_____ Chapter 9____

Tropical penaeid prawns

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INTRODUCTION

Many aspects of the population dynamics and stock assessment of coastal penaeids have been thoroughly reviewed and critically discussed in Garcia and Le Reste (1981) and Garcia (1983, 1984 and 1985).

Although some duplication with these papers is unavoidable in the present review, it is our intention to point out here some of the main characteristics of penaeids as tropical short-lived animals in order to show differences and similarities with the better-known resources of temperate waters. Readers may look at the above-mentioned references for more details.

The aspects of shrimp biology and dynamics singled out in this chapter are those, biological or technological, of relevance to the process of stock assessment and, ultimately, of provision of advice to fishery managers.

GENERAL OUTLINE OF THE LIFE CYCLE

The penaeid prawns, which are a very important component of the estuarine and marine systems in the tropics, can be found from very shallow fringes of tropical estuaries down to about 1000 m depth on the continental slope. The degree to which each stage of the life cycle is linked to the marine or estuarine environment is greatly variable. Some species spend their entire life cycle in the estuaries (e.g. *Metapenaeus mastersii*), others in the strictly marine environment down to 1000 m (*Plesiopenaeus edwardsianus*), but many species use both environments for a variable time (most of the *Penaeus* species).

The present chapter deals essentially with 'coastal' amphibiotic species living both in the estuaries and on the continental shelf down to about 200 m. The females of these species spawn demersal eggs at sea, often after a short shoreward migration. A few littoral species can even spawn in the most saline areas of the estuaries. Hatching occurs within a few hours, starting a long and

complicated development process through a series of nauplii, protozoae, mysis and post-larval planktonic stages, most, or all, of which take place at sea. The post-larvae enter the estuaries through a complex and not yet well-understood mechanism involving vertical migrations, advection and tidal currents, reaction to salinity gradients, etc. (see, for example, Rothlisberg et al., 1985). As a result there are substantial seasonal variations in post-larval abundance and size, related to temperature, salinity and upwelling or rainfall seasonal patterns (Garcia, 1977). The understanding of the larval migration into the nursery area, and the identification of the factors affecting it, are key issues in the stock recruitment question.

The post-larvae reach nurseries at night with the tide flow and become rapidly semi-benthic. The juveniles (with a complete rostral formula) settle in shallow areas rich in detritus, such as seagrass beds, mangrove swamps or floating sargassos, depending on the site and species, until they become subadults with a completely developed petasma and thelycum. Survival during this phase depends heavily on appropriate matching between date of arrival of larvae in the nursery and favourable climatic conditions in the estuary (Ford and St Amant, 1971).

At a size depending on the species but also on the local salinity, the subadult starts its migration to deeper or more saline estuarine areas. In classical estuarine systems, average individual size increases seawards and most prawns migrate out to the sea after reaching a given size (usually around 8–10 cm total length). In anti-estuary systems, size gradients tend to be reversed with bigger sizes observed in upstream hypersaline areas (Lhomme and Garcia, 1984; Garcia and Le Reste, 1981). These gradients fluctuate seasonally and from year to year in relation to environment (Le Reste and Odinetz, in preparation).

The interaction between ontogenetic changes in osmoregulation capabilities of prawns and seasonal climatic factors such as abrupt changes in rainfall, salinity, temperature, or water level and currents, triggers the mass migration towards the sea at a size which varies seasonally and from year to year. Migration occurs at night with the ebb-tide, and Boddeke et al. (1977) have shown that it was linked with moulting. In general migration follows a lunar cycle and is maximal at new moon and full moon.

Adult concentrations and fishing grounds off shore are usually found on soft bottoms with varying proportions of gravel, sand and mud from a few metres depth (Penaeus indicus) to 200 m or more (P. marginatus, P. plebejus). In most cases migrations of adults are not important and are limited to diffusion phenomena within a 100 km range. However, at the northern and southern limits of their world distribution (e.g. P. duorarum in North Carolina, USA and P. esculentus in New South Wales, Australia) long-ranging migrations of many hundreds of kilometres have been observed. In areas where a shallow thermocline exists, as in the Gulf of Guinea, seasonal oscillations of the bathymetric distribution of the species are also observed in relation to movements of the thermocline (cf. Figure
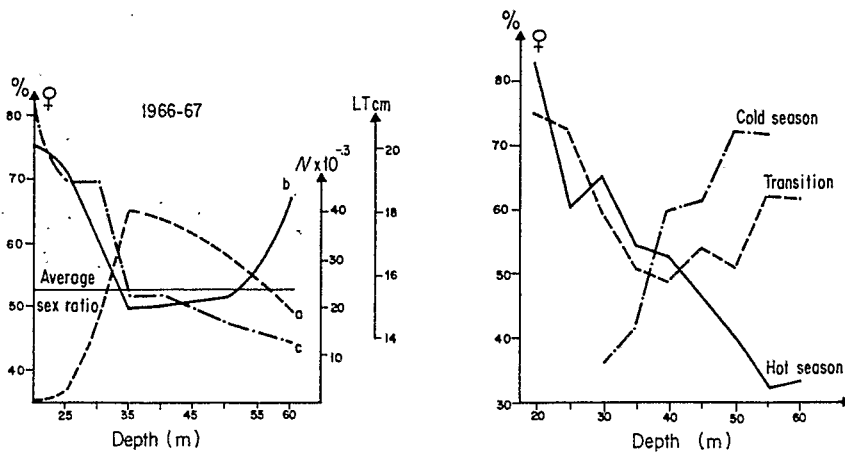
Figure 9.1 (Left) Annual average bathymetric distribution of numbers (a), average size (b), and sex ratio (c), of P. notialis in the Ivory Coast (from Garcia, 1977). The overall average sex ratio is also indicated. (Right) Bathymetric distribution of sex ratio by season for P. notialis, Ivory Coast (from Garcia, 1977). (Reproduced by permission of ORSTOM, Paris)

9.1). Some white prawns like *P. merguiensis* (Dredge, 1985) or *Penaeus setiferus* may even move back in the estuaries.

DESCRIPTION OF FISHERIES

The coastal penaeid prawns discussed in this chapter belong to the Penaeinae family, which consists of 14 genera and 110 species (Holthuis, 1980), but the bulk of the world catch is represented by eight genera (*Artemisia, Metapeneopsis, Metapenaeus, Parapenaeopsis, Parapenaeus, Penaeus, Trachypenaeus* and *Xiphopenaeus*) to which a ninth one, *Sicyonia*, of the Sicyoniidae family, could be added.

Penaeid prawns are found throughout the tropics, where they are one of the most valuable fishery resources, particularly in areas where conditions are favourable (mangroves, lagoons, wide shallow shelf areas, etc.) such as the Gulf of Mexico, some parts of west Africa, and in southeast Asia from the west coast of India to the Gulf of Carpentaria. Annual world catches amount to 700 000 tons (Gulland and Rothschild, 1984), and an additional demand is foreseen in the near future. In developing countries penaeid prawns represent a very valuable commodity for export to Japan, USA, Europe, etc., and a great potential for development both in artisanal and industrial fisheries.

Penaeids are exploited by man at various stages of their life cycle. The post-larvae have been traditionally exploited by artisanal fisheries as wild 'seed' for aquaculture in most of southeast Asia and in the Bay of Bengal area (Funegaard, 1986). In the last 10 years their exploitation has also increased in

Ecuador, and proposals to start exploiting wild 'seed' for aquaculture are being considered in other Latin-American countries, although problems of shortage of seeds have been met, both in the Bay of Bengal and in Ecuador, and fears have been expressed regarding potential damage to artisanal and industrial prawn fisheries potential.

The juveniles can be exploited in very shallow waters with push nets and are usually dried or smoked and often used in a powdered form as condiments.

The migrating subadults are fished with Chinese traps (weirs), stake nets, cast nets, scoop nets, 'baby' trawlers, etc., during their migration. They are a high-value product used locally, dried or smoked, or exported frozen to developed countries, giving a significant source of income to artisanal fishermen.

The artisanal fisheries, both on post-larvae and small prawns, are usually not well controlled because of their remote and dispersed location. In some countries, they are often organized in cooperatives, as in Mexico, where the use of weirs (tapos) is regulated (Edwards, 1978). Small prawns are also exploited for recreational purposes, as in the 'bait shrimp' fishery of the USA.

The adults are exploited at sea either in a mixed trawl fishery for fin-fish and prawns or with specialized industrial 'shrimpers' of 150–400 h.p., using sophisticated technology, i.e. multiple-rig fishing, automatic sorting by sizes on board, blast freezing, etc. In coastal areas prawns can be exploited both by industrial and artisanal fisheries using small trawlers or drifting trammel nets.

