S. Garcia Fisheries Department, FAO, Rome



Reproduction, stock assessment models and population parameters in exploited penaeid shrimp populations

Abstract: During the last few years, penaeid shrimp stocks have been intensively studied over the tropical regions of the world and a wealth of knowledge has accumulated. Some difficulties, however, still remain. The paper summarises the main developments in the understanding of the nature of shrimp fisheries and underlines some of the fields where more research is needed. In order to provide a basis for discussion, a general schema describing the seasonal cycles of reproduction, recruitment and life cycle of the genus Penaeus is presented. It is tentatively concluded that the generation time from birth to massive spawning of these shrimp is essentially one year and the advantages of such a strategy for population maintenance in a seasonally oscillating environment are discussed. The various models used for stock assessment are briefly reviewed and some of their limitations or particular properties when applied to shrimp are discussed. These include production models, stock recruitment relationships, yield per recruit models, forecasting models and DeLury-Leslie estimators. Some emphasis is put on the use of analysis of length frequency data and commercial size categories as well as the potential usefulness of comparative population analysis in a situation of data shortage.

1 Introduction

Coastal penaeid shrimp stocks have become more intensely studied in the intertropical region during the last three decades as their importance in tropical fisheries has increased. Much progress in biological research has been accomplished since the FAO World Science Conference on biology and culture of shrimps and prawns held in Mexico in June 1967. The

Second Australian National Prawn Seminar

scientific work on population dynamics and stock assessment has greatly developed in Australia, as shown by the First Australian National Prawn Seminar held in Maroochydore (Queensland) in November 1973 (Young 1975). Similar developments have also occurred in Latin America, North America, West Africa, Madagascar, Persian Gulf, eastern Indian Ocean and South East Asia. More recently the progress in biological understanding and management of shrimp has been reviewed at the Workshop on the Scientific Basis for the Management of Penaeid Shrimp, Key West, Florida, November 1981 (Gulland and Rothschild 1984).

Critical review of available knowledge is always important and a first attempt was made by Garcia and LeReste (1981) who examined in detail the most important aspects of the shrimp life cycle (including abundance, variability and sampling methodology, exploitation systems, collection of fishery data, tagging, growth, mortality, changes in catchability, modelling, selection, recruitment, stock assessment and management, using literature up to 1979. The present paper tackles particular issues that received little attention in the above review.

The limiting factor in shrimp stock assessment and management at present does not appear to be a shortage of methodologies, at least for single species, but rather in the scarce knowledge of the mechanisms of shrimp production as well as superficial knowledge of the fleet dynamics. For these reasons, the first part of this paper is focused on life cycles especially for the genus *Penaeus* and presents some speculations about reproduction strategies. Unless these mechanisms are understood, it will not be possible to determine the most appropriate of the available methodologies and the need for new ones.

3.



139

The paper recalls first the differences between brown and white shrimp. It then presents a schema for a typical *Penaeus* life cycle including a review of seasonal spawning and recruitment cycles and discussion on the generation time. I am perfectly aware that this may be an oversimplification but it should offer a basis for future comparison between species and regions especially with respect to the consequences of the shrimp life history strategy on the fishery and on our stock assessment concepts. It is intended to stimulate more analysis along similar lines for as many stocks and as many genera as possible in the future.

The paper also examines some typical characteristics of shrimp fisheries. It reviews the main assessment methodologies and deals briefly with the problems of using length frequency data and commercial categories for stock assessment. The conclusion presents some thoughts about specific research needs for the future.

Brown and white shrimp

To facilitate comparison within the group Penaeus it may be useful to distinguish between white and brown shrimp. Boddeke and Kat (1979) have shown that basic differences exist between the subgenera Litopenaeus and Farfantepenaeus (Melicertus). This division of the genus Penaeus into subgenera is taken from Holthuis (1980). The Litopenaeus group, which includes P. setiferus, P. vannamei, P. schmitti, P. stylirostris, P. occidentalis consists of white shrimp which generally fetch higher prices in the market. They are active in daylight and therefore fished during the day. They live in more coastal areas as adults and they seem less sensitive to salinity fluctuations than brown shrimp. They are essentially grazers of benthic micro-organisms.

In contrast, the Farfantepenaeus species which include P. duorarum, P. notialis, P. aztecus, P. brasiliensis, P. californiensis, P. subtilis, P. paulensis tend to be active at night when they are normally fished. Apparent exceptions to this rule, like P. notalis in Ivory Coast, are due to peculiar local conditions of very high turbidity (Garcia 1977a). They are more predatory than white shrimp in both the field and aquaculture situations (Pedini¹, pers. comm.).

Penn (1984) added to this separation between white and brown shrimp by indicating that P. (Fenneropenaeus) merguiensis (a white shrimp) in Australia is active during the day, and tends to school, while P. (Melicertus) latisulcatus and P. (Penaeus) esculentus, two brown shrimp, tend to be active at night and do not school. This difference in behaviour could, according to Penn, affect their catchability and resilience to fishing. As P. (Fenneropenaeus) indicus tend to behave like P. (Fenneropenaeus) merguiensis, one could be tempted to consider together the subgenera groups P. (Farfantepenaeus) and P. (Melicertus) as brown and separate them from the subgenera P. (Litopenaeus) and P. (Fenneropenaeus) as white.

In many countries, when both groups are present, historically the offshore fishery has started in shallow coastal waters on whites, exploited only during the day and has developed later on browns, fishing day and night and expanding into deeper waters.

The group of brown shrimp, as previously defined, contains the striped or tiger shrimp. Usually the latter are separated commercially but it seems difficult with the information available to distinguish them clearly from other brown shrimp on the basis of their population characteristics or fishery related behaviour.

Seasonal patterns

In shrimp stocks, seasonal patterns should not be concealed by the averaging effect of using annual time intervals as is done for many long lived fish in traditional fishery science. The patterns of seasonal recruitment, growth, behaviour and catchability, fishing mortality, age structure of the exploited population, reproductive potential, biomass, etc have important consequences to the outcome of specific management measures (Garcia 1977a; Garcia and Le Reste 1981).

Spawning cycle

. 0

50

Spawning is the base of the resource renewal mechanism and stock conservation. More work is still needed before we really understand the mechanisms of reproduction in shrimp at the population level. Most studies available on the subject are far from satisfactory. For instance, the widely used percentage of mature females is a biased index of population reproduction and must be combined with an index of adult [,] ۲

¹ M. Pedini, FAO Fisheries Department, Via delle termi di Caracalla, 00100 Rome Italy.

abundance and with fecundity at size data (Garcia 1977a: Le Reste 1978; Penn 1980). Furthermore, studies on monitoring of larvae or postlarvae abundance are often too short for a good average annual cycle to be obtained. Short time sampling variability is sometimes as high as the annual signal to be observed (see Garcia and LeReste 1981 for a review of sampling problems). These problems affect large parts of the literature available and complicate any attempt to generalise on penaeid life cycles. The shape and chronology of the potential fecundity seasonal cycle is largely governed by the shape and chronology of the recruitment cycle of juveniles in the sea. The recruitment cycle of these juveniles depends itself on the larval abundance cycle (and therefore on the preceding year class spawning and environmental cycle) as affected by environmental conditions during the estuarine phase.

Under these circumstances, attempts to correlate seasonal spawning indicators with seasonal environmental parameters are likely to produce spurious relationships. The long term evolutionary adaptation of the population to the oscillating environment is often wrongly interpreted as a short term cause and effect relationship. Garcia (1977a), for instance, showed that, by simulating the seasonal changes in population structure of P. notialis in Ivory Coast, the calculated theoretical maximum fecundity was coincident with the observed abundance of larvae and with the seasonal maximum abundance of phytoplankton (Fig. 1). He suggested that this coincidence was in accordance with the match/mismatch theory of Cushing (1975) which hypothesised that, in north temperate waters, fish populations are adapted to spawn in relation to phytoplankton blooms.

