FAO Fisheries Technical Paper No. 203 FIRM/T203

LIFE CYCLES, DYNAMICS, EXPLOITATION AND MANAGEMENT OF COASTAL PENAEID SHRIMP STOCKS

FOOD AND AGRICULTURE ORGANIZATION OF THE UNITED NATIONS

LIFE CYCLES, DYNAMICS, EXPLOITATION AND MANAGEMENT OF COASTAL PENAEID SHRIMP STOCKS

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FOOD AND AGRICULTURE ORGANIZATION OF THE UNITED NATIONS
Rome 1981

First printing 1981
Second printing 1983

M-43
ISBN 92-5-101069-2

FOREWORD

This review is intended on the one hand for all biologists and personnel or organizations responsible for the assessment and management of resources and in this sense is directed to qualified personnel who already have basic knowledge which will allow them to benefit from this text where the information has had to be presented in a rather concentrated form.

On the other hand it is also intended for beginners who are starting their scientific activities by working with penaeid shrimps since a full review of methods of study, sampling, calculation of dynamic parameters, assessment, and management of such resources is provided in this document.

It should however be accepted that this document is not a manual of fishery science since it cannot be used alone. If some aspects specific for penaeids have been somewhat expanded, those which are more concerned with classical population dynamics have been, for the most part summarized or treated superficially by referring to relevant published work for further details. With this in mind, the review has no other intention than to serve as a guide for the beginner by advising him of the difficulties he can expect to meet, of references to similar work and of the theoretical elements he should acquire by referring to basic texts. Since the document has been written in the laboratory of a developing country where the information available is certainly far from exhaustive, the authors apologize in advance for any involuntary omissions that they may have made in spite of their efforts to be comprehensive.

The cited examples have as far as possible been taken from papers dealing with penaeids and are given for purposes of illustration. This does not imply that some of these studies might not be subject to criticism, because the scarcity of studies available on some subjects did not permit the authors to be as selective as they would have wished.

This document has been translated from French and in case of any difficulty in understanding, the reader could usefully refer to the original version: Cycles vitaux, dynamique, exploitation et aménagement des stocks de crevettes pénaeides côtières. FAO Doc.Tech.pêches, (203):210 p.

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For bibliographic purposes this document should be cited as follows:

Garcia, S. and L. Le Reste, Life cycles,
1981 dynamics, exploitation and
management of coastal penaeid
shrimp stocks. FAO Fish.Tech.
Pap., (203):215 p.

ABSTRACT

This document deals with the main aspects of the biology, dynamics and exploitation of the coastal penaeid shrimp stocks, essential for the elaboration of a rational management programme. It describes, in particular, the life cycles, the exploitation systems, the tagging techniques, the methods of analysis of growth and mortality. It summarizes our knowledge of catchability changes, on interannual variation of production and related predictive models, on recruitment and selectivity. It finally reviews the stock assessment models presently used together with the reservations expressed about them, and the advocated management methods.

ACKNOWLEDGMENTS

We wish to express our gratitude to L.K. Boerema who kindly accepted to review the original draft of this paper and made many constructive suggestions. However, the authors are fully responsible for any errors or misinterpretations.

We are also grateful to the editors of the various publications from which we obtained our information and figures, for their kind authorization to use them.

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1. INTRODUCTION

The exploitation of penaeid coastal shrimps of the tropical areas is an extremely ancient activity. Traditionally exploited by artisanal fisheries in many countries (Mexico, Senegal, Benin, India, etc.), shrimps, since the beginning of the fifties, have had to sustain an enormous increase in exploitation through the development of more and more improved and specialized industrial fishing.

After acquiring the seal of success in the Gulf of Mexico, industrial fishing spread very rapidly to South America, Africa, the Indian Ocean and Oceania so that at the present time there are probably not many stocks which remain undiscovered. During the same period, helped until the end of the seventies by increasingly favourable export markets, artisanal fishing has also greatly extended in many countries, providing invaluable sources of income in rural areas but at the same time instigating inevitable conflicts of interest between two entirely different socio-economic systems.

A chronic scarcity of expertise in the fishery sciences in the tropical areas has resulted in the fact that nearly all the known shrimp resources are highly or completely exploited - some species are even over-exploited - while in too many cases the elementary knowledge required to safeguard and rationalize exploitation of these resources is still sadly lacking.

In view of the urgent nature of the problem and to help to resolve the difficulty, at least partially, it seemed necessary to prepare a general review and commentary of available information on those aspects of penaeid biology and exploitation, which have to be known in order to determine optimal conditions for exploitation and for the establishment of management programmes 1/ .

The composition of this document - its essential subject matter, the nature and relative importance of the chapters - is closely linked to the current state of our knowledge of the specific characteristics of the penaeids in comparison with other living marine resources, and the inherent difficulties of studies in the various areas of fishery science.

As a foundation to the problem, the beginning of the first chapter reviews our knowledge of the life cycles of the penaeids so as to demonstrate on the one hand the general characteristics of such cycles and on the other the diversity of variations which account for the great adaptability of this group to very different hydrological conditions. One of the essential biological characteristics of many coastal penaeids is the presence of an amphibiotic life cycle which includes a juvenile stage living close inshore or in estuaries and exploited by artisanal fisheries and an adult stage in deeper waters exploited by industrial fisheries (Fig. 2). Since any integrated management programme must consider these two factors, the study of the complete life cycle is of fundamental importance. It is in particular important to know the dynamics of the juvenile and adult stages and to determine the chronology of the key points of the life cycle: larval recruitment, juvenile migration, age at successive recruitments in different fisheries, spawning age, life span, etc.

Another characteristic which distinguishes these animals is their extremely short life span, of the order of two years, and their presence in the fishery in significant quantities for a period generally little more than a year. In fact the time unit which can be used to describe the events must therefore be less than a year (week or month is generally used) and seasonal variations in phenomena must be taken into consideration since they are not concealed by the averaging effect of yearly means. These phenomena are for example, seasonal variations in recruitment, in growth, in behaviour and in catchability, in fishing mortality, in age structure of the exploited population, in reproductive potential, in the biomass, etc, which have important consequences to the outcome of a specific management measure.

1/ For excellent supplementary documentation, the reader should refer to the following bibliographies: Chin and Allen (1959); Allen and Costello (1969) and to Proceedings of the World Scientific Conference on the biology and culture of Shrimps and Prawns (Mistakidis, 1968, 1969, 1970).

The quality of the study of a life cycle depends essentially on the quality of the basic biological data used for the analysis. It is therefore closely linked to the problem of sampling through the various stages of the cycle (larvae, post-larvae, juveniles, migrating sub-adults, adults) which depends on the distribution patterns in time and space. In view of the importance of this aspect to the understanding of production mechanisms and the final establishment of intelligent management, Chapter II has been devoted entirely to the analysis, stage by stage, of the distribution of the various development stages, to their variations in abundance, seasonal or in shorter intervals, and to a description of sampling methods.

In addition, the quality of resource assessment, the accuracy of information on the reactions to the exploitation, and the relevance of management measures under consideration, depends essentially on the quality of the data collected on exploitation methods and performance. For this reason Chapters III and IV deal respectively with the description of exploitation systems (artisanal for juveniles and industrial for adults) and the gathering of fishing data with emphasis on the possibility of bias and the difficulties associated with the concept of fishing effort at sea and in estuaries as well as with the problem of discards.

One of the chief difficulties in studying penaeid stocks is the absence of skeletal parts which can be used for age determination. This lack, associated with the fact that recruitment is often continuous, frequently makes it extremely difficult to determine the age of the shrimp. The available methods lead, without exception, to the risk of considerable bias, or are associated with a not insignificant amount of subjectivity, and this difficulty has consequences on the studies of mortality coefficients. Tagging techniques, from the simplest to the most sophisticated, have appeared for many years to be a means of circumventing the difficulty, notwithstanding the risks of bias which these methods contain.

Because these three fundamental aspects, growth, mortality and tagging are key points of any analytical study of penaeids, an important part of the text has been devoted to them.

Catchability variations have considerable significance both for exploitation and for mortality analysis and they have been emphasized in a special section although some repetition was inevitable.

Although much information exists on penaeid biology, in the sphere of recruitment there is still a notable amount of ignorance. Though the mechanism of the migration from the estuaries towards the adult spawning grounds where industrial exploitation takes place is well described, the process of entering the exploitation phase is little known. It is difficult to analyse in many types of artisanal fishing where recruitment varies considerably with the type of gear used, and also remains remarkably little documented in studies on industrial trawl fishing where selection studies are scarce and recruitment curves even scarcer. This area of research is still less explored with respect to the relation between stock and recruitment. Outside a few little supported conjectures, no real analysis has been made, and without a concentrated effort in this direction this aspect will remain for a long time the least known part of penaeid dynamics. This is why the small chapter treating these problems emphasizes much more our ignorance than it summarizes our knowledge.

The annual production of a shrimp fishery depends almost entirely on annual recruitment. Since there is no damping mechanism on biomass variations by older year-classes, production should show an interannual variation similar to that of recruitment. If there is great variability it can be just as important, if not more so, to forecast variations from one year to the other using predictive models as to define a management programme which will produce "optimal" long-term results. Many attempts have been made to carry out such work for penaeids, with varying success. The chapter on this problem has given us the opportunity to summarize and comment on them.

Mathematical models generally used for resource assessment and the identification of the most appropriate management measures for penaeids are the classical analytical or global methods. Specialized literature in this field is prolific enough to make it unnecessary to repeat here the mathematical formulations. It is enough to recall the basic hypotheses implicit in these models to see how far they can be applied to penaeids and to underline the principal difficulties resulting from their use. Approximative methods for obtaining rapid and provisional assessments have also been briefly reviewed.

The document ends by analyzing the problems associated with the management of exploiting shrimp resources. After a presentation of management principles and objectives, drawn essentially from Gulland's (1972) work, it seemed useful, when faced with the general use of the production model for penaeid stock analysis, to recall the comments of numerous authors on the use of the maximum "sustainable" yield (M.S.Y.) as a management objective. A discussion on foreseeable management techniques, illustrated by examples taken from penaeids, concludes the chapter.

2. ECOLOGY AND LIFE CYCLES

Coastal penaeid shrimps are found in tropical and sub-tropical zones.

Most of the time, shrimps live in zones influenced by deltas, estuaries or lagoons, that is on bottoms which are generally muddy of a mixture of sand and mud, rich in organic matter; in addition a part of the life cycle takes place in more or less brackish waters. This is however not always the case as is discussed in more detail in Section 2.2.2. The various parameters of the environment are not independent and it is therefore often difficult to isolate one or several which control one or other aspect of the ecology or biology of shrimps.

It is not proposed to examine here the ecology of the different species. We have attempted, essentially through the use of published data, to identify the characteristics common to the majority of species which determine the sampling techniques and sampling plans needed for the quantitative evaluation of the different stages of the life cycle.

2.1 PRINCIPAL SPECIES

Coastal penaeid shrimps which supply fisheries throughout the world belong to about forty species divided into six genera. Very often catches are not identified by species: for this reason one cannot say what part each species plays in world production. We will therefore indicate only the most important species caught in each of the great production areas. A full inventory has recently been compiled by Holthuis (1980). An earlier inventory was made by Eldred and Hutton (1960) and Holthuis and Rosa (1965).

MEDITERRANEAN

Penaeus kerathurus

KOWEIT (Mohamed et al., 1979)

Penaeus semisulcatus, very dominant; Metapenaeus affinis; M. stebbingi, Parapenaeopsis stylifera. More occasionally: Penaeus japonicus, P. latisulcatus, Trachypenaeus curvirostris, Metapenaeopsis stridulans, T. granulosus.

PAKISTAN (Tirmizi, 1969)

Penaeus semisulcatus, Penaeus merguiensis, Penaeus penicillatus, Metapenaeus stebbingi, Metapenaeus brevicornis, Metapenaeus affinis, Parapenaeus stylifera.

INDIA (Jones, 1967)

Penaeus semisulcatus, Penaeus merguiensis, Penaeus indicus, Penaeus monodon, Metapenaeus brevicornis, Metapenaeus dobsoni, Metapenaeus monoceros, Parapenaeus stylifera.

FAR-EAST (Kristjonsson, 1967)

Penaeus monodon, Penaeus japonicus, Penaeus orientalis, Metapenaeopsis lamellata, Metapenaeopsis acclivis, Metapenaeopsis joyneri, Trachypenaeus curvirostris.

AUSTRALIA (Walker, 1975)

Penaeus merguiensis, Penaeus esculentus, Penaeus plebejus, Penaeus latisulcatus, Metapenaeus endeavouri, Metapenaeopsis macleayi, Metapenaeus bennettae.

EAST AFRICAN AND MADAGASCAR COAST
(Hall, 1966; Marcille, 1978)

Penaeus indicus, Penaeus semisulcatus, Penaeus monodon, Metapenaeus monoceros.

WEST AFRICAN COAST (Garcia and Lhomme, 1977)

Penaeus notialis, Parapenaeopsis atlantica.

EAST AMERICAN COAST (Perez Farfante, 1969)

Penaeus setiferus, Penaeus duorarum, Penaeus notialis, Penaeus aztecus, Penaeus aztecus subtilis, Penaeus schmitti, Penaeus paulensis, Penaeus brasiliensis, Xiphopenaeus kroyeri.

WEST AMERICAN COAST (Gross, 1973; Edwards, 1978)

Penaeus californiensis, Penaeus vannamei, Penaeus stylirostris, Penaeus brevirostris, Penaeus occidentalis.

2.2 BIOLOGICAL CYCLES

2.2.1 Different stages of the biological cycle

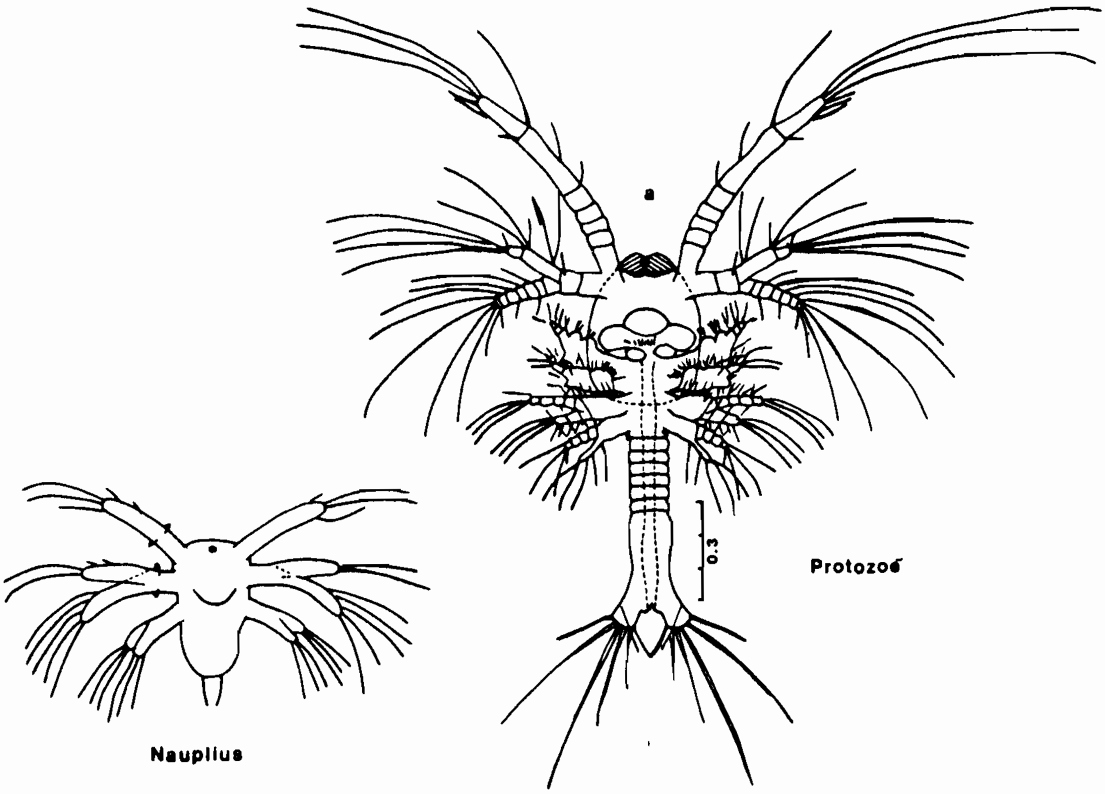
The female lays demersal eggs. The larvae hatch from these eggs in the nauplius stage which is planktonic. Larval development for several species, most of which belong to the genus Penaeus, has been described. It appears that, in general, it progresses, through eleven successive stages, the transition from one stage to another taking place by moulting: there are five "nauplius" stages, three "protozoa" stages and three "mysis" stages (Fig. 1).

The last mysis undergoes a moult which transforms it into a post-larva. Although it only measures a few millimetres, the post-larva already has the general adult appearance but the rostral teeth formula is not complete. The post-larva will pass through several stages each characterized by a particular rostral formula. The first post-larval stages (up to two or three subrostral teeth) are still planktonic whereas those that follow are semi-benthic. When the shrimp has achieved its complete rostral formula, it is considered a juvenile. The external sexual organs (petasma in the male, thelycum in the female) are not yet differentiated. When their formation is complete, the shrimp is known as sub-adult. The adult stage is reached when the shrimp is able to reproduce. Growth varies between 30 and 60 mm/month during the juvenile phase (total length) and decreases subsequently with age. It varies also with population density and surrounding temperature.

2.2.2 Spatial evolution of the life cycle and ecology of the different stages

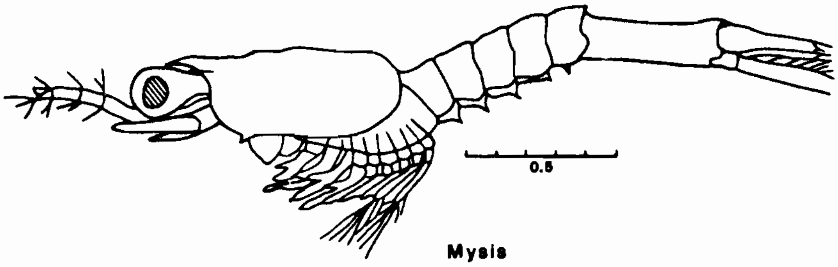
The physiology of shrimps changes during their development, in particular their capacity for osmoregulation evolves. This is related to the fact that during their lives, shrimps migrate through various biotopes which can be characterized for instance by their salinity gradients.

Schematically, the migration cycle is as follows: spawning takes place at sea; the larvae and the first post-larvae are planktonic. The post-larvae later migrate inshore and very often into estuaries and lagoons. The shrimps return to the sea when they have reached a length of about 10 cm. The end of the cycle takes place at sea. A diagram of this cycle showing the phases which are exploited is given in Fig. 2. Kutkuhn (1966) emphasizes that penaeid shrimps can show great differences both in their relationships with brackish waters and in the distribution of adults across a brackish-seawater gradient. In a spiral (Fig. 3) where the diminishing width of the spiral indicates the comparative length of time each new generation spends during early development in estuarine waters have been represented twenty-five species according to his own observations and data taken from published work; the positions along the axis indicate the relative location of the adults along the estuary-sea water salinity gradient.

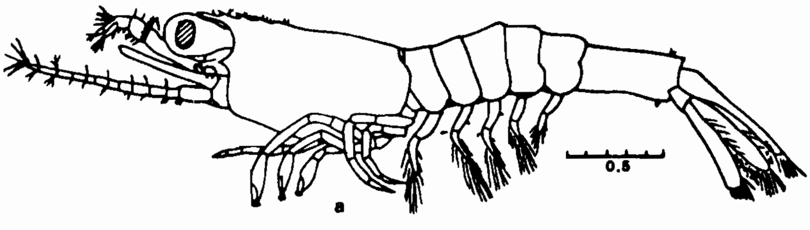


Nauplius

Protozoe



Mysis



Postlarva

Fig. 1 Larval stages of *Sycionа brevirostris*, Penaeoidea (from Cook and Murphy, 1965)

In the centre of the spiral is found for example *Metapenaeus mastersii*, an Australian species which spends its entire life in estuarine waters (Morris and Bennet, 1951). This is also the case of *M. bennetae* (Racek, 1959) and *M. dalli* (Penn, in Press). At the narrow end of the spiral is found an important atlantic species *Plesiopenaeus edwardsianus* which completes its entire cycle in depths of about 900 m (Springer and Bullis, 1956; Maurin, 1965) and cannot therefore be classified among the coastal peaneids. Between these extreme cases can be found all the examples of intermediate types. In the Gulf of Mexico, the adults of *Penaeus aztecus* live and reproduce principally in depths of 55-75 m (Kurkuhn, 1962) and the juveniles do not penetrate very far into estuarine waters. The adults of *Penaeus setiferus* are not found in depths greater tnan 35 m, but the juveniles can travel great distances into the estuary and have been found as far as 210 km upstream from the inlet (Joyce, 1965). The adults of *Xiphopenaeus kroyeri* are confined to a narrow coastal strip and the juveniles do not penetrate very far into estuaries (Burkenroad, 1934; Neiva and Wise, 1964). As a last type case we would refer to the Indian species *Parapenaeopsis stylifera*, the adults of which live at sea at depths less than 40 m and complete their entire cycle at sea. Although it has not yet been studied in detail, it seems that *Parapenaeopsis atlantica* of the West African Coast must be a similar type since the adults live in depths of 0 to 45 m (chiefly 15-25 m) and the larvae are not found in estuaries (Crosnier and De Bondy, 1967). The same has been reported for *P. semisulcatus* in the Gulf between Iran and the Arabian peninsula (Basson *et al.*, 1977). Kirkegaard (1975) has also given a description of the different types of distribution and migration of Australian penaeids (Figs. 4 and 5). The great adaptability of the genus *Penaeus* to different hydrological conditions must be noted. For instance, *P. notialis* juvenile stages are found in nearly fresh water in the Casamance river (Senegal) but also in hypersaline waters in the Sine Saloum in the same country. In the same way *Penaeus esculentus* can be found in waters below 35o/oo but sometimes over 45o/oo (Penn, in Press). Moreover, if most of the *Penaeus* have an amphibiotic life cycle with an estuarine phase, some others like *P. latisulcatus* and *P. esculentus* have their nurseries in the marine littoral zone. This is also the case of *P. marginatus* which adults are found at more than 200 meters (Crosnier and Jouannic,1973; Struhzaker and Yoshida, 1975) when most of the species of this genus are found in waters shallower than 80-100 m.

Shrimps do not migrate solely along an inshore-offshore axis. Requirements related to the nature of the substrate, to the trophic conditions, to the hydrology, can force shrimps to migrate along the coast. *Penaeus setiferus* can migrate as far as 580 km (Lindner and Anderson, 1956), along the Atlantic coast of the USA. Ruello (1975) reported that in Australia a shrimp of the species *Penaeus plebejus* has travelled 930 km.

Plentiful information on the life cycles of the penaeids can be found in the synopsis of FAO (Mistakidis, 1970) and of the C.S.I.R.O. (Kirkegaard and Walker, 1970; Kirkegaard *et al.*, 1970).

2.3 Variability and methods of collection of biological data

A study of a stock of coastal penaeids which is made with the aim to develop a rational management of the resources requires a good knowledge of the chronology of the life-cycle and the relationship between different stages of the cycle. As a matter of fact, because of the lack of a method for the direct determination of the ages of shrimps, only a detailed analysis of the different stages can establish the chronology of the main phases (spawning, larval migration, juvenile migration, recruitment, etc.) by superimposing seasonal variations when they are sufficiently measurable. Figures 6 and 7 give an example of the results obtained in the Ivory Coast and a representation of the chronology of the cycle of *Penaeus notialis* in the region, according to Garcia (1977). Moreover, the development of predictive models (Chapter 9) and the study of recruitment are based on the collection of quantitative data on the different phases of the life cycle.

The study of time-space variations in these different stages requires the establishment of sampling programmes where the techniques used will depend on the kinds of predictable variability; the different sources of variability and the methods employed are set out in the following section.

2.3.1 Larvae and planktonic post-larvae in the sea

One of the main interests in studying the larvae is to arrive at a knowledge of the seasonal variations in the reproduction of the population. It is in general a painstaking study which should not be

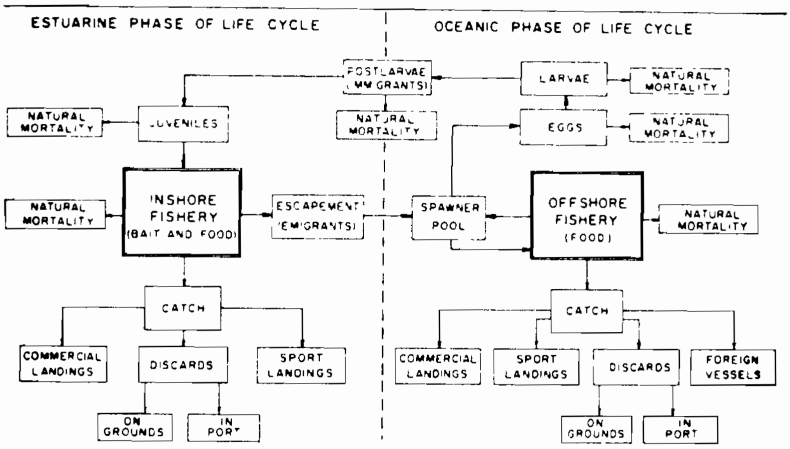


Fig. 2 Relationships among components of the life cycle of penaeids and the fisheries (from Caillouet and Baxter, 1973)

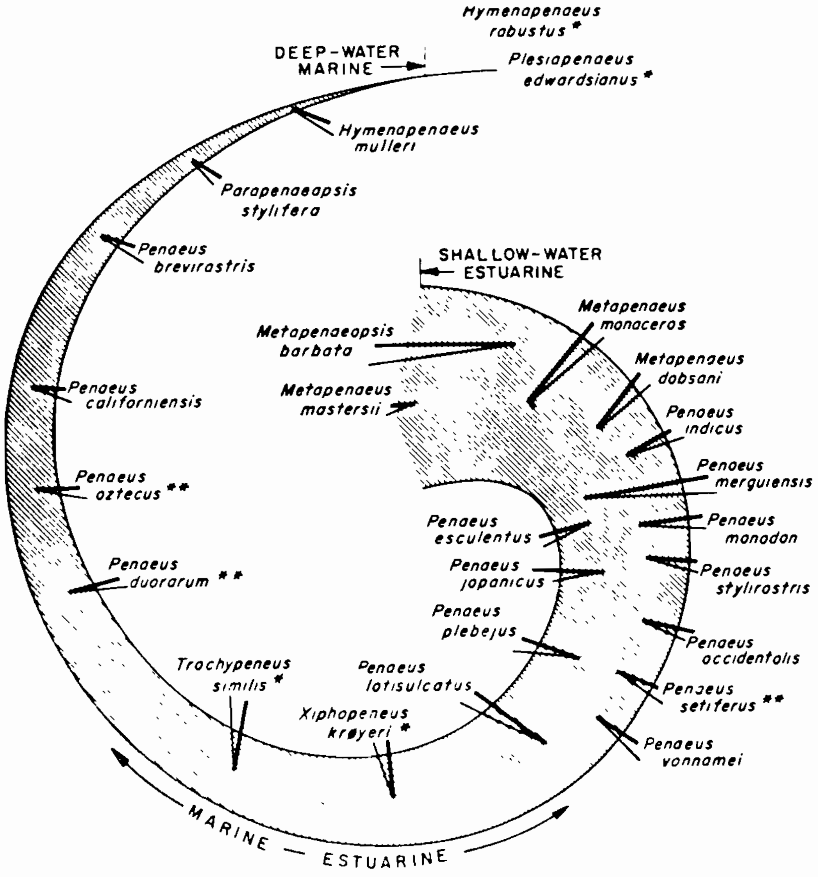


Fig. 3 Expected degree to which penaeid species inhabit the estuarine environment during its ontogenic development (see text) (from Kutkuhn, 1966

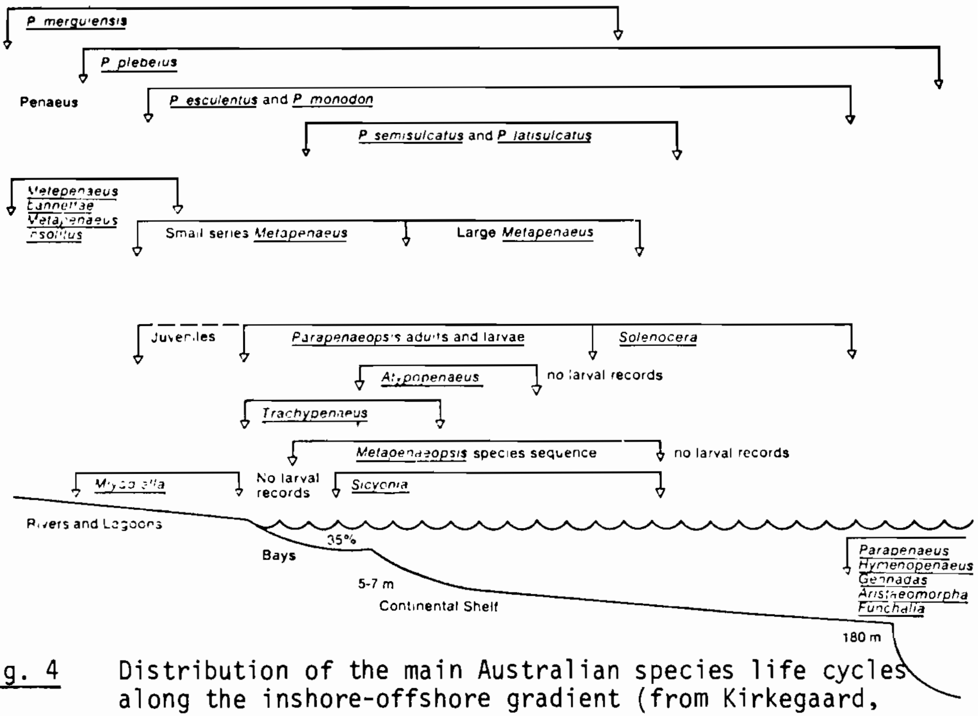


Fig. 4 Distribution of the main Australian species life cycles along the inshore-offshore gradient (from Kirkegaard, 1975)

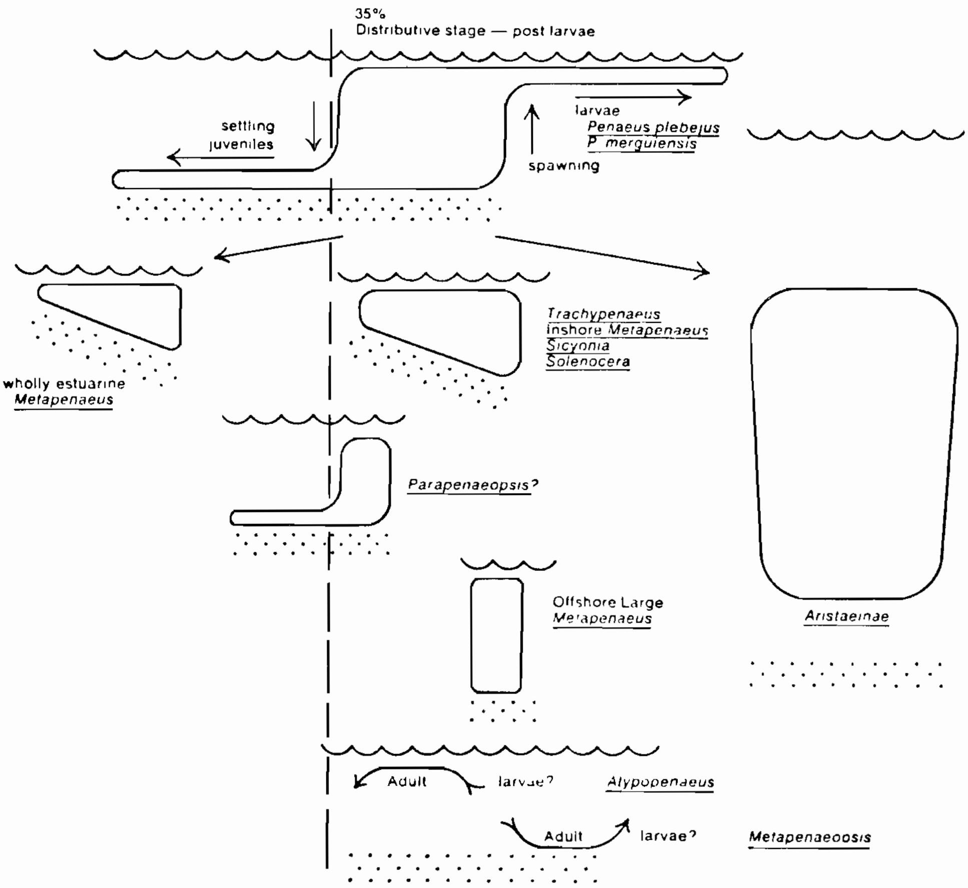


Fig. 5 Different types of life cycles; distribution in relation to the surface (∿), the bottom (:::), and the 35% isoline (from Kirkegaard, 1975)

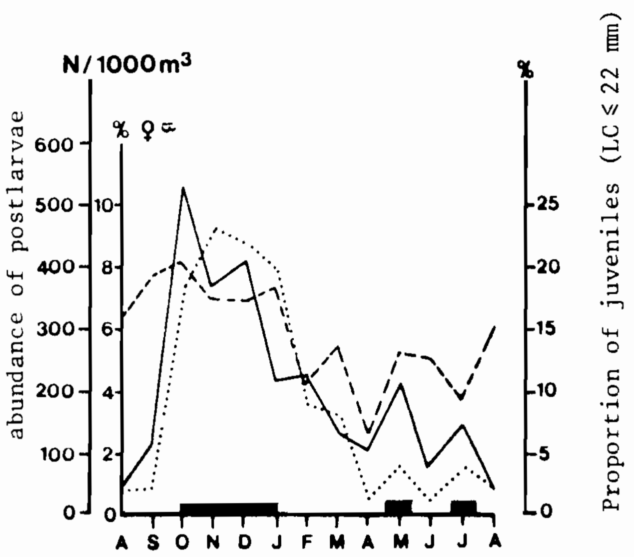


Fig. 6 Comparison of seasonal variations in reproduction (—), postlarval abundance in the region (--), and recruitment of subadults at sea 3 months later (···) (from Garcia, 1977)

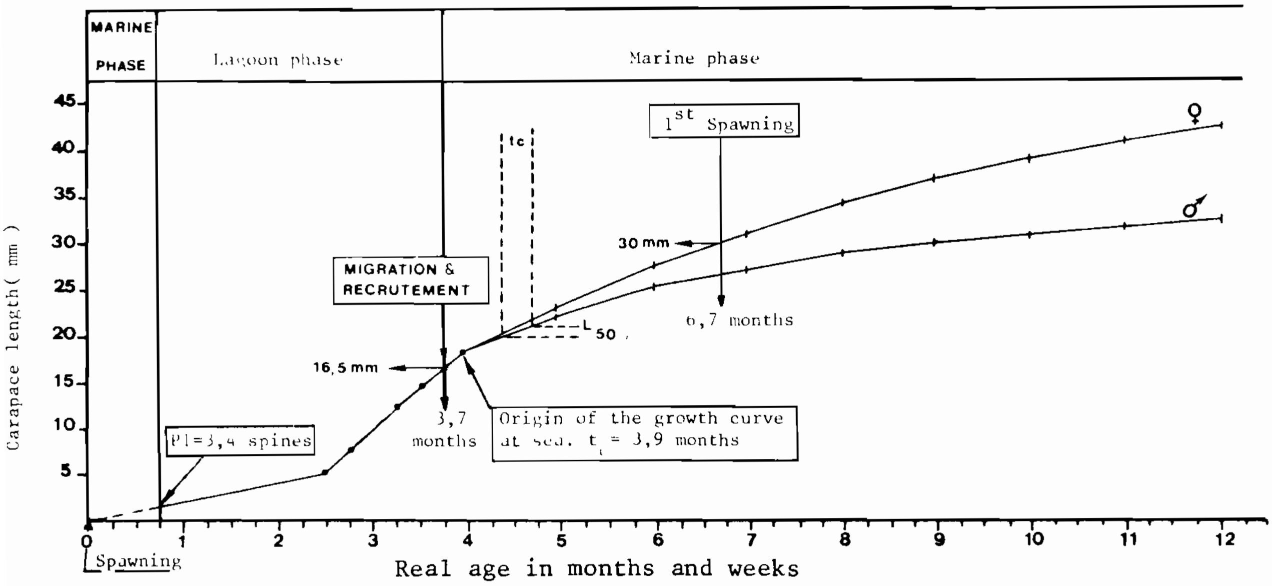


Fig. 7 Reconstruction of the life cycle chronology of *P. notialis* in Ivory Coast (from Garcia, 1977)

undertaken lightly. In particular, even though one can foresee a certain homogeneity of behaviour it is desirable to be able to separate clearly the different species because reproduction periods are sometimes not superimposed (Inglis, 1962). In general even when the larvae have been correctly described, classification at the species level is long and arduous. It is easier if identification of the genera is sufficient.

