurs (temps t), du recrutement ($t+r$), et de la relation apparente stock-recrutement.

available, i.e. where the maximum seasonal potential values for each time stratum will be significantly represented in the data.

4. DISCUSSIONS

4.1. Environmental variability and measurement errors in recruitment indexes

As far as SRR in general is concerned we would agree with SHEPHERD (1982) that "the data on which to base an SRR are generally poor. One can

hardly even have any confidence that the form of the curve and its parameters are reliably determined and therefore many people (1) have felt that the exercise is at best of little value and at worst potentially misleading."

It has always been recognized that at least part of the recruitment survival variability was related to environment (see for instance OTTESTAD, 1942 quoted by CUSHING, 1972, for the Arcto-Norwegian cod). More recently CSIRKE (1980) produced a modified SR Ricker model for the Peruvian anchovy including a variable taken as "representative of

(1) The usefulness of SRR has been questioned again recently in IOC (1981) and SHARP (1981).

the size of the total area or volume inhabited by the population", related to year-to-year changes in oceanographic conditions. The natural variability of recruitment data in various stocks has been analyzed by HENNEMUTH, PALMER and BROWN (1981).

On the other hand, WALTERS and LUDWIG (1981) draw the attention to the effect of measurement errors in SRR. They demonstrate that they can easily mask completely a strong relationship or produce artificial "dome-like" curves.

It is interesting to note that in the case of shrimps the observed relationships are indeed often very good, pointing more towards statistical spuriousness due to the regression approach than to measurement errors.

WALTERS and LUDWIG also point out that "a common reaction by biologists faced with noisy stock-recruit data has been to seek for environmental factors that might explain variation in recruitment" and that "such efforts could well be as deceptive as the SR analyses they seek to replace." I believe that in the case of shrimps the effects of environment are so well-documented that it is an error to forget it in SR analysis, and agree with WALTERS and LUDWIG (1981) that "it is worth questioning the wisdom of trying to fit simple models to the data rather than multi-variate models that account for the various environmental influences on recruitment."

4.2. Systematic bias due to fishing on pre-recruits

SRR's for shrimps are established using data on the adult stock i.e. from the offshore trawl fishery. The recruitment is estimated as the number entering the trawl fishery (dividing Y by Y/R , by backwards cohort analysis, or by the cpue in numbers at the time of recruitment). However juvenile shrimps are very often fished also in estuaries at artisanal level before or during migration. When the data concerning this early exploitation is not taken into account the lagoon fishing mortality is implicitly included in the SRR as an additional "natural" mortality factor lowering the apparent recruitment produced by a given adult stock size by an amount (in %) roughly equal to the exploitation rate in the lagoons.

As a consequence the existence of an artisanal fishery is a very serious source of bias when not taken into account. The impact on the shape of the SRR will depend on the trends of the inshore and offshore fishing mortality. Different cases can be examined:

- .
 (1) As opposed to "natural".

(a) Developing offshore fishery/constant inshore fishery

If we assume that 20 percent of the potential recruits are taken before actual recruitment offshore, this is equivalent to an additional constant mortality at all effort (and stock size) levels. The result will be an apparent SRR of the same shape as the actual one but 20 percent less than they actually are. This bias is not likely to produce an artificial straight line.

(b) Stabilized offshore fishery/developing inshore fishery

This will have the same effect as increasing pollution or land reclamation. The increase in exploitation rate of pre-recruits having the same effect as a decrease in survival due to environmental changes. The SR data points will follow the replacement line corresponding to the stable level of fishing mortality, just as in Figures 16 or 11, producing an apparent linear SRR. This bias has been excluded in the case of the linear SRR for *Penaeus semisulcatus* in Kuwait by using total yield and adjusting the yield per recruit accordingly, but might have to be taken into consideration in the Gulf of Mexico where catch data on inshore fisheries were not used and recruitments were estimated by cohorts analysis on offshore catch data only.