The interactions between these fisheries, operating sequentially at various stages of the life cycle, is potentially important. Fishing at one stage reduces recruitment to the next fishery, and ultimately may affect spawning potential to the extent that recruitment to the post-larval and, above all, to the subadult and marine stock could be negatively affected.

Managing for an appropriate balance between these competing modes of exploitation involves major trade-offs which need careful evaluation. This must take account of economic and social aspects, which differ between fisheries. Each type of fishery has different cost–benefit parameters, and involves greatly differing amounts of manpower or investment in local or foreign currency, and different patterns of distribution of benefits to various strata of the human population.

The complexity of the life cycle and of the various sequential fisheries means that fishing mortalities on different age/size groups differ considerably and that there may not be a simple relation between the amount of fishing (in simple terms) and the fishing mortality, especially in lagoons and estuaries.

By using small try-nets before and during fishing operations, industrial trawlers can aim their activities on the places of highest abundance (and value). Because of the different distribution of different ages, the distribution of fishing mortality by-ages, i.e. the fishing mortality vector, is similar to the distribution of abundance or value at age (Garcia, 1977, 1985; Sluczanowski, 1984). Tagging experiments had shown that size-specific recapture rates were proportional to

abundance (Garcia, 1973). As fishing intensity increases and population struc-
ture changes, the fishing mortality vector will also change, invalidating one of the
most important assumptions of production modelling (see section on modelling,
below). The interpretation of historical data on industrial prawn fisheries meets
with various other problems related to progressive changes in, *inter alia*:

    – the total number of hours of trawling per day, from 8–10 hours of fishing
during the day at the beginning of a fishery, to 16–20 hours of fishing during day
and night in well-developed fisheries. Because of the existence of important
circadian cycles in catchability, these changes affect the relationship between
average abundance and average CPUE and consequently between effort and
mortality;

    – target species (for instance, from coastal fishing on white prawns when
fishing only during the day in the early days of a fishery to shelf-wide fishing of a
mixture of white, brown and tiger prawns when fishing all day round in a mature
fishery);

    – species behaviour: from highly schooling to non-schooling behaviour when
abundance decreases (e.g., banana prawns). This affects catchability.

These problems are discussed in Marcille (1978) and reviewed in Garcia and
Le Reste (1981), while Penn (1984) has particularly elaborated on the issue of
schooling and catchability.

Another important aspect of prawn fisheries is their multispecific nature. Even
when targetting solely on prawn, some 75–90% of the catch may be fin-fish,
much of which is discarded. In fisheries off developed countries, e.g. in the Gulf
of Mexico, where little market is available for 'trash' fish species, or on board
sophisticated freezer trawlers with limited storage capacity and high processing
costs, most of the fish by-catch is discarded. Discussions on the extent of fish
discarding practices in prawn fishing around the world (1 400 000 tons per year)
and on their potential positive or negative effects on prawn production can be
found in FAO/IDRC (1982) and Gulland and Rothschild (1984).

POPULATION CHARACTERISTICS

One of the most striking characteristics of prawn populations which differs most
from those of temperate stocks is their seasonality. Because of their short
lifespan, the abundance, mean size and other parameters of prawn stocks vary
greatly from season to season, and studies on dynamics of prawn populations
must refer to time intervals of less than a year, and monthly (sometimes weekly)
intervals are usually used. Although lunar cycles in moulting, reproduction,
migration, etc. can usually be disregarded, seasonality of key phenomena, such
as spawning, recruitment, population age structure, catchability, etc., cannot be
neglected and masked by conveniently averaging within annual intervals.
Because of the existence of one main generation developing in time and moving
in space, seasonal patterns in reproduction generate seasonal patterns in

population spatial characteristics. These patterns are significantly modified by fishing and the potential consequences on the overall stock conservation or fisheries economy and management are important, as will be shown later.

Growth is very often seasonal in areas when the winter temperature decreases below 16°C, and prawn born in different months have different growth curves. Pauly (1984) proposed a seasonally oscillating von Bertalanffy model which, by adding a season factor, c, to a single K and L_∞, could be used to give a unified description of growth of all cohorts in an area.

Fishing mortality is also usually seasonal. The seasonality increases rapidly as fishing effort increases, because catch rates and profitability decrease below the break-even point earlier and earlier in the season, and fishing concentrates on the few best months, soon after peak recruitment. Natural mortality is also likely to vary seasonally and with size because of the seasonal changes in the feeding habits and the size preferences of the populations of predators, but no information is available on this aspect at present and natural mortality is always considered constant.

Under these circumstances, the traditional concept of equilibrium is difficult to comprehend for a prawn stock as there is no equilibrium (and, for example, no stationary length distribution) at the seasonal level. A stock is made of many different cohorts with different birth dates, their own seasonal growth pattern, fishing pattern and possibly even natural mortality pattern. Although total annual fishing effort is a convenient measure of fishing pressure to use on production models, its relationship to overall fishing mortality will never be straightforward and will depend *inter alia* on its seasonal distribution. Most stock parameters will vary both with age and time (season) and the databases do not generally contain enough information to discriminate between these two effects.

The review by Garcia and Le Reste (1981) contains a compendium of methods used to estimate population parameters, illustrated by examples of application to prawns. A more recent review (Garcia, 1985) touches again on some particular methodological problems. The following sections on growth, mortality and recruitment will therefore briefly summarize the main traits of prawn populations.

Growth

Penaeid prawns have a discontinuous growth pattern at individual levels, but the apparent lack of synchronism of moulting at the population level and the relatively high number of moults per year lead to the consideration that continuous growth models of the von Bertalanffy type are appropriate (Parrack, 1979; Frechette and Parsons, 1983). Growth is very fast and the maximum size, which varies from 15–16 cm total length in some smaller penaeid species (*Metapenaeus* spp., *Xiphopenaeus* spp.) to 30 cm in the giant tiger prawn, *Penaeus monodon*, is reached in about 2 years.
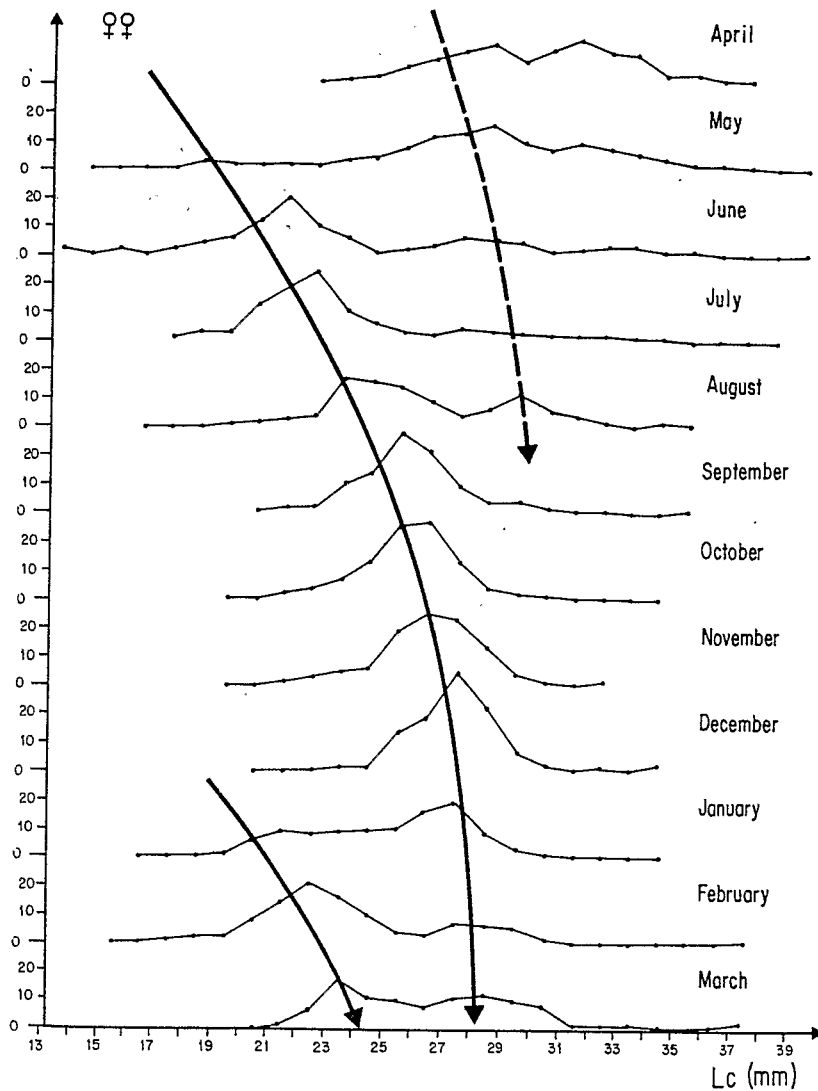
Figure 9.2 P. longirostris. Monthly size distribution of females (carapace
length in 1 mm classes) in 1981–2 (from Arrobas and Ribeiro-
Cascalho, 1982). Modal filiation added. (Reproduced by permis-
sion of FAO)

Growth parameters have been estimated usually by tagging or by modal
progression analysis on length frequency data. The results of this latter method
are fairly reliable if one or two main recruitments occur every year (Figure 9.2).
However, the analysis is often complicated by a continous fairly uniform
recruitment and by the fact that commercial catches are taken in places of higher

density and their size composition varies from trip to trip, requiring intensive sampling. For all these reasons, a significant number of analyses on growth of prawns involve a fair amount of subjectivity and sometimes lead to unconvincing results.