Individual shrimp are partial spawners and can lay several batches of eggs every year. At the population level, however, spawning appears to be more or less continuous, but very often seasonal, showing at least one peak, and sometimes two per year. These frequently occur during the transition periods which separate cool and warm seasons and are characterised by particular hydrological and climatological features such as rising or falling temperatures, low current velocity and wind speed, peaks in primary productivity, as well as high rainfall and severe drops in salinity. Examples can be found in Penn (1980) (*P. latisulcatus,* Australia), Garcia (1977a)



Figure 1. Comparison between observed seasonal patterns of primary production, copepod abundance and postlarval abundance and the calculated seasonal change in fecundity in *Penaeus notialis*, Ivory Coast (from Garcia 1977a). The data have been smoothed by a running mean on three values and reduced to a relative scale by subtracting the mean and dividing by the standard deviation. Postlarval data are lagged by one month.

(P. notialis, Ivory Coast), Berry and Baxter (1969) (P. aztecus, Gulf of Mexico), FAO (1982) (P. semisulcatus, Kuwait), Lhomme and Garcia (1984) (P. notialis, North Senegal), Le Reste (1978) (P. indicus, Madagascar), Motoh (1981) (P. monodon, Philippines), Garcia (1977a) reviewed briefly the various types of spawning seasonal patterns and in spite of the shortcomings of the methods used for quantifying spawning activity, it seems that the double peaked pattern is the most frequent. By analogy with temperate waters we may consider the existence of a spring spawning (it occurs when seawater temperature increases and may extend somewhat into early summer) and an autumn spawning period, these two giving rise to two generations (consisting of many cohorts) per year. When two peaks occur, the spring spawning is usually the more regular in timing and amplitude. The importance of the autumn spawning varies from year to year and place to place, as well as in time of occurrence (Garcia

2

£

1977a) for *P. notialis;* Le Reste (1978) for *P. indicus*). This double maximum spawning cycle seems to be very general for many marine species in the tropics and it has also been found in most coastal fish stocks in the Gulf of Guinea (ISRA/ORSTOM 1979) and in many other tropical areas (Johannes 1978). As a consequence it will be considered in this paper as the typical pattern although it is likely that shifts from this pattern may occur with latitude, or particular local conditions.

The larvae produced during the spawning cycle enter the inshore waters to grow. It has been shown (Ford and St. Amant 1971) that the survival and growth of a cohort in the estuaries is strongly affected by the inshore environment (offshore transport, tidal currents, date of entry in the estuaries, temperature during the estuarine phase). The duration of the estuarine period as well as the size (age) at migration towards the sea are affected by hydrological or climatic events (see Garcia and LeReste 1981 for a review). The seasonal cycle of recruitment is therefore expected to be an image of the spawning cycle lagged by about four months but distorted by the conditions met during the inshore phase.

Migration and recruitment

The number of shrimp leaving the estuary at any time depends on both the abundance of juveniles in the nursery area and their age structure. Both factors are directly linked to the spawning cycle and external factors which trigger emigration (like salinity, temperature, current speed, etc). It should therefore be expected that the seasonal migration oscillation mimics the spawning cycle but is also distorted by the interference with the seasonal oscillation of the environmental conditions inshore. In examples where migration has been carefully analysed it is generally observed that a main migration period occurs in summer through autumn and follows the spawning peak in spring by about four months. Secondary peaks may occur during main flooding or rainy periods, once or twice a year, in spring and again in autumn. Juveniles coming from the secondary spawning in autumn overwinter in estuaries and migrate in spring. When the temperature signal is of low amplitude, and spawning more or less continuous, the migration cycle may show one or both of these secondary peaks and the time lag (age at migration) between spawning and migration may be quite difficult to establish unless intensive sampling of the various cohorts is

undertaken in the inshore waters. Double peaked recruitment patterns in shrimp seem to be common (for example Garcia 1977a, in Ivory Coast; Lhomme and Garcia 1984 in Senegal; Pauly et al 1984 in various regions; Le Reste 1978 in Madagascar). These patterns are also frequent in cephalopods (Pauly 1984a, FAO/CECAF 1982).

Migration generally results in massive recruitment into the small scale inshore fishery and is followed rapidly by recruitment in the offshore trawl fishery. In most cases the shrimp appear in offshore catches in less than a month or so after migration. The more coastal the trawl fishery the shorter the time lag is. The rate of recruitment in the offshore catches depends on the availability of juveniles inshore and therefore on the migration cycle, but also on their vulnerability to trawling. The latter depends on the average depth fished by the fleet at any time. Experience shows that the main generation is generally highly vulnerable because the fleet is waiting for it close inshore, and the main depth fished increases during the fishing season as the fleet tends to follow the main generation as it grows and migrates to deeper waters (Fig. 2). As a consequence, the young pre-recruits of the secondary cohorts will probably be less vulnerable.

The recruitment cycle will, therefore, mimic the migration cycle with a possible distortion due to the behaviour of the fleet. In stock assessment, this implies that the age specific fishing pattern may vary from one cohort to another and that the seasonality in recruitment might be exaggerated when determined from abundance of small sizes in catches of professional trawlers. Another distortion may be introduced by water temperature offshore. If it is low at the moment of recruitment (of the winter cohorts for instance) and below, say 16-17° C, growth is nearly stopped and will start again only in spring. In this case, apparent recruitment can be largely delayed until spring. It should be remembered that because size and age at migration varies seasonally, size and age at recruitment could vary as well. Measuring recruitment by the abundance of small shrimp below a given fixed size in the catches could, in some cases, lead to biased results.

Despite the difficulties foreseen above, it might be said that most *Penaeus* stocks have a seasonally oscillating recruitment pattern with a main generation recruited offshore during



Figure 2. Seasonal variation of average depth (± 2 standard deviations) in French Guiana (from Garcia et al 1984). Fathom = 1.85 m.

summer and autumn and a secondary generation recruited in spring.

There are some variants to this pattern depending on the latitude for the same species (Staples 1979; Penn 1980; Lhomme and Garcia 1984) or on the species concerned when many *Penaeus* species share the same inshore areas. In this latter case, slight differences in timing seem to exist which combined with slightly different biota requirements apparently result in reducing the competition between closely related species (Young and Carpenter 1977).

In the cases where the main spawning peak is in summer, eg for *P. latisulcatus*, in Australia (Penn 1980) or *P. setiferus* in the Gulf of Mexico (Lindner and Cook 1970) the main recruitment is in autumn. When the main spawning occurs in autumn the growth can be low in inshore waters leading to recruitment in the following spring—*P. notialis* in North Senegal (Lhomme and Garcia 1984), *P. semisulcatus* in Kuwait (FAO 1982).

Life cycle and generation time

There seems to be fair homogeneity in the timing of the life cycles of shrimp and it is tempting, albeit risky, to try and describe the life cycle of a typical *Penaeus*. There certainly are deviations from the typical model from place to place and especially at the extreme geographical limits of distribution of the family. There are also obvious deviations from one cohort to another in highly seasonal environments but the following sketch could probably be considered as the most typical.

The typical *Penaeus* is spawned at sea and enters the inshore waters at an age of about three weeks to one month as a postlarva. It grows there for about three months before migrating back to sea where maturation of females can start (maturation of males can apparently start in the inshore waters). It is then about four months old and measures 80 to 100mm (total length). This migration is more clear cut for brown shrimp than for white shrimp and in lagoon systems than in estuaries or open mangroves where the phenomenon can start earlier and is more progressive.

Penaeus continues maturing as it grows and spreads on the fishing grounds in deeper and deeper waters and will spawn after reaching the minimum size for maturation and when environmental conditions are adequate. The size at first spawning, when the very first individuals of a cohort can lay some eggs, is reached at about 6-7 months but the massive maturation, ie the age at which the bulk of a cohort spawns, is closer to one year (10 to 12 months). It is very important to distinguish between the individual size at which first maturation can take place and the average individual size in the population when massive reproduction occurs. This second parameter is more important for stock renewal and therefore the definition of the generation time is from birth to the first massive spawning of that generation.