2.3.1.1 Dispersion of the larvae and treatment of the data

The way in which the sampled stages are dispersed has a direct bearing on the variability of the abundance estimates. Statistical methods used to quantify the variability and to compare the estimates obtained in different periods or zones require that the distribution of the observations obtained within each period and zone is normal, which imply that the spatial distribution of the animals is random, and the value obtained for the mean and the variance are independent. These conditions are not generally met in plankton where the usually observed dispersion of the larvae is in clusters (over dispersion). An appropriate transformation of these data will however bring them closer to the conditions required for statistical analysis. Such transformations have been used by various authors.

To our knowledge there have been no studies on the way shrimp larvae disperse. One can however suppose that the dispersion is of the type that Frontier (1969-1971) has demonstrated for the larvae of the tropical brachyures, which are also meroplanktonic, and the Lucifer. When the taxon is represented by only a small number of organisms the distribution generally follows a Poisson's law where the variance is equal to the mean. For the usual range of sizes of the plankton samples taken Frontier shows that when the amplitude of the variations of observed numbers is high the relation between the mean and the variance is non-linear (Fig. 8). The slope, which is close to 1 for small values (Poisson's law) falls between 1 and 2 for mean values and is greater than 2 for high values; for each range of abundance a different conversion factor is necessary to stabilize the variance. To overcome this obstacle, Frontier proposes a single conversion factor of the form square log (n+1); the addition of a unity to the count allows nil observations to be included. This transformation has moreover the advantage (as compared to the log transformation) to reduce much less the high values and to exaggerate less the random variations of the small ones.

This conversion has been used by Le Reste (1973) for a study of Penaeus indicus in Madagascar.

Other authors used a conversion factor of $\log_{10}$ (n+1) which can be considered to be of value for small counts. Others again, using the results of Anscombe (1948) have applied a conversion factor of $\sqrt{n+3/8}$.

Frontier (1974) nevertheless points out that the log conversion factor is preferred for living individuals because biological responses elicited by environmental variations are often exponential.

In general, the treatment of shrimp larvae data can follow the usual methods of plankton analysis and for a more detailed study one can usefully refer to Windsor and Clarke, 1940; Silliman, 1946; Barnes and Marshall, 1952; Alsthrom, 1954; Frontier, 1971; Hemple, 1973; Bougis, 1974. For shrimps, some examples will be found in Munro, Jones and Dimitriou, 1968; Roessler and Rehrer, 1971 in Florida and to Kutkuhn et al., 1969, Temple and Fisher, 1967 in Texas.

The representation of the spatial distribution of the larval densities also presents a problem. The use of isopleths generally gives a good synthetic picture but an adapted numerical progression of abundances must be chosen. In the conclusion of a study on basic variability Frontier (1974) suggested that statistical laws of dispersion might exist which were largely independent of the zoological group since they were probably linked to the physical phenomenon of dispersion in a turbulent liquid phase. This would lead to the use of the $\log^2$ transformation as we have previously pointed out. According to this author the converted data have then an almost normal distribution with a stable variance of 0.7026 (or σ = 0,838) in samples taken at the same point. This is a residual variability to which spatial variabilities must be compared. The isopleths should thus be chosen on the basis of an interval of constant amplitude of 2 x 1.96σ which is equal to 3.29 on the scale of converted values (0 - 3,29 - 6,58 - 9,87 - etc.). One will then have the following progression of the non transformed values 1 - 64 - 365 1 400 - 4 200 - 11 500 - 27 000 etc. This scaling of isopleths has additional merit in that high values are less flattened and the random fluctuations of the smaller ones are less exaggerated.

2.3.1.2 Cyclic variations

A sound knowledge of these variations allows optimization of sampling.

2.3.1.2.1 Diel rhythm

Temple and Fisher (1965) found that penaeid larvae were located near the bottom during the day and near the surface at night. They noted however that when the water-mass was unstable the distribution was more homogeneous. In contrast Kutkuhn *et al.* (1969) found in the same region *P. setiferus* and *P. aztecus* larvae in the surface water layer during the day while samples taken at night showed a maximum number of larvae in the bottom-layer. Roessler *et al.* (1969) noted that protozoa I of *P. duorarum* were more present in the bottom layer but that protozoa II and III carry out vertical migrations which lead to increased surface abundance at night.

Temple and Fisher (1965) and Roessler *et al.* (1969) found that planktonic postlarvae were distributed near the surface while Kutkuhn *et al.* (1969) observed a homogeneous distribution.

The results obtained are therefore not consistent.

2.3.1.2.2 Lunar rhythm

Roessler *et al.* (1969) noted an increase of larval abundance on moonless nights and related it to an increase in spawning activity. These observations confirm those of Munro *et al.* (1968).

2.3.1.3 Some sampling principles

The location of sampling points must take into account the distribution of the adults. It will a priori be preferable to increase the number of sampling points in zones of greatest abundance. Periodic sampling at a certain number of stations taken at random from a predetermined grid of stations will tend to reduce the variance for a given number of samples and to allow for its estimation (stratified or direct random sampling).

Because of the brevity of the larval stages, a high frequency of sampling should be maintained. At any given moment the observed composition of a larval cohort will depend in part on its absolute age, that is, of the time between sampling and spawning. Since the larval phase lasts about one month, sampling should be performed with a higher frequency.

If spawning has been shown to follow a lunar periodicity, the same frequency could be used for sampling. It should be noted that any frequency of sampling which differs slightly from the base frequency of the sampled phenomenon will bring an artificial oscillation into the results. The ideal, if means allow, would be to sample at each lunar phase. It would be better to increase sampling frequency during the favourable periods of the year (for example when there is a high percentage of mature females).

Bearing in mind the heterogeneity of the data on the vertical distribution of larvae the taking of oblique samples is strongly recommended, especially if sampling takes place during the day.

2.3.1.4 Sampling equipment

In practice any plankton net can be used successfully by adopting a mesh suitable for the stages sampled. Some examples follow:

The Gulf V type net is kept open by a metallic frame. The opening diameter measures 0.40 m. A flowmeter allows the estimation of the filtered water volume. Munro *et al.* (1968) have used a mesh of 293 microns which allows passage of the nauplii but ensures proper sampling of the more advanced stages. Kutkuhn et al. (1969) used a mesh of 190 um with which, in their opinion, they achieved proper sampling of all stages. Le Reste (1978) has used a Clark-Bumpus net as modified by Petit and Bour (1971) with a 0,30 m opening and 180 micron mesh size.

As regards the manipulation of the nets, the density of penaeid larvae in the plankton is too low to obtain usable samples by vertical hauls. The net is therefore hauled horizontally or obliquely. Oblique hauling is probably preferable because bias due to the possible stratification of the larvae in the water column can be reduced.

Hauls should always be of short duration (less than 10 minutes) so as to avoid clogging. With the "Clarke Bumpus" previously mentioned clogging begins when the filtered volume exceeds 50 cubic metre. This is an approximate figure since it depends on the solids and biological content of the water. The plankton is preserved in 10% neutralized formol.

2.3.2 Migrating post-larvae

These are the post-larvae which are already in the process of entering the estuaries after about three weeks of pelagic life at sea. They display increasingly benthic behaviour.

2.3.2.1 Dispersion and treatment of the data

The essentials were covered in paragraph 2.3.1.1. Most authors accept that the variance is proportional to the mean of the population harvested and use a log (n+1) conversion to stabilise the variance to allow the use of the classical statistical methods. It should also be remembered that Frontier (1974) proposes the use of a square log (n+1) transformation.

2.3.2.2 Periodic variations

2.3.2.2.1 Diel rhythm

Whichever catching gear is used, the number of post-larvae observed is almost always higher at night than in daytime (Tabb et al., 1962; Baxter, 1963; Eldred et al., 1965; Copeland and Truitt, 1966; Caillouet et al., 1968; Roessler et al., 1969; Subrahmanyam and Rao, 1970; Roessler and Rehrer (1971); Garcia, 1977; Young and Carpenter, 1977; Lhomme, 1979).

Some authors have not however observed any differences (Eldred et al., 1965; St. Amant et al., 1966; Caillouet et al., 1970).

Observations on the abundance of migrating post-larvae as a function of the depth are somewhat contradictory. Roessler et al. (1969) and Roessler & Rehrer (1971) observed that the most important catches at night, both at full and new moon were made at bottom levels. Eldred et al. (1965) found many more post-larvae at the surface than at the bottom during the day and slightly more on the bottom than at the surface at night. Copeland and Truitt (1966) observed no differences between the bottom and the surface during the day but noted greater abundance at the surface at night.

2.3.2.2.2 Lunar rhythm

Catches are generally higher during new moon (Subrahmanyam, 1966; William and Deubler, 1963; Roessler et al., 1969; Subrahmanyam and Rao, 1970; Roessler and Rehrer, 1971; Garcia, 1977). A second less important peak at full moon has sometimes been recorded. However it should be noted that Eldred et al.(1965) and Subrahmanyam and Ganapati (1971) observed that the maximum occured sometimes at full moon.

2.3.2.2.3 Tidal rhythm

Practically all authors record more abundant catches at flood tide (Tabb et al., 1962; Eldred et al., 1965; St. Amant et al., 1966; Caillouet et al., 1968 and 1970; Roessler et al., 1969; Subrahmanyam and Rao, 1970; Roessler and Rehrer, 1971; Garcia, 1977; Young and Carpenter, 1977; Lhomme, 1977).

Caillouet et al. (1968, 1970) record however that the daily maximum they observed was associated with the ebb tide or slack water at low tide.

The results for benthic post-larvae are therefore in reasonably good agreement: the most abundant catches are generally obtained at night with a new moon at flood tide.

2.3.2.2.4 Seasonal rhythm

Post-larval abundance in estuaries is the resultant of mechanisms of reproduction and of transport by currents during a period when survival most probably depends on surrounding conditions, although in general there is a tendency to consider that variations in reproduction are the only source of seasonal fluctuations.

The action of environmental factors on larval migration is well reflected in the size of the post-larvae during their migration into the estuaries. This type of variation has been observed by Baxter and Renfro (1966), Copeland and Truitt (1966), Temple and Fischer (1967), Garcia (1977), Le Reste (1978); Lhomme (1979). Garcia (1977) and Lhomme (1979), showed that the variations are synchronous for all stages (as defined by the rostral formula) and are positively correlated with phytoplankton abundance at sea and negatively correlated with the temperature. Other hypotheses have been also advanced to explain this phenomenon: variations in the distance between the spawning zone and the mouth of the estuary, variations in growth rate, action of flood water preventing larvae from entering lagoons in rainy seasons and over-wintering of larvae outside lagoons.

2.3.2.3 Some sampling principles

Post-larvae are collected in shallow water with muddy bottoms, or bottoms covered with vegetation, or in deeper water in the axis of the channels. Sampling in the main channel, if possible, has the advantage of being made in an area of concentration of the larvae, often agitated by turbulence where spatial and sampling variability will probably be less than in the estuary itself. Diel and lunar rhythms are very clear in these circumstances and sampling is easier to standardize. If some experiments verify that in the studied area the catches are generally higher at night than during the day (especially at the surface, in the channels) and during flood-tide and with the new moon (as is usually the case) it will be sufficient to sample once a month at new moon at night when the tide is rising. If the means allow it, it is also advantageous to make observations at full moon.

Since abundance varies with the state of the tide, samples can be taken during the entire period of flood-tide by short net hauls to avoid clogging which can be rapid. The index of abundance is then obtained by plotting the numbers caught against the time on a curve and integrating the area under the curve.

Garcia (1977) in the Ivory Coast showed that when the tide is semidiurnal, the two high tides which occur at the beginning and the end of the night give duplicate information and that sampling of a single tidal cycle is sufficient.

Effort can be reduced by sampling only when the tide is rising, from low to high water, by short net hauls and discontinuing sampling after the maximum has been obtained (a little after slack water at high tide).

When samples are taken from a bridge, several hauls can be made simultaneously so as to calculate the variance. When sampling is done from a small boat, this is in general not possible.

When samples are taken from the bottom in shallow areas, St. Amant et al. (1965) showed that the variance can be minimized by taking samples at stations selected at random from a predetermined grid rather than by periodical visits to fixed points.

Since the bathymetric distribution of post-larvae during migration is not clearcut, it would be better to make oblique hauls (difficult to achieve with a light boat) or bottom and surface hauls simultaneously (this is only feasible from a fixed platform when there are adequate currents, or from a large boat).

2.3.2.4 Sampling equipment and its operation

The problem of sampling shrimp larvae is largely the same as that of plankton in general: for a good bibliography one can usefully refer to Jossi (1970).

2.3.2.4.1 Sampling along the banks in shallow water

(a) The Renfro (1963) (Fig. 9) trawl for post-larvae.

This is the most frequently used gear. It has a conical form and the cloth has 50 meshes per cm^2. It has been used in particular by Baxter (1963) in Texas, by Brisson and Lucet (1975) in Brazil and by St. Amant *et al.* (1965) in Louisiana. In operation, the net is pulled by hand by means of a bridle fixed to the ends of an iron bar. When the net is towed slowly the bar scrapes the bottom driving the post-larvae towards the net entrance. The net is fixed by a rope to a post embedded in the river bank. At the beginning of the haul the rope is stretched parallel to the bank and is used as a constant radius when the net is towed. Thus the net describes a half circle. In this way the haul is always made from the same point, its length is constant and also covers several bathymetric strata.

A statistical analysis of the performance of this equipment has been made by Caillouet *et al.* (1968) who found that the abundance of the post-larvae caught by unit of length covered was independent of the radial length for distances between 1·5 and 45 m; they recommended therefore a radial length of 15 m. They also advised at least one two-way haul to eleminate the possible effect of tidal currents, and confirmed that the variance of their abundance estimates was proportional to the average.

Berry and Baxter (1969) showed that the variability between two successive hauls is only 2% but that the variability over a period of 4 days is equal to the seasonal variability, because of the fact that in a given place the post-larval abundance can vary from 0 to a very high number in a few hours.

(b) Sleds or roller nets

Pullen, Mock and Ringo (1968) used a small sled pulled by hand along the banks. According to the authors this very simple apparatus is easier to use than the Renfro trawl.

Allen and Hudson (1970) developed a sled which worked by suction created by the venturi effect. This made it possible to suck in and sift the total surface layer of the sediment. This apparatus which samples a narrow surface layer enabled a detailed study of the bathymetric distribution of larvae to be made. About twice as many young shrimps can be caught than with the simple net of Pullen, Mock and Ringo (1968) and the gear is effective for making an overall assessment of the benthic biomass.

Brusher and Marullo (1970) developed a sled equiped with a flowmeter and an excavatory roller at the front which could be used in areas of medium depth.

With all these devices it was also possible to capture juveniles, with variable efficiency.

2.3.2.4.2 Sampling in open water in channels or bays

(a) Fixed nets

Young and Carpenter (1977) used a net with a lozenge-shaped opening with a mesh of 1mm. The fishing depth was controlled by a rope linking the net to a surface buoy. The lower part of the net was moored to an anchor with a ballast weight of 13,6 kg. Swivel-hooks allowed the net to swivel freely and to stay permanently in the axis of the current. The latter was always strong enough to keep the net open. Every 10 to 20 minutes the net was taken in to avoid clogging and replaced by a new one. The nets were placed at several points across the channel.

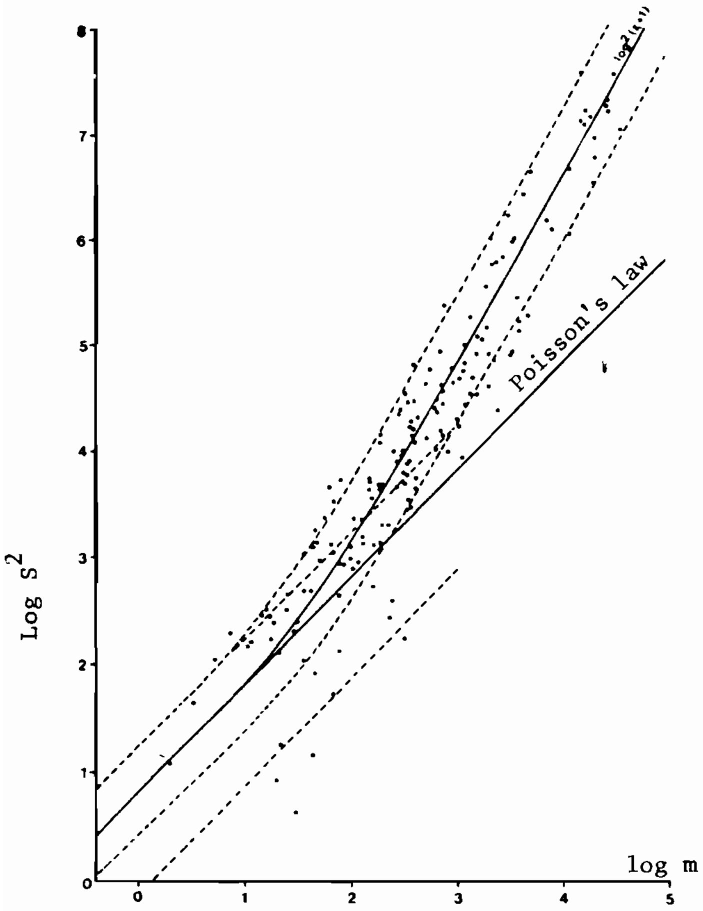


Fig. 8 Relationship between mean and variance in a tropical zooplancton population (from Frontier, 1871)

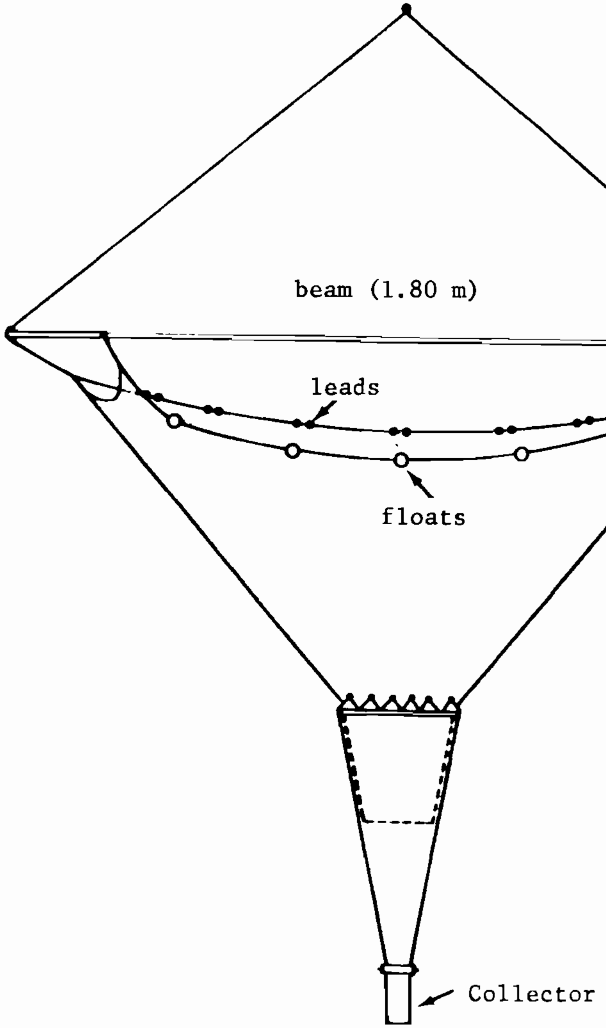


Fig. 9 Postlarval beam trawl (from Renfro, 1963)

(b) Towed plankton nets

Different types of nets have been used. It is preferable to select one with the diameter of the opening large enough to limit the avoidance effect. Roessler et al. (1969) used a net with a 1 m diameter opening, which seems convenient for sampling post-larvae. The authors however used a mesh of 467 microns which is perhaps needlessly small. Garcia (1977), comparing catches from two nets with meshes of 500 microns and 700 microns respectively, did not observe any difference and chose the second mesh which allowed an appreciable decrease in clogging. The net must be fitted with a flowmeter.

(c) Continuous sampling

Fontaine et al. (1972) developed an apparatus which allows the harvesting of large quantities of living post-larvae. Two nets are kept just below surface level on both sides from an anchored boat (or from a platform) (Fig. 10). A pipe is fixed at the end of each net and the two pipes joint into a single one on the deck of the boat. A pump draws up the water and with it the organisms which enter the nets. The water is filtered through three screens made of rods with different spacings. The material collected in the last tank contains a large proportion of penaeid post-larvae although about 10% of them may be retained during filtration. This material is thus very easy to sort.

Marullo (1973) developed an apparatus which could sample automatically in open water. At regular time intervals, a pump drew in water which was filtered through a small net with a mesh of 1 square mm. This net, and eleven others, were fixed on a circular horizontal frame. Every two hours the frame turned slightly on its axis so that a new net came under the water inlet. While one net was in operation, all the others soaked in a trough filled with diluted formal which ensured preservation of the samples. Unfortunately the number of post-larvae caught per hour was rather low (5 on average), much less than in catches obtained simultaneously with the Renfro trawl. Morevoer the seasonal variations in abundance obtained with the two types of gear were not synchronous. The author thought nevertheless that sampling could be improved by increasing the diameter of the water intake, by concentrating sampling in the floodtide period and by choosing a better suited sampling point.

2.3.3 Juveniles in estuaries

2.3.3.1 Distribution

After entering the estuaries the post-larvae concentrate in shallow areas of less than one meter deep. Their distribution is extremely heterogeneous and sampling them is therefore particularly difficult.

Salinity has for a long time been cited as an essential factor in the distribution (Gunter, 1950, 1956; Gunter, Christmas and Killibrew, 1964; Williams, 1955). Slightly different preferences have been noted, for example for *Penaeus setiferus*, *P. aztecus*, and *P. duorarum* inhabiting the same estuaries. Zein Eldin and Aldrich (1965) showed however, that salinity did not have an effect either on growth or survival and that other factors must be responsible for the distribution (food sources, vegetal cover, type of sediment, currents, etc.). Williams (1955) noted that shrimps preferred a silt bottom rich in organic matter. These results were confirmed by Loesch (1965) Galois (1970) and several others.

According to Garcia (1977) the marine influence was the limiting factor in the distribution of *Penaeus notialis* influence, and particularly the tidal currents are factors which determine the distribution limits. Within these limits, other factors, in particular nutritional factors, affect the distribution.

The estuarine distribution of shrimps is also marked by considerable time-space variations. The importance of movements within the estuaries has been shown for example by Tabb et al. (1962), Galois (1975), Parker (1970) and Le Reste (1978). Alternating movements between the banks and the channels appear to be linked to changes in environmental factors such as decreased salinity associated with rain (Galois, 1975). Such quantitatively small movements can only be identified by very meticulous sampling.

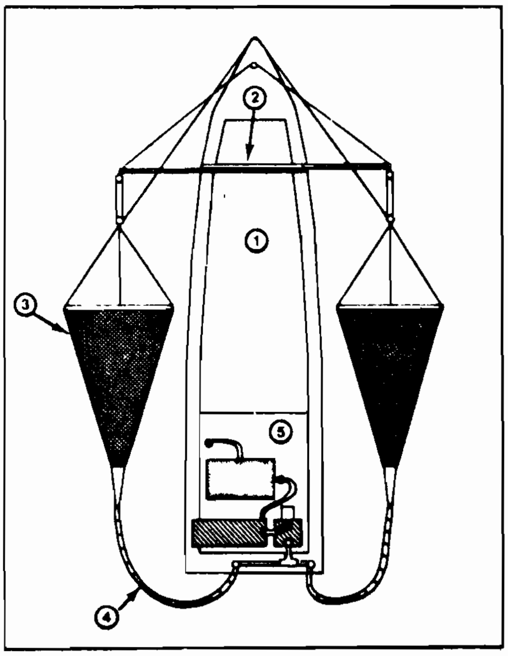


Fig. 10 Diagram of the continuous sampling system:
1. boat; 2. beams; 3. rectangular frame nets; 4. pump hose; 5. pumping and sorting system (simplified from Fontaine et al., 1972)

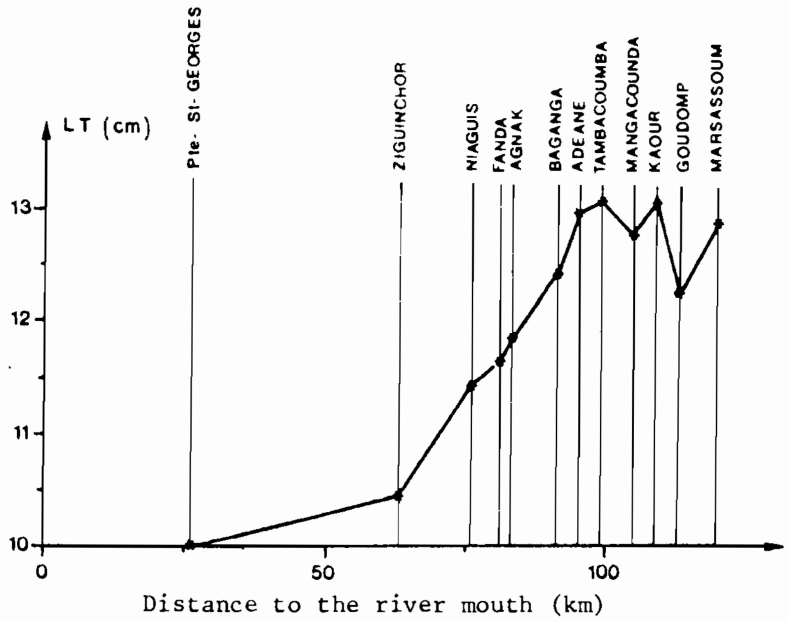


Fig. 11 Variation of the average size along the upstream-downstream axis of the Casamance estuary (Senegal) - (from Lhomme, 1979)

As they grow, shrimps migrate towards the deeper zones and channels and there is always a gradient of increasing sizes from the interior of the estuary to its mouth and from the banks to the channels (Williams, 1955; Dall, 1958; Tabb et al., 1962; Gunter et al., 1964; St Amant et al., 1965; Saloman, 1965; Parker, 1970; Ruello, 1975; Galois, 1975; Le Reste, 1978).

In Senegal, in the "river" Casamance where there is a nucleous of high salinity in the intermediate part of the "river" the variation of sizes from the inner parts to the mouth of the estuary is reversed (Lhomme, 1979) (Fig. 11).

2.3.3.2 Periodic variations in catch rates

The nocturnal character of the burrowing activities of shrimps tends to generate a diel rhythm of catch rates (Saloman, 1968). Garcia (unpublished) has also noted a clear increase in yields at night using an otter trawl). Clark and Caillouet (1973), on the other hand, working with the same kind of equipment in a small bay, caught more P. aztecus in daytime than at night and found no difference between day and night for Penaeus setiferus.

These disparities can be explained by the fact that in shallow zones, classical variations in catchability between day and night are distorted by water turbidity and by the action of boat propellers. In addition, in very soft substrates the digging action of the trawl is considerable - often sufficient to catch burrowed shrimps. Munro (1975) pointed out that this depended on the shrimps species. Saloman (1968) however, achieved better catches in new moon, first and last quarters than at full moon.

Clarke and Caillouet (op. cit.) noted maximum catches at hight tide.

2.3.3.3 Some sampling principles

It is practically impossible to sample the entire range of sizes in a population (from 2 to 10 centimetres) with the same equipment because of the differential size distribution in regions of variable accessibility. The banks, whether covered with grass or not, and attainable on foot or not, according to the consistency of the mud, are sampled with a seine net or a towed net while the channels are most often sampled with a trawl. It would therefore be extremely difficult to build up a picture of the size structure of a population in a small bay and more so in a lagoon.

Because shrimp growth is very rapid, sampling frequency must be high (1 survey per week). To examine growth or movement on a small scale, it is often necessary to limit the zone studied to a small area (avoiding for instance migration channels) carefully chosen after a preliminary general survey. Galois (1975) has obtained excellent results with limited means.

Although no studies have been made on this subject, techniques for stratified random surveys should preferably be used taking a higher number of samples in zones of greater abundance.

2.3.3.4 Sampling equipment and handling

Sampling equipment is extremely diversified in order to cope with the wide range of habitats which must be sampled.

2.3.3.4.1 Roller or sled nets

These are of different forms although their action is always based on the same very simple principle.

Allen and Inglis (1958) have used a small sled pushed from the rear by a long handle. This method avoids agitation of the substrate before the passage of the apparatus, which moreover catches post-larvae as well as juveniles. Having a small opening the net does not take good samples of the larger juveniles.

Penn and Stalker (1975) have developed a design which allows daylight sampling of juveniles which are burrowed into the sediment. The net is attached to a rectangular frame on skis and fitted with a roller to prevent sticking in the mud. A pump throws a jet of water on the front part of the net which agitates the sediment to a depth of 3 cm and causes the shrimps to emerge. The authors considered that there was no escapement of shrimp

2.3.3.4.2 Equipment derived from the artisanal fisheries

Such equipment is often used, in its original form or modified; one can give as an example the Kili (in Senegal) which is a small trawlnet kept open by two rods handled by two men who push it in front of them along the water's edge.

The principle of the beach seine-net is also employed. Having a very fine mesh (mosquito-net for example) it can retain post-larvae and juveniles of small size.

The otter and beam trawls are also often used. The first is preferred because it can be easily handled from a small boat. More often the classic try-net is used, sometimes with modified meshes (2.5 to 6 meters of head rope, about 50 cm high, 6 to 8 meters long and variable mesh).

The usefulness of the trawlnet for sampling shallow bottoms is uncertain because of the disturbance caused by propeller agitation and the avoidance action which it must cause. On this point Loesch et al. (1976) demonstrated that the efficiency of the trawlnet in shallow bottoms is only 30 to 50%.

This result is confirmed by Edwards (1977) who calculated an efficiency of 35% for a small beam trawl in shallow water.

If the efficiency varies with the depth of water under the hull - always possible though never established - a source of bias is introduced.

The beam trawl and its various versions used in local fishing in the United States are also excellent sampling devices (Tabb and Kenny, 1969) (cf. para. 3.1.1.2) and have also been used by Young (1975) in Australia.

2.3.3.4.3 Electrical fishing

Lamarque, Therezien and Charlon (1974), in the course of their experiment in adapting electrical fishing to warm and conductive tropical waters, have obtained rewarding results with Madagascar shrimp in a mangrove swamp. The hourly yields with the electric scoop were from 0.3 to 2.7 kg/hour.

The electrical trawl which has been thoroughly tested at sea (cf. section 3.2) does not seem on the other hand to have been used in estuarine waters. It is true that the water temperature, stratification , salinity gradients and their effects on water resistance create technical problems which are difficult to solve.

2.3.4 Migrating sub-adults

2.3.4.1 Distribution

Beardsley (1970) made a detailed study of migrating juveniles in a channel. He showed that 83% of the shrimps caught were in the surface layer. The distribution depended on the lunar cycle and the number of shrimp at the surface varied from 90-70% between full moon and the first quarter (Fig. 12). He did not demonstrate differences related to salinity, size, sex, tide or temperature. He however observed differences in lateral distribution as a function of moonlight; the shrimps apparently preferred the illuminated side of the channel.

2.3.4.2 Periodic variations

A summary of findings on rhythms and migration was made by Allen (1966).

2.3.4.2.1 Diel rhythm

In very general terms, shrimp do not migrate during day-time, barring exceptional cases (Idyll, 1964; Idyll *et al.*, 1964; De Bondy, 1968; Yokel *et al.*, 1969; Hoestlandt, 1969; De Labretonne and Avault, 1971; Garcia, 1977). However in Madagascar Le Reste (1978) did not observe differences in the catches of *Penaeus indicus* using Chinese barrier traps.

2.3.4.2.2 Lunar rhythm (Fig. 22)

Catches are almost always greater at new moon and full moon than at the quarters, and the absolute maximum is at new moon (Copeland, 1965; Subrahmaniam, 1967; De Bondy, 1968; Yokel *et al.*, 1969; Garcia, 1972, 1977). This is probably due for the most part to the fact that fishing is carried out with fixed stake nets during ebb tides and gives consequently greater catches during strong tides. Yokel (1969) has in fact shown that in the Everglades (Florida) 52% of the variations in catch rates observed could be attributed to variations in the volumes filtered in association with velocity changes in current and the height of the tides.

Boddeke, Dijkema and Stemelink (1977) however, confirming the observations of Racek (1959), showed an identical rhythm for *Penaeus brasiliensis* in a closed pond fed by pump and without any tidal rhythms, which would lead to the supposition that currents are not the only operative factors. These authors pointed out that the sensitivity of shrimps to migrational stimuli depended on their moulting stage. Moulting is centred around the full moon, inhibiting migration which begins after the last quarter when moulting is completed.

De Bondy (1968) in Senegal also noted variations in sex-ratio in the catch as a function of lunar rhythm.

2.3.4.2.3 Tidal rhythm

When the shrimps are fished with fixed gears they are always caught in greater quantity during ebb than flood tide (Idyll *et al.*, 1964; Yokel *et al.*, 1969; De Bondy, 1968; Hoestlandt, 1968; De Labretonne and Avault, 1971; Garcia, 1972, 1977; Le Reste, 1978; Lhomme, 1979).

With othe sampling gear, the greatest apparent abundance can be found at other phases of the tidal cycle. For example, De Labretonne and Avault (op. cit.) observed such high apparent abundance with a fixed net during ebb-tide but with a cast-net during flood-tide.

The difference may arise from the fact that certain gears catch an active phase swimming in open water towards the mouth of the estuary while other gears catch a phase of the population which has burrowed into the sediment. It is also possible that the indices of abundance obtained with the two types of gear (passive and fixed or active and towed) are not really comparable.

In general then, we can note that the catch rates of migrating juveniles are at a maximum at night with ebb tide and at new and full moon if sampling is carried out with fixed gear. When using towed gear and raking the bottom one must ensure, if this is the objective, that it is the migrating phase which is being measured and not that of the resident population of which the growth cycle is not yet completed.

2.3.4.2.4 Seasonal rhythm

Information on this rhythm is most important to obtain; knowledge of previous rhythms is mostly useful to optimise the sampling scheme but it is in fact this particular rhythm which provides information on seasonal variations in recruitment, an essential parameter for stock assessment.

Although reproduction is commonly continuous among the penaeids, a clear seasonal fluctuation in migration can in general be observed which can be associated with an abundance of mature females or with post-larvae some two or three months earlier (cf. Fig. 6).

The seasonal fluctuations observed are in fact the variations of the apparent abundances, defined as the product of the true abundance and the catchability. This latter is associated with tidal currents and flood periods, and the effects of fluctuations in catchability can sometimes be observed as distortions of the basic annual oscillation, corresponding to the annual equinoctal tides or river floods. The basic fluctuation can also be distorted by sudden drops in temperature in autumn which tend, in the northernmost limits of distribution of the penaeids, to force the shrimps into deeper waters (Tabb et al., 1962).

Certainly there are many factors which can trigger the migration of shrimps (for a review see Garcia (1977)). It should be noted that these factors interact, as is the case with regard to their influence on behaviour (Zein-Eldin and Aldrich, 1965). Furthermore, one can imagine that the decisive (limiting) factors are not necessarily the same in regions with low annual thermal variations and high rainfall (India, Madagascar, Ivory Coast) and in those with the opposite characteristics (Senegal, Florida, Texas).

The average size of migratory shrimps also follows a seasonal fluctuation (Fig. 13). This has been observed by many authors (Tabb et al., 1962; St. Amant et al., 1965; Trent, 1967; Yokel et al., 1969; Pullen and Trent, 1969; Parker, 1970; Ruello, 1973; Garcia, 1972 and 1977; Le Reste, 1978; Lhomme, 1979). Several hypotheses have been proposed to explain the phenomenon: growth and recruitment, competition for food, variable length of stay in lagoons. In fact, it is probably true that the size at migration is a complex resultant of the conditions of nutrition and temperature during growth as well as of the length of stay which, at the end of the growth period can be abbreviated by the occurrence of unfavourable conditions (decreasing salinity, low temperatures).