(c) Developing inshore and offshore fishery

When both fisheries develop with time the resulting trajectory of the SR data points will be more complex and will depend on both rates of change, the chances that a straight apparent SRR, *passing through the origin*, is generated, is likely to be very small if the actual SRR is significantly curved.

It is obvious from the above example that the existence of any artificial (1) source of mortality should be taken into account when analyzing the SRR and that particular attention should be given to trends in the artisanal inshore fisheries.

4.3. Conclusions

In our paper we have shown that the SRR presently published for shrimps are likely to be statistical artefacts or biological misinterpretations. It has not been proven that the recruitment of shrimp stocks was independent of stock size, and this was not the purpose of the paper, but these conclusions should lead us into being extremely cautious before accepting for granted, on the basis of limited data, the existence of a simple, deterministic SRR (in the traditional sense) in shrimp populations.

The existence of SRR's are still to be demonstrated. Their analysis has started surprisingly late, considering the high value of shrimp stocks, but the information accumulated during the last three years is important and may be summarized as follows:

— The analysis of the relationship between stock and recruitment at seasonal level (e.g. monthly cohorts) would certainly be a fruitful approach (cf. BODDEKE, 1982, PARRACK, 1981, and Figure 18). When there are two main cohorts (generally coming from spring and autumn spawnings) there will probably be two different SRR's. In this type of analysis, seasonal changes in the proportion of adult stocks actually available for spawning must be taken into account.

— There probably exists an upper limit in the SRR corresponding to the carrying capacity of the nursery which can be affected by man (cf. BODDEKE, 1982).

— For any stock level, the proportion of this maximum which will actually be reached will vary from year-to-year, or seasonally, according to the environment.

— Taking into consideration the important natural year-to-year variability, the concept of an annual stock-recruitment "surface" would be more appropriate than a SR line, and many more data points than presently available, *at all levels of fishing effort*, are necessary before the shape of that surface can be defined (flat-topped, dome-shaped, etc.). Because of the facts that adults and nursery grounds are completely separated and that the nursery conditions and area seem to be the limiting factors, a Beverton and Holt-type of surface would probably be the most likely (as in Figure 14). The important fact, however, is that within that surface, the variations of recruitment are not random but serially correlated, and the data show that in the short-term it is recruitment that drives the stock size and not the reverse.

4.4. Consequences for management

Not very much can be said on this subject because of the uncertainty on the SRR but the already available knowledge should however be usefully taken into consideration. Shrimp stocks (and the yearly catches) being more controlled by the recruitment of the year than other longer-lived stocks, it is therefore even more crucial for management purposes to identify the factors responsible for the variations. The relevant questions to be answered are:

1 — What are the factors influencing the recruitment level?

2 — If fishing (i.e. stock size) and environment are the regulating factors what are their relative impact on the recruitment level?

3 — Can the determinant factor(s) be significantly effected by man, either purposely (by fishery management), or inadvertently (pollution, land reclamation, etc.)?

We would also like to note that the causes of any changes (trends) in recruitment should be identified in order to assess whether the phenomenon is reversible (due to fishing, or periodic environment changes) or not (habitat destruction).

4.4.1. ENVIRONMENTAL ASPECTS

WALTERS and LUDGWIG (1981) state that "in the long term view of management it is simply irrelevant to comment that recruitment can often be predicted more accurately from environmental factors than from spawning stock (because) it is the spawning stock that can be controlled through management decisions." In the particular case of shrimps this last statement may be questionable because stock size is strictly controlled, first of all by recruitment and therefore will be significantly controlled by fishing only if fishing has a major, measurable effect on recruitment (beyond the likely negative effect of a very high "collapse" level of effort). This has not yet been proved (or disproved), while environmental effects are well documented. As a consequence the validity of Ludwig and Walter's statement in the case of shrimps should be assessed by answering the three questions listed at the beginning of Section 4.4. It is likely that the short-term variations in stock size might be difficult to predict from environmental factors in order to adjust the exploitation. A lot of regression models have been established (a review was given by GARCIA and LE RESTE, 1981) but most of them have not been confronted with the test of time to evaluate their actual usefulness. However the long-term oscillations when identified can probably be taken into account.