The use of the automatic processing method ELEFAN has been advocated by Pauly et al. (1984) to reduce subjectivity and it offers the possibility of calculating the seasonal growth parameters, but the statistical limitations of this method when the data are subject to error (Majkowski and Hampton, 1983) require a very critical examination of results, especially when sampling has been poor and when the recruitment pattern is not highly seasonal. The recent version of this method (Brey and Pauly, 1986) is, however, useful as it offers the possibility of obtaining a range of possible estimates of growth parameters which can be narrowed by using additional ancillary information. Tagging has given reliable results despite the obvious problem created by the potential interference of the tag with moulting (see Garcia and Le Reste, 1981, for a review).

Mortality

The mortality values presently available refer essentially, if not exclusively, to the genus *Penaeus* and could possibly be different for smaller species. The scientific literature of the last decade points towards an average natural mortality rate for penaeids of the order of 2.4 ± 0.3 per year for adults (Garcia, 1985). These values have been obtained by estimates of total mortality of lightly fished stocks, by tagging and by relating total mortality estimates to fishing effort. In a recent work, not available when the above estimates were made, Sluczanowski (1984) found that the estimate of natural mortality (M) for *P. latisulcatus* was $M = 1.6$ per year (range from 0.6 to 2.5 per year), using a modified version of the cohort analysis and Monte Carlo simulations.

Although these values are only approximate and may be affected by long-term or seasonal changes, due to predation for instance, they clearly indicate that the very high estimates (of sometimes more than 25 per year) referred to in the early 1960s literature are to be definitively discarded. Although the fishable lifespan is about 1 year, the maximum longevity of penaeid prawns of the genus *Penaeus* is about 2–3 years.

Reliable natural mortality estimates for juveniles in estuaries are scarce. If it is assumed that M increases as size and age decreases, juveniles should die at a faster rate than adults. However, Doi (1981) found $M = 0.18$ per month (or 2.2 per year) for *P. japonicus*, a value close to the one given above for adults.

Fishing mortality in fairly well-developed fisheries (where catch and effort have been stable for a long time after an initial period of rapid increase) has been found to be around 1.6 ± 0.3 per year (Garcia, 1985). This average value, considered close to the traditional FMSY, refers to fisheries where effort has sufficiently

increased to have caused substantial decrease in catch per unit effort (CPUE), but where overall abundance is still high enough to allow for some fishing all year round. In the Gulf of Carpentaria (Australia) fishing on white banana prawn, *P. merguiensis*, has reached such a level that the fishing season lasts only a few weeks. There, fishing mortality has been estimated as 0.9–1.4 per month—equivalent, if sustained, to 10.8–16.8 per year (Lucas *et al.*, 1979). Therefore, values of fishing mortality (*F*) largely in excess of *M* are possible in fisheries where total catch has remained constant despite very substantial increases in fishing effort, and where fishing is heavily concentrated on recruitment early in the biological year. Some reasons for this apparent stability of the catch and discrepancy within the production models theory will be given later.

Fishing mortality is not constant with age. It varies during the exploited estuarine phase of the life cycle and usually increases abruptly during the migration to sea because of intensive artisanal fishing.

In the sea, industrial fishing concentrates on the areas where highest returns per hour of trawling are obtained. Therefore, as fishing pressure increases fishing concentrates more and more on small sizes and during the recruitment period. Fleets of different nationalities fishing for different markets may have different cost–benefit structures and may concentrate on different age classes. In the Guyana–Brazil prawn fishery, for instance, the US and local fleets fishing for the US market concentrate on small and average sizes of brown prawn, while the Japanese fleet concentrates on large sizes of pink spotted prawn.

Recruitment

Because of the sequential nature of prawn fisheries, there are many phases of recruitment, tentatively indicated by R_1 to R_4 in Figure 9.3. These phases correspond respectively to:
- the arrival of post-larvae at the entrance of estuaries and their first settling on shallow areas when they are exploited as wild seed for aquaculture;
- their reaching a first commercial size in shallow areas where they are exploited by push nets, beach seines, etc.;
- their massive departure from estuaries towards the sea at migration, when they are exploited with weirs, stake nets, channel nets, etc.;
- their progressive recruitment into the trawl fishery at sea. The last phase is the combined result of the arrival of the subadults on the fishing grounds out of the often protected coastal sanctuaries, the sudden seasonal concentration of fishing boats in shallow water on the new incoming generation and the mesh size selection. This latter process is not very efficient. The selection range of the usual 40–50 mm (stretched) mesh covers a large part of the lifespan of the animal but the filtration effect can be altered easily by the fishermen, and in practice few prawns of marketable size may be released by the nets in commercial use. Garcia (1985) has pointed out that the age at first capture of each cohort, and in fact the
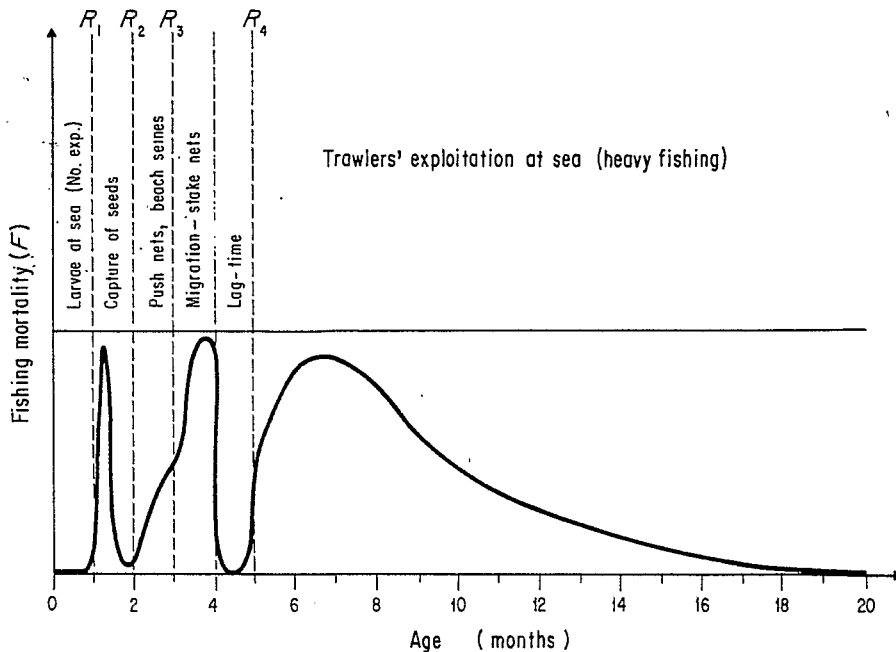
Figure 9.3 Sketch of the variations of fishing mortality in the sequential exploitation of post-larvae, sub-adults and adults. Relative height of peaks is arbitrary and depends on relative intensity of the various exploitation sectors. (Reproduced by permission of A. Ribeiro Coscalho)

whole fishing pattern of such cohorts, depends at least as much on the seasonal changes of the depths fished by the fleet as on the mesh size used. Regulation of the age at first capture by closing coastal zones permanently (where recruitment occurs throughout the year) or for a month or two (where recruitment is seasonal) is therefore more effective than controlling mesh size.

The typical pattern of recruitment as measured, for example, by the abundance of small sizes entering the catch is of one main peak around late summer and autumn corresponding to the main generation spawned the preceding spring, and a secondary and inconsistent peak in spring corresponding to recruitment of prawns born in autumn and having often overwintered in estuaries or in coastal waters. In some cases the autumn recruitment peak is the main one.