2.3.4.3. Some sampling principles

Samples must be taken at night. It is best if the gear can sample a surface layer deep enough to include the greater majority of the shrimp present in the water mass. It is also preferable, if the sampled channel is wide, to take several simultaneous samples across the entire width: this is only possible with fixed nets. It must also be noted that at very low current speeds, the shrimps are able to swim against the current out of the nets. Narrow channels and bridges are good working points. The gear must be set at the beginning of the ebb-tide and withdrawn as soon as the current slackens. It could be worthwhile to measure the current or to position flow-meters close to the nets to estimate the volume filtered. During one tidal phase regular catch samples can be taken from the stake nets so as to ascertain the variation in the numbers caught in relation to the tidal cycle.

It should also be noted that if an index of recruitment is required (that is an amount proportional to the quantity of shrimps which have left the nursery) it is the number per tide cycle which is of value and not the number per unit volume filtered.

In addition, an excellent index with good precision can be obtained from the catch data of the artisanal fishery, especially when fixed nets are used. An example of an in-depth analysis of the data obtained by this method can be found in Garcia (1977). Yokel (1969) and Beardsley (1970) have done excellent work on rationalized experimental sampling.

2.3.4.4 Sampling equipment

2.3.4.4.1 Experimental fixed nets

Yokel et al. (1969) used a net of 1.8 m x 1.07 m opening stretched on a rectangular framework, and 5.2 m length (wing net). Two nets with a stretched mesh size of 1.9 cm were kept near the surface on either side of a small boat. Large anchored nets of the "channel net" type were also tested by Yokel but are now little used.

Beardsley (1970) carried out a detailed analysis of the distribution of shrimp in a water mass by sampling an entire vertical section of a channel using a group of 13 conical nets of 50 cm diameter.

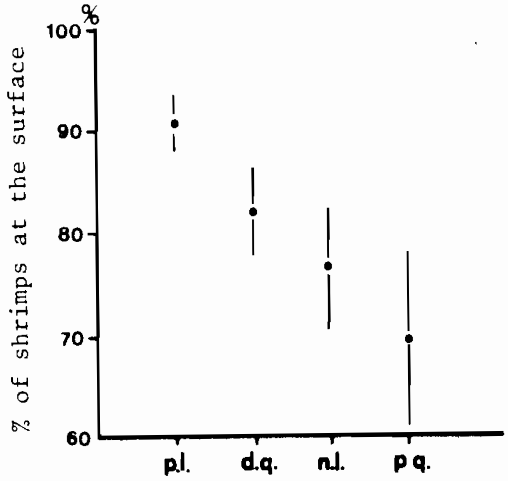


Fig. 12 Vertical distribution of migrating shrimps at different lunar stages (from Beardsley, 1970)

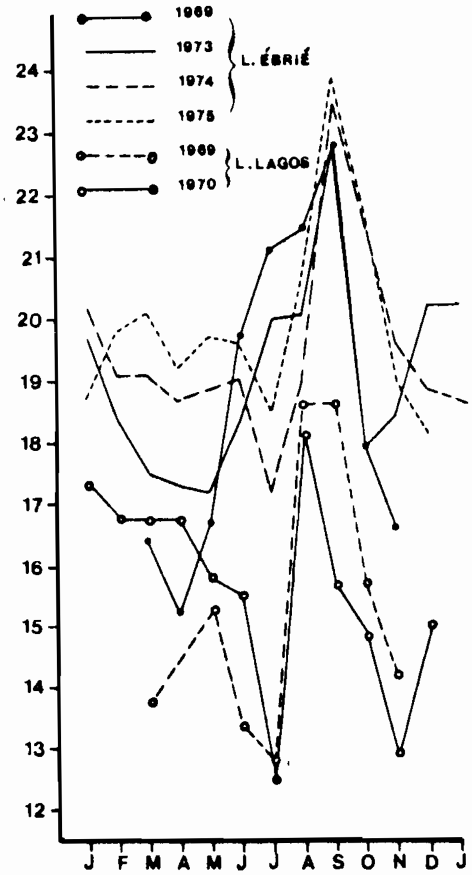


Fig. 13 Seasonal variations of size at migration in Ivory Coast (Ebrié lagoon) and Nigeria (Lagos lagoon) (from Garcia 1977)

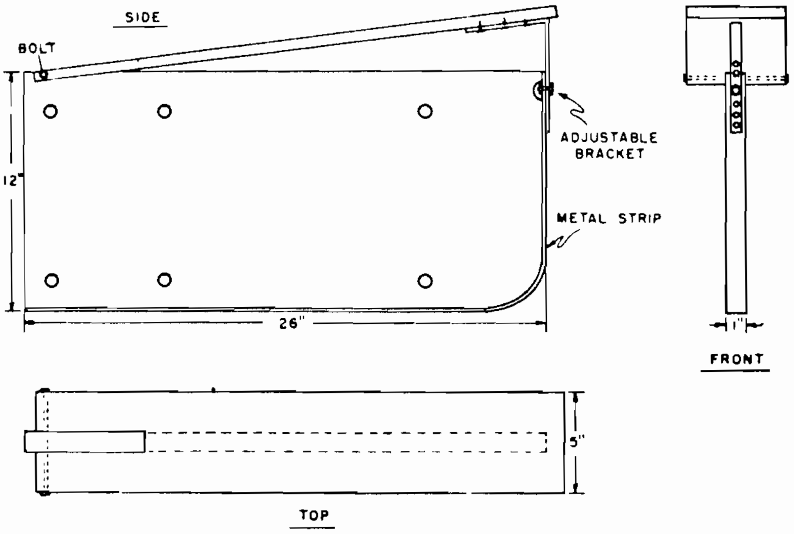


Fig. 14 Modification of otter board with hydrofoils for surface trawling (from Trent, 1967)

2.3.4.4.2 The bottom or the pelagic otter trawl

At the entrance of Galveston Bay, Pullen and Trent (1969) took their samples using an otter trawl with a 3 m opening. The trawl was dragged successively on the surface, at mid-depth and on the bottom. Samples were taken in the daytime: the catch per unit effort increased from the surface towards the bottom. Surface trawling is carried out by attaching two simple hydrofoils to the doors of a normal trawl (fig. 14). This equipment is easy to handle and gives yields 5 times greater than the classical bottom trawl (Trent, 1967a).

2.3.5 Sub-adults and adults at sea

2.3.5.1 Distribution

2.3.5.1.1 Geographical distribution

Distribution is associated with environmental conditions. Strong concentrations suitable for exploitation are found above soft sediment with a content of silt and organic matter which varies for different species (Grady, 1970; Garcia, 1974).

When there are several species in a region their relative distribution appears to be related to hydrological conditions and in particular to their tolerance to variations in salinity or other associated factors. This is the reason for the absence of P. duorarum off the mouth of the Mississippi or the Amazon (Burkenroad, 1939) and for the relative distribution of the three principal west-atlantic species.

Details of the distribution appear to be sometimes associated with turbidity (Crosnier, 1965; Lindner and Bailey, 1968).

The general distribution seems to be stable, except at the extreme geographical limits where shrimps are liable to undertake large-scale migrations in winter (Lindner and Anderson, 1956; Burkenroad, 1939). In other fringe regions there is no seasonal migration; instead a metabolic modification takes place (cessation of growth and lowered activity) as for instance in Senegal (Garcia et al., 1973).

2.3.5.1.2 Bathymetric distribution

Locally shrimp distribution is heterogeneous. The shrimps are not uniformly distributed and are concentrated in at certain depths.

Although geographic limits are usually easy to relate to the nature of the bottom and the presence of estuaries, bathymetric limits are more difficult to explain. Garcia (1977) showed that the upper limit of the distribution of P. notialis on the West African coast is determined by the nature of the sediment and that the lower limit seems to be more associated with hydrological conditions. Rather curiously, the prevailing conditions (absolute hydrological values and annual variations) are the same as those found at the northern and southern geographical limits of the species distribution.

According to zones and species, abundance is maximal either at the centre of the bathymetric distribution (Fig. 15) (Garcia, 1974; Costello and Allen, 1970) or towards the coast (Lindner and Cook, 1970).

In addition the size distribution on a fishing ground is generally not homogeneous. Along the axis of migration from estuaries towards deeper water younger shrimps are often found in the coastal region and the bigger adults in deeper water (Burkenroad, 1939; Lindner and Anderson, 1956; Iversen, Jones and Idyll, 1960; Renfro and Brusher, 1964; Costello and Allen, 1966, George et al., 1968). This is not always the case however and Garcia (1977) noted on the Ivory Coast a central zone, in which shrimps have a medium size situated between a coastal and deep-water zone, where older individuals predominate (Fig. 15).

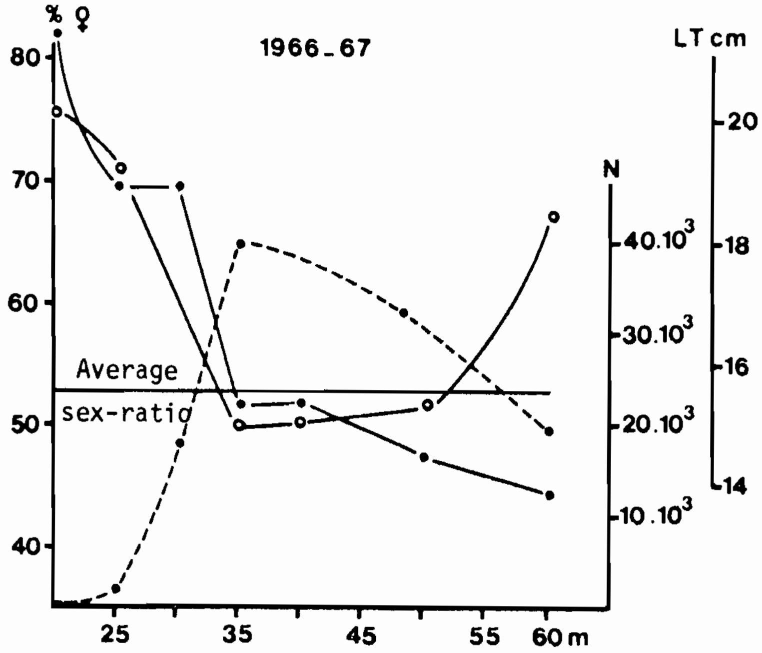


Fig. 15 Bathymetric distribution of numbers (---), average size (o—o), sex ratio (•——•), in Ivory Coast (from Garcia, 1974)

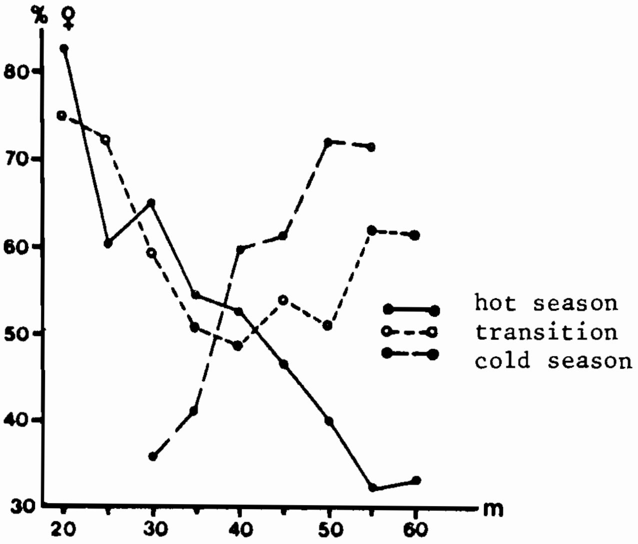


Fig. 16 Bathymetric distribution of sex ratio by season (from Garcia, 1974)

The sex distribution has been little studied. Kinju (1968) however pointed out that in India *Solenocera indica* females spawn at the limits of the distribution area while the males remain in the shallow regions. Garcia observed that during the reproduction period a higher percentage of females is found in the coastal zone, decreasing regularly towards deeper waters (Fig. 15).

In sub-section 3.5.2 it shall be seen that all these distributions are liable to periodic variations.

2.3.5.1.3 Pattern of distribution

The distribution of individuals in a given area can sometimes be considered homogeneous. Certain authors have in fact noted the absence of schooling behaviour, for example in *Penaeus aztecus* (Cook and Lindner, 1970). More generally it seems that penaeids show some phases where they assemble in schools or swarns (*P. duorarum* (Costello and Allen, 1970), *Parapenaeopsis sculptilis* (Kirkegaard and Walker, 1970), *Penaeus merguiensis* (Kirkegaard *et al.*, 1970), *Metapenaeus dobsoni* (Panikkar and Menon, 1956; De Bruin, 1965), *Penaeus schmitti* (Perez-Farfante, 1969), *Penaeus indicus* (Crosnier, 1965), *Penaeus merguiensis* (Munro, 1975)).

2.3.5.2 Periodic variations

2.3.5.2.1 Diel rhythm

Adult shrimps generally burrow into the sediment during the day and swim near the bottom at night; they are then more easily caught by classic trawl nets (Idyll, 1950; Williams, 1955 and 1958, Viosca, 1957; Eldred, 1958, Iversen and Idyll, 1960; Dall, 1958; Eldred *et al.*, 1961; Egusa and Yamamoto, 1961; Fuss, 1964, Crosnier, 1964; Fuss and Ogren, 1966; Wickham, 1966; Le Guen and Crosnier, 1968; Garcia *et al.*, 1973; Wickham and Minkler, 1975; Moller and Jones, 1975, Marcille, 1978).

This may not be true when little light penetrates the water layer (turbid water, cloudy sky); shrimps normally caught plentifully at night may then be taken in daytime. It is for this reason that seasonal changes in the "apparent" diel rhythm were shown in several areas of the gulf of Guinea, in relation to hydroclimatic variations (Garcia *et al.*, 1973).

In certain species catches are greater in daytime than at night. This is true for *Penaeus indicus* (Chabanne and Plante, 1971; Marcille, 1978) *Penaeus setiferus* (Idyll, 1950; Joyce, 1965), *Penaeus schmitti* (Perez-Farfante, 1969), *Metapenaeus macleayi* and *Penaeus plebejus* (Racek, 1959), *Xiphopenaeus kroyeri* (Neiva, 1969), *Penaeus notialis* on the Ivory Coast (Garcia, Petit and Fonteneau, 1973; Garcia, 1975).

In zones where several species cohabit, their different rhythms cause diel variations in the species composition of the catches. Thus in Madagascar, the catches obtained between 02h00 and 06h00 contain 10% *P. indicus*, 75% *Metapenaeus monoceros* and 14% *P. semisulcatus*, whereas the catches made between 06h00 and 18h00 contained 96%, 2% and 2,5% of these species respectively.

Special rhythms can be observed during the reproduction period. In Madagascar for example, during the most favourable period for the ripening of the gonads the females of *P. indicus*, normally caught in daytime are then, for the most part, fished at the beginning of the night.

2.3.5.2.2 Lunar rhythm

It seems that shrimps which are usually fished at night can be caught in the greatest quantities at new moon (Iversen and Idyll, 1960; Fuss, 1964; Idyll *et al.*, 1969; Penn, 1976). But it is often difficult however to demonstrate a clearly defined lunar rythm: for example in the case of *Penaeus semisulcatus* and *Metapenaeus monoceros* in Madagascar, Marcille (1978) pointed out that catches are higher at full moon at the end of the hot season and at the beginning of the cool season, and during the first quarter of the new moon at the end of the cool season and the beginning of the hot season. He also showed that the results obtained vary from one year to the next. The differences observed between the different phases are on the average, small and their significance uncertain.

2.3.5.2.3 Seasonal cycle

This cycle affects many characteristics of the shrimp stock.

(a) Variations in bathymetric distribution

The average bathymetric distribution described in the previous section is liable to seasonal variation, especially in regions where hydrological conditions vary considerably. Crosnier (1963) suggested that this type of variation existed in Penaeus notialis. Garcia (1974) using precise data from the log books of the Ivory Coast fleet, confirmed the existence of periodic displacements of the greatest shrimp densities which were closely related to oscillations of the thermocline (Fig. 17).

In Madagascar, in the bay of Ambaro, shrimps of the species Penaeus indicus are almost completely restricted to the intertidal zone during the dry season, while during the wet season they are widely distributed throughout the bay (Chabanne and Plante, 1971, Le Reste, 1978). The variations in distribution may be related to food availability. In India this type of migrations of many species is related to the monsoon and upwelling (FAO, 1973a, page 24).

(b) Variations in the relative distribution of the sexes

Garcia (1974) showed in the Ivory Coast that the bathymetric distribution of the percentage of females underwent seasonal variation. In the hot season females predominated on the coast and the males in deeper water, and in the cold season exactly the opposite took place. During the transition periods the females predominated both in deeper water and on the coast (Fig. 16).

(c) Variations in the distribution pattern

It has been shown in some cases that the behaviour of the shrimps and their schooling activity could vary seasonally.

Marcille (1978) using fishing data in Madagascar showed that P. indicus, captured essentially during the day, has a stable schooling behaviour. This "over dispersion" gives a slope of clearly more than 1 in the ratio between the mean catch per trawl and its variance. Metapenaeus monoceros and Penaeus semisulcatus essentially caught at night, show seasonal variations with gregarious behaviour at the beginning of the year and a distribution close to random at the end of the year (Fig. 18). He has also demonstrated that seasonal variations occur in the vertical height of the schools of P. indicus. This aspect will be taken up later in the chapter on changes in catchability.

2.3.5.3 Sampling schemes

Sampling should take into account possible seasonal modifications in the zones of distribution, as well as the bathymetric distribution of the densities and the sexes. The work will be facilitated by knowledge of the principal axes along which the variation occurs.

The difficulties caused by diel variations in yield or by changes in vertical distribution are for the most part impossible to resolve satisfactorily. On the other hand, seasonal changes in nycthemeral rhythm could be taken into account by changes in sampling hours if a particular species is under examination.

Two sampling schemes can be used: the equidistant transects (systematic) method, or the random or stratified random survey. In the first case each trawl haul is taken to be representative for a certain surface (element) and all the stations are examined in every fishing campaign. The composition of a population on a transect is calculated by combining all the data per haul weighted by the area of the elements. This method is justified for the very first surveys, when no information at all is available on the structure of the biotope or the population (Grosslein, pers. comm.).

Simple random surveys, where the distribution of all the stations is determined on a random basis have an advantage in that they allow the variance to be calculated, which enables one to apply statistical tests to determine the significance of variations observed between one fishing campaign and the other or one zone and the other.

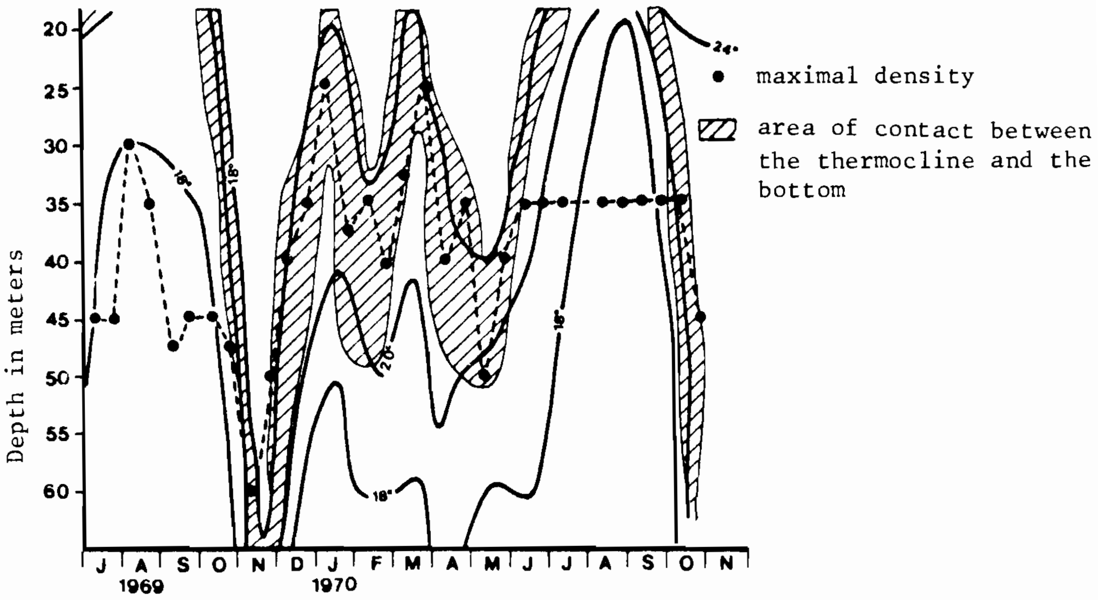


Fig. 17 Seasonal variations of the depth of the termocline and maximum density in Ivory Coast (from Garcia, 1974)

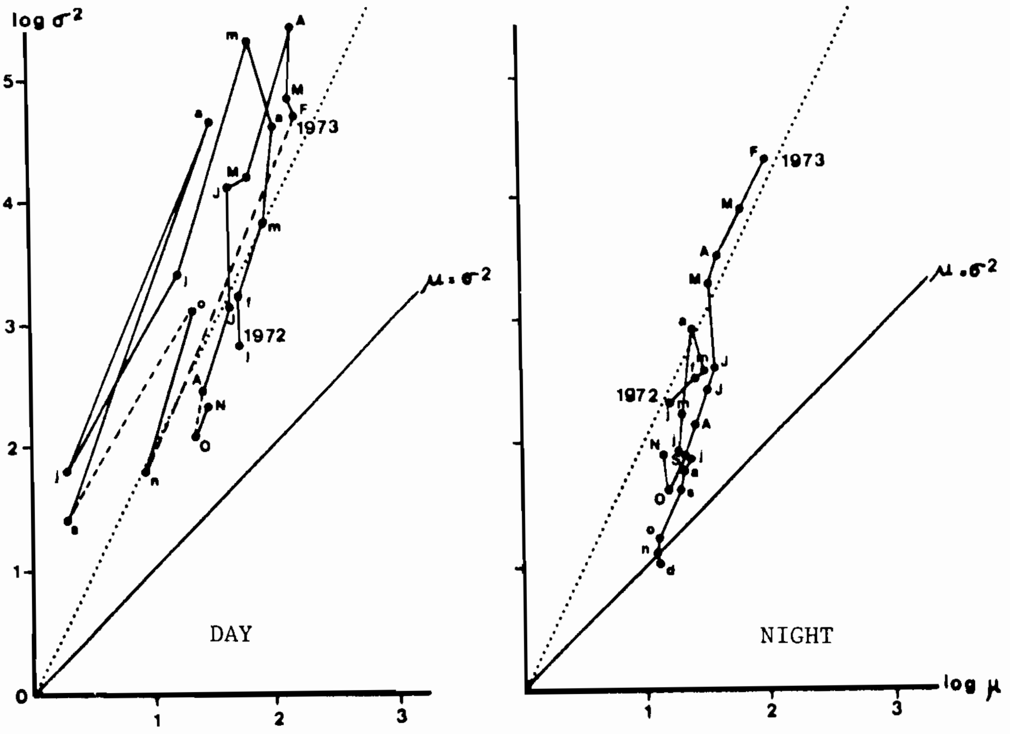


Fig. 18 Relationship between the mean (μ) and the variance (σ^2) of the catch rates, for day fishing on *P. indicus*, and night fishing on *P. latisulcatus* and *Metapenaeus monoceros* (from Marcille, 1978)

In addition, stratified random surveys where the stations are determined at random within predetermined strata permit optimized sampling and lead to an increased precision in the indices of abundance obtained for a given number of hauls (Cochran, 1963).

The stratification scheme must be drawn up before and without using data from the campaign, using for example the of data collected from a preliminary survey.

In general, the problem is the classical one of sampling demersal populations by trawl. For a study of the analysis of the trawl data and the value of the trawl, as a sampling tool Barnes and Bagenal (1951) and the report of the ICES Special Scientific Meeting on Sampling, held in Paris, 1954 (ICES, 1956) are useful references.

For survey methods, survey schemes, data analysis and reporting of the results, Alverson, 1971; Gulland, 1975; Mackett, 1973; Alverson and Pereyra, 1969; Abramson, 1968; Doubleday, 1976; Grosslein, 1971, 1974; Pitt, 1976; Ultang, 1977; FAO, 1976; Saville, 1977 have published excellent works which can be usefully consulted.

A marginal aspect of surveys which should not nevertheless be totally ignored is that of tracks optimisation. Leming and Holley (1978) proposed a computer program allowing such an optimization to be determined. In practice technical difficulties of all sorts are such that they tend to render this approach more theoretical than really useful.

Sampling frequency must be adapted to the species. For subtropical deep sea species monthly sampling may be sufficient. For tropical coastal penaeids weekly sampling is desirable, especially for the juveniles, but sometimes difficult to achieve in practice. A compromise must therefore be found but generally speaking the sampling frequency should always be rather high.

3. EXPLOITATION SYSTEMS

Coastal penaeid shrimps are generally exploited at two stages of their life cycle: during the juvenile stage in the estuaries they are fished more or less artisanally and sometimes very intensively, as in West Africa, sometimes under some surveillance as in the United States, but most frequently without real control. In their adult stage they are exploited on an industrial scale by the trawl fishery, which catches both immature and adult shrimps.

These two types of fishing are sequential and therefore, there should theoretically be interactions between the two: artisanal fishing affects the adult stock by reducing the number of contributing juveniles. Catching the adults can theoretically affect the production of juveniles if the level of exploitation reaches the point where the reproductive potential of the stock is decreased. This case however has never, to our knowledge, been demonstrated for penaeid shrimps, either because of lack of pertinent data or more probably because the very high reproductive rate of the penaeids gives the stock a high resilience. It should be noted however that the rapid collapse of the shrimp resources of the gulf between Iran and the Arabian peninsula these last years has been attributed to recruitment overfishing (Van Zalinge, personal communication).

3.1 The artisanal fishery

Under this heading are grouped all types of low investment fishing. This includes, in addition to small subsistence fishing and similar activities, recreational fishing as well as the highly organized "bait shrimp" fishery or some fisheries for human consumption, organized in fishermen cooperatives.

3.1.1 Gears used

They are extremely variable, depending on the country considered.

The gears can conveniently be divided into passive or fixed and towed devices.

3.1.1.1 Fixed gear

The principle is simple. The seaward transit of migrating shrimps is impeded and they are concentrated into appropriate receivers.

(a) Trap-barriers

Lefebvre (1908) described their use in Benin. The channel is blocked perpendicular to the current, with a compact fence extending to the surface. Bamboo traps are placed behind openings made in the barrier. The fisherman fixes torches above each trap. Kristjonsson (1969) provides an illustration of the equipment. In Mexico, light is also used to attract the shrimps (Castello and Olinto-Moller, 1978). The development of industrial nets has caused this somewhat antiquated set-up to be replaced by a barrier of stake nets.

(b) Stake net barriers (stownets)

In shallow zones (less than 5 m depth) the waterway is barred with one or several rows of evenly spaced wooden or bamboo posts. In the evening or at the beginning of ebb-tide, pockets of fine mesh net which break the surface are stretched between the posts (Fig. 19). These are used throughout West Africa and in the Far East (Menon and Raman, 1961; George, 1961; George and Rao, 1965; Garcia, 1974). The yields depend on the abundance of migrating shrimps but also on tidal currents and, in particular on the volume of water filtered.

In areas where the water is too deep for driving posts, the nets are of larger dimensions and are fixed either to oil drums moored to the bottom, or between pirogues as in Senegal (De Bondy, 1968), or suspended from bridges ("channel nets" as used in USA; Tabb and Kenny, 1969).

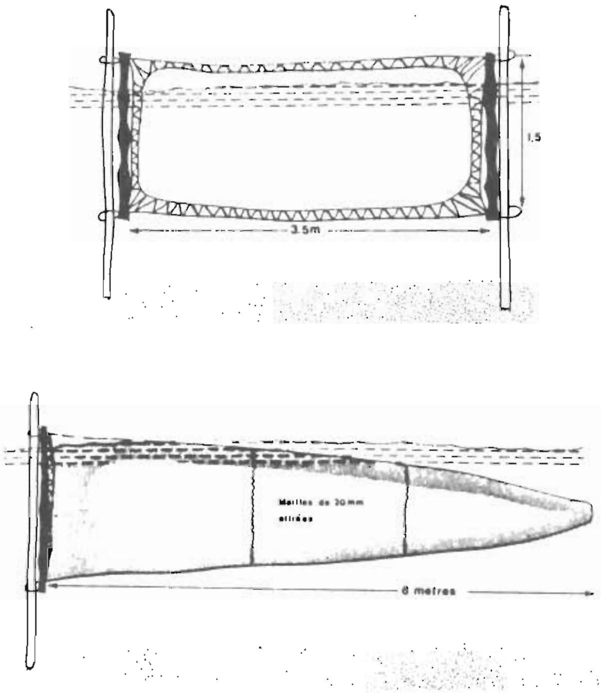


Fig. 19 Stake-net used in West Africa for the lagoon artisanal fishery (from Garcia (1972)

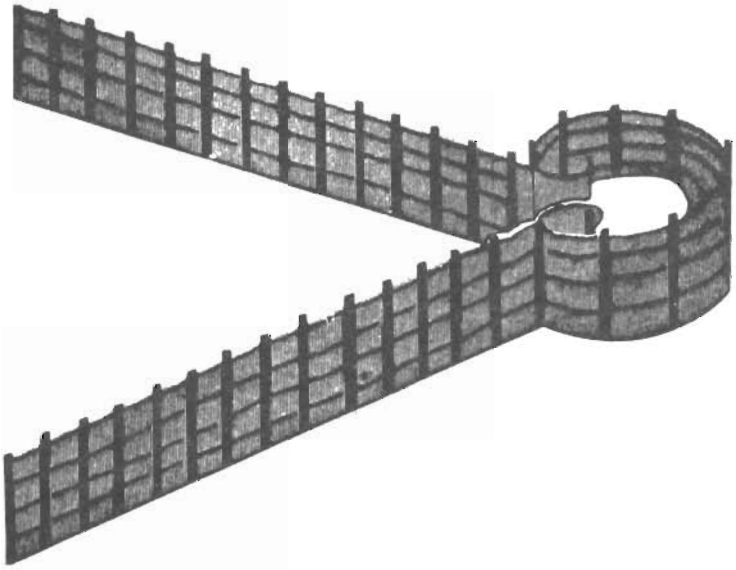


Fig. 20 Bamboo weir used in Madagascar (from Crosnier, 1965)

(c) Chinese barriers (Fig. 20)

These bamboo weirs are made of very fine lattice fences (about 7 mm spacing according to Le Reste and Marcille, 1973) which drive the shrimps towards catching compartments which vary in shape from country to country. These retain the shrimps at ebb- tide. Several individual traps can be linked together to form a complete barrier. The traps originally constructed in wood or bamboo, are nowadays sometimes modernized as is the case with the "tapos" of Mexico where concrete posts linked by galvanized meshwork close off certain channels completely (Edwards, 1978).

3.1.1.2 Towed gears

(a) Seines

These are pocket shaped and are handled from boats; they do not exceed some 10 m in length (Kuriyan and Sebastian, 1976). The beach seine with or without pockets can be several hundred metres long.

(b) Trawls

Manufactured with more or less elaborate designs, these are dragged along the bottom by two men or by a motorized boat; they are of several types:

- the small trawl is sometimes held open by two poles and is dragged by two men walking close to banks, in 1 - 1.5 m of water,

- the classical otter trawl can be used, in particular the "try- nets" developed in the Gulf of Mexico for double-rig fishing at sea. In India trawling is carried out with 8-11 m trawls from 20-60 horse-power boats, the larger of which are fitted with a winch (Kristjonsson, 1969).

In Madagascar 25 horse-power 7-8 m "catchers" trawl a net with a 7 m headrope and a 1 m vertical opening (Marcille, 1978). In the gulf between Iran and the Arabian peninsula the "dhows" of 8 to 23 meters long operate trawls of 12 to 25 metres opening (Van Zalinge et al. M.S.).

- Beam trawls and similar gears. These are also called frame trawls. They have been used for many years in the southern United States and their design has evolved over the years to what presently looks like a climax: the roller frame trawl. These trawls of 2-4 m are drawn by 6-15 m boats. Tabb and Kenny (1969) have reviewed their development since the 1950's.

3.1.1.3 Other gears

Various other equipment, much less efficient than those described above, have been used. These are for example push-nets. Kept open by two poles ("Kilis" in Senegal) or a frame, they are pushed from behind. They are often used in areas where the tidal currents are insufficient to allow the use of stake-nets. They frequently catch very small juveniles before migration and completion of the estuarine phase.

Drift-nets with one end fixed to a boat or a buoy, cast-nets, and dip-nets, have also been used, the latter often in conjunction with oil lamps (Inglis and Chin, 1966; Tabb and Kenny, 1969). A description of the various equipment used in India in artisanal fisheries is given by Kurian and Sebastian (1976).

3.1.2 Fishery characteristics

Whatever the gear used, catches consist generally of small young shrimps which may or may not have completed their estuarine phase. However, under some particular hydrological conditions (high salinity) the shrimps can stay in the estuary until an abnormally advanced age. This is the case in Madagascar (Crosnier, 1965; Le Reste, 1978) and in Senegal (Le Reste, 1979).

The artisanal shrimp fishery requires little investment and commands large returns, if the commercial network is well organized. This is the reason for its rapid development, in the USA, but also in particular in developing countries.

When fishing for exportation, factories or cooperatives may discard undersized shrimps, even in the absence of any regulation on size limits. These "discards" can be sold fresh on the local market or sold smoked or dry and powdered. In the United States they are kept alive and used as bait for recreational fishing.

Very often the activity of a non-powered artisanal fishery is cyclic and follows even short-term variations in abundance. In most cases the fishermen do not hesitate to undertake other work when yields decrease (Garcia, 1977). Fishing effort thus tends to vary with the available shrimp population (Fig. 21). Variations in abundance of the latter are then better expressed by differences in the catches landed than by variations in the catch per unit effort which may be damped by variations in competition between gear, especially in the case of stake nets.

Sometimes however the variation in fishing effort may be independent of the size of the shrimp population. The necessities of the agricultural calendar for example can induce the peasant-fishermen to temporarily abandon fishing. It can also happen that the delivery of the shrimps at the factory becomes difficult in certain seasons because of transport difficulties, especially during the rainy seasons; under such circumstances fishermen who cannot commercialize the catch cease their activities. Variations in the catch per unit effort give in these cases a more reliable picture of changes in the shrimp population abundance than those of the total catch.

3.2 Industrial fishing

Industrial fishing has expanded rapidly since the 1950's in the gulf of Mexico and in the sixties in the rest of the tropical seas.

It is undertaken more and more often by trawlers with freezing equipment or ice storage, equipped with the double-rig gear. This rigging which has been described by Kristjonsson (1969) is characterized by the use of two trawls of 12 to 24 m dragged by a single boat at the extremities of two booms which make an angle of 20 to 30° to the horizontal. It is said that the double rig gives a 30% improvement in catch rates.

The equipment is complemented by a try-net with a 2-4 m opening which is towed at the same time but which is raised at intervals to monitor the abundance of shrimp on the ground. Since skippers know empirically the relation between the yields of the try-net in numbers/minute and those of the main trawls (in kg/hr) they can modify the route of the ship during trawling to stay as close as possible to the depths where the yields are highest. This characteristic enables the fishery to follow the bathymetric movements of the stock rather accurately.

They are many models of trawls and the gear varies according to the regions. Kristjonsson (1969) has made a rather complete inventory. Other information can be found in Bullis (1964) and Knake *et al.* (1958). More recently Gorman (1975) has made a comprehensive statistical analysis of the gears used in Australia.

A recent modification has been made to the classical Florida double-rig trawl with the "twin" equipment in which two trawls are fixed to each of the booms. (Bullis and Floyd, 1972; Moya, 1973). They are separated by a central sled. This system is said to give a further 30% improvement in yield.

In shallow waters, Japanese fishermen use a trawl which is pulled between two boats. This system avoids loss of shrimps which could be disturbed by propeller turbulence and motor vibrations and escape from the net.

The differences in behaviour, from one species to another or one season to another, and between day and night for the same species, can lead to frequent changes being made in the gear used (in the otter boards, vertical opening, etc.).