This average life cycle can of course be modified by environmental factors like currents, which may delay the recruitment of larvae in lagoons, unusual floods and cold strikes or droughts in estuaries that may shorten or protract the duration of the inshore phase and therefore modify, seasonally or from year to year, the size and age at migration, recruitment or spawning. Good information is necessary to reach some understanding of the stock and



Figure 3. Theoretical model of the essential features of the life cycle and fishery of Penaeus.

recruitment relationship at the cohort, generation and population level. It is therefore important to find the link between the seasonal pattern of recruitment and the subsequent seasonal spawning cycle or in other words the link between the recruits at a given time and spawning stock at a subsequent time. It is also necessary to determine the basic time frame of stock reproduction and renewal or generation time.

In order to do this it is necessary to combine information collected on—

- (a) seasonal patterns of spawning, inshore abundance, migration, recruitment and average size by sex in the offshore stock;
- (b) population parameters: size at migration, size at 50% retention by the trawl and selection range, size at first maturation, age and size specific fecundity;
- (c) growth, and in particular, seasonal changes of growth and observed modal progression;
- (d) natural and fishing mortality.

A theoretical example of a graphic integration of this information is given in Fig.3. Other examples can be found in Staples (1979), FAO (1982), Garcia et al (1984).

If, as represented in Fig.3 and as implied from previous sections, the generation time is one year (this seems to be the case for P. semisulcatus in Kuwait (FAO 1982) or *P. notialis* in Ivory Coast and North Senegal) then the main spring generation would reproduce itself one year later as would also the autumn generation. Both generations would meet with different environmental conditions and would have different survival rates, especially before recruitment, and hence would have different stock recruitment relationships (Fig. 7). Some genetical mixing between generations could still occur as there might be limited spawning by each generation out of its main spawning period (for instance a limited first spawning in autumn for the spring generation in Fig.3). Oscillating on the basic annual cycle of the environment the population appears to be placing its most important egg output during the most favourable time window and being more opportunistic during the rest of

• 1

the year with the other cohorts (for instance, the irregular autumn generation).

The other important consequence of the existence of a one year generation time is that, because fishing concentrates on the main generation and drastically decreases its abundance before the main spawning can occur, there is a high risk that the capacity of the main generation to reproduce itself is impaired. This can easily be deduced from simple spawning potential per recruit calculations (Garcia 1977a; Garcia and Le Reste 1981; FAO 1982) and according to Penn² (pers. comm.) this may have already happened for a stock of *P latisulcatus* in Australia.

As it is not yet proved that all Penaeus stocks have a generation time of one year, it may be interesting to speculate about the potential value of a shorter generation time. I suggest that the population would then oscillate in asynchrony with the environment. If the generation time was six months (the first spawning just after recruitment would also be the massive one) the important spring generation would give birth to an autumn generation and vice versa. Such a scheme was proposed by Staples (1979) for P. merguiensis in the Gulf of Carpentaria and also by LeReste (1978) for P. indicus in Madagascar but the evidence given in this last case for seasonal spawning success is not entirely convincing and might be interpreted differently. This strategy would imply a high cost for the stock but might be considered the best one if a high potential fecundity was necessary to bridge over an unfavourable season as assumed by LeReste (1978). The risk of extinction of the stock would, however, be very high because the autumn secondary generation is very irregular and often disappears totally for a few successive years. If this generation would have to bear the responsibility of ensuring permanence of the stock by giving birth to the main spring generation then the system would appear to be very unstable.

Any other generation time longer than six months but shorter than a year would induce an oscillation in the population perpetually out of phase with the environment. The clear and stable seasonal spawning patterns actually observed in the population would then have to be purely the result of the environmental

² J.W. Penn, Department of Fisheries and Wildlife, North Beach, Western Australia. oscillation, with no relationship whatsoever to the size and fecundity of the cohort. The loss of energy for the stock would be even higher than with a six month generation time and one can speculate that a better adapted group of species would have replaced the genus *Penaeus*.

In conclusion, it is suggested that an annual generation time seems to have more virtues for thriving in a seasonal environment than any other and that the case for *P. notialis* in Ivory Coast and Senegal or *P. semisulcatus* in Kuwait might be a general case. More detailed analysis and simulations on other species are needed to confirm this point.

Exploitation sector

Exploitation of adults by trawl fisheries The seasonality of recruitment has very important consequences for the fishery. It will be responsible for the seasonal variations of catch per unit effort and abundance, of average size of the stock, of spawning potential, etc. Combined with the progressive migration of the various generations towards greater depth, it will also be responsible for the great spatiotemporal heterogeneity of shrimp stocks.

Industrial penaeid shrimp fisheries around the world are very similar. The shrimpers tend to exploit the spatio-temporal heterogeneity in the best possible way, concentrating their effort (and hence fishing mortality) on the most profitable space and time allocations(Fig. 4). In multispecies fisheries, the elements of choice will be multidimensional (species, space and time). During the day, they may allocate effort to white shrimp on coastal areas whereas at night they may fish deeper for browns. During the year, they concentrate effort in the months where the expected financial returns are higher. In French Guiana for instance, because of market differences, the Japanese fleet fish mainly for big *P* brasiliensis offshore while the US fleet fishes more for small or average size P. subtilis closer inshore. The consequence of this is that many undetected changes occur in fishing strategy and in the relationship between effort and fishing mortality during the development of a fishery (see Garcia and Le Reste 1981 for a review). This in turn affects the reliability of the results obtained through surplus production modelling using catch and effort data.

The more seasonal the pattern of recruitment the higher the time space heterogeneity and the



Figure 4. Bathymetric distribution of effort (upper histogram), abundance (lower histogram), average sizes for females (----), males (-----) and combined sexes (----) and ages (combined sexes only) for *Penaeus subtilis* in French Guiana from Garcia et al (1984). Ages have been calculated using growth parameters for *Paztecus* from Parrack (1979).

more seasonal the fishery behaviour. The consequence of this extremely well aimed fishing strategy is that the catches may give a biased image of the stock, underestimating for instance the spawning potential available in deep waters during the recruitment months or underestimating the importance of the second recruitment peak when the first one is abundant.

The complex combination of spatio temporal heterogeneity of the resource with the economic motivations of fishing results in a particular fishing pattern or age specific fishing mortality vector. Fishing effort is distributed on the bottom (and on the stock) proportionally to abundance or, more exactly, proportionally to value. Figs. 4 and 5 show a pattern that might be considered general. This fundamental and well known aspect of shrimp fisheries seems to have received little attention when modelling the exploitation, particularly in yield per recruit (Y/R) calculations where fishing mortality (F) is usually assumed to be constant with age.

Artisanal fisheries

A review of artisanal fisheries with an emphasis on stake net fisheries is given in Garcia and LeReste (1981). Detailed analyses of these



Figure 5. Age specific fishing mortality vector for Penaeus notialis in Ivory Coast (from Garcia 1977a).

fisheries are still scarce. Artisanal fisheries for juveniles have a direct effect on trawl fisheries for adults but these effects in biological or economical terms are still largely unstudied in most areas. Garcia (1977a, 1978) provided a first analysis of yield and value as a function of exploitation rate in the lagoons, and fishing effort at sea, in the Ivory Coast. Griffin and Grant (1982) completed this analysis using economic parameters. These types of studies remain scarce despite their importance, probably because of the difficulty of obtaining accurate socio economic data on the artisanal fishery and the complexity of the artisanal exploitation sector in some countries (multigear, multispecies fisheries, links with the wider rural sector). In general, it does not seem to pay to catch small shrimp as stated already by Lindner (1966), Lucas (1975) and more recently, by Willmann and Garcia (in press). The relative benefits for each sector and for the nation as a whole, however, have to be estimated case by case and include not only financial, but also aggregated social benefits.

Assessment methods and models

A review of the methodologies used for penaeid shrimp stock assessment was given by Garcia and Le Reste (1981). An analysis of stock recruitment relationships in shrimp (Garcia 1983) followed. It is easily seen that traditional temperate waters fishery science has largely been applied to date, despite the tropical character of the animals concerned. Most of the so-called new methods (either elaborate or quick and dirty) proposed in recent years for tropical populations have their roots in the very first steps of this classical fishery science and Ursin (1984) has recently pointed out some of the similarities between temperate and tropical environments and resources. The basic concepts will therefore, still be used for some time but minor adjustments have to be made by using shorter time scales, and paying more attention to seasonal patterns and

environmental variables.