REPRODUCTIVE STRATEGY AND GENERATION TIME

Tropical prawns are highly fecund organisms and may lay 50 000 to 1 300 000 eggs depending on size and species. Spawning activity is linked to moulting and prawns may spawn once in each intermoult period during the spawning season, in relation to the lunar cycle. At 27°C, the basic moult frequency of adults is
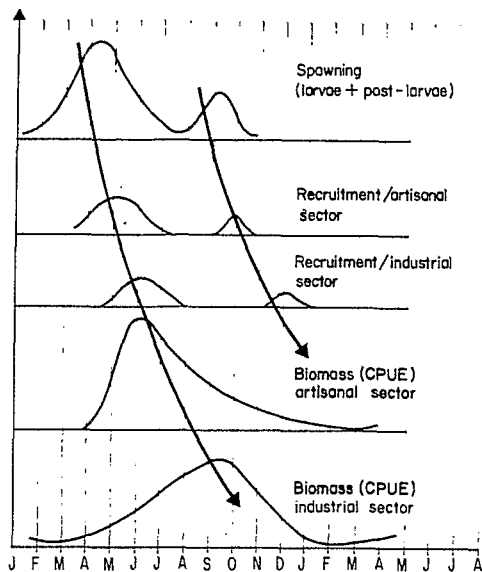
Figure 9.4 **Seasonal cycles of population characteristics and filiation (simplified from Figure 22 in FAO, 1982 — Penaeus semisculcatus in Kuwait). Reproduced by permission of the Food and Agriculture Organization of the United Nations)**

27–30 days, as shown in the excellent work of Crocos and Kerr (1983). It is, however, difficult to find any synchrony in the process among individuals (Crocos, 1985). Garcia (1977, 1985) discussed the relationship between environmental factors and reproduction at the population level for *P. notialis* in the Ivory Coast and concluded that the long-term (evolutionary) adaptation of the animal to the seasonal pattern of environmental conditions seemed to have led to the tuning of the population reproductive pattern to the environmental cycle. The combination of growth, mortality, recruitment and maturation seasonal processes generated an oscillating spawning potential of the population, with maximum reproductive output coinciding with rising temperatures (the hydroclimatic spring) and favourable conditions for larval survival. Similar adaptive mechanisms are advocated by Murphy (1977), Johannes (1978) and Jones (1982), who state that 'the life history involves a succession of choices which culminate in the optimum life history strategy which maximizes the reproduction output of viable reproductive material'. The good relationship between environment and reproduction at seasonal level is often wrongly interpreted solely as a direct cause–effect relationship in the short term. Preston (1985) assumes that
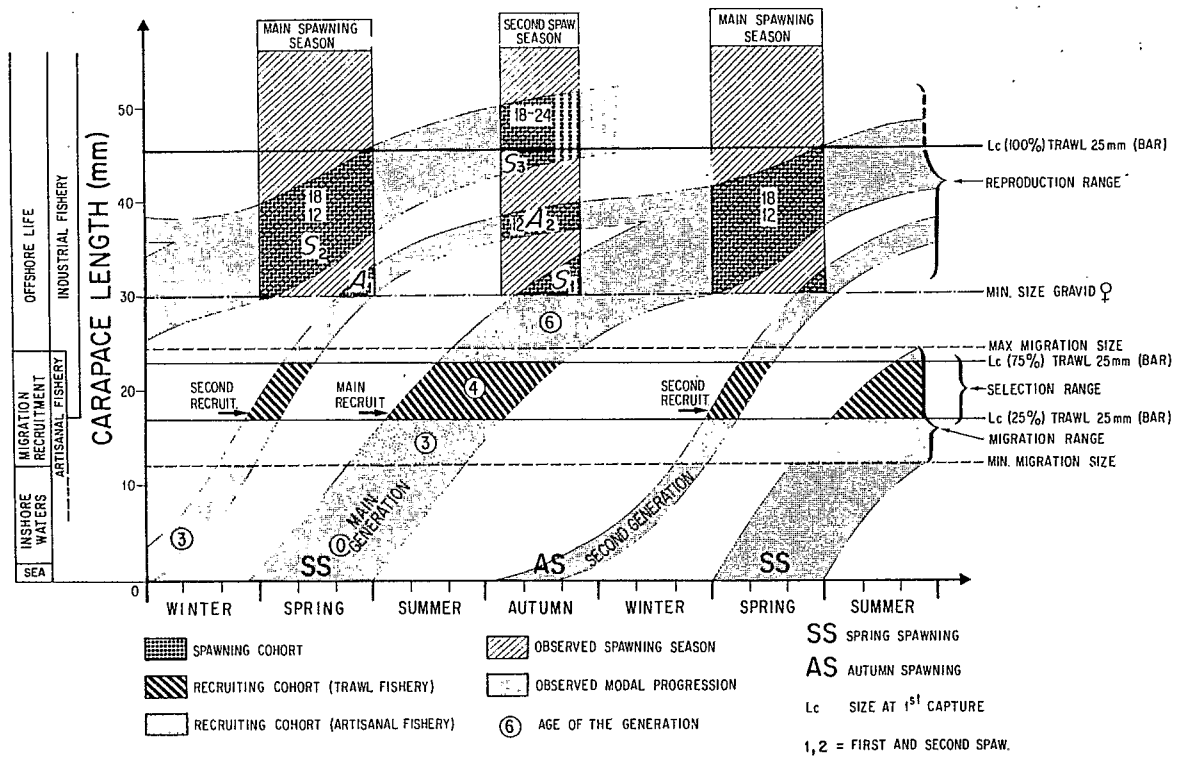
Figure 9.5   Theoretical model of the essential features of the life cycle and fishery of Penaeus. (From Garcia, 1985) (Reproduced by permission of NPS2, Cleveland)

tolerance limits and survival of larvae to hydrological conditions after hatching are, however, also determined more actively by acclimatization of the eggs to the conditions which prevail during the development of gonads. A recent review of the problem of seasonal environmental tuning of the reproduction can be found in Grahamme and Branch (1985).

Since the beginning of the 1980s more systematic attention has rightly been given to the understanding of the reproductive strategy of prawns at the population level (Dredge, 1985; Rothlisberg et al., 1985; Garcia, 1983, 1985). Although some problems of understanding still remain, a useful level of generalization has been reached.

Combining enough information on seasonal cycles of egg production indices (calculated from CPUE data for adults, size frequency distribution, proportion of mature females and fecundity), larval and post-larval abundance, juveniles and emigrant subadult abundance, and recruitment, it is often possible to make inference about the timing of the life cycle and on the generation time of the species (Figures 9.4 and 9.5). Because the spawning activity is continuous, the characteristic generation time of a species can be defined as the time between the average date of birth of the main generation and the average date of birth of the main group of offspring from this generation. The seasonal reproductive patterns are usually bimodal, with a main and stable generation of spring spawners, born in spring and reaching a first minor reproduction in autumn at the age of about 6–7 months and a massive reproduction at about 1 year in spring. The secondary irregular generation of autumn spawners, born in autumn, reaches a first minor spawning in spring and has its main reproductive output in the following autumn (Garcia, 1985), i.e. the generation time is about 1 year. One can assume that even in the cases where, because of particular local conditions in summer, the main generation is in autumn, the generation time is still 1 year.

The synchrony between the reproductive and the seasonal environmental cycles has obvious advantages for a short-lived animal.

When a prawn stock is heavily exploited, as in the Gulf of Carpentaria, where 85% of the population is scooped out by fishing in the 2 months following recruitment (Lucas et al., 1979), the rapid depletion of the stock modifies the natural seasonal patterns of abundance and fecundity, leading to a 'maximum' reproductive output of the main spring generation in autumn. This has been interpreted as a basic generation time of 6 months (Dredge, 1985; Rothlisberg et al., 1985) but should most likely be considered as a severe distortion of the basic cycle by fishing (see also next section).

The theoretical inconvenience of a cycle with such an alternation between spring and autumn generations is discussed by Garcia (1985), who stresses the fact that because the autumn larval peak and the following recruitment are, in most cases, very irregular in strength and sometimes non-existent for many successive years, a natural 6-month generation time strategy would be a very risky one as the most inconsistent generation is supposed to ensure the perpetuity of the stock.

It is interesting to note that Munro (1975), studying the same species in the same area when the stock was unexploited, did find two age groups, a main spawning season in early summer, and came to the conclusion that a 1-year generation cycle existed. It is also interesting to note that under the alternating generation assumption of Rothlisberg et al. the present 'maximum' spawning potential corresponds to unfavourable conditions and maximum offshore transport of larvae. On the contrary, the 1-year generation time would lead to maximum spawning in the season of maximum inshore transport, in line with the optimization theory illustrated by Johannes (1978), Garcia (1977) and Grahamme and Branch (1985).