One of the basic problems of this type of fishing is that of the by-catch species. This by-catch usually constitutes a large proportion of the catch, much greater than that of the shrimps, with a low market value, and which also complicates the sorting operations. If often contains juvenile fish of valuable species, the destruction of which is wasteful. Experiments have been made to develop selective trawls which separate shrimps from fish by taking advantage of their different behaviour in the net. Very interesting results have been obtained (High, Ellis and Lusz, 1969; Brabant, 1964; Kurk, Faure and Laurent, 1965). Although such trawls have been recommended by the experts, provided tha certain precautions are taken (FAO, 1973) this type of net has not found widespread use.

To cope with the effect of day-night variations in the catchability, another special trawl has been developed which can expel burrowing shrimps from the sediment by electrical impulses (Klima, 1968); Bullis and Thompson, 1966; Ellis, 1972; Klima, 1967; Pease and Seidel, 1967). At the moment the equipment does not appear to be commonly used.

Trawlers have very different characteristics which contribute to their relative fishing power. One may arbitrarily define industrial fisheries to include boats with engines of more than say 100 horse-power. Some may go as far as 1 200 horse-power but the majority have a horse-power of between 150 and 400. Trawlers may fall into two classes according to their storage facilities: boats with storage on ice and the freezer trawlers. The latter can sometimes function as factory ships in which case the whole shrimp processing operation takes place on board. While ice boats can only undertake short trips from 3 to 7 days which obliges them to work near their home ports, the freezers are only limited by their storage capacity and therefore have greater autonomy.

Shrimp searching is done by using a try net or by high frequency echo-sounding (100-200 kc/s) (Kristjonsson, 1969).

In general, catches are sorted on deck and stored in bulk on ice and treated to avoid blackening, or sorted into size grades, whole or headless, packaged on board and deep frozen.

4. FISHERY DATA

Two types of data can be identified: fishery statistics (catch, effort) on the one hand and biological data on the catches (sex, measurements, age, sexual state, etc.) on the other.

4.1 COLLECTION OF FISHERY STATISTICS

The collection of statistics which enables one to monitor the simultaneous developments of the stock and the exploitation system is one of the essential aspects of stock assessment. For practical reasons a differentiation into the two main types of shrimp exploitation systems will be made: industrial trawling of adult shrimps and artisanal fishing of juveniles.

4.1.1 Industrial fishing

Shrimp fishing at sea is a classical example of bottom trawling. It gives no specific statistical problems and for the basic theory, reference can be made to the classical publications of Beverton and Holt (1956) and Gulland (1969). The essential information required concerns the fleet itself and its operations. This information should for ease of later treatment, be stratified according to predetermined geographical areas.

4.1.1.1 Sources of information

(a) The files of fishery administrative bodies. When they are available, they permit one to follow the fleet development both with regard to number of vessels and eventually the total power of the fleet and other overall characteristics

(b) Daily movement records obtainable from port authorities or kept by statistical offices allow one to get exact data on boats in port and, by difference, those at sea. From this information absence from the port, or time at sea can be estimated.

(c) Interview records obtained by interviewers questioning the skippers after their return from each trip, can provide information for all or part of the fleet on the dates of departure and return, fishing area, species sought, weight of catches, etc.. The details and completeness of these records depends mostly on the good will of the skippers and the relationship between the interviewer and the fishermen. They allow one to calculate the effective fishing time and eventually to check the data on landings reported by factories or auctions. Experience shows that skippers can make a very close estimate of the tonnage caught (fig. 22).

(d) Records of the landings obtained from the auctions or factories, provide the catch by species (target species as well as by-catch) and the selling price for each boat. The date of landing allows these data to be allocated to a specific trip for which other information is obtained as described above.

(e) Fishery log books. These are a source of very valuable data for the fishery biologist. The volume and precision of the data obtained will depend on the possibilities and the educational level of the skippers. In the best cases data for each haul are available (time of shooting, time of hauling, position, depth, species captured, quantities, changes in discarding practices, information on the gear used). Detailed data of this kind often require computerized treatment, an example of which is given by Slack-Smith and Stark (1969).

If properly utilized, such data allow one to follow closely the development of the fishery, and the fishing strategy, to study in detail the geographical and bathymetric distribution of different species, and to determine the rhythms in the fish activity (see e.g. Garcia, 1976).

The information will generally only be obtained for a portion of the fleet and the representativity of the sample will require analysis.

Some examples of studies of shrimp fisheries with a description of the data collected can be found, in addition to the publications already quoted, in Snow (1969) for the Gulf of Mexico; Slack-Smith (1969) for Australia; Chabanne and Plante (1970) and Marcille, (1978) for Madagascar. An inventory of statistical collecting methods in the Caribbean has been made by Mackett (1972).

These various sources provide basic data for the estimation of the total effort expended and the catches achieved.

4.1.1.2 Fishing effort

Several measurements of effort can be obtained, depending on the efficiency of the information collecting network. Progressing from the most crude to the most precise, the following can be identified:

(a) The size of the fleet. In the absence of any detailed information, the total number of operating units, the overall engine power or any other approximation of nominal power can be used as a measure of the effort. The time during which the power is applied is usually the year. It is however not possible to detect variations in the actual use of this power (variations in the gear used, in effective fishing time, etc.).

(b) The number of trips is also an approximate figure of fishing effort which can still be seriously biased if complementary information is not available on the average duration of the trips or the engine power of the boats concerned.

(c) Number of days of absence from port or time at sea is easily available from daily movement records but these do not allow assessment of lost time (travel time to fishing grounds for example).

(d) Effective fishing time represents the true time spent on the fishing grounds, when travelling time has been subtracted. It does not allow calculation of "lost" time (stops for repairs, for processing the catch or waiting for a more favourable phase of the diel catchability cycle when catch rates are too low).

(e) Trawling time. This represents effort actually spent on the stock. Lost time spent moving between fishing grounds, in processing catches, sorting the catches, is not included. Practically speaking, this effort can only be estimated from log books or lacking these, from very detailed enquiries on an adequate number of boats.

4.1.1.3 Standardization of effort

The classical conceptions of fishing effort, nominal or standard, and of fishing intensity and fishing power can be found in the classical works of Beverton and Holt (1956), Ricker (1975); Gulland (1969). A special meeting on this problem was held in 1970 (ICES, 1975).

Rothschild (1972, 1977) tried to redefine a more modern concept of effort. A recent FAO document (1976) has reviewed the essential principles of the use of effort for evaluating abundance.

As a preliminary to standardization, a file of fishing boats with their characteristics (name, number, size, power, tonnage, gear type, mesh size, date of construction, date of entry into the fishery, method of preserving catches, etc.) should be established. This record must be kept up-to-date regularly; this can be a difficult task at the beginning of the fishery when the composition of the fleet is not yet stable.

Problems encountered for shrimp-fishing are those associated more generally, with trawl fishing for which the litterature is very abundant. We will therefore only mention that in fishery resources research the fundamental requirement of good estimate of fishing effort (f) is that it is proportional to the fishing mortality (F) and is related to the latter by the equation:

$$F = q.f$$

where q is the coefficient of fishing mortality per unit of effort, or Ricker's catchability coefficient.

In order to fulfill this requirement the nominal fishing effort must be standardized. The essential objective of this operation is to remove important variations and especially the trends of the f/F relationship. In the case of shrimp-fishing the main foreseeable factors causing such trends are:

- the increase of engine power
- the evolution of fishing gear progressing from normal rig (the Vigneron-Dahl type) to double rig or "twin" type
- the evolution in trawls and the tendency to increase their size for a given engine power or to introduce changes in design affecting their efficiency
- the evolution of fishing tactics: adoption of the try net, increase in number of hours trawling per day; trawling by night or by day or both; variation in the proportion between effective fishing time and the duration of absence from port with the modernization of fishing fleets and a widespread use of deep-freezing allowing longer trips to be made; changes in the specific distribution of effort in a multispecies fishery; change from individual search of schools to fleet searching (Marcille, 1978).

One of the essential characteristics of shrimp-fishing is that it can be undertaken either at night or in daytime, or throughout the twenty-four hours. This depends on season, region, species and type of boat.

Garcia (1977) showed that on the Ivory Coast, the 400 HP freezer-trawlers which processed the catch on board, sometimes chose the most favourable hours for fishing, and remained at anchor during the remaining hours of the day, to save fuel or to sort and pack the catch. He identified two fishing tactics:

- Day or "selective" fishing (an average of 11 hours of trawling)
- Night and day or "normal" fishing (15 hours of trawling).

It is evident that the choice of the more favourable fishing hours gives an increased yield per hour, to the detriment of the yield per day. The relative fishing power of a freezer-trawler using these tactics will depend on the unit of effort used (number of fishing hours or fishing days) and on the number of hours of effective work. From Fig. 23 it can be seen that when effort is expressed in trawling hours the relative fishing power [1] passes from 1.25 during "normal" to 1.8 during "selective" fishing. Conversely if the effort is expressed in fishing days it passes from 1.25 during "normal" to 1.0 during "selective" fishing.

If a fleet contains units which are fishing during different periods of the day and if either the tactics or the composision of the fleet change with the season, or over the course of the years then a very important source of bias is introduced. This difficulty can be avoided simply by adopting a measure of relative fishing power which differs according to the tactics used. Marcille (1978) demonstrated seasonal variations in the daily number of hours trawling in Madagascar as well as a progressive increase in this number from 1969 to 1973 (Fig. 24A). He also showed a seasonal variation for the relative fishing power of boats (Fig. 24B). He suggested a relationship between this phenomenon and the seasonal variation in shrimp availability that affected different types of boats differently. The change from semi-pelagic behaviour (from January to June) to a benthic behaviour (from July to December) in shrimp would have a different effect on small and large shrimpers, since in the former the catch rate is related to the areas of the trawl openings while in the latter it is related only to the head rope lengths.

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[1] By comparison with a standard shrimp vessel of 250 HP fishing night and day

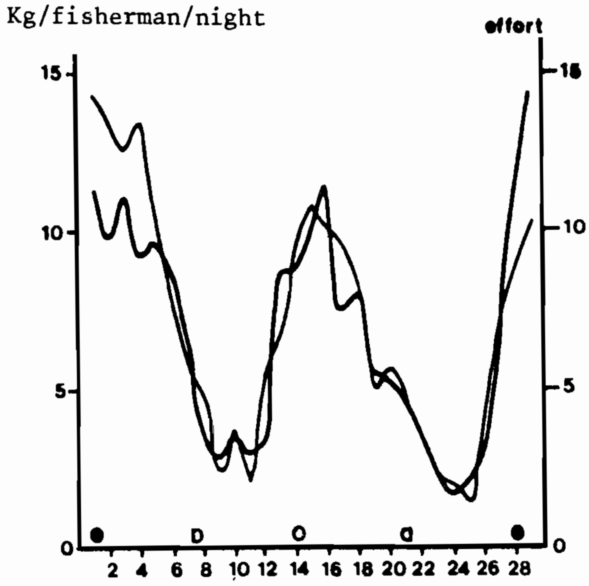

Fig. 21 Lunar variations of effort (in n.b of active fishermen) and catch rates in the Ivory Coast artisanal fishery (from Garcia 1973)

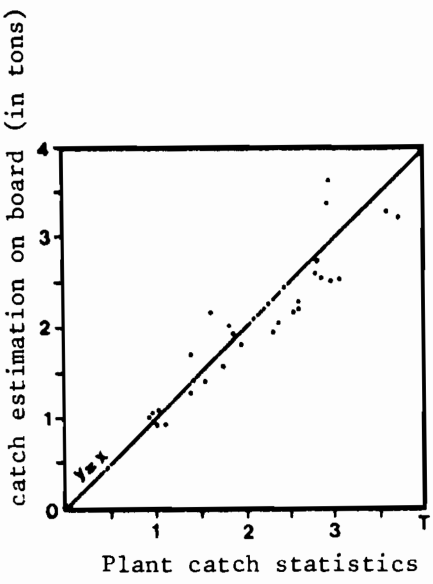

Fig. 22 Relationship between the catch estimation of the skipper and the true catch, measured at the plant (from Garcia, 1977)

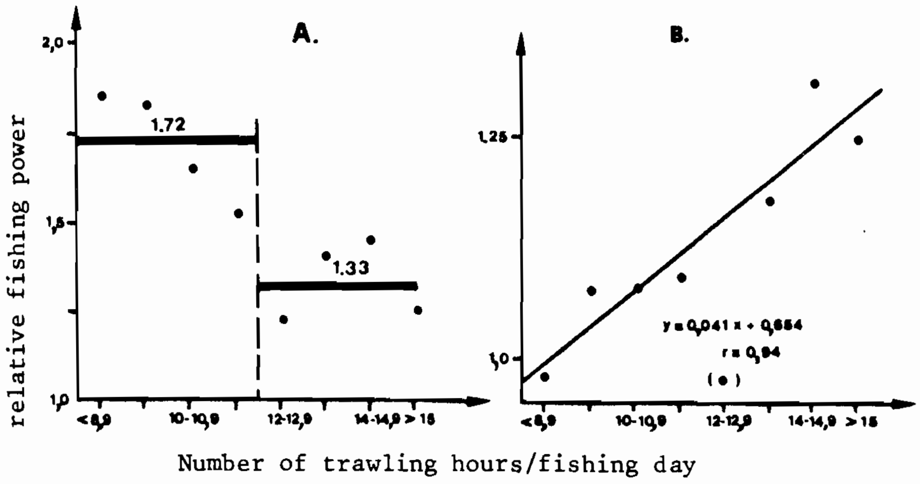

Fig. 23 Variation of the relative fishing power of the freezer-shrimp trawler in Ivory Coast in relation to the average daily duration of fishing (from Garcia, 1977):

A: when effort is expressed in hours of trawling

B: when effort is expressed in fishing days

The main methods of standardization are well-known. In trawl fishing the relative fishing power of the boats is generally closely related to their engine power or their gross registered tonnage (GRT). Standardization is therefore most often established through a relationship between the catches per nominal effort and the engine power or tonnage.

Relative fishing powers are defined by comparison with a standard boat. Where there are many fishing zones, and different types of boats are distributed heterogeneously, Robson's (1966) method allows the calculation of relative fishing powers with good statistical precision and the identification of possible space-time variations. A programme written by C. Berude is available (Abramson, 1971).

One of the characteristics of the relationship between relative fishing power and the engine power in shrimp vessels is its low slope. Doubling the engine power from 200 to 400 HP results in an increase of only roughly 50% in the relative fishing power, both in the Ivory Coast (Garcia, 1977) and Madagascar (Marcille, 1978). The following table gives some of the published relationships.

References	Regions	Equations
Marcille (1978)	Madagascar	$Pr = 0{,}0029\ Pm + 0{,}530$
Garcia (1977)	Côte-d'Ivoire	$Pr = 0{,}0020\ Pm + 0{,}460$
Neal (1970, 1975)	U.S.A.	$Pr = b.L + a$ $0{,}424 < b < 0{,}630$ $0{,}022 < a < 0{,}036$

Table: relation between relative fishing power (Pr) of shrimpers and their characteristics
Pr = catch per hour of the particular boat/catch per hour of standard boat
L = boat length
Pm = engine power

Griffin, Nichols and Lacewell (1973) provide a more complex equation

$$Pr = \frac{(Pm)_i^{0,1385} \ (LCD)_i^{0,4064}}{(38,0)^{0,1385} \ (14,6)^{0,4064}}$$

in which $(Pm)_i$ and $(LCD)_i$ indicate engine power and the trawl head rope length of a boat of class i and 38.0 and 14.6 are the engine power and trawl headrope length of the standard boat, respectively.

Another important characteristic of the relation between relative fishing power and boat characteristics is the great scatter of the points around the regression line. This is due in part to the variety in the types of trawl used (flat, balloon, semi-balloon, etc.) and the tactics employed (day fishing, night fishing, day and night fishing solitary or fleet-searching) and apparently also, to an important degree to the personal factor related to the skill of the skipper and his own experience.

In the case of multispecific shrimp fisheries the most complex problem is to identify the effort devoted to each species. This can be very difficult if there is not a clear geographical separation between species. For want of something better, it is often assumed that fishing effort is randomly distributed among the different species and that catches per unit effort (c.p.u.e.) are proportional to the true densities of these species. This is probably not accurate when fishing is as well "aimed" as shrimp fishing and the risks of bias become significant when the concentration of the fleet on one or other species changes with time (which is equivalent to a change in q). This is the usual situation in multispecific fisheries (Louisiana, Madagascar) where the main species is the only objective at the beginning of the fishery, especially when it is abundant during daytime (*Penaeus setiferus* and *Penaeus indicus*) and it is only when yields for the main species decrease that other species are sought. Boerema (1974) indicated for the Panama fishery a progressive change in emphasis between *Penaeus* and *Xyphopenaeus*, when catches of *Penaeus* decreased as an effect of fishing.

When the species composition of the catches depends on the time of trawling as in Madagascar (Chabanne and Plante,1971) a simple modification in the fishing effort distribution during a day is sufficient to modify the overall catchability coefficient for the different species. These changes tend in general to overemphasized variations in the abundance indices.

4.1.1.4 The catch

The total catch must be known for each species fished.

4.1.1.4.1 Target species

Data on the catch are sometimes easy to obtain at the factories because, due to the high commercial values of shrimp, they are carefully processed and, often, separated by species. However when fishing covers several species, factory statistics are sometimes difficult to use because the shrimp species may be mixed. In Madagascar for instance, Marcille, 1977, noted the following commercial categories.

- HL white: *Penaeus indicus* headless and graded
- HL pink: *Metapenaeus monoceros* headless and graded
- HL tiger: *Penaeus semisulcatus* headless and graded, with in addition some *P. japonicus*
- HO: whole shrimps consisting of a majority of *M. monoceros* head-on with some small *Penaeus indicus* and *P. semisulcatus*
- Tiger HO: include large head-on *P. monodon*, *P. monodon* headless and sometimes, some *Penaeus semisulcatus*
- Mixed: a category which can include various non-graded headless species.

HO is used for "head-on" and HL for "headless" shrimp.

In case of mixtures only regular sampling can distinguish the proportions of different species. When two species of different size distributions are mixed in one category, there is sometimes a bimodal distribution of the size gradings which allows approximate classification.

In each commercial category, shrimps are often graded, sometimes following a local standard, but more often the American standard (in number/lb) is used. It is important to collect such important information, which allows one to reconstruct the size distribution of the catches (section 4.2).

Bearing in mind the different processing possibilities, it may be necessary to convert the data (whole into headless or vice versa). One can use for this purpose an overall empirical coefficient, obtained by weighing a significant quantity of shrimps before and after heading. In the United States the ratio used is 1.680 (whole/headless or 0.595 headless/whole). Other very similar ratios are used elsewhere. A list can be found in Fao (1972) and Squires (1974).

Nomograms can also be used for more exact conversions from commercial categories (size grading) into average sizes or average individual weight or to convert from one processing type to another (head-on to headless, etc.). These nomograms are based on classical biometric relationships (Fig. 25). Kutkuhn (1962) gives some examples and the way in which they can be constructed. However, remembering that the line must be used in both directions, it would be preferable to calculate a functional relationship such as a GM regression (or Tessier's line) (Ricker, 1973).

Because of the required accuracy, it is also preferable to use for each species its own carefully calculated relationship.

A later section (4.2) shows a method to obtain the size distribution of the catches from the landings reported by size gradings with greater precision, using conversion keys.

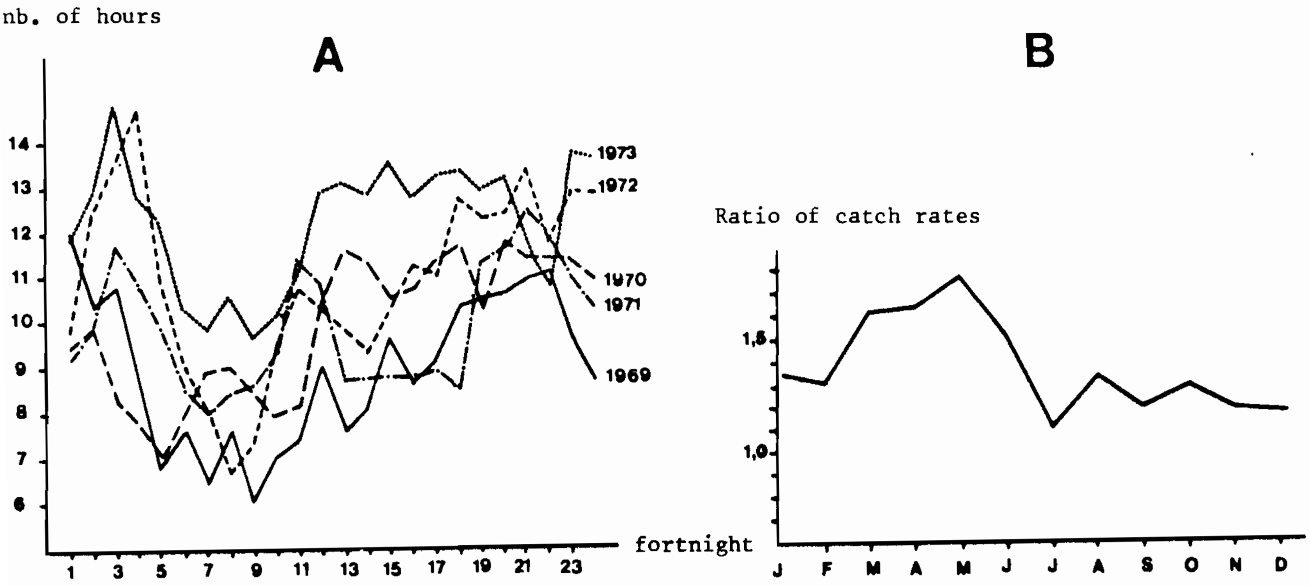

Fig. 24 Seasonal variations of the characteristics of fishing effort (from Marcille, 1978)

A : Changes in the number of trawling hours per day from 1969 to 1973 in Madagascar
B : Seasonal changes in relative fishing power

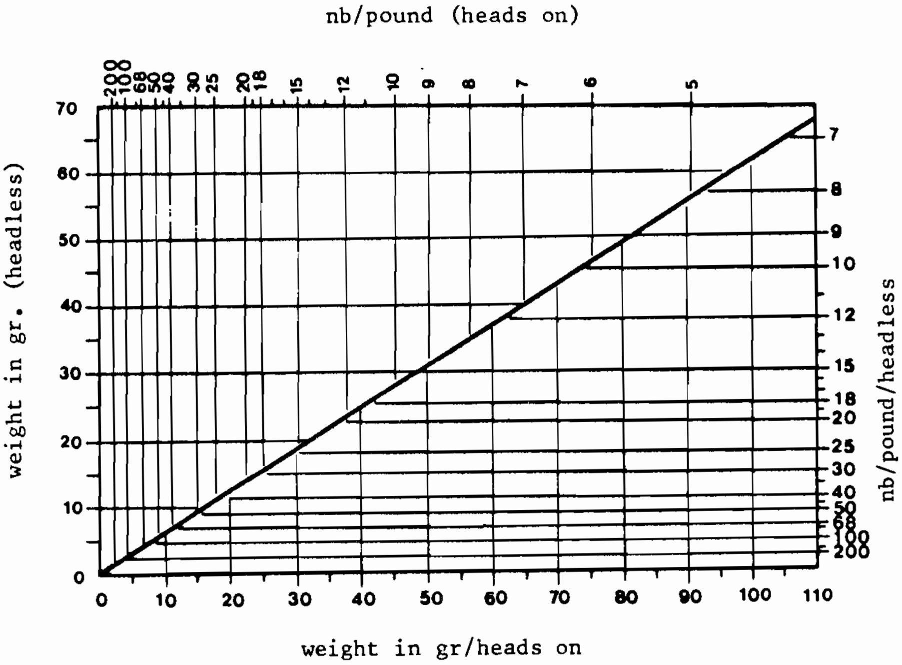

Fig. 25 Nomogram for conversion of weight and numbers of whole or headless shrimps (from Kutkuhn, 1962)

4.1.1.4.2 By-catch

The fish which are caught together with the shrimp are generally discarded, and only very small quantities are landed because boat storage space is limited. Thus, only good quality species are kept on board. These are nevertheless a significant element of the economic balance of the boat and must therefore be included in any economic study.

Also, any overall resource management policy in a region must take into account all species because of possible interactions on a given species by two types of fisheries (for example trawl-fishing and shrimp- fishing on the Sciaenids),

We have already seen that in general the skipper of a boat is able to make an accurate estimate of his catch (Fig. 22) and that, lacking precise data on shore (in the case of transhipment at sea, for example) the catch data obtained through interviews are usable.

4.1.1.4.3 Discards (Fig. 26)

The combination of the data on effort and catch allow the calculation of catches per unit of effort (c.p.u.e.). If the effort is correctly expressed, the catch is proportional to the stock density

$$C/f = q\,\frac{\bar{N}}{A} = q\bar{D} \quad \text{from Gulland (1969)}$$

where $\bar{N}$ and $\bar{D}$ represent respectively the average numerical abundance and the average density during a certain time interval and A the area of the fishing ground.

As a consequence the basic data must be the real catch of the investigated species and not the amount landed, when part of the catch may be discarded.

Most often, only the landings are known and this can cause serious bias since the discarding practices often change with the evolution of the fishery, or with the market prices, by size grading.

It should be noted that discards have been studied by Berry and Benton (1969), Baxter (1973) and Juhl and Drummond (1977) in the Gulf of Mexico and the Caribbean region. They are of considerable importance, not only for the target species itself but for all by-catch species.

Previously the resources of the shrimp fishing grounds have often been considered as mono-specific or consisting of a few species only and in any case consisting only of shrimps because of their high commercial value and because of the slight interest which the fish by-catch has for shrimp fishermen. Nevertheless an overall resource management scheme in a region requires knowledge of the effort applied by shrimp fisheries on associated fish species. The great majority of fish species currently discarded in the Gulf of Mexico and the Caribbean, is estimated by Juhl and Drummond (1977) at 350,000 t/year. Klima (1976) estimated a maximum of 900,000 t on the basis of 1.4 to 9.0 kg of discards per kilogramme of shrimp caught.

There are several methods of estimating discards; they are of two types:

(a) Direct methods - Skippers can be interviewed at the end of each trip so as to obtain their estimate of the tonnages discarded and some idea of the principal species involved. If the usual reluctance of fishermen to speak on this subject can be overcome, an approximate estimate of discards can be made. This method can be refined if skippers agree to fill in fishery log books. If a more precise assessment of discards is required the best method is direct observation on board of the fishing vessels by a scientist who takes catch samples before and after sorting.

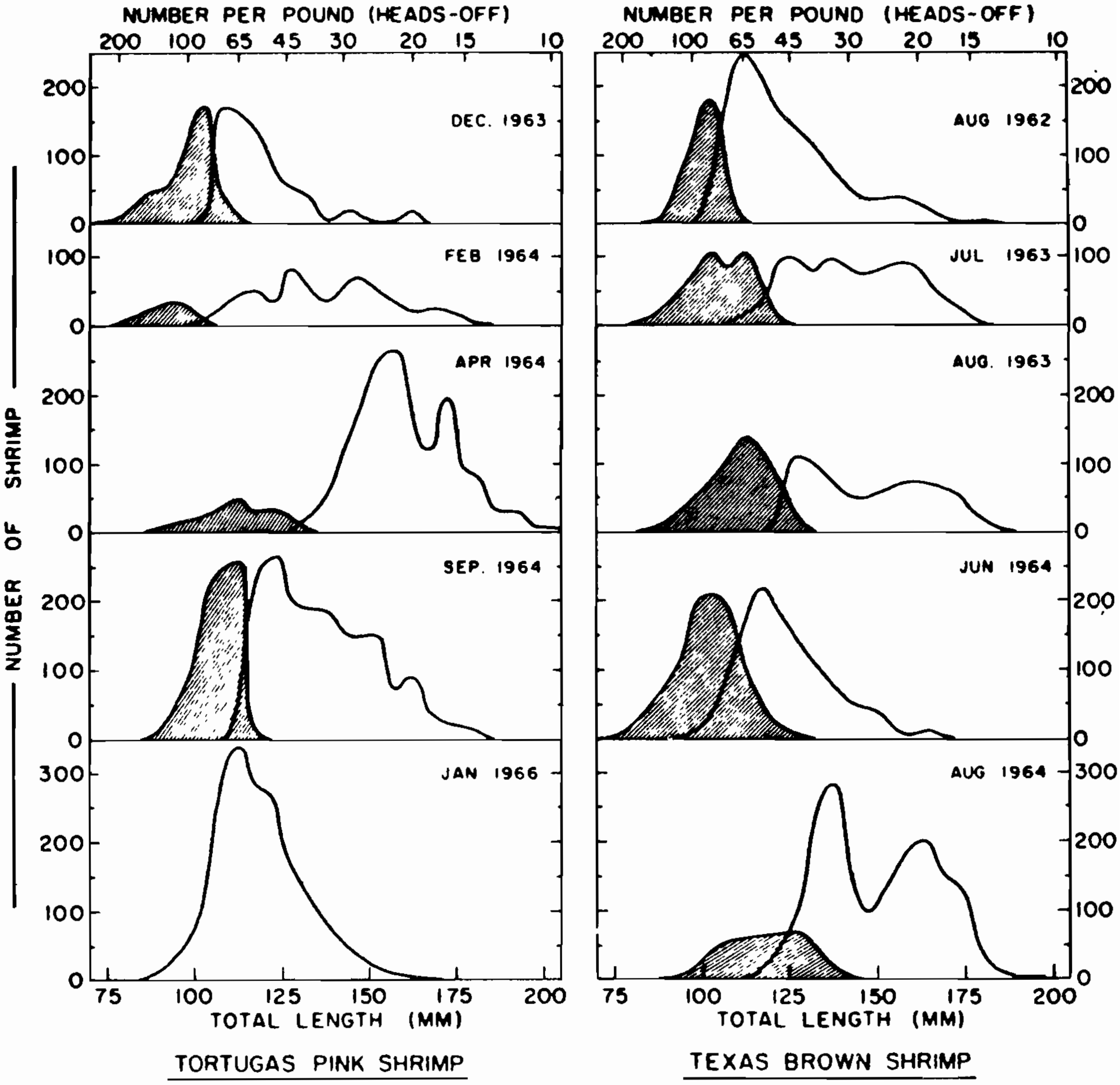

Fig. 26 Length-frequency distributions of shrimp that were culled and discarded (shaded areas) or kept (unshaded) during fishing trips to Florida and Texas fishing grounds

(b) Indirect methods - An estimate of the quantities discarded, their species composition and size distributions can be obtained by a research vessel using a gear identical to that used by the fishermen. The specific composition of the experimental catches is afterwards compared to that of landings. For each species a "discard curve" analogous to a selectivity curve can be determined.

Also, a fisherman can be put on board the research vessel and asked to carry out sorting of the catch as though he were on board of his own ship. A direct and an experimental approach to determine the discarding practices are thus combined.

How much and what sizes of shrimps are discarded depends on several factors such as:

- The quantity of small-sized shrimps in the catch
- Their landing value
- The sorting method (Berry and Benton, 1969)
- Possible regulations on the minimum commercial sizes.

Discards of associated species depend on:

- The catches obtained of the target species
- The size of the associated species caught and their market value
- The storage methods available on the boat.

The amount of discards is therefore subject to important seasonal variations, and analysis of these variations can lead to the construction of a simple model. Berry and Benton (1969) established a multiple regression of the form

$$Y = a + b X_1 + c X_2 + d X_3$$

where Y is the tonnage of shrimps rejected per month, X_1 the total tonnage of shrimp landed, X_2 the tonnage of small shrimps landed, and X_3 the selling price of small shrimps per unit weight.

They also used the equation

$$\frac{Y}{Y + X2} = a + b \frac{X2}{X1} + c X3$$

These two models however can only account for 42 to 55% of the total variance of shrimp discards.

4.1.2 The artisanal fishery

4.1.2.1 Sources of data

These depend on the organizational level of the fishery. If the organization is good, the problem comes back to that of the preceding chapter, compounded by the fact that landing sites are numerous and widely dispersed; this is the case, for example, in the artisanal fisheries which have developed in the lagoons and estuaries in the United States, where the classical statistical collecting forms can then be used.

In the case of an artisanal system with organized collection of catches such as those which are found in West Africa, good statistical data can be obtained through the processing plants.

In all such cases the discards will have to be estimated as previously described for the industrial fisheries.

Where fisheries are completely unorganized, the possibility of using several sources of data must be investigated.

(a) Fishing records

Although difficult, it is sometimes possible to obtain the cooperation of educated fishermen who will agree to make records of the setting and hauling time of, e.g. stake nets, the catches made, and the number of nets employed. This system was used with success by one of the authors on the Ivory Coast (Garcia, 1978). This would of course be difficult to apply to a whole country and can therefore only be used for some elements of the whole fishery.

(b) Commercial data

When the marketing networks are not too diffuse or when there are obligatory passage sites (ferries, secondary ports) statistics on the quantity transported can be obtained by checking the vehicles (vans or boats) and estimating their contents. The part of the catch consumed by the fishermen themselves cannot be estimated. In general this is negligeable if commercialisation is well organized, since the fisherman prefers to sell all his catch because of the high price of shrimps. But it can be important if there is a regulation forbidding the sale of small sizes which are then processed and consumed locally or sold through traditional circuits.

(c) Classical interview techniques at landing sites

It is evident that even more than for industrial fishing, a detailed knowledge of local fishing requires a good sampling network and excellent contacts between researchers, fishermen and the fish traders.

4.1.2.2 The concept of fishing effort

This is extremely complicated in the case of artisanal fishing with fixed nets. Garcia (1977), using fishing records which were completed each evening at some stations in the Ebrie lagoon (Ivory Coast), outlined several sources of variations which we summarize as follows:

(a) Unproductive effort

When statistics are used from factories or cooperatives, trips without catch have not been recorded. There is therefore an underestimation of the effort and an overestimation of the catch per unit of effort. The bias is at its maximum during the slack season.

The unit of effort used was one night of fishing by one fisherman or the setting of a net during one ebb- tide. If the number of nets per fisherman is stable, the two units are equivalent.

(b) Lunar cycle

From Fig. 21 it can be seen that the catch per unit effort and the nominal recorded effort follow the same lunar fluctuation. This is an almost general observation in West Africa where the artisanal effort is often related to the shrimp abundance. Nearly everyone fishes when the abundance is high, but a great proportion of fishermen abstain in the slack season in order to concentrate on other work, in particular agriculture.

A closer study shows that this rhythm, which influences the number of active fishermen, is superimposed by another one - that of the number of hours fished per day. The latter is controlled by the interaction between dusk and ebb-tide and is maximum a few days after full and new moon (Fig. 27).

(c) Seasonal cycle

Whatever the phase of the moon, the number of hours fishing per night varies throughout the year. In the Ebrie lagoon it increases from February to August when it is at a maximum, and undergoes a second maximum in December. In October-November there is a clear decline which appears to be related to flood periods (Fig. 28A). The seasonal pattern may be different in successive years at the same fishing site or at different sites during the same year (Fig. 28B). These phenomena are probably affected by hydrological factors (tidal or flooding cycles, tide resonance phenomena, interaction between floods and tides) but have not been explained.

(d) Geographical variation in fishing duration

The shape of the tide wave changes as it advances up the estuary, so that the time at which fishing begins and its duration (and also current velocity and consequently the volume filtered,) vary from the mouth of the estuary upstream in a complex fashion (Fig. 29).

(e) The selection of a unit of effort

- Stake nets: the cubic metre of filtered water should be the best unit of effort, as shown experimentally by Yokel (1970 - cf. section 2.3.4.2.2), since the catch per cubic metre is a good index of the shrimp density in the water mass. This information however is often lacking.

In addition, if the object of the study is to define an index of recruitment, it is not the density of migrating shrimps in the water mass, but the total number going seawards, or a corresponding index, which must be known. In this case an integrated figure is preferable: for example a night of fishing with one net. The catch per net per night in a given location will depend on shrimp density, on the time the net is working and the current velocity. We will see in the section dealing with mortality that it also depends on the place where the net is set in the upstream-downstream axis and the width of the lagoon at the fishing site.

- Trawls: if they are towed by boat the fishing time (hours) will be the best unit. If they are pulled by two men, the trip will probably be the only type of information, with all its associated possible biases. If fishing is well organized the situation comes much closer to industrial fishing and identical methods can be used.