Production models

In the context of high spatio temporal heterogeneity of the resource exploited by a well aimed fishery, it is obviously dangerous to summarise a fishery as a set of catches and nominal efforts plotted on a bivariate graph to produce a production model and generate information on catch potentials and some sort of optimal fishing level. Many sources of drift in effort or fishing pattern can distort the model and lead to biased conclusions. Garcia and LeReste (1981) give a review of the problem in the case of shrimp. A description of this sort of change in fishing power is also given by Lucas et al (1979) for the Gulf of Carpentaria fishery.

However, in a single year class fishery, despite the lack of dependence of the biomass in one year to the biomass and fishing mortality in the preceding year, the production model approach can still provide an empirical knowledge on the apparent reaction of the stock to exploitation.

Because of the strong influence of the environment on annual shrimp production, the potential errors when this influence is not taken into account is serious, especially when the data series is short. More use should be made of multivariate models of the form—

Catch = g (effort, rainfall, temperature, etc.)

as used by Griffin et al (1976). A preliminary correlation of the residuals from the relationship between catch and effort with environmental variables known to affect recruitment or catchability could also be useful as a first step (see for instance Lhomme and

 Garcia 1984 for *P. notialis* in Senegal). The comparison of time series of such residuals for neighbouring stocks may also show the wide scale effect of some environmental factor (an example is given for Kuwait by Garcia and Van Zalinge 1982). A short analysis of the effect of environmental variability on production modelling is given in Garcia (1984b) and it is pointed out that the fishery trajectory across a catch, effort and environment multidimensional



EFFORT

Figure 6. Theoretical example of the trajectory of a fishery (dots) across a catch, effort and rainfall production model.

space could be wrongly taken as a production model on the catch effort plane while all the basic properties of this model have, in fact, been lost. Above all, the possibility of reversing the observed evolution of the fishery stock along the same observed trajectory by reducing the amount of effort (Fig.6) is often not feasible.

Stock and recruitment models

Despite the fact that it is relatively easy in many instances to measure the spawning stock size and the recruitment index in *Penaeus* populations, stock and recruitment relationships (SRR) have been studied only since the beginning of the 1980s. In a review of the available literature, Garcia (1983) has indicated the various types of recruitment indexes that could be used and stressed the following—

- (a) annual shrimp catches have been shown to be strongly related to environmental factors. The cohort survival in lagoons and estuaries and therefore the level of recruitment are largely dependent on local climatic conditions;
- (b) environmentally driven changes of stock size in short-lived species are likely to be serially correlated and therefore very likely to produce artefactual linear stock recruitment relationships (SRR) which in fact are an approximation of the opposite recruitment stock relationship (RSR) or replacement line;



Figure 7. Theoretical example of stock recruitment for the spring and autumn generation of shrimp. A and B indicate the respective areas of equilibrium of the two generations when fished with the same intensity. Two levels of the stock recruitment relationship (SRR) are shown, corresponding to good and low survival of prerecruits. Recruitment stock relationship (RSR) or replacement lines shown as sector XOY to allow for natural variations of catchability for a fixed fleet size. X'OY' is the replacement sector when F, the fishing mortality, reaches the critical level.

(c) there are probably many stock recruitment relationships (SRR), or more strictly many pre-recruit mortality levels depending on the birthdate of the various cohorts. In other words pre-recruit mortality is likely to vary seasonally from one cohort to another. For example, a different pre-recruit survival range for the spring and autumn generations can be expected (Fig. 7).

Under a given fishing regime (as well as in a virgin stock) one would therefore have to consider under the classical theory, two equilibrium SRR areas (A and B in Fig.7) corresponding to the two generations. In Fig.7 it is assumed that the RSR or replacement line is the same for both generations but this is probably not so. The existence of seasonally different pre-recruit mortality levels and of a generation time of one year would lock together environmental effects and possible stock reproduction. Garcia (1983) proposed a three dimensional interpretation of a stock recruitment relationship in shrimp (Fig.8).

The bottom plane of the figure shows the seasonal cycle of population fecundity, assumed to depict also the seasonal spawning intensity with the shaded blocks accounting for natural variability of fecundity. Vertical plane I shows the seasonal cycle of recruitment with the shaded blocks again accounting for natural variability in recruitment. The darker three dimensional blocks identified by the month of spawning (J, F, M, etc) give the SRR area and therefore the level of pre-recruit survival for the months of spawning considered. The true SRR therefore, is three dimensional and depends on stock size, recruitment and time. The vertical plane II shows the apparent stock recruitment relationship as a projection of these SRR areas on the recruitment stock plane.

The figure emphasises the differences that exist, despite a similar shape, between this interpretation which shows the result of a longterm adaptation of the animal to its oscillating environment and the traditional stock recruitment relationship which is supposed to depict the effect of fishing on stock size and consequent recruitment.



Figure 8. Seasonal patterns of population fecundity as an index of spawning stock sizes (at time t), recruitment (at time t+r) and apparent stock recruitment relationship (modified from Garcia 1983). Age at recruitment considered constant (r=3) for all monthly cohorts (eg shrimp spawned in January are recruited in April).

The important mechanisms that operate in the reproduction of penaeid shrimp populations need to be carefully considered before making biological inferences from a bivariate stock recruitment plot. This does not intend to rule

- out the possibility of a negative effect of fishing on recruitment. The effect of fishing on spawning capacity per recruit of the main
- cohort and on the seasonal fecundity cycle is potentially very drastic when fishing mortality approaches or passes the level of natural mortality (Garcia 1977a; Garcia and LeReste 1981), and it is obvious that beyond a critical level of fishing mortality (Fig.7) some serious and abrupt detrimental effect might happen, (eg the disappearance of the main spring generation spawning).

The progressively greater mismatch between the seasonal environmental cycle and the overall population fecundity and spawning cycles, which are continuously altered by increasing fishing mortality might result in an apparent SRR as effort increases because of the subsequent progressive increase in average pre-recruit mortality and reduction in recruitment resulting from a given stock size at the population level and on a yearly basis. It is not easy to demonstrate this effect, however, under moderate levels of fishing. A first approach might be to use multivariate models with effort, stock size, recruitment level and environmental indexes as variables following an approach similar to the one used for the Peruvian anchoveta by Csirke (1980).

Yield per recruit models

Yield per recruit models are proving to be very useful for the single species approach to shrimp management. The models of Thompson and Bell (in Ricker 1975), Beverton and Holt (1957), or Ricker (1975) have been widely used. They are justified when recruitment has not been shown to be dependent on stock size. They are flexible enough to be adapted to short time intervals and can easily be used to model for example (1) the interaction between artisanal inshore fishery on juveniles and trawl fishery on subadults and adults offshore (Garcia 1977a, 1978; Grant and Griffin 1979; Willmann and Garcia in press); (2) the effects of closed seasons (Garcia and Van Zalinge 1982) or (3) the effects of other changes in fishing patterns. They can also be used as a basis for simulation models with recruitment and fishing effort varying seasonally in order to try and reproduce the seasonal patterns characteristic of the resource. The results can be expressed, on a per recruit or on an absolute basis when an estimate of the current level of recruitment is available. They can also be expressed in value terms and used for economic analysis (Garcia 1977a; Clark and Kirkwood 1979; Lucas et al 1979). Finally they are useful for investigating the evolution of potential fecundity per recruit when fishing pressure increases (Garcia 1977a). The Thompson and Bell model is particularly appropriate because of its flexibility, capacity to use observed length at age or value at age data, and easily understood form for non-scientists like fishery administrators, (see for example Garcia and Van Zalinge 1982; Willmann and Garcia in press).

Because of the values characteristic of penaeids for natural mortality (M), growth rate (K), and critical length (I_c) and asymptotic length (L_{∞}), the yield per recruit (Y/R) increases exponentially towards a quasi asymptote with increasing fishing mortality (F) and Y/R_{max} is reached only at unreasonably high level of F. This casts doubts on Y_{max} as an objective for management but does not affect the intrinsic validity of the model.