The issue is certainly not entirely settled and in any case deviations from the natural scheme are to be expected with latitude and local conditions, but it would seem unlikely a priori that generation times very different from 1 year can be found in seasonal environments. Buckworth (1985), working on *P. esculentus* and *P. semisculcatus* in the Gulf of Carpentaria, shows that these two species, which are less intensively exploited than *P. merguiensis*, spawn in spring and have a maximum CPUE in the next spring. He stresses that increased fishing would reduce population fecundity at the 'critical moment' for synchronization with the period when conditions lead to highest recruitment success. The work of Arrobas and Ribeiro-Cascalho (1982) on *Parapenaeus longirostris* off Portugal is interesting in this respect because the data show that this 'cold water' penaeid, available in coastal waters in temperate areas as well as in deep waters in tropical areas, also has a 1-year generation time. The issue is worth a sustained research effort because of its bearing on the stock–recruitment relationship. (Similar problems are identified on a longer time-frame and similar conclusions are reached for longer-lived crustacea affected by interannual (instead of seasonal) variations in year class strength (Caddy, 1986).)

THE STOCK AND RECRUITMENT RELATIONSHIP

Because of their short lifespan and the 'single year class' nature of the prawn fisheries, alternative recruitment indexes are easily obtained by dividing annual yield by calculated yield per recruit, average annual CPUE (for periods when effort has been constant), and CPUE at the beginning of the fishing season when recruitment period is short. Spawning stock size indexes could be obtained by annual average CPUE, average CPUE during the spawning season, and population fecundity index (Morgan and Garcia, 1982). These indexes are given in increasing order of reliability.

The importance of the relation between the abundance of the adult stock and the average strength of the subsequent recruitment is as great in prawns as in other stocks, and those studying prawns have the same problems of disentangling the effects of adult abundance from the high variation due to environment. Much of the discussion about prawns has concerned the existence or otherwise

of a stock–recruitment relation (SRR), i.e. whether or not average recruitment (R) is affected by changes in adult stock size (S) due to fishing.

The natural interannual variability of prawns in relation to rainfall, temperature, etc., is well known and the mechanisms have been documented. Ford and St Amant (1971), for example, showed that recruitment success depended more on the date of arrival of post-larval cohorts on the nursery grounds and the environmental conditions upon arrival than on initial larval abundance. Boddeke and Becker (1979) showed that pre-recruit mortality of *Crangon crangon* varied seasonally in lagoons. Long-term effects have also been documented regarding the effect of land reclamation, mangrove cutting, pollution, etc. on prawn yields. A review of the information available is given in Garcia and Le Reste (1981).

The effect of stock size on recruitment has received much attention only since the beginning of this decade and examples can be found, e.g. in Gulland and Rothschild (1984). It is, however, likely that most of the examples of the existence of SRRs in prawns are artefacts and misinterpretations stemming from the combination of autocorrelated environmental changes and short lifespan of prawns.

Considering the SRRs established at yearly level (one data point on stock and recruitment per year), and because of the well-known environmental interannual variability of prawn stocks and observed trends in their recruitment, the SRR could be represented by a family of S–R curves, arbitrarily represented by ramp functions in Figure 9.6 (following Garcia, 1984), corresponding to the various annual environmental conditions. An example of such relationships is given by Penn and Caputi (1986). As R_n determines S_n, if environmental conditions in year n and $n+1$ are highly correlated, this will also be the case for R_n and R_{n+1} and for S_n and S_{n+1}. As a consequence relating S_n to R_{n+1} may generate artefactual relationships, which appear quasi-linear in relatively stable fisheries, and the R–S relationship detected is confounded with the SRR. Garcia (1983) also mentioned artefacts created by the use of inappropriate stock and recruitment indexes, or lag-times, as well as by undetected changes in the artisanal fisheries, or in the nursery environment (land reclamation, pollution, etc.).

Because of the existence of continuous, albeit seasonal, recruitment in prawn populations, stock and recruitment data with seasonal or monthly resolution has been used to increase the number of points available. In cases where the SRR is established for a single monthly cohort across many years (say between the abundance of the January spawners and their recruits 3 months later across one or two decades) the situation is similar to the one described above. If effort varies seasonally—a very likely assumption—different artefactual SRRs are found for different cohorts or generations exploited at different rates (Figure 9.7). When both effort and environment vary from year to year, a multivariate analysis would be necessary to discriminate between environmental and fishing effects (see, for example, Csirke, 1980; Jones et al., 1982).
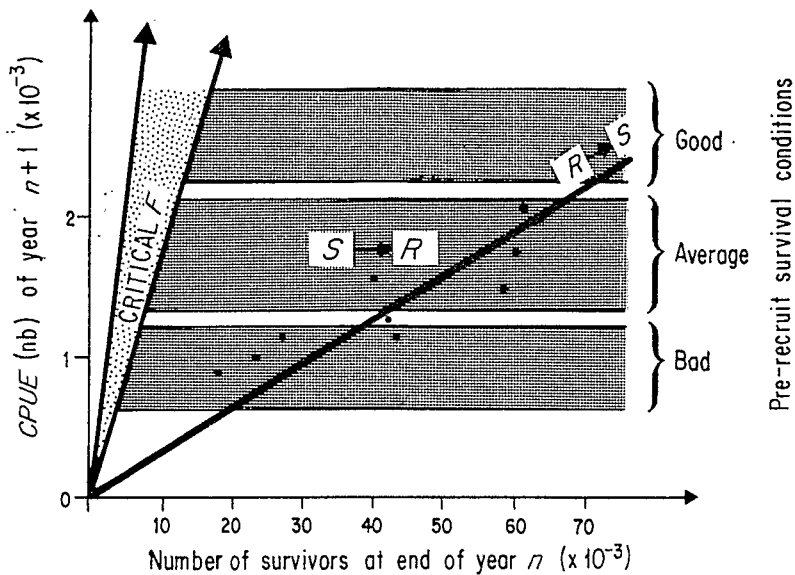
Figure 9.6   Interpretation of the apparent annual SRR for P. aztecus (modified
from Garcia, 1983; data from Brunenmeister, 1981). Recruitment
success is assumed to have changed over the years whilst fishing
mortality remained constant. The apparent SRR (thick line) is in
fact the RSR or replacement line. The data points correspond to
different years. (Reproduced by permission of ORSTOM, Paris)

In cases where time series are short, attempts have been made to combine
seasonal stock and recruitment data from the various cohorts spawned within a
year on a single SRR plot (see, for example, Boddeke, 1982). However, because
of the existence of seasonal variations in pre-recruit survival, artefactual SRRs are
generated (Garcia, 1983). In the preceding section it has been stressed that the
adaptation of the population spawning potential to its seasonally oscillating
environment could be seriously disturbed by fishing. In the virgin stock (Figure
9.8a) the theoretical SRR for the typical Penaeus reproductive strategy described
in the previous section is shown. The spring generation is bigger and less
variable, both in terms of spawning stock size and recruitment, than the autumn
generation. When fishing develops evenly on both generations, the two spawn-
ing stocks are reduced proportionately. When fishing depletes the spring cohort
selectively, the relative size of the spring and autumn spawning cohorts can be
reversed (Figure 9.8b). This latter diagram could describe the evolution of the
banana prawn stock in the Gulf of Carpentaria (Australia), where no stock
recruitment has so far been found (Staples, 1985), in spite of heavy fishing and
where the spring spawners have been selectively decimated and are now much
less abundant than the autumn spawners (see discussion in the previous section).
If, in spite of an extremely severe reduction of the abundance of the spring
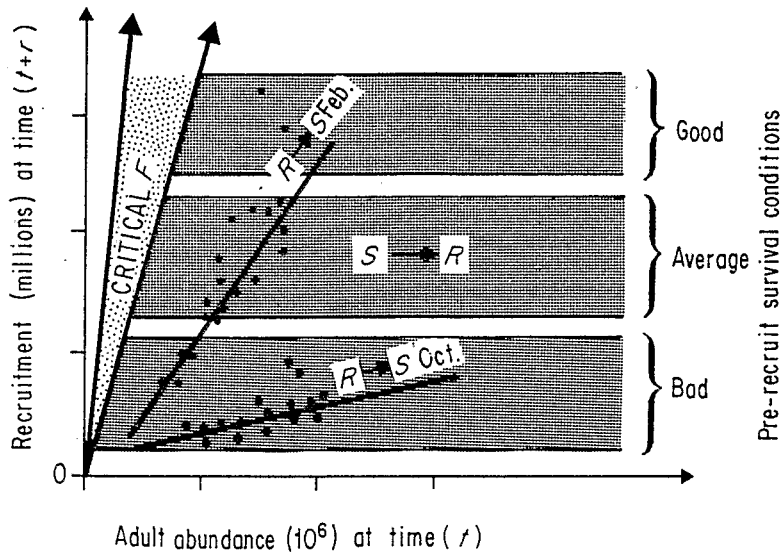
Figure 9.7 Interpretation of the apparent seasonal SRRs for P. aztecus (modified from Garcia, 1983; data from Parrack, 1981). Recruitment success is assumed to have changed over the years. Fishing mortality is higher on the February cohort than on the October cohort. (Reproduced by permission of ORSTOM, Paris)

spawners below the level of the autumn spawners by selective fishing, there has been no change in the respective importance of the spring and autumn recruitments, it is an argument in favour of a weak SRR (if any) within fairly high levels of mortality in accordance with the findings of Staples (1985). It would imply that, at seasonal level, and within a fairly wide range of fishing efforts, the carrying capacity of the environment and the cohorts' specific rate of survival to recruitment are more determinant than the spawning stock size. As a matter of fact, Rothlisberg et al. (1985) have shown that inshore advection at sea and rate of settlement of larvae in the lagoons are both maximum in spring, in line with the finality of the adaptation of the spawning cycle to the environmental cycle discussed earlier.