- Seine nets: fishing time includes searching for shrimp and actual fishing. The unit of effort may be the trip. However, modification of the ratio of fishing time to searching time can be a source of bias when the species declines in abundance. Seine nets are however relatively little used gears.

When different gears are used in the same fishery it is practically impossible to standardize the fishing effort if different age-group structures are exploited.

If the age structure of the catch of the various gears is similar, an estimate of the total effort can be obtained simply by dividing the total catch by the c.p.u.e. of a standard gear for which the effort is easy to define.

4.2 COLLECTION OF BIOLOGICAL DATA

Sampling of the landings for biological data poses a classical statistical problem which can be resolved with the usual techniques.

The essential objective of the sampling is to estimate the size composition of the landings of the different species (since age cannot be directly determined), with the smallest possible variance, taking into account the means available. The biological properties of the two sexes (growth in weight and size) being very different, it is advisable to collect the data for each sex separately. This is important to obtain the best possible assessment of the consequences of regulatory measures, even although it is evident that the two sexes cannot be managed separately.

Excellent analyses of the general problem and of the methodologies are given by Gulland (1955, 1966) Pope (1956), ICES (1956).

4.2.1 Size composition

The dimensions most generally measured are the carapace length (from the orbital notch to the posterior dorsal margin of the carapace) or the total length (from the tip of the rostrum to the tip of the telson). The first one is the most precise and is not liable to variations in "elasticity"of the shrimp which depends on its degree of decomposition and its method of preservation.

If all or part of the fleet land whole iced shrimps for processing ashore, sampling can be made by classical methods before they pass through the sorting machine. The only problem is that boats which keep shrimps on ice land small quantities which are quickly sorted. The sampling operation must therefore be very rapid.

It is usually preferable to take advantage of the fact that shrimp are nearly always processed by commercial categories (size gradings). The variance will therefore decrease appreciably if the whole catch statistics are collected by commercial categories which are thereafter converted to obtain the estimates for the whole catch size distribution.

The conversion is made using a table (cf. table I) giving the size frequency distribution in each commercial category, obtained by sampling the shrimps falling into these categories during the sorting process. These tables allow for the conversion of the catches by commercial category into catches by size class (centimetric ones for instance). The global size distribution in the catch for the considered period of time is then simply obtained by adding together the elementary distributions of the catches in each commercial category. If the information so obtained covers only part of the landings the partial distribution will be raised to the total catch.

In this way, good information can be obtained at little expense. If there is however a possibility that the adjustment of the sorting machine is changed, the frequency distributions corresponding to each commercial category must be checked periodically.

If part of the fleet land whole shrimps in bulk and another headless ones already sorted and packed it will be necessary to decide which source of data will be the most appropriate in order to extrapolate to the total catch in the safest way. Alternatively both size frequency distributions will be elaborated by sampling of both types of catches and then pooled together.

It should be noted that commercial categories often concern shrimp tails and hence the frequency distributions sampled are in tail length (or weight). By determining the relationships between tail length (or weight) and tail or capacace length it is possible to transform the frequency distribution available in any other size units. The conversion table is then used as above. The measure of the tail is however not very precise and this introduces a lack of precision into the reconstructed size distribution. Squires (1974) proposed to measure the tail weight, which can more accurately be obtained.

It is also possible to work directly with tail-length if the growth curve in these units is available but the problem of the lack of precision still remains.

Caillouet, Patella and Jackson (1980) proposed a very synthetic way of expressing the size composition of catches. If the weight of the catches of each size grading in the American grading system is expressed as a percentage of the total weight, the relation between the $\log_e$ of the cumulative percentages and the category is a straight line. They found that

$$F_i = ae^{bC_i}$$

where F_i is the cumulative percentage in weight of headless shrimps in the category i,
C_i is the lower size category limit (for instance 21 for the 21-25 shrimps/lb category),
i = rank of the category,
a and b are constants. The $\log_e$ conversion allows a linear expression of the results.

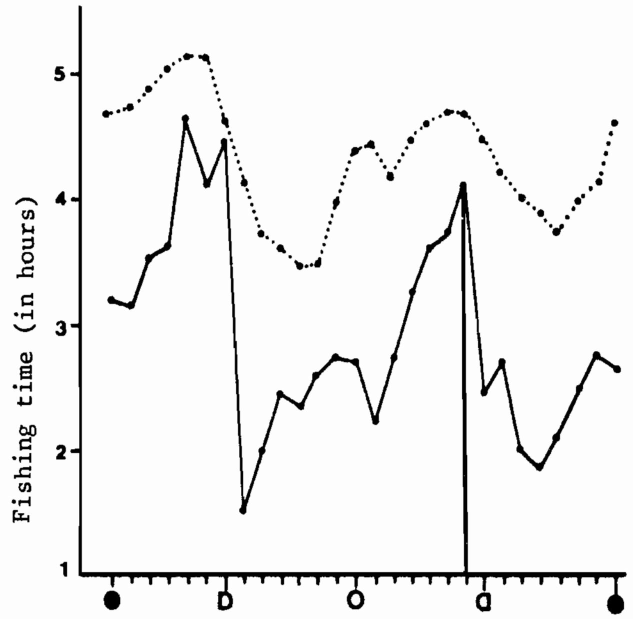

Fig. 27 Duration of fishing in connection with the lunar phase in the Ebric lagoon (Ivory Coast) at Ngadykro (—) and Adoukro (:..) (from Garcia, 1977)

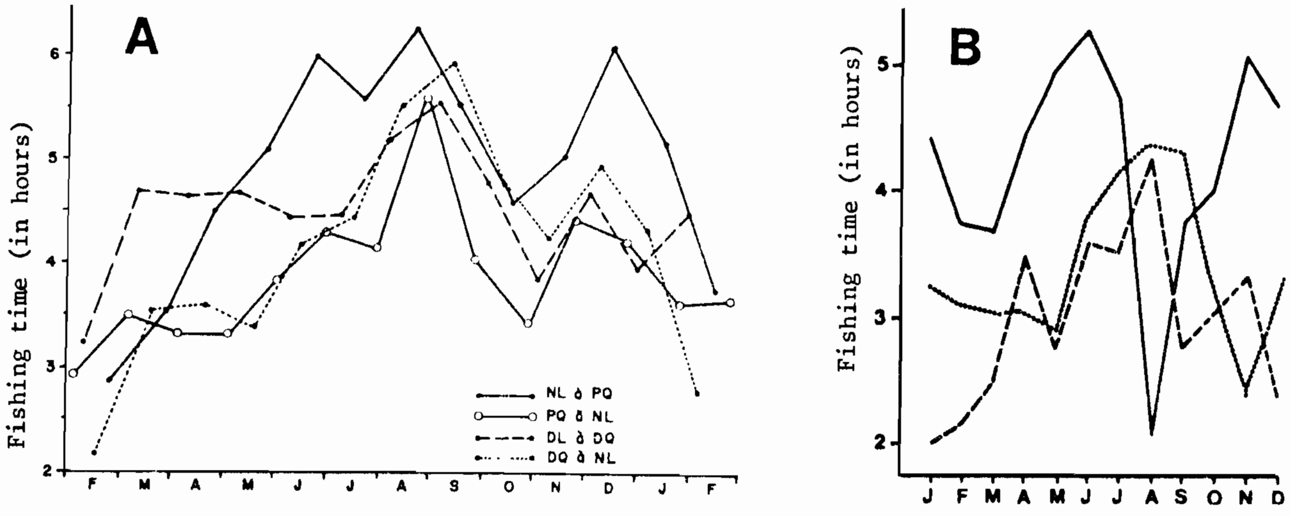

Fig. 28 Seasonal variations of the fishing time/night in the Ebrié lagoon (Ivory Coast) - (from Garcia, 1977):

A: in 1974-75 at Adoukro, by lunar phase

B: in 1975 at Adoukro (—), Ngadykro (--), and Ndiemi (···)

If this model is used, the study of the long-term variations in the slope (b) of the relationship allows the identification of the trends in the size composition and hence also in the total mortality rate.

4.2.2 Composition by sexes

When factory data on shrimp landings are used the sex distribution is obviously not available. The males, being smaller than the females, are more frequently found in the smaller size categories. Also, within a category, the sex ratio is not uniform because it varies with size. The size-age relationship being different for each sex the size distributions cannot be used as such for growth or mortality analysis.

Garcia and Albaret (1977) following Wenner's (1972) work, proposed, with the necessary precautions, that the use of the relationship between sex-ratio and size should be considered for the *a posteriori* separation by sex of size frequency distributions established for mixed sexes, in cases where sex could not be easily determined, or was not specified in the available data. The average relationship obtained on the Ivory Coast from experimental surveys in 1969-1970 (Fig. 30) was applied to the size composition of *Penaeus notialis* landings in April 1974 as an example of the use of this method. The size composition of males and females in the landings obtained by this method were compared with those determined directly and showed excellent agreements (Fig. 31).

It is of course necessary to confirm that the method can be generally applied. The relation can probably be used for large numbers (monthly landings) but one must be certain that seasonal changes through differential migration or catchability variations in one or the other of the sexes, do not occur. Boerema (pers. comm.) pointed out that when the seasonal variations of recruitment are important changes in the relationship are likely to occur from one month to another. Marcille (1978) used the method and showed the similarity among the sex ratio/size average curves obtained for *P. indicus* over several years and the differences in curves obtained for different species. Lhomme (1980) working on *P. notialis* in Senegal demonstrated the existence of an average curve similar to that of Garcia and Albaret but clearly shifted. This indicates that the curve may be a characteristic of a given fishery and must not be generalized to the species.

4.2.3 Other data

Among biological data worth collecting, the frequency of soft "shelled" shrimp and the state of the sexual maturity in the female might be recorded. The first information, which is easy to obtain, allows one to determine moulting periodicity which is of great importance in growth studies. The second allows one to determine the seasonal reproduction cycle and will be discussed in more detail in the following chapter.

4.3 CONCLUSIONS

The availability of reliable statistics is one of the essential conditions for rational management of the resources.

Such statistics can be obtained:

- if a permanent data collection system is established at the places where the catches are landed. The scientists, users of the data, must then be closely associated with the design of the system;
- if a scrupulous attitude towards professional secrecy is maintained and if it has been agreed that statistical data will remain anonymous and will not be used for tax purposes;
- if a minimum of useful information is returned to fishermen and industries, e.g. through informal personal contacts between scientists and fishermen or in the form of news bulletins for factories, fish traders or ship owners (Statistical bulletins, market news).

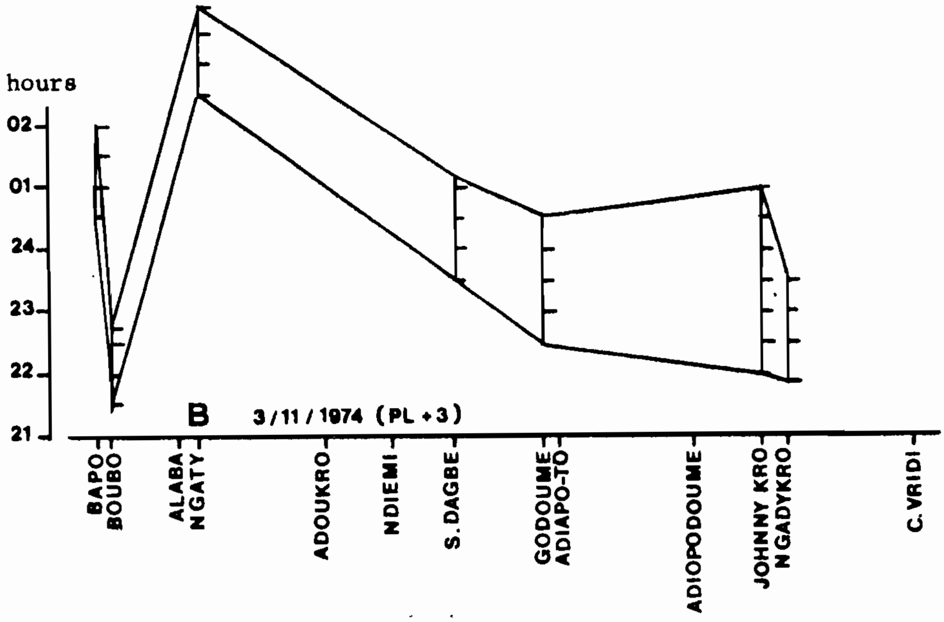

Fig. 29 Variations of the time and duration of the fishing (in hours) along the upstream-downstream axis of the Ebrié lagoon (from Bapo to the Vridi Channel) (from Garcia, 1977)

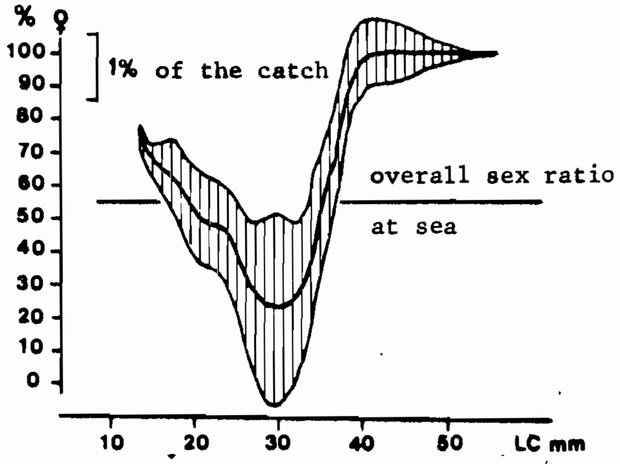

Fig. 30 Relation between size and sex-ratio for *Penaeus notialis*. The vertical lines are proportional to the abundance of each size class in the catch (from Garcia, 1974)

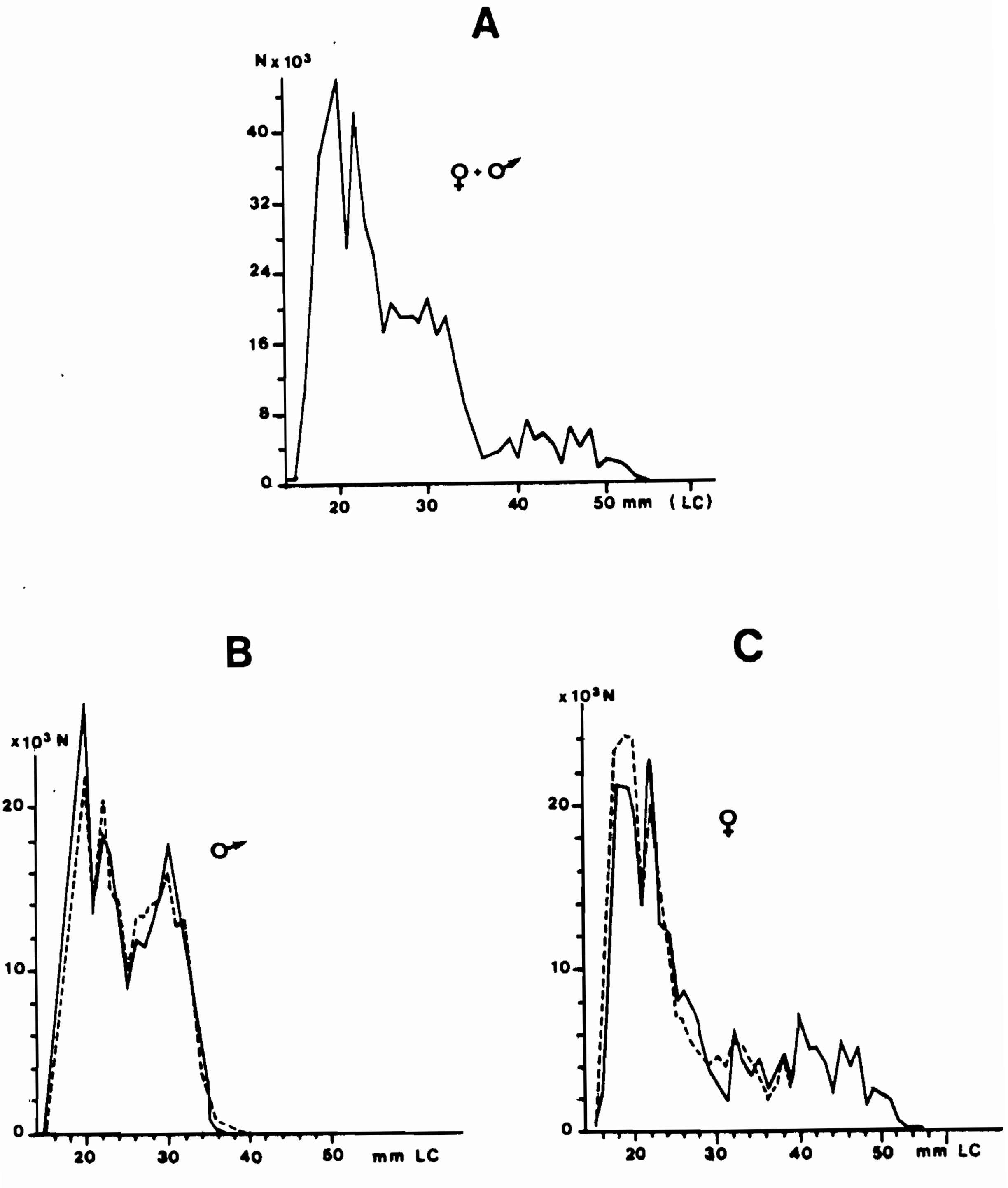

Fig. 31 Comparison of length frequency distribution by sexes observed and calculated using the size/sex-ratio relationship for *Penaeus notialis* (from Garcia and Alabaret, 1977)

In addition, the complexity and the quantity of collected data requires automatic data processing and this means that basic equipment and adequately trained people must be available. The system of the collection of the data, their coding and processing is always that described above, but since each fishery represents a special problem in a different context, it is difficult to suggest a general outline. Some publications already quoted may be consulted (Snow, 1969; Slack-Smith and Stark, 1969; Berry, 1967; Garcia, 1978; Marcille, 1978).

In addition to the data on the shrimp landings, it is important to devote attention to the by-catch of fish. Until very recently the information about the fish caught, kept on board or discarded in coastal shrimp fisheries has been neglected most of the time. This is because of the disproportionately higher price of shrimp and the high specialization of the fishing units. This state of affairs is unsatisfactory. Because a multispecies approach of management needs to be considered, the direct consequence for statistics collection is the necessity to give special attention to data so far neglected, such as the catch and discards of by-catch species. Also, better estimates of the effort directed to each species of shrimps are necessary when there are several species exploited together.

Tableau I: Key to convert catch data by commercial categories into length distributions for *Penaeus schmitti* (from Cadima *et al.*, 1972)

Total length (cm)	FREQUENCY (%) OF THE TOTAL LENGTHS IN EACH COMMERCIAL CATEGORY								
	61/70	51/60	41/50	36/40	31/35	26/30	21/25	16/20	11/15
8	-	-	-	-	-	-	-	-	-
9	-	-	-	-	-	-	-	-	-
10	-	-	-	-	-	-	-	-	-
11	15	12	1	-	-	-	-	-	-
12	72	43	26	1	4	1	-	-	-
13	13	38	56	8	9	1	-	-	-
14	-	3	15	24	14	2	-	-	-
15	-	3	1	52	25	21	4	-	-
16	-	-	-	14	33	44	33	5	-
17	-	-	-	1	12	26	29	22	2
18	-	-	-	-	2	5	20	43	20
19	-	-	-	-	1	1	4	23	33
20	-	-	-	-	-	-	1	6	35
21	-	-	-	-	-	-	-	1	9
22	-	-	-	-	-	-	-	-	-
23	-	-	-	-	-	-	-	-	-
24	-	-	-	-	-	-	-	-	-

5. GROWTH

This is one of the basic parameters for population dynamics, but its study is less precarious than that of mortality because results are easier to obtain and analytical models are more robust regarding parameters of growth than of mortality. As a rule, individual growth is studied, and population growth is considered to be only a simple addition of its single components.

In the case of peaneids, several difficulties arise.

- The crustaceans do not have a bony structure which records an imprint of internal and environmental variations, which would allow age to be read directly. We should note however that, according to Yano and Kobayashi (1969) the number of lamellae in the endocuticle increases with size and thus may give some possibility of age determination.
- Growth is discontinuous and the occurrence of moulting makes tagging techniques and, in particular, the use of external tags a risky operation (Petersen discs etc.). According to Boddeke, Dijkema and Siemelink (1977) however, growth in length continues during the period between moults by stretching of the supple parts of the carapace, while the size of the dorsal-lateral shields remains unchanged. They showed moreover that the ratio of shield length to total length varied in a cyclic manner between moults.
- Like many tropical species, penaeid shrimps show most often a protracted reproduction period which makes it difficult to use polymodal length frequency curve analysis for distinguishing and separating age groups from the modes in the curves.

Basic work on the subject is plentiful and among others, the publications of Kurata (1962) and Mauchline (1977) can be consulted for studies on moulting and growth in crustaceans, and for more general growth studies those of von Bertalanffy (1938, 1964), Walford (1946), Gulland and Holt (1959), Tomlinson and Abramson (1961) Fabens (1965), Southward and Chapman (1965) and Ebert (1973), the classical work of Beverton and Holt (1956), Gulland (1969) and Ricker (1975), and the excellent synthesis of Ricker (1979).

The estimation of growth parameters is made in two stages. First of all the basic data must be collected (age-length keys, instantaneous rate of increase average lengths, etc.) and later this information must eventually be expressed in a more or less simple mathematical formula (of a logistic, linear, monomolecular type, etc.). This second stage is more and more often optional since the current use of computers allows the observed age-length keys to be used directly. The formula is in any case approximate since a single mathematical law can rarely be applied to the growth of an individual from birth to death and the price to pay for simplicity is some degree of approximation.

It should also be remembered that Knight (1968) stated that the calculated parameters have no biological significance, while Kruger (1969, quoted by Ricker, 1979) questions this opinion.

5.1 METHODS OF DETERMINING GROWTH

5.1.1 The modal progression analysis

This method which originated from Petersen is applied by following, over a period of time, the observed modes in the length distribution of samples taken periodically from the catches. Among the penaeids, where the absolute age is unknown, a relative age is defined starting from an arbitrary point (size at recruitment, the first mode observed at sea, etc.). Later, complementary data on the juvenile phase will perhaps allow one to revise these relative ages and relate them to the date or period of birth, when this appears to be necessary.

The main limit of this method is in fact founded on the difficulty of distinguishing size groups in coastal penaeids and to follow them over a period of time (Fig. 32). With a little experience, however, some success can be achieved in certain cases, of which there are several examples (Neiva *et al.*, 1971;

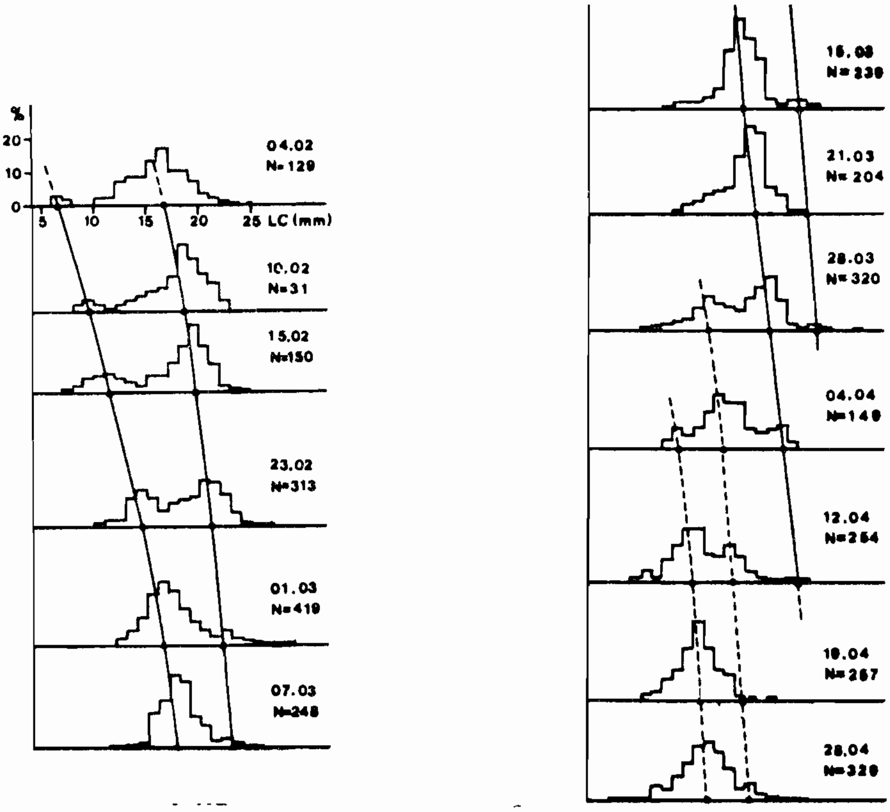

Fig. 32 Growth of Penaeus notialis in the Ebrié lagoon (from Galois, 1975)

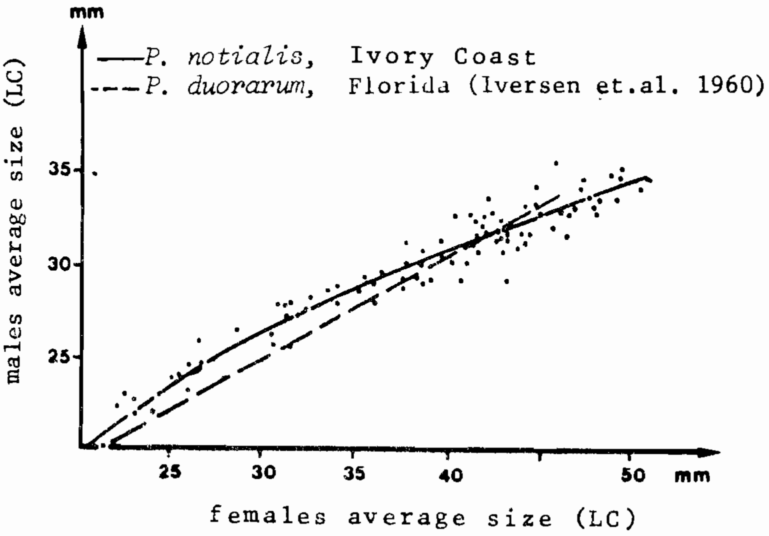

Fig. 33 Relationship between the average size of females and males for Penaeus notialis (from Garcia, 1975) and P. duorarum (data from Iversen et al., 1960)

Galois, 1975; Garcia, 1975; Edwards, 1977). The facility of the analysis will depend on the seasonal spawning pattern and on the sampling quality. In areas of strong seasonal fluctuations in reproduction the principal cohort (or groups of cohorts) can often be followed; in estuaries where growth is very rapid, frequent and careful sampling (once a week) should often make it possible to follow micro-cohorts generated by lunar (tidal) periodicity in the larval recruitment into nurseries.

It is sometimes possible to break the total size distribution down into a series of simple distributions, each representing a different cohort, by using one of the many available methods, sophisticated or otherwise (Harding, 1949; Cassie, 1954; Tanaka, 1956; Battacharya, 1957; Hasselblad, 1966; Gheno and Leguen, 1968; Gregor, 1969). Some programmes compiled by Macdonald (1969) are also available. Only the simplest methods have been used for penaeids (Cassie and Gheno-Leguen) and the results are not always, at first sight, unequivocal. However, on the Ivory Coast the growth estimates of Penaeus notialis determined by the modal progression analysis have been verified using tagging techniques (Garcia, 1975).

The greatest drawback of all these methods is their evident or hidden subjectivity. Intended originally for determining the number of individuals in age classes which appear as clearly distinguishable modes in the length distribution curve, they are too frequently used to subdivide size frequency curves, the structure of which is not obvious at all. This distortion in the use of the methods can cause serious errors.

The possibility of studying shrimps growth by modal progression analysis (because of rapid growth and continuous reproduction), depends very much on the space-time configuration of sampling and the precision of the measurements. In particular, precise measurements (carapace length to 1/10 mm) allow higher discrimination in the large size groups. Measurements are often made with normal callipers but Cole and Mistakidis (1953) and Mauchline (1958) developed high precision instruments which are of great service in measuring small sizes.

The existence of a heterogeneous geographical or bathymetrical distribution of sizes and sexes is undoubtedly a handicap which makes the reconstruction of a representative histogram of the population a difficult task. This is the reason for the difficulties which generally arise when industrial fishery samples are to be analyzed. The variation in the relative concentration of effort on different population strata in association with variations in catchability, sometimes results in changes in the length distribution curves of the catch, from one trip to another, which are unrelated to growth, due to the non-random character of the "sampling" by the fishing boat.

One can get round the difficulty if a research vessel is used with a satisfactory sampling plan (stratified sampling).

Observations on growth of migrating sub-adults (Loesch, 1965; Lhomme, 1979) are particularly difficult to interpret. Indeed, in an absolute sense, if the migration of juveniles seawards takes place at a given size, fixed modes would be observed and no growth would be apparent. On the other hand if migration takes place at a certain development stage (for instance, the maturation stage), the size at migration will vary as a function of growth conditions existing in different parts of the estuary and at different seasons. If size at migration depends on the time spent in the estuary, itself dependent on environmental conditions, it will vary as a function of the environmental factors and in particular of the salinity (Garcia, 1977; Le Reste, 1979) or of the temperature (Trent, 1966).

Migrating populations consist in general of numerous micro-cohorts[1/] and unless there is well defined sampling allowing their identification, the attribution of variations in average size at migration

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1/ Small groups with different time-space origins to growth can lead to false results which would in general underestimate true growth. This type of data must therefore be considered with caution.

5.1.2 Tagging

The difficulty in identifying shrimp age groups can be overcome by the use of tagging techniques.

The principle is that an individual or a group of individuals can be identified by a visible tag and growth can be determined between tagging and recapture, the basic hypothesis being that tagging has not interfered with growth.

Coloured injections, properly used, do not affect metabolism (cf. chapter 6). They are used for tagging of a group with a limited size range, sorted from the catch, of which the development of the average size can be followed. To cover the full range of sizes present in a population, different tagging operations using different colours are required.

The simultaneous use of secondary tags (section 6.5) increases appreciably the number of possible combinations. Plastic numbered internal secondary tags allow even the identification of individuals. An additional advantage of external tags (Petersen discs and derivatives) is that they allow the marking of all sizes caught without previous sorting and individual identification. All types of stratification are then possible when the data are processed: by size groups, by sex, sometimes by sexual phase, etc.

Although the coloured injection technique properly executed is probably the least harmful, external tags give more possibilities for interpretation. The main data obtained by tagging are: size at marking, size at recapture, length of period at liberty. Since the recapture is generally carried out by fishermen, the length of time at liberty is extremely variable for the same group of tagged individuals.

5.1.3 Male growth

Their growth is usually less than that of the females (smaller L_∞ and higher K - see section 5.2). As a consequence the length frequency distributions contain a smaller range of sizes and are therefore more difficult to analyse than the females one, because they are more compact. However, when the growth curve and the age-length relationship is known for females, Garcia (1975) showed that one could use a relationship between average size of males and females to infer the age-length relationship of the males and their growth curve.

Such a relationship is obtained by plotting the average size of the males in a sample (from a trawl haul at a given depth for instance) as a function of the average size of the females in the same sample, for a series of samples collected at different trawl stations. The scatter of points is small enough and the curve can be drawn by eye. Figure 33 shows the curve obtained by Garcia (1975) for Penaeus notialis and for comparison the one found by Iversen et al. (1960) for Penaeus duorarum.

If it is assumed that the observed average differential distribution of the sizes of shrimps on the bottom (Fig. 15) reflects an age specific segregation and that males and females caught together are on the average of the same age despite possible variations of sex-ratios, one can very simply infer the age-length key of males from that of the females (provided, of course, the latter is known).

On the Ivory Coast this method gave results identical to those obtained by modal progression analysis and by tagging (Garcia, 1975 a and b). Lhomme (1977b) has used the same method in Senegal.

When the "observed" or assumed modal progressions for the males are not very obvious, as it is often the case, this method can help to avoid big mistakes.

5.1.4 Concept of maximum age

Because the age of shrimps cannot be determined directly and cohorts are usually difficult to follow, the maximum age of shrimps is difficult to determine.

The analysis of growth curves shows a higher K and a lower L_{∞} value for the males than for the females. The study of the changes of the sex-ratio in relation to the size (Fig. 30) also shows a clear predominance of females beyond a certain size. These data have sometimes been used, for other marine species, to infer a lower life-span for males (Beverton and Holt, 1959; Holt, 1962).

However a study of sex-ratio as a function of age in P. notialis on the Ivory Coast over a complete two-year period has shown that there was no clear trend in this parameter and that the life-span of the two sexes should be considered comparable (Fig. 34).

Iversen, Jones and Idyll (1960) also showed for P. duorarum that if the sex-ratio in different samples is plotted against the average size of the females in each sample no trend is apparent. This observation leads to the same conclusion of comparable life-span of males and females.

To give some idea of maximum age, shrimps over two years of age are rarely found in significant amounts in catches, although shrimps of at least 27 months old have been observed in tagging experiments (Baxter, 1971).

5.2 MATHEMATICAL EXPRESSIONS FOR GROWTH

Once the basic data (age/length and growth as a function of size) have been obtained, a mathematical expression or model may be required which gives the best possible expression of growth using a simple formula. The literature is rich in basic studies and reviews on this subject and it is not necessary to make an exhaustive review here. The reader could more usefully refer to such basic work as Beverton and Holt (1956), Ricker (1958, 1975 and 1979), Gulland (1969). A single model would rarely be sufficient to represent the growth of an individual from birth to death and an approximation must often be accepted.

The model most frequently used is that of Von Bertalanffy (1938) because Beverton and Holt (1956) decided to integrate it into their yield equations. Other models have been proposed, such as those of Gompertz (Riffenburgh, 1960), a logistic model (in Ricker, 1971) and an exponential model (Ricker, 1958). The properties of the Von Bertalanffy's model have been studied by a number of the authors already quoted and by Fabens (1965) and Southward and Chapman (1965).

The Gompertz and Von Bertalanffy models have been compared by Silliman (1969) and Parrack (1979) for fish and penaeid shrimp respectively. Their results show that Von Bertalanffy's model as now used is appropriate.

Some modifications or a generalization of the Von Bertalanffy equation have been proposed by several authors such as Richards (1959), Chapman (1961) and Taylor (1962). Although their application to the Beverton and Holt models is possible (Paulik and Gales, 1964) they do not yet seem to have been used. Knight (1969) has also proposed a modified equation in which the true growth rate (growth per unit of time) appears as a parameter.

We will not dwell on the important biological significance that Von Bertalanffy (1938, 1964) wished to attribute to his model and that Ricker (1975) and others (quoted by Von Bertalanffy, 1964) have contested. We note with Ricker that the proposed model most often agrees with what is observed and therefore can be applied as an empirical model, an opinion shared by Brody (quoted by Ricker, 1975) who laid the basis for the model.

We will therefore only refer to Von Bertalanffy's model and will review very briefly the most commonly used methods for calculating the parameters of the equation.

The classical expression of Von Bertalanffy's curve is of the form:

$$l_t = L_{\infty} (1-e^{-K (t-to)}) \qquad ......(5.1)$$

where L_{∞} is the average asymptotic size to which the individual grows. On this point we must note that the principle of asymptotic growth itself is sometimes questioned (Knight, 1968; Ricker, 1979). K is Brody's growth coefficient (Ricker, 1975, points out that it is inappropriate to speak of "growth rate" for this parameter) and t_o is the theoretical age of the individual at zero size. There are numerous methods for calculating the parameters.

5.2.1 Ford-Walford's method (1946)

This is based on the following form of Von Bertalanffy's equation (Ford, 1933):

$$l_{t+1} = L_{\infty} (1 - k) + kl_t \qquad \text{......(5.2)}$$

where k is Ford's growth coefficient, (= e^K). Walford showed that where L_{t+1} is plotted against l_t and a straight line is adjusted to these points this line has a slope k and cuts the diagonal at $l_t = L_{oo}$ (Fig. 35A).