Use of the DeLury-Leslie estimators

The use of the De Lury-Leslie methodology for estimating fishing mortality and population size in shrimp goes back to Iversen (1962) who used it on *P. duorarum*. The method (see Garcia and Le Reste 1981 for a review) is usable only if F is sufficiently high to affect significantly the stock size in a time interval short enough for M to be negligible, unless M is counterbalanced by recruitment. For short-lived animals like shrimp, changes in catch per unit effort (CPUE) during time intervals small enough for M to be neglected, are likely to be also largely due to behavioural changes in catchability and this complicates the interpretation of the data.

This method, correctly used by lversen and also by Clark and Caillouet (1973) in conjunction with tagging data has been very widely used in the last 10 years in Latin America. The tendency has been, however, to plot the CPUE in numbers for the whole stock against cumulative catch for a long period of time (many months) starting after the recruitment has been completed. Within such a time interval the decrease in numbers is not only due to fishing but also to a significant natural mortality. In that case the slope of the regression is not F/f=g but F/f+M/f=q+M/f (Ricker 1975) where F=fishing mortality, M=natural mortality, q=catchability, and f=fishing effort. When this is not taken into account serious biases are introduced in the calculated F and, consequently, in M when this last parameter is estimated by difference between total mortality (Z), independently obtained, and biased F. The problem can be solved if M is known independently (Yew-Hu and Condrey 1985).

The other potential errors in the application of this estimator to shrimp should be carefully examined. By applying (correctly) the method only to the portion of the year where the CPUE decreases (and recruitment can be considered terminated) it is obvious that the Y axis intercept (in theory equal to q x initial population size (N₀) would be proportional to the population size at the starting point of the analysis and not proportional to the overall recruitment that entered the fishery in the preceding months. This value, better called qN'₀, depends not only on the true total recruitment but also on fishing mortality applied during the progressive recruitment period. It is therefore not a stable recruitment index. If the recruitment period is well determined and lasts for say, three months, a better, and more stable recruitment index might be obtained, as a first approximation, by the value of y when x=-1.5 months (assuming knife edge recruitment).

Forecasting models

Because of the high spatio temporal heterogeneity of shrimp resources and their year-to-year fluctuations in recruitment and abundance, there is need to develop short term **Table 1.** Estimates of annual natural mortality M and fishing mortality at full exploitation, F_{MSY} (or equivalent) for penaeid shrimp. Z=Instantaneous rate of total mortality, f=fishing effort and q=catchability. SE = standard error.

Area and species	М	F _{MSY} (or equivalent)	Reference (method)
Gulf of Mexico P. aztecus	2.8	(0.36) ¹	Rothschild and Brunenmeister 1984 (tagging)
P. aztecus	1.8-2.5		(average age and regression of Z on f)
P. aztecus	1.8		(decline in CPUE of cohorts)
P. aztecus	1.9	1.12	(decline of CPUE)
P. setiferus	2.2	1.5 ²	(decline of CPUE)
Ivory Coast P. notialis	3.0	2.1 ³	Garcia 1977a,b (tagging and production modelling)
P. notialis	2.5	1.9 ³	(catch curve, relation Z/f and production modelling)
Madagascar P. indicus	2.5	1.3-1.5 ³	LeReste 1978, for M and q; Marcille 1978 (tagging and production modelling)
Australia P. plebejus P. merguiensis	2.4 2.4	 (12.0)4	Lucas 1974, Lucas et al 1979 (tagging) (tagging)
Mean \pm 2 SE	2.4 ± 0.3	$1.6 {\pm} 0.3$	

¹ Unlikely low value for such an old and intensive fishery-not used

² Close to full exploitation

³ Full exploitation

⁴ Exceptionally high value—very flat topped yield per recruit curve. Yields level off between 1.8 and 2.4 year⁻¹ on their Fig.4.

equilibrium is not met. Similar problems in sampling length frequency distribution of pandalid shrimp are discussed by Frechette and Parsons (1983). Problems of sampling (of the population by the fleet and of the fleet by the scientist) seem to be largely responsible for a lot of chaotic length frequency distribution series found in the literature and lead to dubious estimates of growth parameters, no matter what sophisticated or objective methodology is used.

Commercial size categories which are used for reporting landings contain similar information but have seldom been used. They could potentially be very useful. They often represent an exhaustive compilation of the size structure of the annual landings and the categories used are standard for most fisheries around the world. The information is very often easily available, at least for the industrial trawl fisheries together with elementary data like catch and nominal effort.

In theory this information could be used for length cohort analysis with unequal time intervals (Jones and Van Zalinge 1979). The additional difficulty here is that when sexes

have very different growth rates and therefore different K and L_{∞} values, it is not advisable to analyse a mixed catch structure using average growth parameters. The sex ratios within each commercial category should be taken into account in order to split the annual data for mixed sexes into monosex catch structures. A similar procedure applying the size to sex ratio relationship to length frequency data was advocated by Garcia and Albaret (1977) for P. notialis (Fig. 9) in Ivory Coast. Such relationships have also been used by Lhomme and Garcia (1984) for P. notialis in Senegal and Marcille (1978) for P. indicus in Madagascar. These studies show that the sex ratio to size relationships are similar from year to year for a given stock, different from stock to stock and of course from species to species.

The problem of using appropriate growth parameters when studying commercial categories data are similar to those for length frequency data. The Jones and Van Zalinge (1979) method developed in Kuwait has apparently been used up to now only in Kuwait (Mathews and Al Hossaini 1982). It seems to generate excessively high mortality values (Z=12 to 38 year⁻¹ for some species) and predictive models to guide the fisheries. Many attempts have already been made and a review can be found in Garcia and LeReste (1981) and Witzell and Allen (1983). Generally, empirical regressive models have been used relating total catch to some environmental parameter. The relationship can be quite good. In most instances the real predictive ability of these models cannot be assessed from the literature as the model has generally been elaborated using all the data available and the test of the model in the following years has either not been made or not reported in the literature. Predictive models using a pre-recruit abundance index seem to work better, especially when using juvenile abundance during migration as a predictor. These models can be used to predict total annual catch.

The inclusion of effort as a variable in predictive models might improve their predictive ab_ility in most cases. When long time series of data on the fishery and environmental data known to affect shrimp catch are available, multivariate autoregressive integrated moving average (ARIMA) models could be tried for forecasting. An example of application to crustaceans is given by Fogarty (1984) which shows that annual and monthly catches could be predicted for the Maine American lobster (*Homarus americanus*). This methodology does not seem to have been applied yet to penaeid shrimp.

When detailed information on the biological patterns of migration, recruitment, distribution and spawning, as well as on population parameters of growth and mortalities are available, detailed forecasting is possible when data on recruitment strength of the main generation can be rapidly obtained, for example, through reporting by professional trawlers of their CPUE early in the season. Detailed forecasting of the CPUE and catch structures by month (and possibly by area) and of the likely extension of the profitable fishing season would be very useful for fleet management. The appropriate time structured simulation models are available (based on Y/R models for instance) and are presently used in operations research in a limited number of countries like Australia (Kesteven et al 1981) and Cuba (Baisre 1983). Structuring the models also in the space dimension to predict CPUE by areas could be done in theory when good information is available on the dispersion rate of shrimp from the nurseries to the various grounds. However, in most cases the variability of the spatial structure of the stock may be so

high in the short term and so stable (and therefore known to fishermen) in the medium term that the exercise might not be worth its cost.