On the other hand it should be noted that a clear littoral and freshwater management policy is needed because the potential indirect effect of their misuse may be a much greater cause of trouble in the long-term than the fishing activity per se.

4.4.2. THE EFFECT OF FISHING

It must be noted that shrimps are adult at 8 months but that the fishery starts at a much earlier age (2-3 months and even earlier in some artisanal fisheries). In this case the spawning potential in

terms of potential fecundity-per-recruit (1) can be reduced to very low levels by fishing as was shown by GARCIA (1977) for *P. notialis*, and some sort of limitation of effort may therefore be necessary.

It is generally accepted that there must be a level of stock size below which the recruitment will decrease on average (cf. point E in Figure 14) and a level of effort beyond which the stock cannot replace itself (line OZ in Figure 14) and collapses. Because of the importance of year-to-year variability in shrimp recruitment, it is better to think about a range of exploitation levels between which the risks of collapse increase drastically (YOZ in Figure 15), and remember that it in fact begins to increase as soon as fishing starts on a virgin stock, as demonstrated by LAUREC *et al.*, 1980. GARROD (1973) has pointed out that in the traditional concept of stock-recruitment, the collapse level is attained for $F = F_{\infty}$, but that if high fecundity is an adaptation to strong variations in the environment, the level of high risk of collapse may be reached at much lower values of F , especially for late-maturing species (which is paradoxically the case for shrimps because they are recruited at 3 months, are adult at 8 months and live only 12 months in the fishery). This collapse level may even be reached earlier if the natural variability of recruitment is taken into account (Figure 15).

It has however often been assumed that "it is not economically or technically feasible to take so many shrimps that there are too few survivors to provide an adequate supply for the following year" (2) (NEAL, 1975 and TURNER and CONDREY, 1981), or in other words that the maximum-allowable-yield is virtually "all the shrimps that can be caught" (point of view challenged by ROTHSCHILD and PARRACK, 1981) leading to an optimum management of the adult stock on a yield-per-recruit basis (in weight or, better still, in value) as advised by GULLAND (1972).

This assumption refers to the industrial trawl fishery and may hold, provided governmental aids and subsidies do not help the fishery to develop beyond the critical level, and the exploitation system is flexible enough to allow excess fishing effort to be diverted out of the fishery when the

stock size is too low. In fact PENN (personal communication) indicates that in 1980 and 1981 two Australian stocks of *P. esculentus* have experienced acute recruitment problems following a documented concentration of fishing effort.

The assumption should also certainly be considered with caution where artisanal lagoon fisheries on juveniles are concerned because of the low operating costs and high efficiency of the net-barrier fishery systems can reach (bamboo traps in the Indian Ocean, "Tapos" in Mexico, stake nets in West Africa).

For the want of better information it therefore seems advisable (both for economical and biological purposes) to manage a shrimp fishery by limiting the effort below some threshold level corresponding to an "acceptable" level of risk. This is of course rather theoretical because this level is difficult to define in practice (except by trial and error, progressively increasing the level of effort allowed). It is likely that with the present fishing conditions, keeping the industrial fishery profitable (without government subsidies), would allow the biological objective (avoiding the critical level of effort) to also be met on average, even when an artisanal fishery on juveniles exists, because its biological effects (reduced recruitment) will affect the profitability of the trawl fishery on adults.

In any case it is clear that any good management policy based on some sort of fishing effort regulation will lose efficiency in the absence of a clear freshwater and estuaries management policy.

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(1) Concept introduced by LE GUEN (1971).

(2) This point seems to be supported by the observations of GUNTER (1966) who indicated that despite nearly complete destruction of the shrimp resources on the Atlantic coast of the U.S.A. during the cold winter of 1940, the catch in autumn 1941 was normal.

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