Beverton (1954) proposed that the value obtained for L_{oo} should only be considered provisional and that $\text{Log}_e (L_{oo} - l_t)$ should be expressed as a function of t since

$$\text{Log}_e (L_{\infty} - l_t) = \text{Log}_e L_{\infty} + Kt_o - Kt \qquad \text{......(5.3)}$$

The linearity of this relationship is sensitive to small variations of L_{oo} and some trials with slightly different L_{oo} will help to determine a more exact value of this parameter (Fig. 35B). The slope of the relationship (which is in this case a classic predictive regression if t is precisely known) is equal to K and, the x-axis intercept being equal to ($\text{Log}_e L_{\infty} + Kt_o$), t_o can be obtained.

Ricklef (1967) also proposed an approximate graphic method using a rather similar approach for the Gompertz and von Bertalanffy curves and the logistic curves by weight. This method however is rarely used.

Gulland(1969) showed that t_o can also be obtained graphically from the same elements. In fact, according to the above equation, when $l_t = 0$ (and thus by definition $t = t_o$) the ordinate is equal to $\text{Log}_e L_{\infty}$. Thus when $\text{Log}_e (L_{\infty} - l_t)$ is expressed as a function of t, the point which has $\log_e L_{\infty}$ as ordinate has t_o as abscissa (Fig. 36).

The true age is rarely known. It is thus possible, either to assume that $t_o = 0$ or to take as the origin an observable point of the life cycle: migration for example. The average age at migration would then be taken as the origin ($t'_o = 0$) and the growth curve using a relative age (t') would be defined as in the preceding sections. The estimation of the real average age at migration, made from data on spawning and migration, would allow the curve to be adjusted to a real time scale.

Since the age at migration is apt to vary according to the environmental conditions in the estuary, the first mode observed in the length frequency distributions at sea can also be taken as representing the origin of the relative ages. This method has been used by Garcia (1970, 1975, 1977) and Galois (1975) for Penaeus notialis on the Ivory Coast and by Lhomme (1979) in Senegal, for the same species.

The Ford-Waldford method has been adapted to the use of tagging data by Manzer and Taylor (1947). When data are available on individuals of different sizes which have been at liberty for approximately the same length of time, the Ford-Walford graph can be used by plotting the individual size at recapture as a function of the size at release (Manzer and Taylor, 1947; Hancock, 1965). This method has been used for penaeid shrimps by Lindner (1953), Lindner and Anderson (1956), Iversen and Jones (1961), Kutkuhn (1962), Klima (1964, 1974), Berry (1967) and many others.

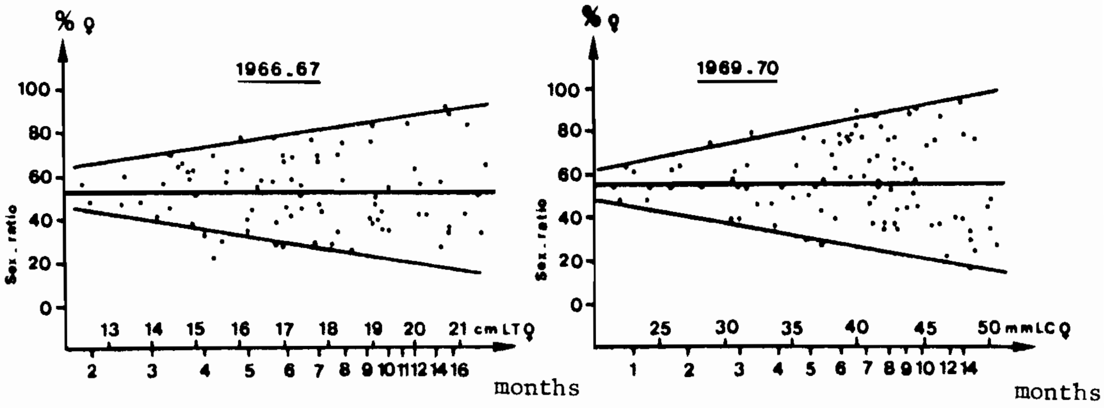

Fig. 34 Variation of the sex ratio as a function of age and size of the females in samples collected in Ivory Coast (from Garcia, 1977)

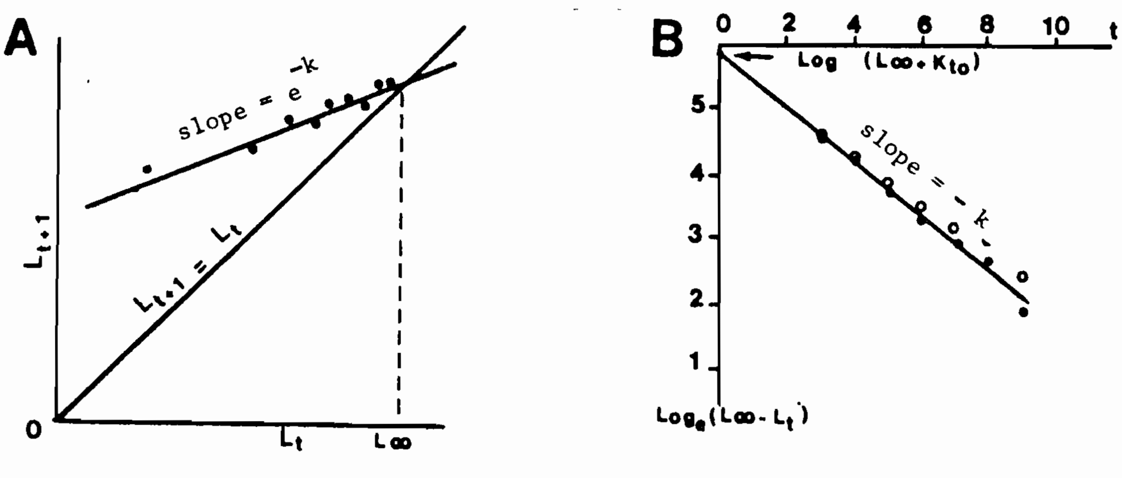

Fig. 35 Estimation of the Von Bertalanffy growth curve parameters
A. Ford-Walford plot. B. Beverton plot
(from Ricker, 1975)

The procedure is relatively simple. The recaptured shrimps are grouped by equal intervals of days at liberty, which should be as short as possible (a week or 10 days). For each period the relation between the size at recapture ($L_{t+10\ \text{days}}$) and the size at release (l_t) is analyzed. One obtains as many growth curves as there were time intervals with sufficient recaptures for the estimation, which requires that enough shrimps have been tagged to ensure sufficient shrimps in each recapture period.

5.2.2 Chapman's method (1961) (Fig. 37)

This method attributed to Chapman by Ricker (1979, page 709) is often also called Gulland's method (1964, 1969). It derives from the following form of Von Bertalanffy's equation

$$(l_{t+1} - l_t) = (L_\infty - L_t)(1-e^{-K}) \qquad \text{......(5.4)}$$

The functional regression line of $(l_{t+1}-l_t)$ on l_t has a slope - $(1-e^{-K})$ and the intercept with the x-axis at L_∞.

This method can be used for tagging data if the length increase per time L is expressed as a function of the average size at marking. The growth is thus calculated in the absence of all knowledge of true age, which justifies the use of the word "atelic" given by Diaz (1963), for the method.

If the times at liberty are unequal, Gulland and Holt (1959) propose a calculation method based on a hyperbolic tangent correction. This is particularly valuable when the number recapture is insufficient for distinguishing different size groups having equal times at liberty. The method is explained in detail by Jones (1976).

To illustrate, if (a) is the length of time at liberty with $y = (l_{t+a}-l_t)/a$, the increase per unit time, and (x) is the average size during the period of liberty, $(l_{t+a} + l_t)/2$, the regression of (y) on (x) can be made as a first operation and the slope will give a provisional value of K. If $b=\frac{1}{2}Ka$, the regression of yb/tanh b on x can be made so as to obtain a second value of K. The process is repeated until the K value is stabilized. For short periods of liberty (less than 2 months) the correction is not necessary and the K value is stabilized at the first step. Campbell and Phillips (1972) proposed a different solution to the same problem but Gulland and Holt's (1959) method is preferable when there are large time intervals.

5.2.3 Discussion of regression methods

Ricker (1975, page 225) pointed out that the direct use of a predictive regression of l_{t+1} on l_t is not satisfactory since the two variables are liable to error; the distribution of the points along the line is not normal and all the points are used twice (as l_t then l_{t+1}) except for the two extremes which are used only once. Beverton's modification (section 5.2.1) is aimed at overcoming this difficulty.

The problem is the same when the increments method is used (section 5.2.2), Diaz (1963) used a functional regression line (Wald, 1940). Troadec (1968), as well as Garcia et al. (1970, 1975) used a GM regression (or Tessier line). In his latest manual Ricker (1975), applying the results of his work about the use of regressions in fishery biology (Ricker, 1973), recommends the use of this latter method and recalls that Chapman (1961) had already discussed the possibility of obtaining the parameters of Von Bertalanffy's equation by regression.

5.2.4 Automatic calculation methods

The increasingly current use of computers makes it possible to use improved methods of calculation which provide estimations of parameter variance. In the case of classical growth data, the programme VONB established by Allen (1966a) allows the use of data spaced at regular or irregular time intervals.

In the programmes BGC2 and BGC3 (Abramson, 1971) regularly or irregularly spaced data can be used respectively.

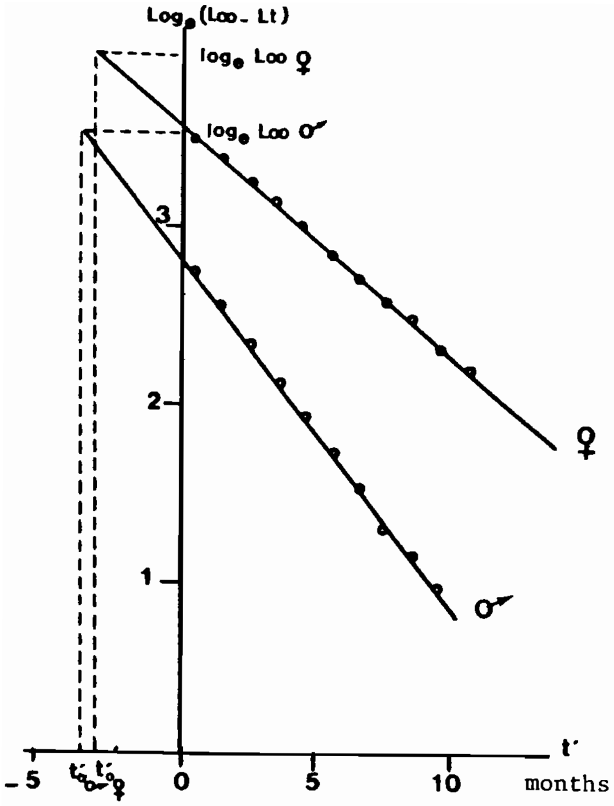

Fig. 36 Estimation of t'_0 by Gulland's method (1969) for *P. notialis*. The origin of ages (t' = 0) is arbitrary (see text)

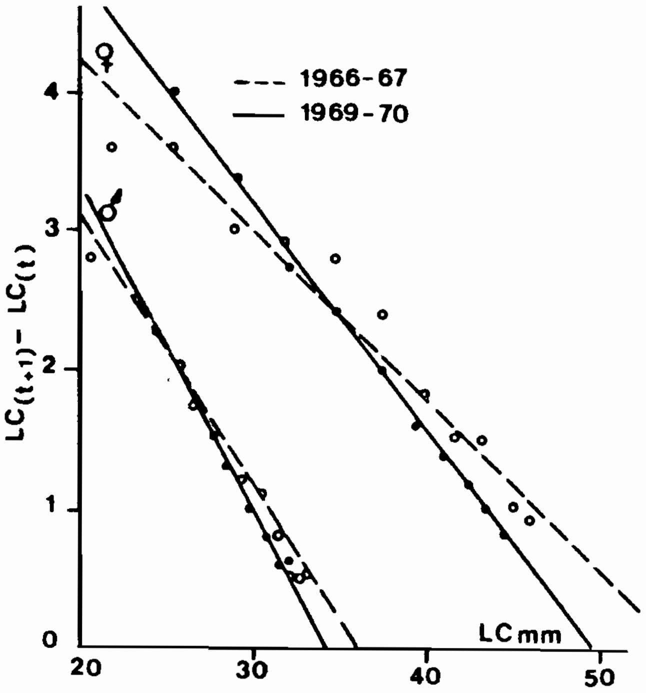

Fig. 37 Estimation of growth parameters by Chapman's method (1961) for *P. notiatis* in Ivory Coast

Psaropoulos' programme CIAT DO5[1] applies Tomlinson and Abramson's method (1961). This programme has been used by Garcia (1975) for Penaeus notialis.

For tagging data Fabens (1965) proposed a programme[2] allowing the parameters of the growth equation from Brody's original equation to be calculated by the least square method. It has been utilised for instance by Le Reste and Marcille (1976). This programme has been modified by Allen (1967, programme FABVB) and by Tomlinson (in Abramson, 1971, programme BGC4).

Southward and Chapman (1965) proposed a programme for the computation of the 4 parameters equation of Richards (1959) by the least squares methods.

5.2.5 Seasonal growth variations

The quantification of these variations is of particular importance for animals with short life-spans. They can have different origins, climatic (Ikematsu, 1955; Lindner and Anderson, 1956; Garcia, 1975, 1977; Lhomme, 1977; Klima, 1979, Fig. 38) or biological and related for instance to reproduction (Garcia, 1975; Penn, 1975). Lhomme (1977) demonstrated a relation between the value of K and the temperature of the environment in Senegal (Fig. 39). A detailed review of this problem will be found in Ricker (1979).

When these variations exist, they can seriously affect growth results of analysis by modal progression analysis. They can easily be revealed by repeated tagging during different seasons.

It should be remembered that, although this possibility has not yet been employed for shrimps, the von Bertalanffy equation can be adapted to give mathematical expression to seasonal variations (Lockwood, 1974). Moreover Ursin (1963) had already proposed the incorporation of temperature in the von Bertalanffy model, the time being then expressed in day-degrees.

The most serious consequence of the seasonal variation of growth rates is that each cohort of an annual shrimp generation will have a different growth pattern according to its birthdate and that a single age-length key is no longer available but there are rather as many age-length keys as basic cohorts that can be identified (12 monthly cohorts for instance).

5.3 CONCLUSIONS

Considering the difficulty of analyzing size distributions in penaeids, tagging seems to be a fundamental technique for analyzing growth and its seasonal variations, in spite of the constraints mentioned in the chapter on tagging techniques and their effect on metabolism.

The direct use of observed age-length data, for example in stimulation models, helps to avoid the use of too complex, and often only approximate equations, to describe growth.

Since growth is closely related to environmental conditions, it is extremely important to determine the concomitant hyroclimatic conditions to make it possible to compare results from one region with another.

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[1] Available at the I.A.T.T.C., La Jolla, California, USA

[2] To our knowledge, this programme is also available at Shimizu University, Japan, where Professor Suzuki kindly made the calculations for us (Le Reste, 1978)

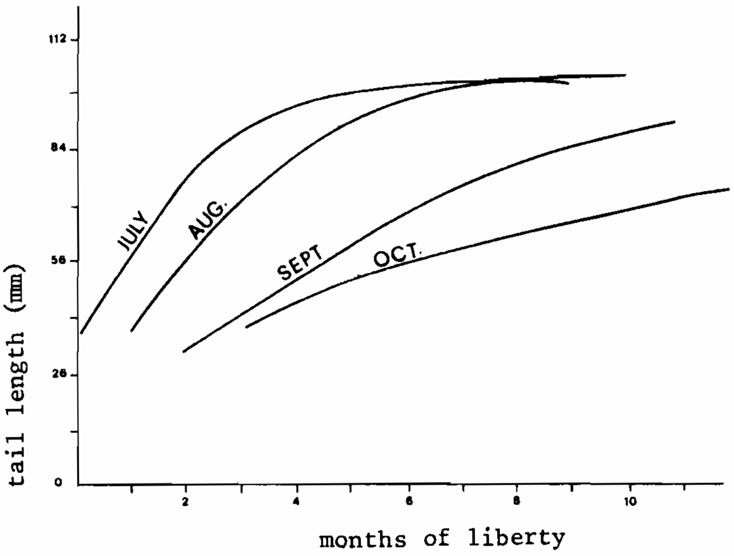


Fig. 38 Comparison of growth curves between different white shrimp *(P. setiferus)* cohorte (from Klima, 1980)

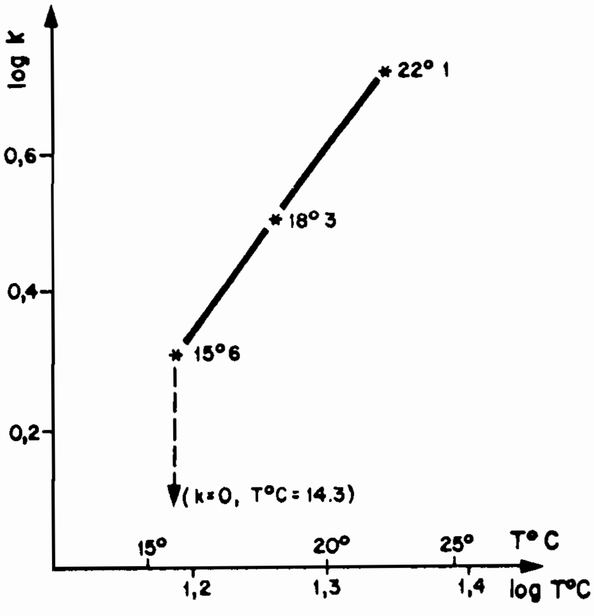


Fig. 39 Variations of K as a function of the temperature (from Lhomme, 1981)

Before its incorporation into population models the Von Bertalanffy equation, expressed in length, should be converted to an equation expressed in weight in the following way:

$$W_t = W_\infty(1-e^{-K(t-t_o)})^n \qquad \ldots\ldots(5.5)$$

where n is the exponent of the length-weight relationship

It should be rembered that the equation can also be calculated directly if weight-age data are available as in section 5.2.1 (Ricker, 1975, p. 231), by using the regression of $\text{Log}_e\ (W_\infty - w_t)$ on t, the linearity of which is very sensitive to small variations in W_∞ and the slope of which is equal to K.

Kutkuhn (1966) used Allen's method (1967) for P. duorarum by employing the $W^{\frac{1}{3}}_{(t+1)}$ regression on $W^{\frac{1}{3}}_t$.

The use of this type of curve means that growth is treated as a continuous function. Because of moulting it would perhaps be more advisable to use step-wise functions. However, since moulting is not simultaneous in all individuals and partial growth continues during the intermoulting period (Boddeke, Dijkema and Siemelink, 1977), the approximations of a continuous function should not introduce too much bias.

It should be noted that in cold regions, where there is a prolonged intermoult period (several months) by comparison with the basic time interval (one year), one approaches nearer to "simultaneous moulting" conditions and moulting becomes an important seasonal component of biomass development. Examples of the approaches used in this case for other crustaceans can be found in Kurata (1962), Hepper (1967), cited by Conan (1975) and Conan (1976). The last author demonstrates the bias resulting from the use of the von Bertalanffy curve by comparison with a step-wise simulated growth model.

6. MARKING TECHNIQUES

Tagging is a method of long standing which has been used to study migration, growth and mortality in marine animals. A general review of the tagging techniques used in fish and invertebrates was given by Rounsefell in 1963 and, more recently by Jakobsson (1970) and Neal (1970).

In the particular case of shrimps one meets the following main difficulties:

- their small size and their consequent frailty
- the moulting process. Any disturbance in this process can produce growth irregulatities or increased mortality.

There are two kinds of tagging methods, those which allow individuals to be distinguished and those which allow only the tagging of a group of individuals which are then followed as an artificial cohort.

A marking operation must be planned carefully from the beginning so as to ensure the best chance of survival of the tagged animals. For tagging in estuaries for example, it is best to select locations where hydrological parameters (temperature, salinity, dissolved oxygen) are favourable for the species under examination, avoiding for example too low salinities or too high temperatures.

The marking equipment (including water circulation, available tank volume, aeration) must be designed to insure the best conditions.

6.1 CATCHING

In carrying out this operation, the maximum precautions must be taken to avoid damaging the shrimps. Use of a trawl should preferably be avoided when possible, particularly in estuaries, where stake nets or traps are better.

If trawling is inavoidable it should be carried out in short hauls (10-15 minutes for example). Trawling time can be reduced according to the abundance of the species under examination and of by-catch species, and to the amount of "detritus" on the bottom (stones, sponges) which could crush the shrimps when the trawl is hauled in.

Costello (1964) suggested that the pressure in the cod end could be reduced by fitting rigid rings sewn to the inside so as to hold the pocket open.

6.2 STORAGE ON BOARD OR ASHORE

The problems of maintenance of live shrimp are especially acute if tagging is carried out on the shore. At sea, good water circulation is usually sufficient. Problems may arise if the salinity of the surface water pumped by the ship is very different from that near the bottom, where the shrimp live. The temperature should also be monitored; it may sometimes be necessary to stop tagging during the hot hours of the day.

On small boats in estuaries a simple solution is to attach some floating cages to the anchored boat. Circulation is thus ensured by the natural currents.

If tagging is carried out on the shore, the equipment will be more complex and should include a pump and an air supply. The latter can be eliminated by injecting water with special spouts giving a Venturi effect which will ensure aeration, or even simpler, by letting the water strike the surface with sufficient force.

The marking bench must have two flat basins containing seawater where shrimps can be held during the tagging operation (Fig. 40) and if possible a channel which carries the tagged shrimps to the recovery tank. It might be necessary to lower the temperature of the storage tanks and Emiliani (1971) described a system used in the Galveston laboratories (USA).

The use of an anaesthetic might be advisable to reduce the jumping of the shrimps during tagging: nevertheless Zein- Eldin (quoted by Neal, 1970) showed that high concentrations of anaesthetic were required and emphasized how difficult it was not to exceed the narrow non-lethal dosage limit within which rapid sedation could be induced.

It is often preferable to tag the shrimps immediately after catching when they are still under shock and relatively immobile. Experience shows that their subsequent recovery is very rapid and that they become extremely active after 20-30 minutes. Tagging then becomes more difficult for the operator and a greater stress for the shrimp.

6.3 MARKING A GROUP OF INDIVIDUALS

The aim of the operation is to mark a group of individuals of given characteristics, so as to follow them over a period of time. It is preferable to tag homogeneous groups, especially when the phenomena under observation may vary with age.

6.3.1 Sorting into groups

Young migrating shrimps are generally "naturally" selected in that their range of sizes and ages is small. This is not the case at sea and sorting is therefore necessary. Allen and Costello (1962) developed a simple method using separators made of properly spaced plexiglass tubes. The passage of the shrimps through the side and bottoms of successive separators of different spacing between tubes resulted in the sorting of groups of homogeneous sizes, the larger sized shrimp staying in the first compartment and the smaller escaping through the bottom into the second.

6.3.2 Use of vital stains

Menzel and Racek have used vital stains since 1955.

Arnold (1965) has reviewed their use in fish. Several methods can be used:

6.3.2.1 Total immersion in a staining solution which impregnates membranes and the digestive tract. The colour persists for only a few days according to Dawson (1957).

This method has been discussed by Racek (1955). The persistence of Tripan blue is two weeks but with 50% immediate mortality. Nile blue sulphate gives, according to the author, better results. The mark disappears at moulting (Meyer-Waarden and Tiews, 1965).

6.3.2.2 The ingestion of coloured food pellets will also colour the alimentary tract. Dawson has, since 1957, experimented with both techniques which are however, not in common use, because of the rapid disappearance of the mark. Persistence is sometimes good - more than 200 days, nevertheless over-ingestion of the colour causes fatal poisoning. According to the author, however, this drawback can be avoided.

6.3.2.3 Intra-muscular injection

This has been used in shrimp by Menzel (1955) and by Dawson (1957), Costello (1959), Costello and Allen (1965), Klima (1965-1974), Berry (1967), Kutkuhn (1962) and McCoy (1968) and seems to give the best results.

Costello (1964) has described a detailed operational procedure for this technique, from catching to releasing, and we will here summarize the essential details of his work.

The standard equipment consists of 0.5 or 1 cc tuberculin syringes with very small hypodermic needles. An automatic syringe can be used (Fig. 41).

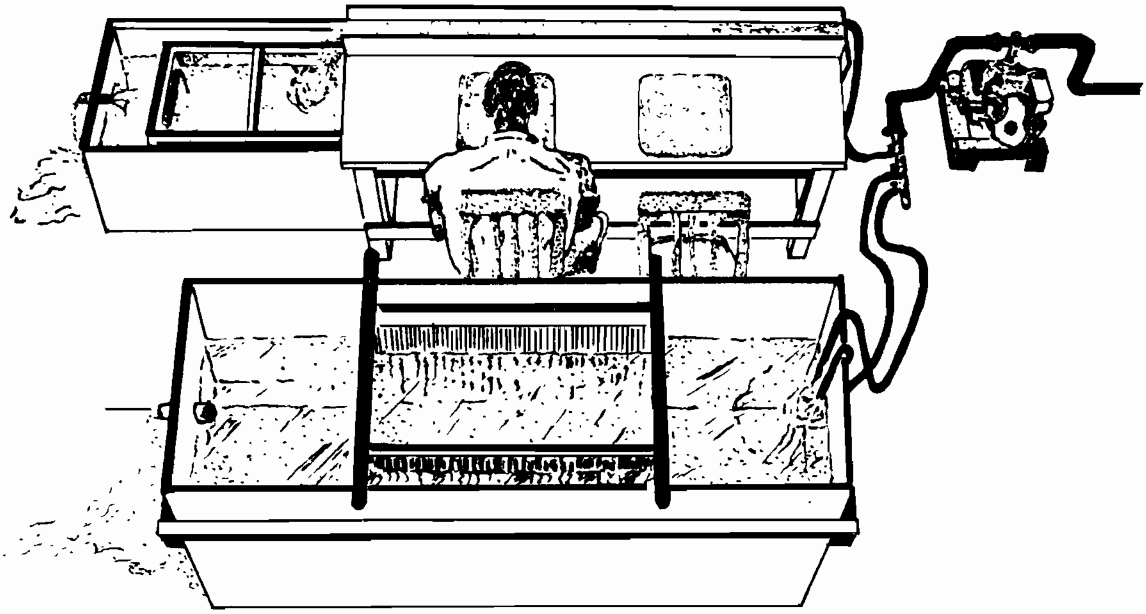


Fig. 40 Equipment for field marking (from Costello, 1964)

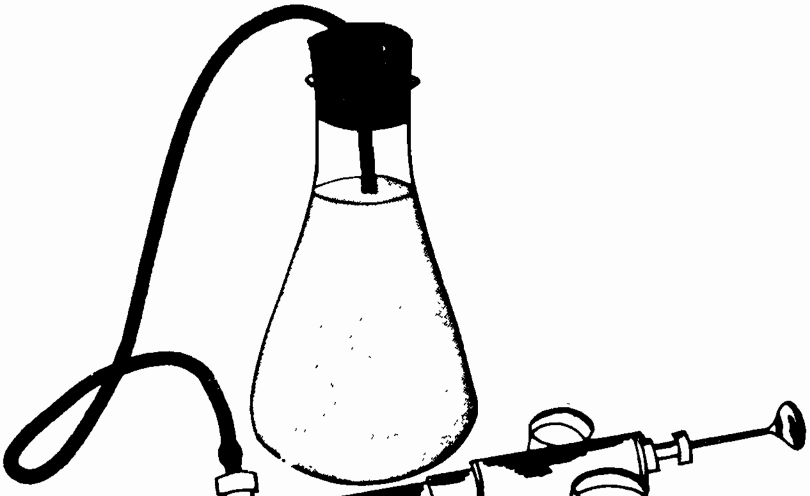


Fig. 41 Automatic injection system (from Neal, 1969, FAO)

The filtered staining solution is injected laterally through the articular membrane, between the 5th and 6th abdominal segment (or between the 3rd and 4th, Neal, (1970)). Shrimps of less than 60 mm, (total length) can be injected through the first abdominal segment.

The marking speed was 200/240 shrimps per hour and could reach 300 shrimps per hour.

Shrimps must be counted as and when they are marked. Shrimps which, because of their bad condition, are withdrawn later are substracted from the total.

The stain injected into the vascular system through the dorsal abdominal artery settles in the gills (Fig. 42A) where it can persist for several weeks 1/. The drawbacks of this technique is in the risk of rapid fading of the colour which can produce an artificial reduction in the recovery rate during the recapture period.

6.3.3 Fluorescent pigments

6.3.3.1 Mass spraying

Shrimps can be sprayed under high pressure (14 kg/cm^2) with a fluorescent powder (Benton and Lightner, 1972). The particles of the powder penetrate into the flexible membranes of the shell and can be observed by fluorescence under UV light. This method has several disadvantages:

- the most important is that the tag has low persistence; it disappears at the first moulting, except under exceptional circumstances, when it has been retained for 130 days. Loesch *et al.*, (1976) using this method showed that the particles can pass through the shell and persist during several moults;
- the necessity of using ultra-violet light for detection which limits its use to marking and recapture experiments completed by scientific operators;
- mass spraying at sea could possibly contravene regulations with regard to the use of food dyes, since undetected shrimps could be accidentally eaten.

Fluorescent marking of this type has the advantage that in short term studies it is possible for one person to mark several hundred shrimps per hour (Neal, 1970).

6.3.3.2 Injection

This can be accomplished using a fluorescent product dissolved in paraffin oil (Klima, 1965). The dye has strong persistence (276 days) but requires the use of ultra-violet light and the personal supervision by the scientist for detection. Smith (1970) studied the use of these dyes for marking young fish. In his experience the mark persisted for 8-11 months. Clark and Caillouet (1973) used the technique on juvenile *Penaeus setiferus* and Edwards (1977) on *Penaeus vannamei*. Neal (1970) and Penn (in press) pointed out however that paraffin oil particles progress slowly towards the gills where they may accumulate, especially if too much product is injected.

6.3.4 Printing inks tested by Klima (1965) for secondary marking were not found satisfactory because they did not stay at the point of injection but diffused toward the gills where they masked the primary mark.

6.3.5 Clipping

The partial clipping of a uropod is a useful method for short term experiments, which have been utilised by Barr (1971) on caridean shrimps.

1/ Shrimps carrying a still visible mark have been recaptured after 6 months (Fast Green FCF) and 10 months (Trypan Blue).

6.4 INDIVIDUAL TAGGING

The advantage here is that each individual can be identified by a number. This tagging can be applied to all individuals which can support a tag and its extension in time and space causes no difficulty since the characteristics of the tagged individual when recaptured can be easily identified because of the specific number.

6.4.1 External tags

These are visible externally and can be fixed to the shrimp by several techniques.

6.4.1.1 Atkins tag (Fig. 42B) consists of a nylon thread passing through the shrimp from side to side, tied in a loop and carrying a coloured and numbered plastic disc (Allen and Costello, 1962; Penn, 1975; Ruello, 1970, 1975, 1977). A similar tag, which is simply tied around the carapace, has been used by Tiews (1964) on *Crangon crangon*. The Atkins' tag is fixed by Costello and Ruello through the first abdominal segment and by Penn between the first and second abdominal segments so as not to hinder the moulting.

6.4.1.2 Vinyl ribbon

Marullo *et al.*, (1976) used a flexible plastic ribbon threaded through the shrimp which has the advantage of not damaging the tissues very much and not hampering the shrimp. Its colour can however fade which makes the tag less conspicuous. Tagging is quicker than with the previous tag but the toxicity of the coloured plastic has not been tested. In conjunction with aureomycin to limit infection, such tags have recently been used with success in the United States (Klima, 1979 and Klima and Parrack, 1979) and in Koweit (Mohamed *et al.*, M.S.). To date it is the most effective external tag for marking of juveniles since shrimps of 50 to 100 mm (total length) can be tagged and give an excellent recapture rate.

6.4.1.3 Petersen discs and variants (Fig. 42C)

This long-standing technique has been very widely used for many years and has developed considerably. The tag was originally in the form of two discs of 7.9 or 9.5 mm diameter placed on either side of the shrimp and joined by a steel wire through the body at the middle of the first abdominal segment (Iversen and Idyll, 1960; Potter, 1975). The method was improved by Neal (1970) who decreased the disc size and used a stainless steel needle to avoid rusting. Attachment of the tag to the shrimp was simplified by using printed circuit pliers. The needles were dipped in an antibiotic solution (2% chlortetracyclin) before use.

This type of tag, to which Kurata (1962) objects because of its inevitable interference with moulting, has been widely used in the USA (Lindner and Anderson, 1956; Iversen and Jones, 1961; Neal, 1969) on the Ivory Coast (Garcia, 1973, 1975), in Senegal (Lhomme, 1977) in Madagascar (Le Reste and Marcille, 1976) and in Australia (Lucas, Young and Brundritt, 1972) giving apparently good results.

Welker *et al.*, (1973) have compared this type of tag with dye injections and internal tags and have found no significant differences in growth or recapture rate.

The latest step in the development of tags of this type is the "toggle tag" used by Penn (1975) in Australia. A plastic numbered label is attached to the prawn by threading it into a flexible PVC toggle (35 mm long, 0,5 mm diameter) which was passed through the body between the first and second abdominal segment and secured by a 10 mm "T" bar at each end which protrude on either side of the shrimp. The tag is positioned with a special gun (Floy tag). The flexibility of the PVC connection reduces tissue ulceration. The "toggle tag" and Atkins tag give similar results.

6.4.1.4 Dart tags

Because they are attached to the muscle tissue of the shrimp, these tags (dart and anchor tag) have been shown to be disastrous for the shrimp. Dell (1968) has described the tag and the tagging gun.

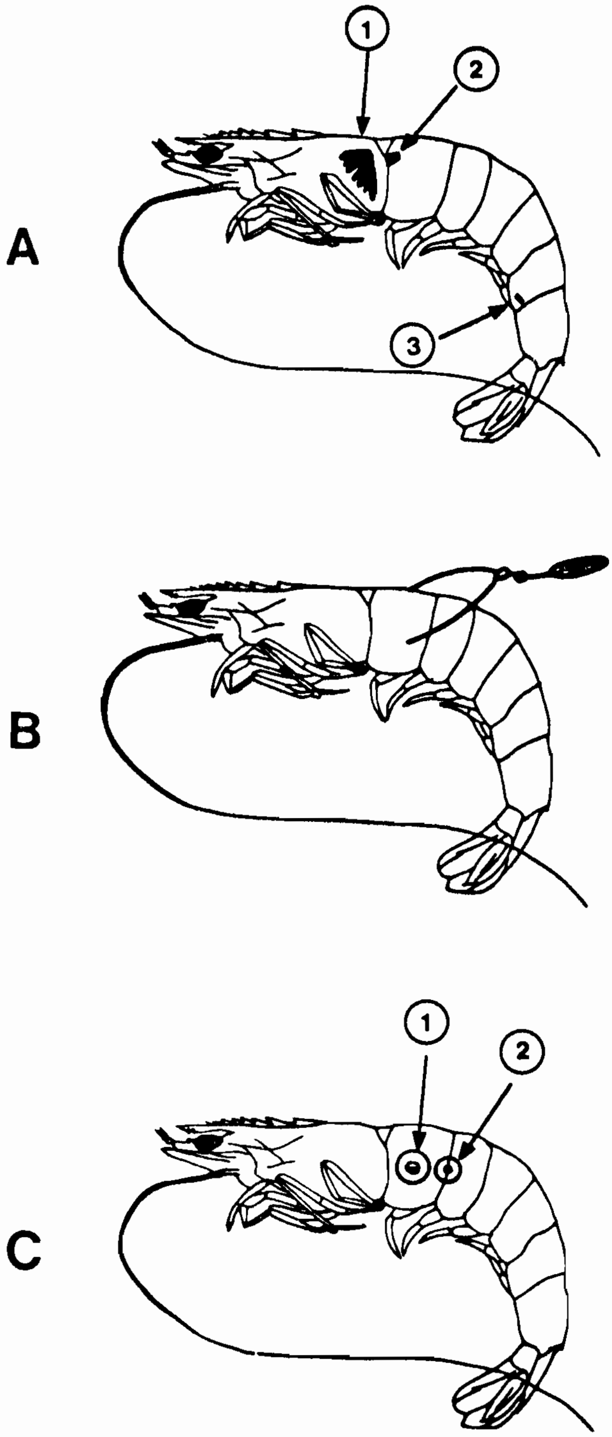


Fig. 42 Different types of internal and external marks
A - injected stain (1) internal vinyl tag,
and fluorescent dye
B - Atkins tag
C - Petersen discs = original method (1) and
modifications by Neal, 1970 (2)

They have been used for example by Bearden and McKenzie (1972), and have the disadvantage of being assymetric; the tag appears only on one side of the shrimp and unbalances the shrimps during swimming. Excessive movements of the tag causes permanent ulceration and consequent additional mortality (Neal, 1969; Lucas et al., 1972).