Alternative models and techniques

The modern trend for tropical fisheries is to make better and more complete use of length frequency distributions for parameter estimations (Pauly et al 1984, Munro 1984). Some of these methods still need further examination to test their sensitivity and accuracy (Majkowsky 1982, Hoenig et al 1983) but the trend will persist and the use of these techniques will be developed in the near future (see for instance Sainsbury 1982). When using length converted catch curves (Pauly 1983, 1984b) or various types of length cohort analyses (Jones 1979, or Jones and Van Zalinge 1979), there is a problem in using an age length relationship (average length for a given age) for calculating the average age for a given length. Jones (1985) points out that the L_{∞} values can be biased downwards and suggests some ways of correcting them, as well as adjusting the K values accordingly. Bartoo and Parker (1983) stressed that, using the usual growth curve parameters, the calculated ages for given length are increasingly overestimated as the lengths approach L_{∞} . Majkowski and Hampton (1983) have shown that, in fact, the errors increase rapidly on both sides of the length frequency distribution, when they are converted to distribution of ages. They state that this leads to errors, for instance, in recruitment indices based on CPUE of small fish. It can be expected that errors in estimates of exploitation rates are also likely to occur. Pereiro and Pallares (1984) show that the bias introduced by inappropriate growth parameters can be very high. The bias could be reduced by starting the backward analysis at a length as close as possible to the upper limit of the length interval for which growth parameters are valid and by using a final length group (I+) for which the lower limit is as far as possible from L_{∞} .

Sampling produces another difficulty in the application of these methods which often uses stationary (annual) length frequency distributions. In short-lived animals, such as shrimp, the validity of the results depends largely on the representativeness of the annual aggregated size distribution and therefore on sampling. Single monthly size distributions of catches, or aggregated distributions from one single trawl survey cannot be used to estimate mortalities as the essential condition of

151



Figure 9. Example of determination of length frequency distribution by sexes from a mixed distribution using a relationship between size and sex ratio. **a.** Size sex ratio relationship (obtained from a one year trawl survey program in 1969). **b.** Mixed sexes distributions of landings in April 1974 (the distributions by sexes are known but have been pooled to test the method). **c.** and **d.** Comparison between the observed (continuous line) and calculated (broken line) distributions (from Garcia and Albaret 1977).

needs more testing in order to assess its practical value.

í .,

. °.

Comparative population dynamics

Comparative studies could potentially be very useful for tropical regions where a large number of species and stocks and a low number of scientists occur. Some generalisations might therefore provide useful first estimates when data are scarce.

Growth

The Von Bertalanffy model seems appropriate for shrimp (Parrack 1979; Frechette and Parsons 1983) despite the fact that growth in



Figure 10. Comparison of growth parameters (K and log W_{∞}) for penaeid shrimps (redrawn from Pauly et al 1984).

crustaceans is not continuous but stepwise. Pauly (1980), Munro and Pauly (1983) Pauly and Munro (1984) have developed simple methodologies for comparing growth. These tools could be used to investigate similarities in penaeid shrimp_as in Fig. 10. The chain of programs (ELEFAN) applied to shrimp by Pauly et al (1984) can be a useful tool for growth analysis if critically used, especially when seasonal changes in growth are suspected and the seasonal temperature cycle consists of a single annual oscillation (one warm and one cool season of equal duration).

When the growth of females is known, the slower growth of males which is much more difficult to analyse by modal progression may be obtained through the relationship between size of males and size of females in various trawl samples taken at various depths (Fig. 11). Comparisons between species or regions could be simplified. Pauly (1984a) showed that different growth curves (with different growth parameters) corresponding to different environmental conditions could be produced with a single set of K and L_{∞} by taking the seasonality of growth into account in a seasonally oscillating Von Bertalanffy growth model.

Natural mortality

Some of the M values obtained in the 1960s which attained 26.4 year⁻¹ are clearly unrealistic

and the values regularly obtained in the past 10 years by analytical methods are around 1.2 to 5.4 year⁻¹ for adult shrimp at sea. Table 1 shows that when the most extensive analyses are considered, values of M are around 0.20 month⁻¹ or 2.4 year⁻¹ for adult *Penaeus*. The case of the smaller genera (*Metapenaeus*, *Trachypenaeus*, *Xiphopenaeus*, *Parapenaeopsis*, etc.) is less well documented and their most likely values for M are still to be determined. Natural mortality estimates in the juvenile phase are also seriously lacking. Doi (1981) reported a value of M=0.18 month⁻¹ for *P. japonicus* and Lucas (1974) gives a value of 0.44 to 0.88 for *P. plebejus*.

Optimum fishing mortality and F_{MSY} As recruitment is likely to vary from year to year, management may be based on some predetermined effort level. In this case, the value of F corresponding to the level of maximum sustainable yield (F_{MSY}) could be considered a management objective but, because of the general criticism about this parameter (Gulland 1969, Larkin 1977, Sissenwine 1978) it could be considered as a reference mortality level to exceed or not depending on management objectives. A review of F_{MSY} values or equivalents (Table 1) leads to a mean value of 1.6 year⁻¹ \pm 0.3. This value is lower than the mean value of M=2.4 year⁻¹ \pm 0.3 in the same papers, confirming the more general conclusion of Deriso (1982) about the relationship between M and F_{MSY}.

Few stocks in the world seem to have experienced levels of F largely above M, perhaps because this is economically difficult. The case of the banana prawn stock in the Gulf of Carpentaria, Australia, with F/Z = 0.78 to 0.86 is in this regard a notable exception (Lucas et al 1979).

Discussion and conclusions

A lot of progress in research has been achieved in the last two decades, particularly for the larger shrimp of the genus *Penaeus*. Some important aspects will remain obscure and more research effort is needed in order to improve our understanding and management ability.

In the first sections of this paper I have insisted on the need to integrate and cross check all the information available in both the time and space scales in order to build up a basic life history model. This information includes: seasonal



Figure 11. Relationship between mean size of males and females in trawl samples (from Garcia and Le Reste (1981). Data for *Penaeus duorararum* from Iversen et al (1960). Dots and solid line indicates *P. notialis*, broken line indicates *P. duorarum*.

variations of recruitment, average size of massive spawning, adult abundance, fishing effort, modal progressions in monthly size frequencies offshore, weekly modal progressions inshore, bathymetric distribution of abundance, and of effort. This integration is important as the information published by different authors on these various aspects for the same stock and fishery are sometimes contradictory.

When a coherent life history model is available, a time structured simulation model should then be produced and tested on its ability to reproduce the observed seasonal patterns and length frequency distributions. It might then, and only then, be used for evaluating the effect of changes in fishing pattern or mortality levels on the population and on the fishery.

The use of a comparative approach could help by bridging the parameter gap for some species. This comparative approach should be fruitful as far as growth is concerned because much data are already available for various species. It is probably useful also for mortality estimates in the genus *Penaeus* but dramatic scarcity of data limits its application for the small shrimp (*Metapenaeus, Xyphopenaeus, Parapenaeopsis,* etc).

The reproduction mechanisms should be studied more intensively, and particularly the link between spawning and recruitment (and vice versa) at the seasonal level. This is necessary in order to understand the stock and recruitment relationship and also to assess the effect of fishing on the spawning potential and reproductive capacity of the stock.

In order to progress rapidly, particular effort should be made on sampling catches for size distributions by sexes and/or improving the present use of commercial categories, together with more and critical use of the length based methodologies. These methodologies need to be tested for sensitivity to error in input parameters and have been particularly scrutinised at the International Conference on the Theory and Application of Length-Based Methods for Stock Assessment organised by ICLARM in Mazara del Vallo, Italy, in February 1985 (Pauly and Morgan unpublished). The proceedings will be published in 1985 in the ICLARM Report series. The available forecasting models for annual catch for abundance should be tested against time and the results should be published no matter whether they are positive or not. Finally, it must be remembered that a shrimp fishery has a heterogeneous and changing spatial

- structure which is very important to understand, if serious errors are to be avoided in stock assessment and management. Consequently, surveys (or detailed logbooks) are necessary to
- surveys (or detailed logbooks) are necessary to map the distribution of the resource and of the effort. The size structure may help identify migration routes sometimes more surely than tagging. The monitoring of concentrations of fishing effort by areas or depth will be fundamental when planning a tagging experiment, when standardising effort for production modelling, when trying to identify age specific fishing patterns and, last but not least, when trying to assess the potential effect of closed seasons or closed areas.