The identification of serious sources of artefactual SRRs in short-lived animals like prawns does not imply that there are no SRRs and that effort can be increased indefinitely. It does imply, however, that only long data series of stock, recruitment and relevant environmental parameters containing strong contrasts in environmental conditions and effort levels may allow proper discrimination between the respective effects of environment and fishing through multivariate analysis (see Staples, 1985, and the good example given by Penn and Caputi, 1985, and reproduced in Figure 9.9). In addition, the identification of serious disturbance of the seasonal reproductive strategy by intense and selective fishing
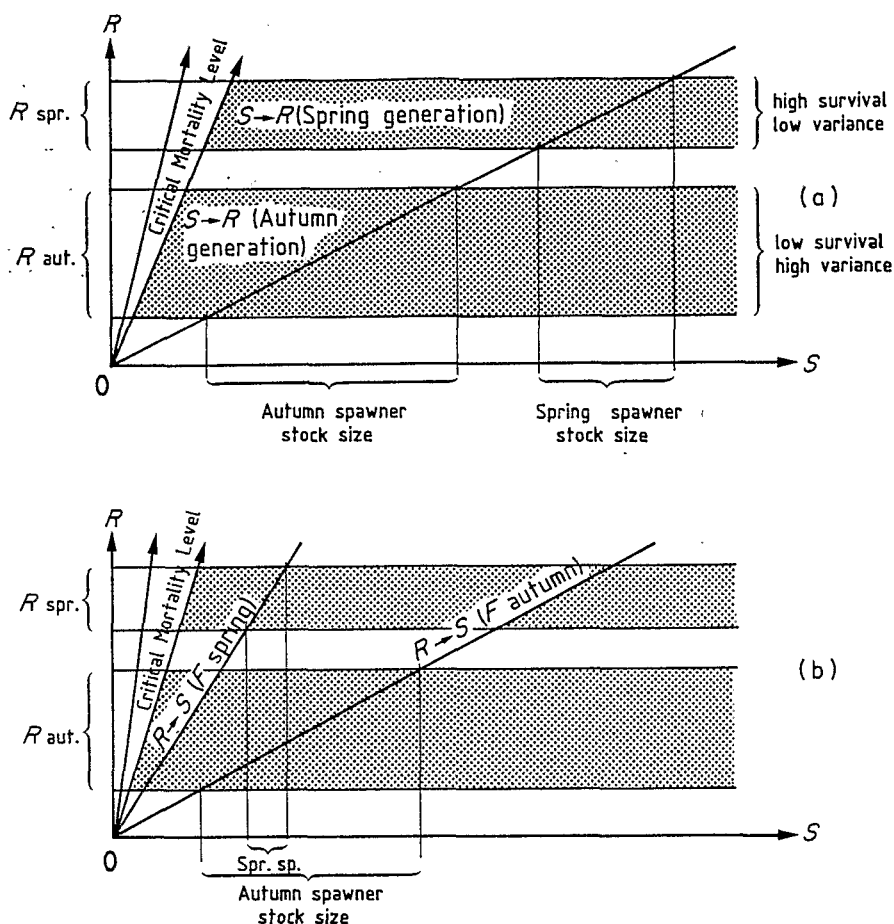
Figure 9.8   Theoretical illustration of the effect of fishing on stock and recruitment for the spring and autumn generations (see text): (a) same fishing pressure on both generations; (b) stock intensively fished with higher levels of effort (*F* spring) directed at the spring generation

should lead to caution when assuming no SRR in prawns because of their fecundity. If the main and successful cohorts are selectively depleted beyond the critical mortality level (see Figure 9.8), a reduction in the overall pre-recruit survival rate will occur and a strong 'SRR' may materialize, although its underlying mechanism may be somewhat different from the traditional concept.

MODELLING, RESOURCE EVALUATION AND MANAGEMENT

Three types of models—surplus yield, analytical and simulation models—are used for analysis of the dynamics of prawn fisheries, in biological or economic terms.
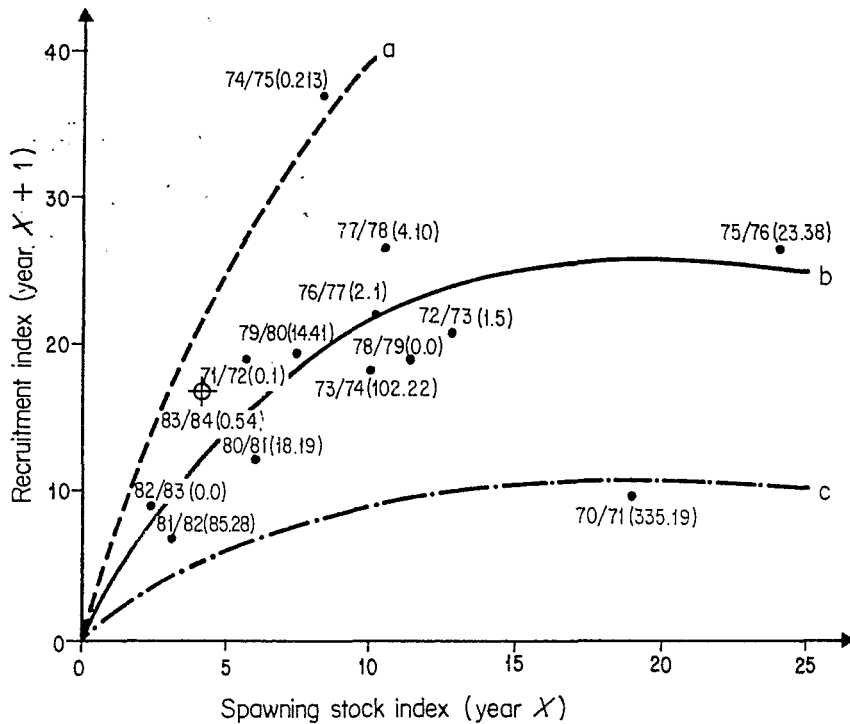
Figure 9.9 The relationship between spawning stock, recruitment and environ-
ment for the Exmouth Gulf stock of the tiger prawn, Penaeus
esculentus. Preliminary data for 1983–4 are shown (Penn and Caputi,
1985) (Courtesy 2nd Australian National Prawn Seminar, NPS2). (a)
Cyclones in February; (b) no cyclones; (c) cyclones in January. (Repro-
duced by permission of NPS2, Cleveland)

The surplus yield (production) models

These are still the most widely used in the first stages of the development of a
prawn fishery, despite their obvious limitations. Garcia and Le Reste (1981)
presented a review of the problems and assumptions concerning the determin-
ism of the model, the equilibrium conditions (also questioned by Kirkwood,
1984), the lack of consideration of the age structure, the 'constant' catchability,
the environmental noise (see also Garcia, 1984), etc.

It has often been stated that despite the lack of relationship between biomass in
year t and biomass in year $t+1$, production models might be more appropriate
for prawns because the short lifespan means that the approximately equilibrium
conditions are reached within a year. This condition can be met even better if
biological years, starting with the main recruitment, are used instead of calendar
years for compilation of catch and effort statistics. However, serious problems
arise when we consider a time-scale more relevant to prawns and to their fishery
such as the week or the month. At this scale, the stock is in constant disequilib-

rium, as its biomass, age structure, reproduction potential, etc., change sea-
sonally. Fishing effort usually also changes seasonally, generating a fishing
mortality that varies with age (cf. earlier sections on description of fisheries, and
mortality) and mortality is concentrated on the more profitable age classes/
months of the year (Garcia, 1977; Sluczanowski, 1984). If the seasonal patterns
were constant, the concept of 'equilibrium' could be replaced by 'dynamic
equilibrium' and surplus yield models could be used. Unfortunately, when
fishing effort increases, the overall abundance decreases, the profitable fishing
season shortens and the seasonal fishing pattern is modified, leading to progres-
sive changes in average age at first capture and fishing mortality at age, even if
there are no changes in mesh size because of the progressive concentration of
fishing in shallow waters and during recruitment. The result is a progressive
change in the yield per recruit function with time, which invalidates the use of a
single production model to describe the whole historical trajectory of a fishery.
(Garcia, 1986). When monitoring a fishery, the observation that the fishing
season is shortening can be considered as a threshold beyond which production
models become inapplicable, and other models must be applied.