6.4.2 Internal tags

A tag of this type has been described by Neal (1970) and consists of a small numbered plastic label of 5 x 2 x 0.25 mm which is introduced into the abdominal muscle across an articular membrane. It is therefore invisible and is not normally lost at moulting. To be detected it must be used together with a primary mark (dye injection). The use of an antibiotic ointment reduces infection (Fig. 42B). Penn (in press) indicates that this tag can be rejected at moulting after local infection and erosion of the surrounding tissues.

Metallic tags in stainless steel coded with colour bands were used by Jefferts, Bergman and Fiscos (1963) and West and Chew (1968) on Pandalus platyceros. They do not appear to increase mortality and growth is normal. An apparatus for their rapid insertion into the shrimp is available. After insertion the tag is magnetized to make detection easier at recapture. The technique was used successfully for penaeids by Welker (quoted by Neal, 1970). Detection during industrial fishing operations would however give some technical problems.

6.5 DOUBLE MARKING

In this type of tagging two marks are placed simultaneously on the shrimp. It is, theoretically, used to detect and estimate accidental losses of tags. In shrimps it has been used to extend the possibilities offered by dye injection. These, which are clearly visible from the exterior, at least at first, are used as a primary mark, to distinguish, for instance, different tagging periods. At recapture the secondary mark allows a more detailed information to be obtained by consequent identification of sub-groups (different size groups, different releasing sites, etc.). The secondary mark could in this case be an injection of fluorescent jelly into the tail (Klima, 1965) (Fig. 42A). The use of two different injection sites increases the available combination possibilities. This author did not observe any noticeable additional mortality.

This method has also been applied by McCoy and Brown (1967) for juveniles. Double marking is applied in one or two operations. In the first case the two dyes (vital and fluorescent) are injected as a mixture. The first reaches the gills in 24 hours and the second after 48 hours. The mixture of the two dyes can be detected until 45 days later by ultra-violet light.

The secondary tag can be used to identify the individuals if it is numbered (cf. section 5.4.2). Double tagging of this type has the advantage of individual tagging (visual identification of individuals) without interfering with moulting and on the other hand has the drawback of coloured injections which fade with time. The method has however been used by Berry (1967).

6.6 THE RELEASE

This is one of the delicate steps in the tagging operation, because predation during the release can be an important cause of additional mortality. The essential principle that must be maintained is that: shrimp must never be thrown back into the water one by one. They should (as far as possible), be released very near the bottom. In addition only shrimps in good condition should be released. These are identified by inspection in a trough of highly aerated running water. Shrimps at first suffering from shock, recover quickly and experience shows that in general a holding period of an hour is enough since the shrimps that survive that period thereafter survive several days in fish tanks (Garcia, 1970, 1976; Lhomme, 1978; Le Reste and Marcille, 1976). Berry (1967) has kept tagged shrimps on board for 24 hours. When tagging juveniles Klima (1965) has extended this period to 18 days.

A recovery period is desirable but should not be too long since, contrary to the desired effect, the tagged shrimps may finally in fact be weakened (Beverton and Bedford, 1965).

For the actual return to the water a special cage may be used which opens at the bottom (Costello, 1964; Le Reste and Marcille, 1976) by a "messenger" released from the surface, or an inexpensive plastic container (Fig. 43) which opens simply by pulling a rope (Garcia, 1972) or simpler still, unattached weighted plastic dismountable containers are put into the sea which open on the bottom through the simple but ingenious process of the dissolution of a block of salt (Emiliani, 1971) (Fig. 44). This system is currently and regularly used in the Gulf of Mexico. In shallow lagoons shrimps can be sent to the bottom through a tube which allows the shrimps introduced above water to reach the bottom directly (Emiliani, op. cit.).

6.7 THE RECAPTURE

In certain cases (in limited zones or small bays) this is done by the research team itself; more often tagged shrimps are recaptured by fishermen and considerable care must be taken in planning the operation before and after tagging to achieve successful results.

6.7.1 Preliminary activities

The fishermen must be very well informed through personal contacts of the scientists with the skippers, crews, shipowners and with sorters in the factories, etc., and through the display of attractive coloured posters indicating clearly the kind of mark used, its position, the return address and the reward offered. The periodic organization of a lottery can encourage the return of tagged shrimp if the prizes are good.

6.7.2 Collecting information on recaptured shrimps

The whole shrimp with all associated information must be retrieved (date and place of recapture). Nevertheless it is not advisable to decrease the reward when only the tag, or incomplete information, is offered since one runs the risk of receiving false information.

Very close contact with the fishermen will ensure the collection of the recaptured shrimps and information under the best conditions. It may be necessary to provide for the distribution of cans of formalin to ensure best preservation of these shrimps.

When the boats undertake long trips, it would be advisable for the skippers to note on the spot the tag numbers in their log books with all the additional information since the shrimp grows quickly and the greatest precision on the date of recapture is needed.

The collection of supplementary information regarding the fishery and particularly the fishing effort must be carefully planned. Extra assistance may be desirable during the few weeks which follow tagging so that particularly accurate information concerning the geographical distribution of the fishing effort can be collected.

6.7.3 Biases

There are numerous sources of bias which affect tagging results; they have been reviewed in the basic studies of Beverton and Holt (1957), Ricker (1975) and lately by Gulland (1969). One should refer to these manuals for an in-depth study of the problems.

Some essential factors for shrimp are summarized here and in the following section. Z, F and M represent respectively the instantaneous coefficients of total fishing and natural mortality. For a better understanding of the following text it will be useful to also refer to chapter 7 on mortalities.

6.7.3.1 Ricker's type A bias

This will affect F but not Z values.

(a) Initial tagging mortality.

This has been studied by Penn (1975). It can be reduced by keeping tagged shrimps from 1 to 2 hours in a tank with circulating aerated water so as to eliminate the weaker shrimps.

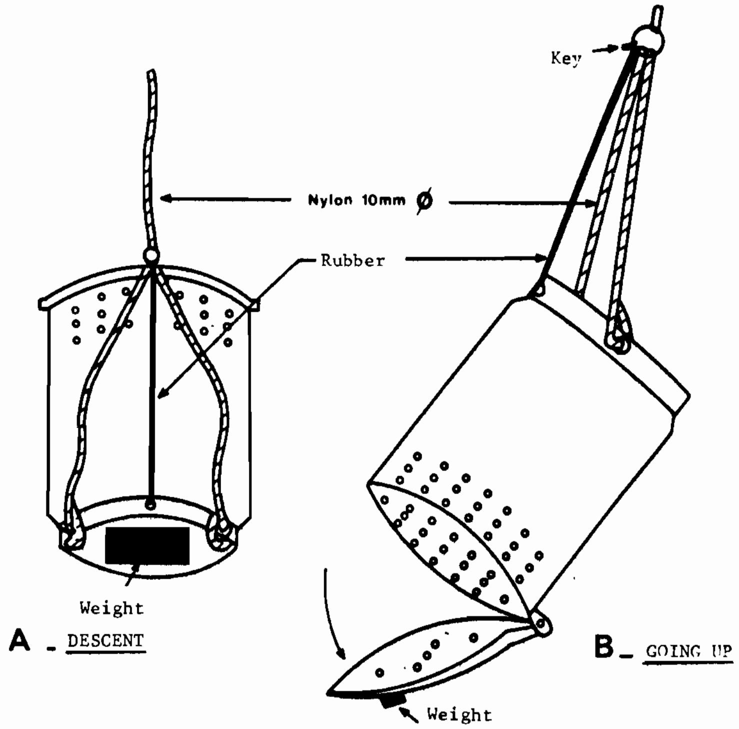


Fig. 43 Simple system for releasing shrimps on the bottom in shallow waters. The cage descends freely, a pull on the nylon rope when the bottom is reached opens it. (from Garcia, 1973).

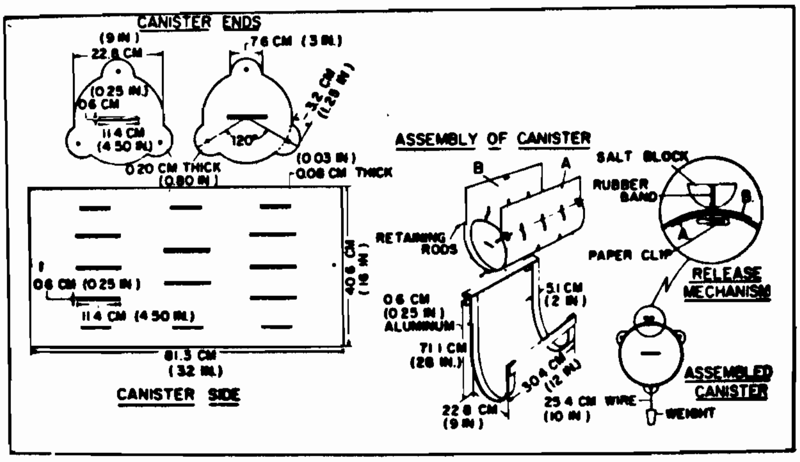


Fig. 44 Disposable canister with automatic opening. The canister descends freely; the melting of a bloc of salt opens it after 10 minutes(from Emiliani 1971)

Shrimps must be returned with great care to the bottom level to avoid predation by fishes which are attracted by the fishing operations and are following the boat. Garcia (1975) showed that the rate of recapture depended on the hour of release and that the difference between recapture rates for shrimps released during the day or during the night was greater when the water was clear.

Tagging mortality can also be reduced by avoiding the tagging of shrimps which are too small. Lucas, Young and Brundritt (1972) showed that Petersen discs caused additional mortality in shrimp of less than 30 mm (LC).

(b) Incomplete reporting of recaptures at constant rate

To reduce this factor to a minimum, it is important to ensure a good tagging information campaign and a good organization of tag collection and payment of the rewards. According to Penn (in press) an important loss of tagged animals occurs particularly among young individuals when a significant proportion of the capture is processed by automatic peeling machines. The amount of tags recaptured but not detected can be calculated by using the "seeding" technique. This consists of introducing directly into the catches of the boats a known number of tagged shrimps so as to observe the numbers reported later. A good statistical treatment of this method is given by Paulik (1961). This technique has been used by Berry (1967) and Costello and Allen (1968) for Penaeus duorarum.

The amount of non-reported tags obviously depends on the type of tag. A priori, it is less when the tag is less conspicuous. In this respect the Petersen disc practically cannot be missed when the shrimp is headed, whereas coloured injections are much less obvious.

In the latter case, the finding of the stain also causes a progressive increase in the percentage of non-detected marks which affects the calculated value of Z. The recapture curve is in this case no longer linear.

Following the same line of reasoning it should be noted that the "interest" of the fisherman for the tagging and the attention devoted to the discovery of the tags decreases as tagged shrimp abundance decreases.

It may, therefore, be important to consider only the recaptures obtained in the first weeks after the tagging (Costello and Allen, 1968).

6.7.3.2 Ricker's type B bias

This affects the Z but not the F value.

(a) Loss of tags at a constant rate

Petersen discs are less liable to cause this bias, but the progressive fading of injected dyes with time can contribute to it. The recapture curve can even loose linearity when the loss rate is not constant and Ricker (1975, p. 114) proposed a method which would allow this difficulty to be overcome. It should be remembered that according to Penn (in press) the P.V.C. internal tags may also be rejected at moulting.

(b) Constant tagging mortality

This is a classical type of bias. It usually shows as an overestimation of the natural mortality calculated by marking. According to Lucas, Young and Brundritt (1973), Petersen discs no longer introduce this error for shrimps of more than 30 mm LC.

(c) A constant rate of emigration out of the fishing area

This error is potentially very important when tagging takes place in a lagoon or an estuary just before migration. The migration rate cannot be distinguished from the natural death rate and appears as an additional mortality rate in the estimation procedure.

These errors are difficult to detect and even more to quantify and correct. It is for this reason that tagging generally is considered to allow a value for Z to be obtained which can be broken down into F+X where X represents a "composite" mortality integrating tag losses, migration, tagging mortality and natural mortality (M). It is sometimes taken as M in the absence of indications to the contrary and may in fact be considered as the upper limit to possible values of M (the term "apparent" natural mortality rate is often used).

In addition, the combination of the F value found by tagging with the Z value found, for example, by analysis of the age distributions, allows a better value for M to be determined.

6.7.3.3 Ricker's type C bias

This affects both Z and F. In this group are included those biases that make recaptures unusable in the initial period, and those arising from the difference in vulnerability between marked and unmarked shrimps because of:

(a) A modification in behaviour of tagged shrimps caused by the tags, which modifies the catchability at the beginning of the recapture period.

(b) Differential distribution of tagged and untagged shrimps associated with a non-random distribution of fishing effort in the first time intervals. During the following ones, effort must be randomly distributed or else the tagged animals must have the same distribution as the untagged ones, in order to be able to use the recaptured numbers as abundance indices of the natural untagged population. This aspect is more extensively looked at in section 7.2.3.

The first type of error can be easily detected when good data are available since the first points on the recapture curve are clearly positioned above or below the alignment of those which follow. The error is of little importance when many tagged shrimps are still caught after the single or several biased intervals but can be serious when the opposite is the case.

Gulland (1969) and Ricker (1975) proposed methods to overcome these errors, the principle being to use only non-biased points (see also section 7.5).

The problem of the differential distribution of tagged and untagged individuals is extremely important and tagging must be carefully planned to avoid this difficulty. The simplest way is to grid the whole distribution area (and not just the fishing area) and to tag all individuals caught per unit of effort at each station, or if they are too numerous, a constant proportion of them. These problems are treated in the chapter on mortality.

However, when the area is too large this may be impossible to achieve and Gulland (1969) proposed an approach for non-mixed populations which consisted of calculating F for the tagged shrimp from which, given the fishing intensity in limited zones where the marked shrimps are found, q can be deduced. If this value can be taken as valid for untagged individuals as well, the evaluation of the overall fishing intensity allows the calculation of a valid value of F.

6.8 SECONDARY EFFECTS OF MARKING

6.8.1 On growth

It is evident that external tags are likely to hinder the moulting mechanism considerably, even if the tags are inserted into the intersegmental membrane rather than through the first abdominal segment as was done originally. Kurata (1962) considered that external tagging was wholly incompatible with shrimp physiology because of this problem.

According to Penn (1975) external tags caused a slowing down of growth during the first two months and there was often no growth at first moulting under experimental conditions. It was also noted (Neal, 1970) that, in the aquarium, "injected" shrimps grew faster than those carrying a rigid external tag.

However, in spite of all these restrictions, tagging has frequently been used, for want of a better method, in many regions (the Gulf of Mexico, Kuwait, Australia, West Africa, Madagascar) and excellent results have been obtained, showing that the growth of tagged shrimps under natural conditions was compatible with those obtained by other methods. Also, tagging provided a useful tool for the demonstration or seasonal growth variations associated with environmental factors or with reproduction (Garcia, 1976, 1977; Penn, 1975; Lhomme, 1978; Klima, 1979).

6.8.2 On physiology

A comparative study made by Zein-Eldin and Klima (1965) did not show differences between oxygen consumption in individuals marked by injection and non-marked ones.

Penn (1975) and Garcia (1975) observed by tagging a retarded growth during the spawning period.

External tagging causes a wound which darkens rapidly. However on moulting this blackening disappears, the wound heals (Penn, 1975) and a newly formed cuticle sheaths the pin of the external tag, isolating it completely from the muscle (Ruello, 1970; Fontaine and Lightner, 1973; Penn, 1975). Penn noted that healing is retarded with rigid tags of the "anchor tag" type because usually an infection occurs which hinders the closing of the wound.

6.8.3 On behaviour

According to Costello and Allen (1961), external tags could affect the swimming and burrowing abilities of the shrimps, thus making them more susceptible to predation. It is true that when the tag is not well placed there is a perceptible imbalance in the swimming movements. Penn (1975) confirmed that burrowing is hindered by a rigid tag, but Lucas *et al.* (1972) did not observe any impediment to burrowing or swimming.

According to Penn, the general activity, for example movement and moulting, is reduced during the first two months after tagging.

6.8.4 On survival

Many authors have noted that the percentage recaptured is less in small-sized shrimps (Fig. 45) (Lindner and Anderson, 1956; Iversen and Jones, 1961; Lucas *et al.*, 1972; Garcia, 1973, 1975; Le Reste and Marcille, 1974; Lhomme, in press). The observed decrease is however often difficult to interpret because the effects of selectivity (reduced catchability of small sizes) are difficult to separate from those due to tagging (increased mortality).

In view of the obvious stress that tagging causes, one may expect that tagging is responsible for some mortality. One should however, distinguish *initial tag mortality* which occurs within a few hours after marking from *additional tag mortality* which occurs in addition to natural and fishing mortality during the entire period of observation.

6.8.4.1 *Initial tag mortality*. That initial mortality can be important and is evident from the number of tagged shrimps dying during the holding period on board before release. Its magnitude depends to a great extent on the conditions of capture and of holding on board.

The effect of this mortality on the experiment can be reduced by keeping the tagged animals on board for some time so that the weaker individuals can be eliminated before release. According to Penn (1975) shrimps which after tagging with an external tag survive the first 72 hours will also survive until the next moult in aquarium. Garcia (1975) noted that 93 to 99% of shrimps marked with Petersen discs and judged to be healthy survive after the first hour and do not show afterwards greater mortality than the non-tagged controls during 12 to 24 hours.

It is never sure that all initial mortality occurs before release and it is very important to identify its eventual occurrence afterwards since the reduction in the assumed initial numbers of tagged individuals cause bias in the evaluation of F.

Lucas et al. (1972) showed that Petersen discs, in contrast with the "anchor tag" (which give 50% losses), do not cause initial mortality. Penn (1975) calculated for "toggle tags" an initial mortality of 20%. Lucas et al. did not note any lethal effect from injected dyes, but it should be remembered that "vital" dyes can be toxic at high doses (Costello, 1964) and that meticulous use of the technique is required to limit these problems (test of the required dose, filtration of solutions, elimination of air bubbles at injection, etc.).

Predation on release can also be an important cause of initial mortality. Most authors agree that mass release at the sea bottom is preferable. Garcia (1975) has observed for different marked batches a rate of recapture which depended on the time of release (Fig. 46) and that the differences were least when the waters were turbid. He suggested that this fact could be due to predators which were attracted to the boat by the trawling and the discards and followed the cage during its descent to the bottom.

6.8.4.2 Additional tag mortality

This mortality is implicitely assumed in all tagging operations for which an estimation of F and X ("apparent natural mortality" or residual mortality, including natural mortality, migration, tag losses and additional tag mortality) is obtained.

Lucas et al. (1972) showed in aquarium that additional tag mortality occurred for small shrimps tagged with discs and "anchor tags", but not for adults. This was confirmed by Penn (1975) with "toggle tags" and Atkins tags. This author also pointed out that the colour of the tag had no influence on survival, confirming the work of Costello and Allen (1961) who asserted that tag colour had no effect on predation. According to Penn (1975) an important tag mortality occurs at the first moulting after tagging.

6.8.4.3 Conclusions

Although the mortality due to the tagging operation and to the presence of a tag is the greatest problem of this research technique, such mortality is very difficult to demonstrate clearly and even more to quantify.

It is obvious that such mortality depends on the conditions prevailing during the tagging operation (equipment, differences between conditions on board and on the bottom, catching and tagging methods, release procedure, etc.).

It is also certain that the results of experimental observations on survival, moulting, etc. should often be accepted with caution. In fact results are often contradictory and, for example, many authors have noted a survival rate in tagged shrimps which is greater than that of the controls (Costello and Allen, 1961; Lucas et al., 1972; Klima, 1965).

The two first authors had even suggested that injected dyes have a prophylactic effect. Penn (1975) thought that this paradox arose because mortality in the aquarium occurs chiefly at moulting, by stress or by cannibalism, and that because the general activities of tagged shrimps is reduced, they have a lower moulting rate than the controls and hence a lower mortality.

Even in control batches very high mortalities have been observed (Lucas et al., 1972; Penn, 1975) which emphasizes that in many experiments the animals are under conditions of stress.

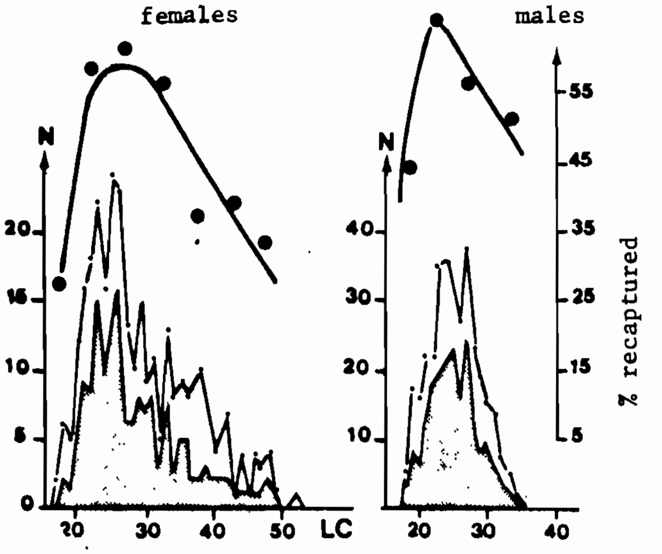


Fig. 45 Recapture rate as a function of size during the first month following the tagging (from Garcia, 1975)
unshaded = tagged shaded = recaptured

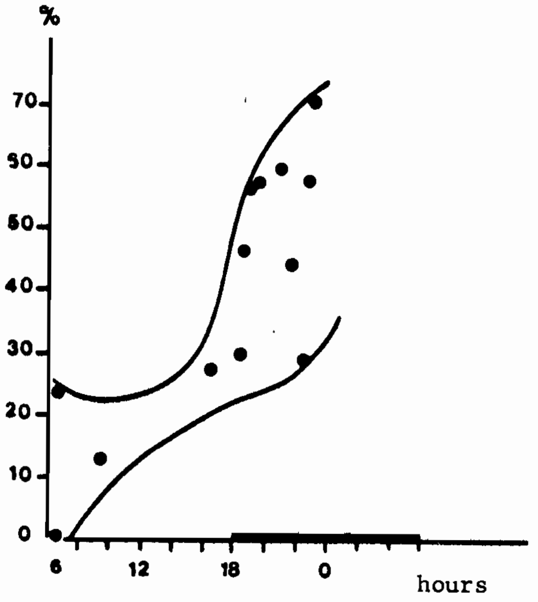


Fig. 46 Variations of the recapture rate in relation to the hour of release (from Garcia, 1975)

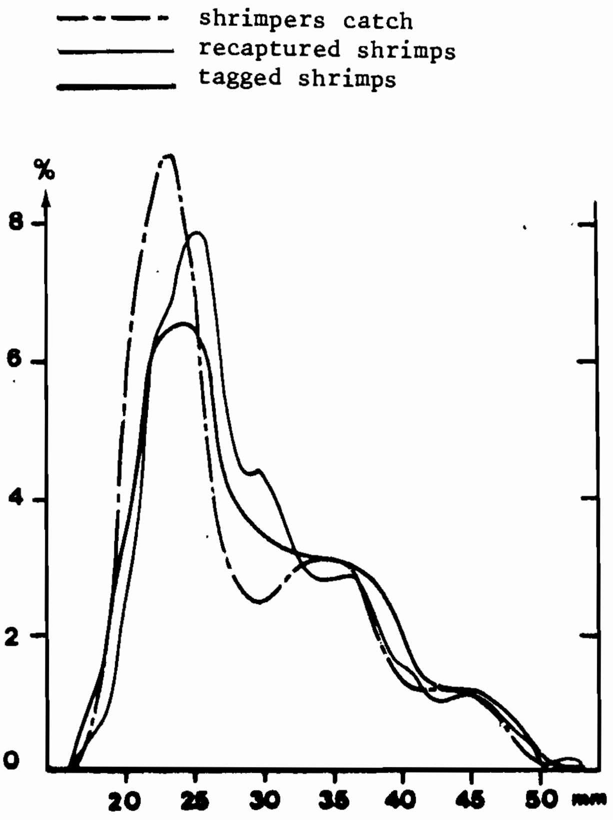


Fig. 47 Comparison of the size frequency curves of the shrimps tagged, recaptured, and caught by the fishery during the same period of time (from Garcia, 1977)

It seems probable that the least stressed animals survive best when the conditions under which the animals are held become limiting.

One could thus well ask how far the results obtained in the aquarium can be extrapolated to real tagging experiments. Penn (1973) has outlined their limitations and Lucas et al. (1972) pointed out that experimental results in the aquarium "depend on the environmental conditions" and that they must only be cautiously applied in tagging data analysis.

It would therefore be very fruitful during tagging experiments to also attempt to identify possible bias by indirect methods: comparison of results obtained with different batches, for different sexes and in different seasons with several types of tags.

A useful test would also be to compare the size frequency distributions of the shrimps tagged, recaptured and those caught by the fishing fleet in order to be sure that tagged and exploited populations were identical (Fig. 47), and that the results obtained for the tagged population can be extrapolated to the total exploited stock.

For the analysis of the data, it is probable that the recaptures obtained later (beyond the first 30 days after tagging) will give the least biased results, for growth as well as for mortality estimations.

7. MORTALITY

Information on mortality is extremely critical to the study of population dynamics since data are difficult to obtain, especially for natural mortality, and that the consequences of the possible biases in the estimates are important. A detailed analysis of possible biases will be found in the available handbooks and apart from a minimal review of the basic theory, we will concentrate chiefly on the methods most frequently used in studying shrimps.

The different possible approaches for estimating mortality are:

- analysis of catch curves
- tagging
- analysis of the c.p.u.e./effort relationship
- analysis of catch vectors: virtual population, cohort analysis
- approximative methods

There are two ways of expressing numerically the mortality in a population: the annual mortality rate or expectation of death and the instantaneous mortality rates (Ricker, 1975, p. 8). The following section will refer to the latter as they have been the more largely used.

If the number of deaths in a small interval of time is at all times proportional to the number of fish present at that time, the fraction which remains alive at time t, of the population at the start of the year is:

$$N_t/N_o = e^{-Zt} = e^{-(F+M)t} \qquad \text{......(7.1)}$$

where M, F and Z are respectively the instantaneous rates of natural, fishing and total mortality.

These parameters which are essential for population dynamics can be estimated in different ways which will be reviewed in the following sections.

7.1 ANALYSIS OF LENGTH FREQUENCY DISTRIBUTIONS

7.1.1 Successive numbers of the same cohort

The survival rate of the shrimp in a cohort can be approximately estimated by the ratio of the numbers in that cohort at two successive ages.

$$S = \frac{N_{t+1}}{N_t} = \frac{\bar{N}_2}{\bar{N}_1} = \frac{c.p.u.e._2}{c.p.u.e._1} \qquad \text{......(7.2)}$$

The formula remains valid if one considers the average numbers during two successive time intervals. They can be replaced by indices of abundance which are proportional to the average numbers by a constant q, that is by the c.p.u.e. in numbers. As it is assumed that the numbers in a cohort decrease exponentially as a function of time, one can write

$$Z = -\log_e S$$

where Z is the instantaneous rate of total mortality.

If the fishing effort can be taken either as a constant during the whole period studied or without distinct trends, a combined weighted estimate over several time intervals can be obtained by arithmetical methods such as that of Jackson (Ricker, 1975).

$$S = \frac{N_2 + N_1 + \ldots N_i}{N_1 + N_2 + \ldots N_{i-1}} \qquad S^2 = \frac{N_3 + N_4 + \ldots N_i}{N_1 + N_2 + \ldots N_{i-2}} \qquad \ldots\ldots(7.3)$$

or conceptually similar methods such as that of Chapman and Robson (1960) which give a better estimation of S;

$$S = \frac{T}{\Sigma N + T - 1} \qquad \ldots\ldots(7.4)$$

where $T = N_1 + 2N_2 + 3N_3 + \ldots\ldots$
and $\Sigma N = N_0 + N_1 + N_2 \ldots\ldots$

If it is thought preferable to obtain a non-weighted average, it can be found by simple arithmetical means from values obtained by equation 7.2 or by regression as a function of time of natural logarithms of the successive numbers in the cohort under examination. The slope of the line is equal to -Z.

These possibilities have been summarized for the sake of conciseness.

However it must be emphasized that in the case of animals with such a short life-span as shrimps, the maximum age of which is about 2 years and which are caught in significant numbers during one year only, the useful time interval is most frequently less than a year. In such a situation seasonal variations in catchability make it difficult to interpret, in terms of mortality, the observed changes in numbers with time.

This difficulty, added to that of breaking down the size composition into age categories explains why the methods outlined here have been very little used.

However, it should be noted that Berry (1967) used successive c.p.u.e.'s over short periods of time for calculating total mortalities. We will return to this example in section 7.1.4.

The evaluation of mortality from tagging experiments is a particular case of this method which will be examined later.

7.1.2 Simultaneous numbers of successive cohorts

One of the main concepts of the computation methods in population dynamics is that in equilibrium conditions (when recruitment and mortality have remained constant during a period of at least the life span of the species in the fishery) the numbers of fish belonging to the successive cohorts in the population at a given time are equal to the complement of one cohort in successive time intervals. All equations listed in the preceding paragraph therefore remain valid if applied to the numbers of each age in a representative sample taken from a stock in equilibrium condition at one particular time. Since direct reading of the age of shrimps is not possible and the breakdown of the size frequency distributions is problematical, Heincke's formula (in Ricker, 1975) is of interest because it only requires a knowledge of the numbers of the first fully recruited age group:

$$1 - S = \frac{N_0}{\Sigma N} \qquad \ldots\ldots(7.5)$$

where N represents the total number of all ages, including N_0.

In the particular case of shrimps, the need to work with a short time interval (one month, for example) implies that the basic hypothesis of this procedure is not fulfilled when monthly catch histograms are used.

For example: if a shrimp lives for 12 months at sea and if one supposes that the population (or annual generation) consists of 12 cohorts recruited monthly during the year ("continuous" recruitment), it is sure that the 12 cohorts present in the catches in any one month of the year have not had the same recruitment if seasonal variations exist, which is generally the case. It is also possible that they have not been subject to the same mortality if there are seasonal variations in mortality and/or fishing effort. Hence, the analysis of the numbers of the different age groups within a monthly size frequency distribution does not allow for the computation of mortality.

This approach is nevertheless valid if the size frequency distribution of the total annual catch is used. An evaluation of mortality can be obtained by "chopping" this annual distribution into age groups using data on the average annual growth, if one assumes that the annual level and the seasonal variations in recruitment are stable1/. This is the classical catch curve method. Garcia (1979) used this method on data obtained for three different effort levels to estimate natural mortality (Fig. 48). To limit the errors due to the "chopping" procedure, which is of course much less precise than a real separation into age groups (see section 5.1.1), only the size distributions of the females (which cover the widest range of sizes) were used and rather wide age groups were considered (4 month intervals). Berry (1969) also used annual histograms of the lengths of the shrimp caught to evaluate total mortality, but with a finer classification since he calculated the average age for each single size class.

The method was also used by Roessler et al. (1969) to calculate the rate of survival of larval stages from the abundance at different stages and the duration of each stage.

It is always possible to calculate mortality directly from the numbers at each size, without preliminary conversion. This process which is the basis of the method described as "catch curve method" goes back to Baranov (1918). Jones and Van Zalinge (M.S.) proposed its use for penaeids in Koweit where the size frequency distribution of shrimp caught from one age class during its whole life-span is known or, alternatively an annual frequency distribution (which is often an adequate approximation because of the high values of M and F which are usually encountered).

In this case, the comparison of the total number caught above a given length L_1 with that caught above another length L_2 gives an estimate of the survival between L_1 and L_2. The time necessary to pass from L_1 to L_2 depends on the growth parameters K and L_{oo}.

The authors showed in particular that

$$\mathrm{Log}_e \ \Sigma_L N = \frac{Z}{K} \ \log_e \ (L_\infty - L) + \log_e C \qquad ......(7.6)$$

where $\Sigma_L N$ is the accumulated number above a certain size L and C is a complex term independant of L. Plotting $\mathrm{Log}_e \ \Sigma_L N$ on $(L_{oo} - L)$ thus gives a line with a slope equal to Z/K, Z being assumed as constant (Fig. 50). If linearity is not maintained over the whole range of sizes examined, only the linear section can be used for regression. The usable interval must however, represent a sufficient proportion of the life- span to allow a certain significance to be attached to the calculated value of Z.

1/ It should be remembered that when the main recruitment occurs over a short period (2-3 months) and when the life- span in the fishery is close to a year (which is often the case), it is profitable to compile the catches by periods of 12 months which begin just before recruitment. The catch is then associated almost exclusively to the recruitment of the year and the catch curve in fact represents successive numbers of the same age class.

It is also clear that the method cannot be used for a size distribution which consists of a mixture of the two sexes; the laws of growth being different there is no single size-age relationship for a combined size distribution.

7.1.3 Conclusions

Since the short life-span of shrimps implies the use of a time interval of less than a year, seasonal variations in key factors such as recruitment or catchability make the use of classical methods for the assessment of mortality extremely difficult. Most often, the variations are such that no analysis can be made from monthly age distributions.

The annual frequency distributions should also be used with caution because its decomposition into age strata is usually very difficult. A simple "chopping" technique can be applied, which, because it is based on an annual average growth curve, can nevertheless be a source of error.

It is moreover preferable to consider only age groups which are sufficiently large to minimize, as much as possible, errors due to this "chopping", at the same time remembering that for important time intervals, age corresponding to average size in a group is not identical to the true average age of the group under examination. Furthermore, the hypothesis of constant mortality with age must be approached cautiously. In fact there can be important seasonal variations in mortality which are difficult to separate from age specific variations (see section 7.5.2).

It should finally be remembered that the quality of the results obtained from the analysis of length and age distributions depends a great deal on the quality of the sampling system and the representativity of these distributions.

7.1.4 The particular case when F varies with time

The methods reviewed in the preceding sections implied that Z be constant. This is however rarely the case in penaeid shrimps because the effort may vary considerably from year to year but also because the use of data corresponding to time intervals smaller than a year - which becomes necessary when dealing with such short lived animals - results in the fact that seasonal variations of effort and F have to be taken into consideration. For more detailed information on this type of situation Ricker (1975, sections 2.6 and 7.4) should be consulted. Two methods will be considered here because they have been used in shrimp studies: the Silliman and the Beverton and Holt iteration methods..

7.1.4.1 Silliman's method

The method can be used when data are available on two or more annual periods of stable effort in a fishery. If the two periods are long enough compared with the shrimp life-span the values Z_1 and Z_2 can be calculated by analysis of the annual age distributions. One then has:

$$\begin{aligned} Z_1 &= F_1+M \\ Z_2 &= F_2+M \\ F_1/F_2 &= f_1/f_2 \end{aligned} \qquad \text{......(7.7)}$$

Z_1, Z_2 and f_1/f_2 are known and these equations can be simply solved for F_1, F_2, M and $q = F_1/f_1 = F_2/f_2$.

Garcia (1977) used this method after having analyzed the annual length frequency distribution for catches made from a stock which was first almost virgin then lightly exploited, and at a later time heavily exploited (Fig. 48).