References

- Baisre, J. 1983. Resultados de la administracion científica de la pesquerias de camarones (*Penaeus* spp.) y langostas (*Palinurus argus*) en la plataforma cubana. FAO Fish. Rep. (278) Suppl.: 120-141.
- Bartoo, N.W. and Parker, K.P. 1983. Stochastic age frequency estimation using the von Bertalanffy equation. US Fish. Wildl. Serv. Fish. Bull. 81: 91-96.
- Berry, R. and Baxter, K.N. 1969. Predicting brown shrimp abundance in the northwestern Gulf of Mexico. FAO Fish. Rep. 57: 775-798.
- Beverton, R.J.H. and Holt, S.J. 1957. On the dynamics of exploited fish populations. Fish. Invest. Ser. II, 19, 533 pp.
- Boddeke, R. and Kat, M. 1979. Differences in food programmes of penaeid shrimp species. ICES paper CM/1979/K: 20, 7 pp.
- Clark, S.H. and Caillouet Jr, W. 1973. White shrimp population trends in a tidal marsh pond. Mar. Fish. Rev. 35: 27-29.
- Clark, W.C. and Kirkwood, G.P. 1979. Bioeconomic model of the Carpentaria prawn fishery. J. Fish. Res. Bd. Can. 36: 1304-1312.
- Csirke, J. 1980. Recruitment in the Peruvian anchovy and its dependence on the adult population. Rapp. P.V. Reun. Cons. Int. Explor. Mer. 177: 307-313.
- Cushing, D.H. 1975. Marine ecology and fisheries. Cambridge University Press, Cambridge, 278pp.
- Deriso, R.B. 1982. Relationships of fishing mortality to natural mortality and growth at the level of maximum sustainable yield. Can. J. Fish. Aquat. Sci. 39: 1054-1058.
- Doi, T. 1981. Population dynamics and management of the shrimp fishing in the Seto Inland Sea. Paper presented at the international shrimp releasing, marking and recruitment workshop, Kuwait, 25-29 November 1978. Kuwait Bull. Mar. Sci. 2: 289-306.

- FAO 1982. Report of the workshop on assessment of the shrimp stocks of the west coast of the Gulf between Iran and the Arabian Peninsula (Kuwait, 12-22 October 1981). Fisheries development in the Gulf. (Bahrain, Iran, Iraq, Kuwait, Oman, Qatar, Saudi Arabia, United Arab Emirates). FI/DP/RAB/80/015: 163 pp.
- FAO/CECAF 1982. Report of the special working group on cephalopod stocks in the northern region of CECAF. CECAF/ECAF Series, 82/24, 178 pp.
- Fogarty, M.J. 1984. Temperature-yield relationship for the Maine American lobster (*Homarus americanus*) fishery: a time series analysis approach. NAFO. SCR. DOC. 84/VI/57, 23 pp. (mimeo).
- Ford, T.B. and St. Amant, L.S. 1971. Management guidelines for predicting brown shrimp, *Penaeus aztecus*, production in Louisiana. Proc. Gulf Caribb. Fish. Inst. 23: 149-164.
- Frechette, J. and Parsons, D.G. 1983. Report of shrimp ageing workshop held at Ste Foy, Quebec, in May and at Dartmouth, Nova Scotia, in November 1981. NAFO Sci. Coun. Studies (6): 79-100.
- Garcia, S. 1977a. Biologie et dynamique des populations de crevettes roses (*P. duorarum notialis*, Perez Farfante, 1967) en Cô d'Ivoire. Trav. Doc. ORSTOM 79: 271 pp.
- Garcia, S. 1977b. Evaluation des mortalités chez la crevette rose, *Penaeus duorarum notialis*, en Côte d'Ivoire: analyse des variations saisonnières de capturabilité. Cah. ORSTOM (Ser. Oceanogr.) 15(3): 51-60.
- Garcia, S. 1978. Bilan des recherches sur la crevette rose, *Penaeus duorarum notialis*, de Côte d'Ivoire et consequences en matière d'aménagement. Doc. Scient. Centre Rech. Oceanogr. Abidjan 9(1): 1-41.
- Garcia, S. 1983. The stock-recruitment relationship in penaeid shrimps: reality or artifacts and
- misinterpretations. Oceanogr. Trop. 18(1): 25-48. Garcia, S. 1984a. Un exemple d'utilisation des
- modèles composites en Mediterranée espagnole. FAO Fish. Rep. (305): 98-105.
- Garcia, S. 1984b. Environmental aspects of penaeid shrimp biology and dynamics. pp.268-271. In: J.A. Gulland and B.J. Rothschild, (Editors) Penaeid shrimps: their biology and management. Fishing News Books Ltd., Farnham, UK.
- Garcia, S. and Albaret, J.J. 1977. Utilisation de la relation sex-ratio taille pour le décomposition par sexes des structures démographiques. Cah. ORSTOM, Ser. Oceanogr. 15(2): 83-87.
- Garcia, S. and Le Reste, L. 1981. Life cycles, dynamics, exploitation and management of coastal penaeid shrimp stocks. FAO Fish. Tech. Pap. 203: 215pp. (original in French, same reference).
- Garcia, S. and Van Zalinge, N.P. 1982. Shrimp fishing in Kuwait: methodology for a joint analysis of the artisanal and industrial fisheries. pp. 119-142. In: Assessment of the shrimp stocks off the west coast of the Gulf between Iran and the Arabian peninsula. Fisheries development in the Gulf. FI/DP/RAB/80/015.
- Garcia, S., Lebrun, E. and Lemoine, M. 1984. Le recrutement de la crevette *P. subtilis* en Guyanne française. Rapp. Tech. IFREMER, 323 pp.

ĺ

- Grant, W. and Griffin, W. 1979. Bioeconomic model of the Gulf of Mexico shrimp resources. Trans. Amer. Fish. Soc. (108): 1-13.
- Griffin, W.L., Lacewell, R.D. and Nichols, J.P. 1976. Optimum effort and rent distribution in the Gulf of Mexico shrimp fishery. Am. J. Agric. Econ. 58: 645-652.
- Griffin, W.L. and Grant, W.E. 1982. A bioeconomic analysis of a CECAF shrimp fishery. CECAF/TECH/82/41, 78pp.
- Gulland, J.A. 1969. Manual of methods for fish stock assessment, Part 1. Fish population analysis. FAO Man. Fish. Sci. 4: 154 pp.
- Gulland, J.A. and B.J. Rothschild, (Editors) 1984. Penaeid shrimps: their biology and management. Fishing News Books Ltd., Farnham, UK., 308 pp.
- Hoenig, J.M., Lawing, W.D. and Hoenig, N.A. 1983. Using mean age, mean length and median length data to estimate the total mortality rate. ICES CM. 1983/D 23: 11 pp. (mimeo).
- Holthuis, L.B. 1980. Shrimps and prawns of the world. An annotated catalogue of species of interest to fisheries. FAO Fish. Syn. 125, 1. 271 pp.
- ISRA-ORSTOM 1979. La reproduction des espèces exploitées dans le golfe de Guinée. Rapport du groupe de travail ISRA/ORSTOM, Dakar, 7-12 Novembre 1978. Doc. Scient. Centre Rech. Oceanogr. Dakar, Thiaroye, 68. 213 pp.
- Iversen, E.S. 1962. Estimating a population of shrimp by the use of catch per effort and tagging data. Bull. Mar. Sci. Gulf Caribb. 12: 350-398.
- Iversen, E.S., Jones, A.E. and Idyll, C.P. 1960. Size distribution of pink shrimp, *Penaeus duorarum*, and fleet concentrations on the Tortugas fishing grounds. Spec. Sci. Rep. USFWS (Fish.) 356: 62 pp.
- Johannes, R.E. 1978. Reproductive strategies of coastal marine fishes in the tropics. Env. Biol. Fish. 3: 65-84.
- Jones, R. 1979. An analysis of a *Nephrops* stock using length composition data. Rapp. P.V. Réun. Cons. Int. Explor. Mer. 175: 259-269.
- Jones, R. 1985. Assessing the effects of changes in exploitation pattern using length composition data (with notes on VPA and cohort analysis). FAO Fish. Tech. Pap. 256: 118 pp.
- Jones, R. and Van Zalinge, N.P. 1979. Estimates of mortality rates and population size for shrimp in Kuwait waters. FAO shrimp stock evaluation and management project, Kuwait. Final Report, Kuwait, TF/KUW/6/R3. 26 pp. Also published in Kuwait Bull. Mar. Sci. 2: 273-288.
- Kesteven, G., Stratton, J. and Carter, D. 1981. KFV launches private, enterprising research programme. Aust. Fish. 40(10): 19-21.
- Larkin, P.A. 1977. An epitaph for the concept of maximum sustainable yield. Trans. Amer. Fish. Soc. 106(1): 1-11.
- Le Reste, L. 1978. Biologie d'une population de crevettes *Penaeus indicus*, H. Milne-Edwards, sur la côte nord ouest de Madagascar. Trav. Doc. ORSTOM, 99: 291 pp.
- Lhomme, F. and Garcia, S. 1984. Biologie et exploitation de la crevette penaeid *Penaeus notialis* (Perez Farfante, 1967) au Sénégal. pp. 111-141.
 In: J.A. Gulland and B.J. Rothschild (Editors).