The need to take into account the environmentally induced changes in stock
size (or carrying capacity) was stressed by Garcia and Le Reste (1981) and
developed by Garcia (1984). The trajectory of a developing fishery across a
catch–effort–environment three-dimensional space will be wrongly taken as a
traditional production curve on the catch–effort plane, while in fact basic
properties of the model will have been lost. In particular, if few data points are
available and environmental changes are autocorrelated, the apparent MSY may
be grossly in error and the curve may not predict correctly the catches obtainable
with substantial changes of effort.

The analysis of the residuals of the CPUE–effort relationships and their relation
with environment is a first and rough approach to the problem (Garcia and Van
Zalinge, 1982; Lhomme and Garcia, 1984), but the use of multivariate produc-
tion models, including an environmental variable, is a better answer. An
example of statistical fit between catch–effort and environment can be found for
prawns in Griffin et al. (1976). Proper multivariate production models have never
been used in prawn fisheries, but Freon (1985, 1986) gives good examples of
applications of multivariate production models to small pelagic fisheries in
Africa.

The management uncertainty generated by the non-stationarity of production
models in relation to environmental or fishing effects is discussed by Walters
(1986). He affirms that changes in the parameters of production models can
never be completely monitored, controlled or explained and proposes to
describe the variations statistically and look at their implications in terms of
management under uncertainty, a point of view developed also by Waugh
(1984) for the Exmouth Gulf prawn fishery in Australia.

Despite their shortcomings, and because of their small data requirements and
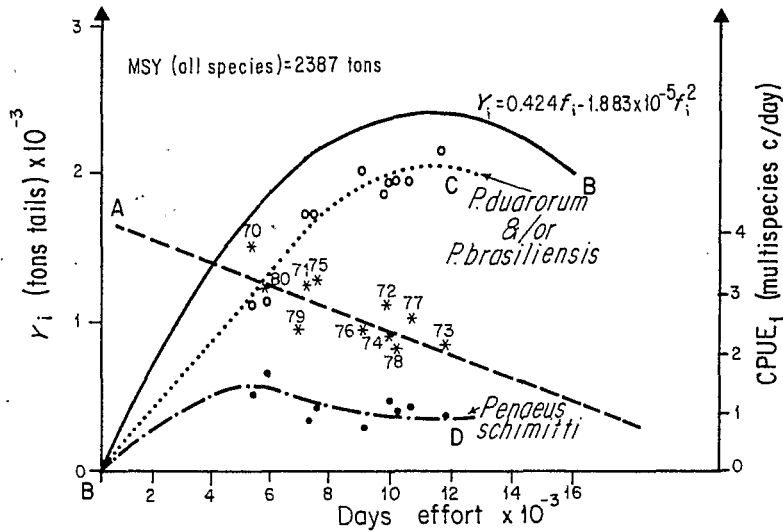
$$Y_i = 0.424 f_i - 1.883 \times 10^{-5} f_i^2$$

Figure 9.10 Multispecies production models (lines (a) and (b)) for Nicaraguan Atlantic (from Caddy, 1985). (Reproduced by permission of the Food and Agriculture Organization of the United Nations)

mathematical simplicity, catch–effort relationships have been, are and will continue to be used for some time on prawn fisheries, even if they are no more than empirical descriptions of the catch–effort trajectories of a fishery. For instance, if effort has undergone various increases and decreases, the identification of 'hooks and loops' (Walters, 1986) will point towards the existence of non-stationarity in the system. Also, if catch is composed of a mixture of species, the decomposition of the overall production curve into its various components may illustrate successive 'overfishing' of the various species (Figure 9.10), although because of the likely changes in the proportion of effort allocated to each species, such sub-models should be taken with a pinch of salt.

Clark (1985) referring to the Gulf of Carpentaria prawn fishery indicated that 'although the Schaefer model may be biologically unrealistic (for prawns) its cautious use as a basis for general economic analysis seems justified, because its principles are in fact quite robust'.

The yield per recruit models

These have the advantage of explicitly dealing with age structure and age- or size-specific changes in economic or biological parameters like value, fecundity, fishing mortality, etc. As prawns are essentially single year class stocks when they are fished, age and seasonal patterns are confounded when there is a short main recruitment season. For example, seasonal variations in fishing mortality can be

taken into consideration by using an age-specific fishing mortality vector and vice versa. Yield per recruit models have, however, also limitations linked to the usual assumptions of constancy of parameters (stationarity of the model), determinism and equilibrium conditions. This latter condition is needed in order to accept the assumption of ergodicity between time and age which allows one to assume that the production of a cohort during its lifespan is equal to the production of all cohorts present in the stock in one year. When the fishery exploits one main generation and the fishable lifespan is one year, the assumption is particularly well met. The simplest yield per recruit models from Beverton and Holt (1957), Ricker (1975), or Thompson and Bell (in Ricker, 1975) require the definition of average parameters (for growth, mortality and recruitment). The results depend on the seasonal variation of these parameters and the validity of the conclusions will therefore depend on the interannual stability of the seasonal patterns.

As stated earlier, the growth is assumed to be a continuous function of time. Stepwise yield per recruit models as proposed by Caddy (1986) have not been used for penaeids and are probably not required because of the apparent lack of synchrony in moulting.

The main recruitment process operates through massive migration out of the nursery and massive concentration of fishing on the new recruits, in shallow depth. This leads to an abrupt recruitment of the main generation into the fishery, for which the knife-edge approximation might well be adequate, although loosely related to mesh size. It should be noted, however, that natural variations of size at first capture at seasonal and interannual levels are to be expected owing to environmental effects on the migration process (Garcia and Le Reste, 1981).

Simple yield per recruit models can easily integrate data on value by age or size category as well as cost of fishing and therefore easily lead to preliminary bioeconomic analysis (see, for example, Clark and Kirkwood, 1979; Lucas et al., 1979). They can also be used to deal with most critical problems in prawn fishery related to the determination of the effects of seasonal fishing closures. They offer a first opportunity to look at the effect of fishing on overall spawning potential and fecundity per recruit (Garcia and Van Zalinge, 1982). They can easily be used to reproduce the catch–effort history of a given fishery with a yearly or seasonal resolution (see Willmann and Garcia, 1985, and Sluczanowski, 1984, respectively). The classical yield per recruit function for the most frequent age at first capture (which is around 3–4 months) is a very flat-topped curve. It should not be taken to mean that prawns can be fished very hard without overfishing because the stock recruitment relationship at high levels of fishing is not known.

However, the conclusions of the simple Y/R models are very sensitive to seasonal patterns of recruitment, catchability, fishing effort, etc., and more elaborate models are necessary for fine-tuning of management measures, especially when the problem related to the stock and recruitment relationship and the uncertainty generated by non-fishery variables has to be taken into account.

Simulation models

The simulation models used for prawn fisheries are basically analytical models. Their degree of sophistication is variable but may consider the development of, say, 12 monthly cohorts, each with its own seasonally varying population parameters (Grant and Griffin, 1979; Garcia, 1977; Willmann and Garcia, 1985). Their economic components can deal with seasonal patterns in fishing effort, landings and markets. The introduction in the models of appropriate error structures for the estimates of population and fishery parameters and for their natural (environmental) variations leads to a more realistic approach to management advice and a better appreciation of the consequences of parameter uncertainties and system noise on the forecasts (Sluczanowski, 1984).

Simulation models may be used to investigate equilibrium situations and determine optimum yields and annual effort, as well as optimum fishing patterns. The outputs, in terms of catch, value, etc., can be scaled to mimic actual outputs of the fishery by adjusting the overall recruitment level. When no stock–recruitment relationship is included in the model the conclusions have to be taken with caution, especially at high effort levels.

Simulation models are useful for investigating seasonal behaviour of fisheries and more particularly for optimizing the dates of the closed fishing seasons and for short-term fleet management.

They can be used dynamically to predict average states of the fishery system (prawn size, abundance, economic returns, etc.) at any time $(t+a)$ starting from an observed state of the system at time t. For instance, length–frequency distributions collected during pre-fishing season surveys in inshore waters have been used as input to simulate prawn population and fishery results at any later time interval and so to consider various options for fleet size or date of opening of the fishing season (Somers, 1985; Kesteven et al., 1981; Sluczanowski, 1984). The latter author shows in his particular study that system noise has more impact than parameter uncertainty, that absolute values of M and q are more critical than the seasonal variations of catchability. The seasonal distribution of fishing effort has, of course, a determinant effect on both the biological and the economic performance of the prawn fisheries. Optimal closures should ideally be flexible and based on the most accurate parameters, but the cost of reaching such optimum can be prohibitive and suboptimal policies might be accepted in exchange for reduced management and research costs.

Further refinements could be made by introducing considerations of spatial structures into the now classical age- and time-structured models. Grant and Griffin (1979) were percursors in this field and modelled the migration of prawns across various depth strata exploited by different competing fisheries. Because of the migration of an annual stock across the depth range in one year, the prawn stock dynamics have corresponding and largely interchangeable dimensions for age, time and space (depth, distance from the estuary, etc.). Where location is

highly relevant (lagoon v. open sea, littoral area v. offshore, shallow v. high
depth, etc.) in relation to costs of fishing (distance to port, type of boat or fishery
technique used) or conflicting use of the resource (when two or more fisheries are
competing for space) the spatial dimensions of fisheries might become critical.
This is the case, for instance, when studying the effect of establishing a sanctuary
in an area along the migration route of prawns from the estuary to the offshore
grounds. It is also the case for prawn fishery complexes consisting of many
different stocklets, where fleet strategy has to be optimized by careful planning
(Kesteven et al., 1981).

Another important application of the bioeconomic simulation models is the
analysis of interaction between the artisanal or recreational inshore fisheries and
the industrial trawl fishery. Violent conflicts have arisen (in India and Southeast
Asia, for instance) because of the sequential or simultaneous exploitation of a
prawn stock by different fleets and different socio-economic communities. The
overall effects of different management policies on values, profits, employment
and other social benefits, net foreign exchange earnings, etc., are of utmost
importance to the manager. The trade-offs involved can be analysed as a guide to
decision-making. Examples can be found in Garcia (1977, 1978) and Willmann
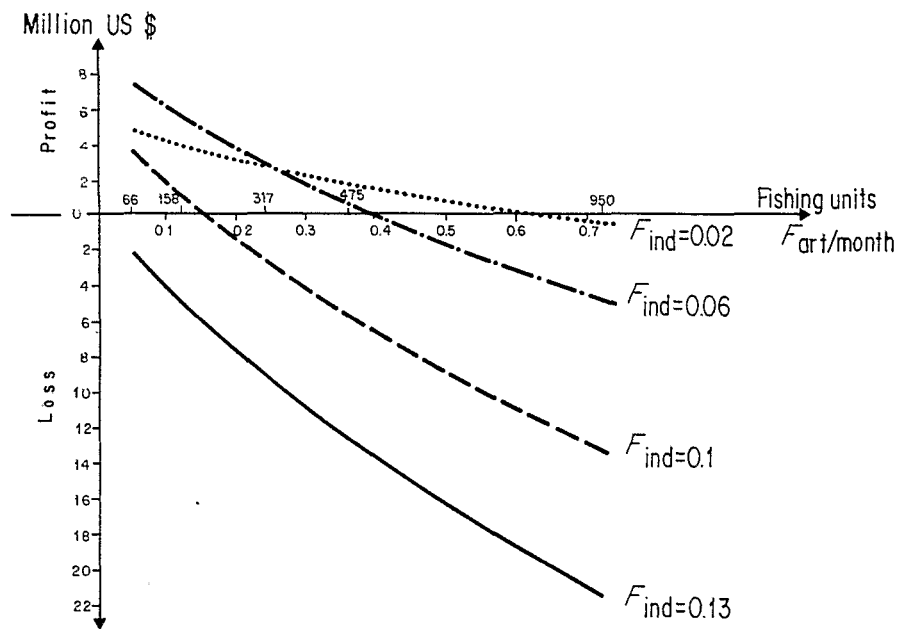and Garcia (1985) (Figure 9.11).

Figure 9.11   Relationship between profit (or loss) and the level of artisanal effort (F_{art}) in
fishing units or fishing mortality for various levels of industrial fishing effort
(F_{ind}). (From Willmann and Garcia, 1985) (Reproduced by permission of
the Food and Agriculture Organization of the United Nations)

MANAGEMENT

Most of the preceding sections have indirectly touched on management in relation to the fisheries description, the population characteristics or the modelling. Reviews on the management of prawn fisheries in the Gulf of Mexico and in Australia are available in Leary (1985) and Bowen and Hancock (1985), respectively. A wider review of management issues, objectives, strategies and techniques has been prepared by Garcia (in press) and a brief account is given in this section in order to put the knowledge of the dynamics of prawn populations in the proper context of its practical application to fisheries management.

Most prawn fisheries around the world are overfished, at least in economic terms. They are developed largely beyond the level of the maximum economic yield (MEY) and suffer from heavy overcapitalization, loss of revenues, shortage of post-larvae (in Ecuador), and sometimes seem to encounter recruitment problems whose origin is not always very clear. The problem of the optimization of the yield per recruit function, in weight or value, is central and leads to measures such as closed seasons and sanctuaries, as well as reduction of fleet size. The trade-offs involved by the solution to the conflicts with artisanal fishermen lead to increased use of the simulation models. The conflicts with aquaculture for wild seed have, however, been very little addressed and their analysis is potentially very difficult because of the uncertainty regarding the relationship between stock and recruitment, the pre-recruit mortality factors and the great sampling difficulties.

A major issue, sometimes underestimated in present management programmes, is the uncertainty generated by the environmental effects on prawn production. Although the problem is less critical than with small pelagic fish, annual production depends on recruitment level under strong influence of environmental factors which cannot usually be forecasted with sufficient precision. This leads to the following strategies which can be followed together:

– assessing the likely level of uncertainty, including it into the models used and providing for it when elaborating management advice (Sissenwine, 1984). The rationale for this is that caution and flexibility should compensate for uncertainty;

– managing on a yield per recruit basis (Gulland, 1972). Most of the sophisticated scientific work done on prawn populations follows this principle and aims at improving yield per recruit in value by optimizing size at first capture, dates of opening and closing of fishing seasons, level of effort, etc.

An important amount of work has been dedicated to analysing environmental effects on annual production with the objective of forecasting, and a review of the work is given in Garcia and Le Reste (1981). As usual, the 'forecasting models' using environmental variables appear at best to be able to reproduce the past events but very few of them have really been tested against time. Based on experience with similar problems in other resources it can be assumed that few will pass this test, that extreme conditions may well be forecast usefully, but that

in average conditions the precision of the forecast will be insufficient.

Short-term forecasting, based on pre-recruitment indexes such as CPUE in the inshore fishery on juveniles or emigrants, has, however, proved to be more successful. The information, plus data collected by pre-recruit surveys (abundance and size structure) have been usefully used in management, reducing uncertainty and improving yield per recruit (Leary, 1985; Somers, 1985).

Recruitment overfishing has also been a central issue in recent scientific meetings (e.g., in Gulland and Rothschild, 1984; Rothlisberg et al., 1985). This issue is widely discussed earlier in this chapter from the point of view of population dynamics. In terms of management the assumption of the existence of an SRR leads to attempts to improve spawning potential by protecting adults during the spawning season, or by protecting juveniles from selective depletion at the time of recruitment by enforcing appropriate sanctuaries (Leary, 1985; Penn and Caputi, 1985, 1986) or closed seasons. Conversely, the assumption that there is no such SRR for a large range of effort levels leads to management on a bioeconomic basis, searching for better employment opportunities, higher revenues, improvement of foreign exchange balance, etc. Whether or not such SRR exist at low fishing effort levels, there is a need for conservation of the carrying capacity of the nursery environment, protection of littoral areas, lagoons, mangroves and seagrass beds.

The large by-catch makes multispecies exploitation and management an important issue for prawn fisheries. The problems are threefold. First, discards represent an economic waste where there are no markets for trash fish or where boats are too sophisticated to be able to keep fish on board economically. Secondly, it would be useful to know the impact of by-catching by prawn fisheries on competing fin fisheries. These gear interactions can be very important and must be analysed, because shrimpers catch young fish which might have been exploitable later by other gears. Finally, it would be useful to know the biological impact of the dead fish discarded on the overall food chains and production. Very few studies are available on these aspects (see Gulland and Rothschild, 1984), but species interactions are very difficult to detect in multispecies communities, either because they are unimportant or because sampling variability masks their effects (Sainsbury, 1982). In fact, according to Larkin (1982) ecologists may well have over-emphasized the role of species interaction and underestimated the role of environment. Consequently, multispecies management will remain empirical for some time (see also May, 1984) and largely dominated by socio-economic considerations.

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