Penaeid shrimp: their biology and management. Fishing News Books Ltd., Farnham, UK.

- Linder, M.J. 1966. What we know about shrimp size and the Tortugas fishery. Proc. Gulf Caribb. Fish. Inst. 18: 18-25.
- Lindner, M.J. and Cook, H.L. 1970. Synopsis of biological data on *Penaeus setiferus* (Linnaeus) 1767. FAO Fish. Rep. 57: 1439-1470.
- Lucas, C. 1974. Preliminary estimates of stocks of the king prawn, *Penaeus plebejus* in south-east Queensland, Aust. J. Mar. Freshw. Res. 25: 35-47.
- Lucas, C. 1975. Does it pay to catch small prawns? Aust. Fish. 34(1): 10-11.

Lucas, C., Kirkwood, G. and Somers, I. 1979. An assessment of the stocks of the banana prawn, *Penaeus merguiensis*, in the Gulf of Carpentaria. Aust. J. Mar. Freshw. Res. 30: 639-652.

- Majkowski, J. 1982. Usefulness and applicability of sensitivity analysis in a multispecies approach to fisheries management. pp. 149-166. In: D. Pauly and G. Murphy (Editors), Theory and management of tropical fisheries. ICLARM/CSIRO.
- Majkowski, J. and Hampton, J. 1983. The effect of parameter uncertainties in age-length relationship upon estimating the age composition of catches. Can. J. Fish. Aquat. Sci. 40: 272-280.
- Marcille, J. 1978. Dynamique des populations de crevettes penaeides exploitées à Madagascar. Trav. Doc. ORSTOM 92: 197 pp.
- Mathews, C.P. and Al Hossaini, M. 1982. Stock assessment of Kuwait's shrimp populations: growth, mortality and life cycles of *Penaeus semisulcatus*, *Metapenaeus affinis* and *Parapenaeopsis stylifera* and the management of Kuwait's shrimp stock. Paper presented at the 3rd Shrimp and Finfish Fisheries Management Workshop, Kuwait, June 1982.
- Motoh, H. 1981. Studies on the fishery biology of the giant tiger prawn, *Penaeus monodon*, in the Philippines. SEAFDEC Tech. Rep. 7, 1-128.
- Munro, J.L. 1984. Estimation of natural mortality rates for selectivity and catch length frequency data. Fishbyte 2(1): 11-14.
- Munro, J.L. and Pauly, D. 1983. A simple method for comparing the growth of fishes and invertebrates. Fishbyte 1(1): 5-6.
- Parrack, M.L. 1979. Aspects of brown shrimp, Penaeus aztecus, growth in the northern Gulf of Mexico. US Fish. Wildl. Serv. Bull. 76: 827-836.
- Pauly, D. 1980. A new methodology for rapidly acquiring basic information on tropical fish stocks: growth, mortality and stock recruitment relationships. In: S. Saila and P. Roedel (Editors), Stock assessment for tropical small-scale fisheries. Univ. Rhode Island. Int. Center Mar. Res. Dev. 198 pp.
- Pauly, D. 1983. Length converted catch curves: a powerful tool for fisheries research in the tropics. Part I. Fishbyte 1(2): 9-13.
- Pauly, D. 1984a. The population dynamics of shortlived species with emphasis on squids. Paper presented at the NAFO special session on the biology and ecology of squids, *Illex illecebrosus* and *Loligo pelaei* in the North East Atlantic. 5-7

September 1984, Dartmouth, Nova Scotia, Canada, 32pp. (MS).

- Pauly, D. 1984b. Length converted catch curves: a powerful tool for fisheries research in the tropics. Part II. Fishbyte 2(1): 17-19.
- Pauly, D., Ingles, J. and Neal, R. 1984. Application to shrimps stocks of objective methods for the estimation of vital statistics from length data. pp. 220-234. In: J.A. Gulland and B.J. Rothschild (Editors). Penaeid shrimps: their biology and management. Fishing News Books Ltd., Farnham.
- Pauly, D. and Munro, J.L. 1984. Once more on the comparison of growth in fish and invertebrates. Fishbyte 2(1): 21.
- Penn, J.W. 1980. Spawning and fecundity of the western king prawn, *Penaeus latisculcatus* Kishinouye, in Western Australian waters. Aust. J. Mar. Freshw. Res. 31: 21-35.
- Penn, J.W. 1984. The behaviour and catchability of some commercially exploited penaeids and their relationship to stock and recruitment. pp. 173-186.
 In: J.A. Gulland and B.J. Rothschild (Editors).
 Penaeid shrimps: their biology and management.
 Fishing News Books Ltd., Farnham, UK.
- Pereiro, J.A. and Pallares, P. 1984. Consequences of introducing errors in the values of the input parameters in the "length distribution analysis" (R. Jones) as applied to the northern stock of hake. CIEM/CM 1984/G: 61, 7 pp. (mimeo).
- Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish population. Bull. Fish. Res. Bd. Can. 191: 1-382.
- Rothschild, B.J. and Brunenmeister, S. 1984. The dynamics and management of shrimp in the northern Gulf of Mexico. pp. 145-172. In: J.A. Gulland, and B.J. Rothschild, (Editors) Penaeid shrimps: their biology and management. Fishing News Books Ltd., Farnham, UK.

Sainsbury, K.J. 1982. Population dynamics and fishery management of the paua, *Haliothis iris*. Population structure, growth, reproduction and mortality. NZ J. Mar. Freshw. Res. 16: 147-161.

Sissenwine, M.P. 1978. Is MSY an adequate foundation for optimum yield? Fisheries 3(6): 22-24, 37-42.

- Staples, D.J. 1979. Seasonal migration patterns of postlarval and juvenile banana prawns, *Penaeus merguiensis* de Man, in the major rivers of the Gulf of Carpentaria, Australia. Aust. J. Mar. Freshw. Res. 30: 143-157.
- Ursin, E. 1984. The tropical, the temperate and the arctic seas as media for fish production. Dana 3: 43-60.
- Willmann, R. and Garcia, S. 1985 (in press). Bioeconomic model for the analysis of net economic benefits of artisanal and industrial sequential fisheries on tropical shrimps. FAO Tech. Pap.
- Witzell, W.N. and Allen, D.M. 1983. Summary of studies relating coastal climatological factors and commercial shrimp production, southern United States. FAO Fish. Rep. (278), Suppl.: 111-119.
- Yew-Hu, C. and Condrey, R.E. 1985. A modification of the De Lury method for use when natural mortality is not negligible. Fish. Res. 3: 23-28.
- Young, P.C. (Editor), 1975. First Aust. Nat. Prawn Sem. AGPS, Canberra, 345 pp.
- Young, P.C. and Carpenter, S.M. 1977. Recruitment of postlarval penaeid prawns to nursery areas in Moreton Bay, Queensland. Aust. J. Mar. Freshw. Res. 28: 745-773.