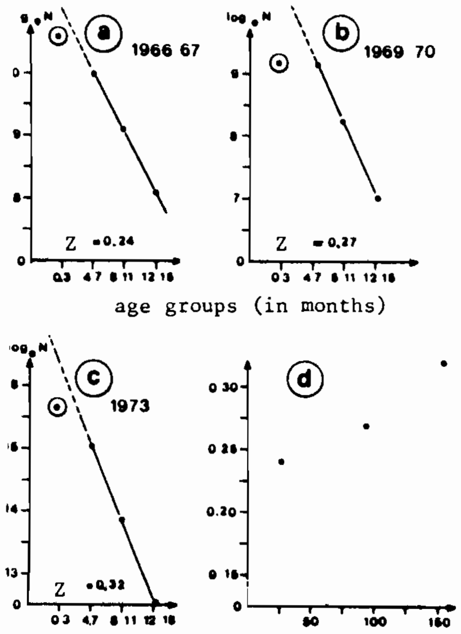


Fig. 48 Catch curves for different levels of effort in P. *notialis* (a, b, c,) in Ivory Coast and total mortality against effort (d), (from Garcia, 1977)

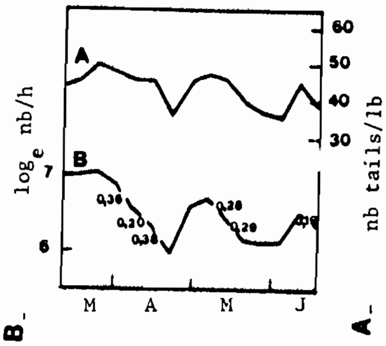


Fig. 49 Short term variations of c.p.u.e. in numbers (A) and average size (B) for *P. duorarum* The numbers are weekly mortaly rates (from Berry, 1967)

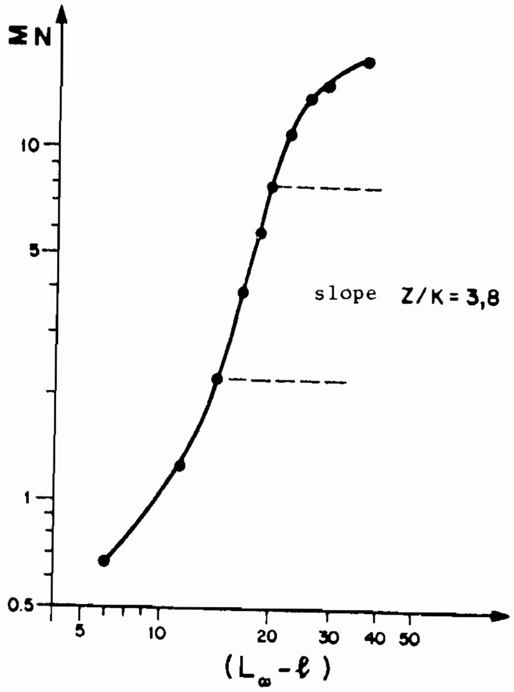


Fig. 50 Relation between the cumulative numbers and (L_∞ - ℓ) for *P. semisulcatus* in Kuwait (from Jones and Van Zalinge, M.S.)

7.1.4.2 Beverton and Holt's method (1957)

When periods of stability are not available and the effort varies continuously, the authors proposed (p. 234) a method derived from the one above and analogous in principle to that used in the section on tagging. If indices of average abundance are available for several successive periods for which the average effort is known, the regression of

$$\bar{Z} = \log_e \frac{(c/f)_i}{(c/f)_{i+1}} \quad \text{sur } f_i$$

on f is a straight line with a slope equal to q, the y intercept of which is equal to M. These two first estimates are then improved by successive iterations involving the computation of a correction term (Ricker, 1975, p. 170).

Paloheimo (1961) proposed a modification of the method permitting, by the regression of Z on

$$\frac{(f_i + f_{i+1})}{2}$$

one to obtain q and M directly without iterations.

Neither of these two methods give values of the parameters which are truly non-biased, but the second give the best possible estimate. Ricker (1973 and 1975) discussed the justification of the predictive regression line used by the two authors and proposed, in view of the probable errors in both the estimates of f and Z, using a functional regression (Nair-Bartlett or Wald) instead.

He even suggested that by using an M value obtained by other methods, the calculation of a functional line passing through M would provide a more precise value of q.

Berry (1967) used this principle in a particular context: that of short-term variations in effort in a penaeid fishery. Assuming that over a few days the composition of the stock remained unchanged, he related the numerical changes in c.p.u.e. to the mortality. Fig. 49 shows variations in c.p.u.e. and those of average size (in numbers of tails/pound). It can be seen that the c.p.u.e. decreases when the size increases (mortality) and increases when the average size decreases (recruitment). Considering that the segments with a negative slope are the consequence of total mortality, Berry calculated the weekly values of Z which he related, quite simply, to the effort, to obtain q and X (natural mortality and, possibly, emigration). The scatter of the points in Fig. 51 gives an idea of the variance not calculated by the author, of the M and q estimates. This variance could have been calculated by using the equations given by Paloheimo (1961).

7.2 ESTIMATION OF MORTALITY RATES BY TAGGING

7.2.1 The general case: F + M are constants

In spite of all the drawbacks of tagging experiments the problem of determining age in crustaceans is such that these methods must be resorted to. They have also the advantage of allowing an estimate of both the fishing mortality and the natural mortality (the latter being generally overestimated).

The theory for these studies can be found in the basic textbooks and has been very thoroughly reviewed by Cormack (1968) and summarized by Jones (1968).

The tagged population can be treated as a normal population and the principles of the estimation of mortality as described in the previous section remain valid, since the problem of recruitment variation is eliminated.

In particular, if F and M are constants, the rate of survival can be found from the ratio of the recaptured numbers in 2 successive time intervals

$$S = \frac{R_2}{R_1} = \frac{R_3}{R_2} = \cdots = \frac{R_2 + R_3 + R_4 + \ldots + R_i}{R_1 + R_2 + R_3 + \ldots + R_{i-1}} \qquad \ldots\ldots(7.8)$$

and another non-weighted, combined estimate of Z can be obtained by calculating the regression line of R_i on i. This latter method is the most frequently used, and deserves more detailed examination.

If Z is considered to be a constant the numbers of tagged shrimps decrease exponentially with time and the evolution of their logarithms is a straight line (Beverton and Holt, 1956 - Gulland, 1969).

If the natural logarighms of the recaptures are expressed as a function of the ranking order of the time intervals, the first being numbered zero 1/, a line with a slope (-Zt) is obtained with the Y intercept being equal to

$$\mathrm{Log}_e \frac{FN_o}{Z} (1-e^{-Zt})$$

where t indicates the length of the time interval. Knowing Z and N_o, the number initially tagged, F can be calculated and by subtraction, a value X representing the residual mortality, attributed to M as a first approximation, that is, if there has been no emigration and no additional mortality. For the several reasons given in section 6.8.4, this estimation would be biased by excess and it would be preferable to calculate M from an independant value of Z obtained by other methods.

If the time intervals are small enough, Gulland (1969) showed that if the natural logarithm for recaptures is plotted as a function of the median point of the interval 2/ a line with a slope -Zt and a Y intercept of $\mathrm{Log}_e\ FN_o t$ is obtained.

Paulik (1963) quoted by Jones (1976) provides, following the same principle, a weighted regression of $\mathrm{Log}_e\ R_i/N_o$ as a function of the rank of the intervals. The weighting factor used is $W = R_i/N_o$. The method can be used as long as the recaptures are neither very small nor nil for any of the intervals. When working on shrimps, the duration of a tagging experiment is generally limited (1 to 2 months) because of the rapid decrease in numbers. It will sometimes be difficult to mark a sufficient number of animals in a time short enough to consider the marking as instantaneous. Jones (M.S.) proposes to consider in this case many groups of tagged shrimps (for periods of tagging of 2-3 days each), to make the computations separately with the appropriate time intervals, and then, to recombine the recaptures so obtained within intervals of identical rank. In this way a unique theoretical marking experiment is reconstructed where the total number tagged is the sum of the numbers tagged in the elementary operations and the date of tagging is the average date of all elementary operations. It is worth to note that given the foreseeable seasonal variations in parameters the recombination must be done cautiously if the elementary taggings are done too far apart in time.

1/ The ranks will be r = 0, 1, 2, 3 ..... etc.

2/ The numbers will be 0,5; 1,5; 2,5; 3,5; etc.

After calculating Z, the fishing mortality can also be obtained from the following equation:

$$\frac{R}{N_o} = \frac{F}{Z} (1-e^{-ZT}) \qquad \ldots\ldots(7.9)$$

which is the equivalent of Ricker's exploitation rate when T = 1. R is the total number of recaptures obtained in the experimen in which the duration is T.

Beverton and Holt (1957) indicated that

$$\log_e R_r = \log_e R_1 - \frac{1}{t} \log \frac{R_1}{R_2} \quad (t_r - t_1) \qquad \ldots\ldots(7.10)$$

where R_1, R_2 are recaptures in the 1st and 2nd interval (rank 0 and 1). The regression $\log_e R_r$ as a function of the rank of the intervals then has a slope

$$- \frac{1}{t} \log_e \frac{R_1}{R_2}$$

which is equal to (-Z) and a y-intercept of $\log_e R_1$.

One can then calculate

$$F = \frac{\frac{R_1}{t} \log_e (\frac{R_1}{R_2})}{N_o \quad (1 - \frac{R_2}{R_1})} \qquad \ldots\ldots(7.11)$$

and X by subtracting F from Z.

This method has been used by Berry (1967) and Allen and Costello (1968) for Penaeus duorarum in Florida.

It is also interesting to remember a method originated by Gulland (1955). This author showed that if the exact duration of the period of liberty (t_i) is known for each recaptured individual, if the numbers decrease exponentially and when the probability of recapturing additional individuals is nil, the average period of liberty ($\Sigma t_i/R = t$) is an estimation of 1/Z.

It would then follow

$$\frac{R}{\Sigma \, t_i} = Z \qquad \ldots\ldots(7.12)$$

The author also shows that

$$\hat{M} = \frac{(N_o \; - \; R)R}{N_o \; \Sigma \; t_i} = \frac{(N_o \; - \; R)}{N_o \bar{t}} \qquad \ldots\ldots(7.13)$$

and that

$$\hat{F} = \frac{R^2}{N_o \; \Sigma \; t_i} = \frac{R}{N_o \; \bar{t}} \qquad \ldots\ldots(7.14)$$

Chapman (1961) proposed a less biased estimation

$$\hat{M} = \frac{(N_o - R)\ (R - 1)}{N_o\ \Sigma\ t_i} \qquad \text{......(7.15)}$$

and

$$\hat{F} = \frac{R(R - 1)}{N_o\ \Sigma\ t_i}$$

......(7.16)

the variances of which can be approximately calculated by

$$\text{Var}\quad \hat{M} = \frac{M(F^2 + FM + M^2)}{N_o}$$

and

$$\text{Var}\quad \hat{F} = \frac{F(F + 2M)}{N_o} + \frac{2(F + M)}{N_o^2} \qquad \text{......(7.17)}$$

......(7.18)

Nicholson and Pope (1978) discussed the precision of the estimates and their robustness when the basic asumptions are not met.

7.2.2 The case where F is not constant with time

The regression methods presume that Z is constant. For shrimps this is rarely the case. In fact the useful time interval is the month or even the week, in which case large fluctuations of fishing effort around the average are experienced. It is thus possible, as a first approximation to use the recaptures per unit of effort, instead of the actual recaptures for the regression. This approximative method has been used by Kutkuhn (1962), Berry (1967), Garcia (1975a), Le Reste and Marcille (1976). When the logarithm of the recaptures per unit of effort is expressed as a function of the rank of the time interval (0, 1, 2, ...) or of the median point of the interval (0.5, 1.5, 2.5, ...) a line with a slope -Zt is obtained with a Y intercept equal to $\log_e qN_o(1-e^{-Zt})/Z$ or $\log_e qN_o t$ respectively. One can then derive q from the Y intercept and calculate F from the relation F = qf. The details can be found in Gulland (1969).

The following, more rigourous, method was proposed by Beverton and Holt (1957) which assumes that effort is constant in each small time interval and changes abruptly between two intervals in which case f is a stepwise function of time.

If one uses the classical equation $F_r = qf_r$ and if the first interval has rank 0 they showed that

$$qf_r + X = \frac{1}{(t_r - t_{r+1})} \log_e \left[\left\{ \frac{R_r . f_{r+1}}{R_{r+1} . f_r} \right\} + \ \cdots \right. \qquad \text{......(7.19)}$$

$$\left. \cdots\ \log_e \left\{ \frac{(q.f_r + X)\ (1 - e^{-(qf_{r+1} + X)\ t_{r+1}})}{(q.f_{r+1} + X)\ (1 - e^{-(q.f_r + X)\ t_r})} \right\} \right] \qquad \text{......(7.19)}$$

and proposed to solve this equation by successive iterations. To begin with, one can consider the term furthest right as nil and carry out the regression

$$\frac{1}{t_r}\left\{\log_e\left\{\frac{R_r \cdot f_{r+1}}{R_{r+1} \cdot f_r}\right\}\right\} \quad \text{on} \quad f_r$$

obtaining a line with a slope equal to q and an Y intercept equal to X. These values thus allow the computation of a complete regression taking into account the term which is furthest to the right to obtain two new values of q and X and to repeat the process until stabilization of the results. The value of q thus obtained allows F to be calculated, if the average effort for the period under examination is known. This method has been used by Kutkuhn (1966) on Penaeus duorarum.

Chapman (1961) criticized this regression method since the two variables are not independent, because the fishing effort f occurs in both terms of the equation. He gave equations for maximum likelihood which are too complicated to solve without a computer. He then proposed an approximative method of multiple regression on which Cormack (1968, p. 495) has commented.

More recently Lucas (1975) working with shrimp data from Costello and Allen (1968) proposed a method of calculation based on maximum likelihood criteria and a computer programme which allowed the solutions to be obtained easily.

Schematically, he uses the classical computation of a regression of the logarithms of the recaptures per unit of fishing intensity on the rank of the intervals (the first being o). Z is thus obtained and F and X can be calculated from the equation

$$\frac{R}{N_o} = \frac{F}{F + X} \quad 1 - e^{-(F + X)T} \qquad ......(7.20)$$

where R is the total number of recaptures, N_o the number of shrimp tagged initially and T the total duration of the recapture period under examination. The values of F and X thus obtained are considered as provisional values which are used to calculate with his programme the final values by maximizing the likelihood function.

The advantage of the Chapman (1967) and Lucas (1975) methods are that they allow calculation of the variance of the parameters F and X thus obtained.

7.2.3 The case where F is not constant in space or where the distribution of the tagged and the natural population are different

One of the basic postulates of tagging studies is that the effects of the fishery on marked and non-marked populations are identical. This supposes, among other things, that the distribution of marked and non-marked shrimps is the same or that fishing effort is distributed at random. This is obviously not so in penaeids where an essential characteristic of the density distribution is its heterogeneity and the existence of gradients.

The best solution in these circumstances is to prepare a grid of squares of the fishing area and to tag in each square the same proportion of the numbers caught by the research vessel per unit of effort (Gulland, 1969; Beverton and Holt, 1966). In this way short hauls can be made in each square with the objective of tagging the whole catch.

The classical treatment of data is then carried out.

However, the fishing ground under examination can be very extensive and it may be impossible to cover it entirely in the time available. It may in such case also be difficult to carry out tagging at a few points only and then wait for a mixing of populations since, because of the high mortality in shrimps, the major part will be recaptured before mixing is complete and the recapture data become useful.

The solution is then to tag in one or several of the richest and most intensively fished zones and to use the recaptures per unit of fishing intensity (effort per unit of area) as in the preceding section (see also Gulland, 1963) so as to arrive at a q value in the zone examined. Calculation of the effective overall fishing intensity allows one then to calculate F for the whole fishing area.

Since shrimp dispersal continues as the experiment progresses, the surface to be considered will also increase progressively (Fig. 52). It will be defined by the zones from which the tagged shrimp derive if it is sure that the entire fishing ground is covered by the fleet.

7.2.4 The case where the first recaptures are unusable

It is possible that during one or several of the first time intervals after tagging the recaptures would not be usable:

- either because the catchability of tagged individuals is different from that of the non-tagged shrimps because of modified behaviour,
- or because the mixing of tagged and non-tagged populations is not complete.

Berry (1967) and Garcia (1975) met this problem with Penaeus duorarum in Florida and P. notialis on the Ivory Coast. It is a particular case of the previous problem in which the time needed for mixing of the populations is short enough for the corresponding data to be discarded without a too great loss of information. It is better then to eliminate the data corresponding to this period and to use the later data to calculate the regression for determining Z. The calculation of F will then need an approximative method by successive iterations to back calculate N_o, the number of marked shrimps at the beginning of the usable period.

$N'O_1'$ is first calculated approximately by subtracting from N_o the number of shrimps (R') recaptured during the period in question (T) and neglecting natural mortality.

$$N'_{0_1} = N_o - R'$$

This value, used in equation (7.11) together with the results of the regression made with the data of the usable time intervals, allows the calculation of F_1 and then $X_1 = Z - F_1$. One can thus make a correction of N_o by putting

$$N'_{O_2} = (N_o - R')\, e^{-X_1 T}$$

The insertion of N'_{O_2} in equation (7.11) allows one to obtain a revised value of fishing mortality F_2 and the process is repeated until the stabilization of N'_O and X. This method was used by Berry (1967) for Penaeus duorarum.

The approach would be similar when using equation (7.9) to calculate F. The initial value of M can also be taken from the literature, if available.

The same procedure can be used when fishing does not begin immediately after marking. There is then a preliminary period where the only mortality is X, and N'_o is determined as previously. An example can be found in Le Reste's (1978) work.

7.2.5 Conclusions

Tagging is an indispensable technique for studying shrimp mortality. The main difficulties are the following:

- It is practically impossible to tag small-sized shrimps without obtaining considerably biased results except perhaps when the vinyl ribbon tag is used;
- The numbers tagged are always ridiculously small compared to the large numbers in the population
- Fishing effort is never constant and varies greatly, around the mean value in the best cases;
- Mortality due to tagging cannot be accurately assessed, and the results of aquarium experiments cannot be applied without risk.

7.3 OTHER METHODS

The methods discussed in this section were chiefly developed and used for the study of natural, closed, non-fished populations. Tagging and recapture are generally carried out by the scientist himself and his team. For a detailed study of the methods involved, the reader could very usefully refer to Ricker (1958, 1975); Jones (1976) and to the very detailed review of Cormack (1968).

Although they have been very little employed for fished shrimp stocks, the few more or less promising trials that have been made on these stocks deserve to be reviewed as examples.

7.3.1 Combination of tagging, catch and effort data: Ketchen's method

Leslie's method allows calculation of the size of the population, fishing mortality, natural mortality and migration. The basic principles will be found in Ricker (1975, p. 150). It should be remembered that the method can only be used when the applied effort is large enough to cause a significant decrease in the c.p.u.e. It can be shown thus that if natural mortality and immigration are nil or counterbalance each other, the regression of the c.p.u.e. on the cumulative catch gives a line with a slope equal to F/f (equivalent of q), a Y intercept = q N_o, and an X intercept = N_o (where N_o is the initial size of the population) (Fig. 53).

Ketchen (1953) proposed a modification of this method, which was used for penaeids by Iversen (1962) and Clark and Caillouet (1973). The natural population is subject to natural mortality, emigration and immigration. The tagged population can only be modified by the first two factors. These two populations are treated as in Leslie's method (Fig. 54).

If F is the fishing mortality
y the rate of emigration
z the rate of immigration
M_1 the number of initially tagged individuals, and
N the initial natural population,

the regression of the c.p.u.e. on the accumulated catch for the two populations, natural and tagged, allows M_{1a} and N_a, the apparent iinitial numbers to be obtained. The slopes of the lines are equal to (F + y)/f and (F + y - z)/f respectively. It can easily be shown that

$$F = \frac{M_{1a}}{M_1}(F + y)$$

that z can be calculated from (F + y - z) - (F + y) and that $N = N_a\ (F + y - z)/F$.

slope = q = 0,000011
intercept = X = 0,226

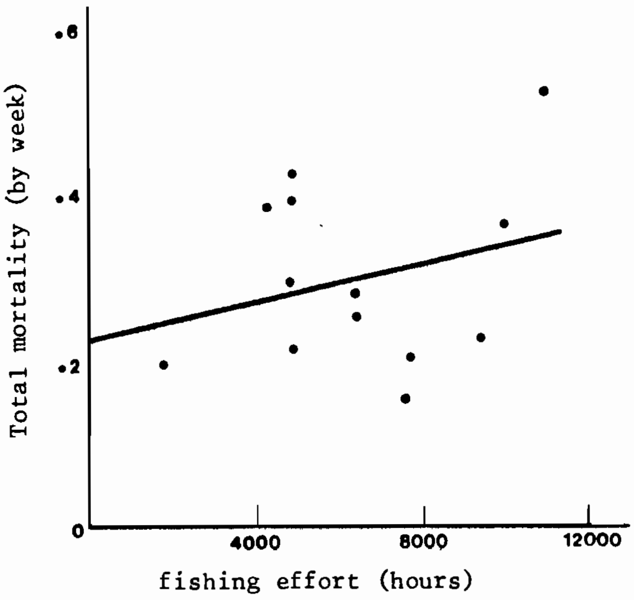


Fig. 51 Estimation of q and X for *P. duorarum* in Florida (from Berry, 1967)

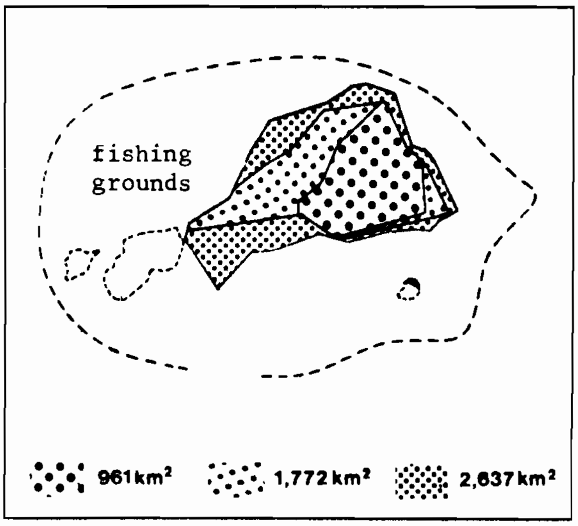


Fig. 52 Successive areas of distribution of tagged shrimps in Florida (from Castello and Allen, 1968)

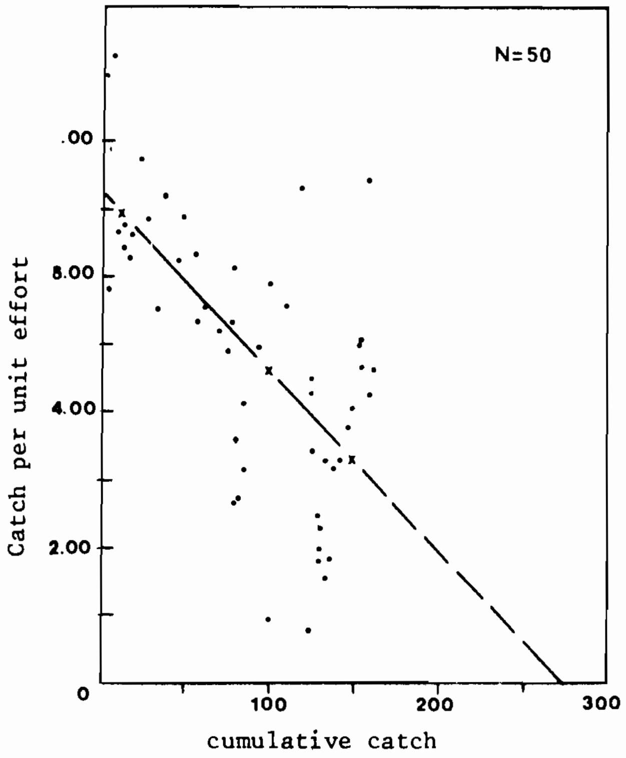


Fig. 53 Application of the Leslie method to a *Penaeus duorarum* stock in Florida (from Iversen, 1962)

One of the main criticisms that can be made of this method is that it implicitly supposes a constant catchability ($F/f = q$). If the catchability varies at random around the mean it will simply show as an important scatter of the points. For shrimps however, catchability is subject to many non-random fluctuations. It varies with the lunar cycle (over a period of about 14 days) as Penn (1976) has shown. It also varies seasonally with environmental and temperature conditions (Penn, 1975) and with turbidity (Garcia, 1977). In these conditions an experiment lasting for several weeks could be seriously biased if there is an upward or downward trend in q.

It is for this reason that Penn (1976) was of the opinion that Leslie's method was not applicable to his experiments.

7.3.2 Successive evaluation of numbers in a closed population: Petersen's method

Petersen's method (single census), known also as Lincoln's method, depends on the following principle: where M tagged individuals are introduced into a natural population of N individuals and a significant sample, n, is taken later containing m tagged individuals the ratio of tagged and non-tagged individuals is the same in the sample as in the natural population.

$M/N = m/n$ from which it can be derived that $N = Mn/m$

This method makes it possible to calculate the size of an isolated population. When used repeatedly, it can give several successive estimates from which mortality can be calculated. At the end of this section an example of this type of use is given.

It has been shown that this formula gives extremely biased results and other methods of calculation have been proposed. One which has been used with shrimps is provided by Bailey (1951).

$$N = M(n+1)/\ (m+1)$$

and

$$\text{Var. } N = N^2(n-m)/(n+1)(m+2)$$

This method has been applied by Penn (1976) for Penaeus latisulcatus, in Australia, by Clark and Caillouet (1973) for Penaeus setiferus and by Iversen (1962) for Penaeus duorarum in the Gulf of Mexico.

This type of method must be used carefully since the implied assumptions impose many constraints which should be pointed out (Cormack, 1968, p. 458):

- the shrimps do not lose their tags
- they are always correctly identified (without errors or omissions)
- either the population is really a closed one or neither recruitment nor immigrations of non-tagged shrimps take place, and mortality and migration of individuals is the same whether or not they carry the tag
- sampling is random: all the tagged or non-tagged shrimps have the same probability of being recaturesd. If the population is heterogeneous, this must apply to each stratum.

Iversen (1962) worked with large stocks of adults in Florida in an environment which was difficult to control. He used moreover a tag, which was later acknowledged to be relatively harmful (Petersen discs which were too big and fixed through the center of the first abdominal segment). The tagging mortality he estimated in aquarium was very high and may have been overestimated if what was said in the section on the estimation of tagging mortality in artificial conditions is taken into account (section 6.8.4 and 7.2.5).

Although he obtained apparently consistent results, it should be recognized that he worked under the most difficult conditions and that his results (as he himself emphasized) must be taken with reserve. Also the number of tagged individuals in his experiments was very small with respect to the size of the natural population.

Caillouet and Jones (1973) approaching somewhat more to ideal conditions, worked in a small shallow bay, isolated from the main estuary by a net so as to avoid interchanges. Marking was conducted using injections of fluorescent paraffin oil, which almost completely avoided tagging mortality. In spite of these precautions the results are not all consistent.

Penn (1976) in his turn made a very interesting study on a virgin stock of Penaeus latisulcatus in an area of 1,700 hectares in which more than 13,000 tagged (toggle tag) shrimps were placed. The operation took place during a period of negligible recruitment. Sampling was done by two chartered shrimpers who worked so as to cover the whole zone with uniform effort. They obtained several successive population abundance estimations using Petersen's method which enabled them to calculate the total mortality and to separate this into natural and fishing mortality by using Ricker's (1958) formula for the rate of exploitation

$$C/N = F(1-e^{-ZT})/Z$$

where N is the population number at the beginning of the observation period and C the catch in numbers during the whole period, of duration T.

Here also disagreement between long and short-term results was noted.

In conclusion, these little-used methods have given, when they were applied, results in which one cannot place great confidence because the basic assumptions are badly met.

7.4 MULTIPLE MARKING TECHNIQUES

To overcome the difficulties met in the application of the methods described in the preceding section, more sophisticated methods have been developed based on the possibility to mark and thereafter recapture and release again the same animal many times. Used by Barr (1971) on pandalid shrimps, the Schnabel's method and other similar ones have never been used on penaeids which, because of their fragility, cannot survive manipulation and stress during several successive capture and recapture operations.

The multiple marking method of Robson (1963) can however be used because it does not imply multiple recaptures. This method has been recommended by Jones (M.S.) for the penaeids in Koweit. The following will be essentially based on his text.

The principle of the method is the following: if N_1 individuals are tagged at the time t_1 and N_2 at the time t_2 one can calculate the survival rate between t_1 and t_2 by comparing the recaptures obtained from t_2 onwards for the two independent taggings. If the recaptured numbers (beyond t_2) are respectively R_{12} and R_{22} and if we assume that the exploitation rates are the same for the two groups during the same period, then:

$$R_{22}/N_2 = R_{12}/N_1\text{-}S_{1-2}$$

where S_{1-2} is the survival rate between t_1 and t_2 and N_1S_{1-2} represents the theoretical number of tagged shrimps remaining from the first tagging at the time t_2. Everything being known but S_{1-2}, the total mortality can be calculated by

$$Z(t_1-t_2) = -\log_e S_{1-2}$$

This method allows for the analysis of seasonal variations in Z (in relation for instance with variations in effort) and for the discarding of the data from the first period after tagging if it is felt that these are not representative.

As a matter of fact, if it is estimated that recaptures are only usable after a time t_3 (where $t_3 > t_2 > t_1$) it can be written:

$$R_{23}/N_2S_{2-3} = R_{13}/N_1\text{-}S_{2-3} \text{ and also}$$

$$R_{23}/N_2 = R_{13}/N_1S_{1-2}$$

where R_{13} and R_{23} are the recaptures obtained beyond t_3 for the two considered taggings and N_1S_{1-2} S_{2-3} and N_2S_{2-3} are the numbers tagged and still alive at the time t_3. S_{1-2} and $Z(t_2-t_1)$ can then be calculated as before.

7.5 CATCH BY AGE DATA ANALYSIS: VIRTUAL POPULATIONS, COHORT ANALYSIS

Although not yet much used for penaeids, the potential of these methods must be examined, for they may lead to the possibility of using catch statistics more intensively. They might also allow to circumvent difficulties sometimes met in the definition of effort.

7.5.1 The method of virtual populations analysis, the principle of which was advanced by Fry (1949), was used by Neal (1967) for *Penaeus aztecus* in the Gulf of Mexico. The virtual population (V) is defined by Fry as being the complete contribution of a population to a fishery. For any given moment it is the accumulated catch achieved in the following time intervals to the point of population extinction. Thus, one obtains a minimum estimate of the actual population (since animals dying by natural causes are obviously not counted) and a maximum estimate of the exploitation rate, called by Ricker (1971) the biostatistical rate of exploitation.

If U (max) is the maximum rate of exploitation (in Ricker's terms),

C_t the catch at age t, and

f_t the fishing effort applied at age t,

the following elements can be defined:

$$U\,(\text{max})_t = C_t/V$$
$$F\,(\text{max})_t = -\log_e\,(1\text{-}U\,(\text{max})_t) \text{ and}$$
$$q\,(\text{max})_t = F(\text{max})_t/f_t$$

If for example, the size (or age) composition of the catches per month (by length groups or by commercial categories) and the seasonal recruitment cycle are known, the time series of monthly catches by size (or age) categories can be reconstructed for a given generation (Fig. 55)1/.

The monthly virtual population, both total and by size (or age) class, can later be calculated as well as the corresponding biostatical exploitation rates.

When the exploitation rates are calculated by size classes which represent different periods of time the use of an annual growth curve allows calculation of the exploitation rate per standardized time unit (for instance per week in the example given below).

It should be however noted that the occurrence of seasonal growth variations would require that a preliminary breakdown of monthly size histograms into age groups is made before pooling these data at the annual level for calculation of the virtual populations.

1/ A generation is defined here as the total of all shrimp recruited in one year, and consists of successive cohorts recruited through a continuous recruitment process influenced by seasonal variations

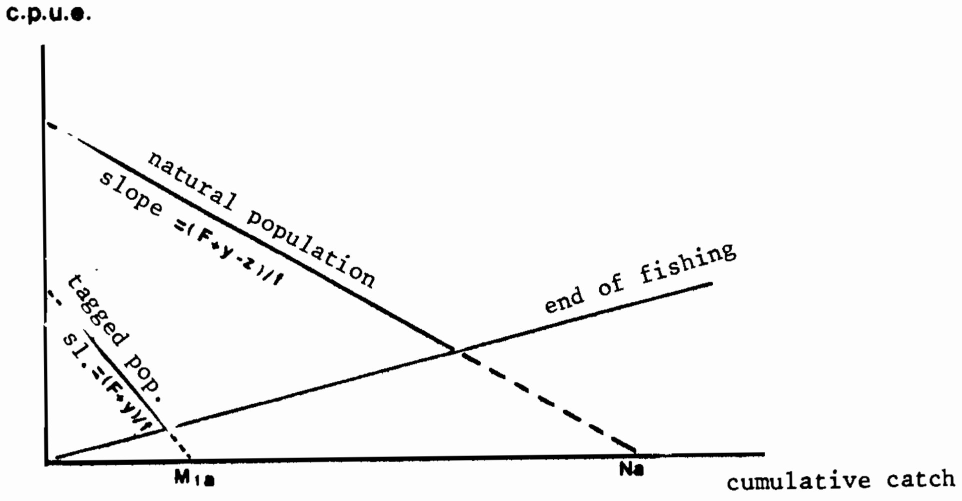


Fig. 54 Principles of the Ketchen's method (from Ricker 1975)

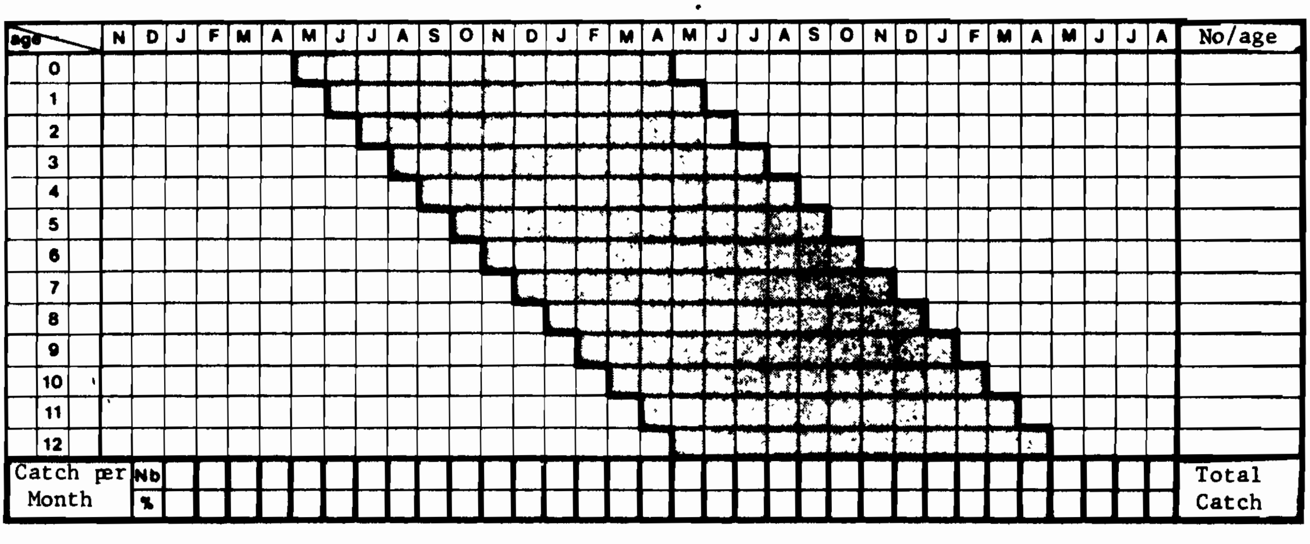


Fig. 55 Schematic diagram for the reconstitution of the virtual population for a year class recruited continuously during 12 months and which life span in the fishery is 12 months. Each column is a monthly histogram of catch by age. For each year class the catch per month in numbers is given in the bottom line and the catch per age (in months) in the last column, (modified from Neal, 1967)

Category (No./pound)	Age class				
	1961	1962	1963	1964	1965
51-67	2	3	4	2	6
41-50	10	10	5	6	8
31-40	27	14	19	17	17
26-30	22	12	18	17	18
21-25	5	9	7	9	11

Maximum weekly exploitation rate (in %) by size group for Penaeus aztecus (from Neal, 1967).

This simple method also enables one to compute the percentage of the whole virtual population which is caught month by month during the fishable life span, and to make comparisons between years (see Fig. 56). The use of economic data (value by size classes) allows one to make a practical study of the relation between the seasonal distribution of effort, the sizes of shrimps caught and their value from one year to the other (Neal 1967). This author has as a matter of fact confined his analysis to this practical aspect and showed that small variations in the seasonal distribution of fishing effort are reflected in significant variations in the catch.

This method has been very little used for penaeids, and the example given is the only one the present authors are aware of. It has however been used extensively in other fisheries. An analysis of the errors inherent in the method and a discussion of the results obtained can be found in the work of Bishop (1959) and Ricker (1971, 1975).

In so far as the results of virtual population studies are of limited scope and are difficult to interpret, it seems preferable to employ the method of cohort analysis.

7.5.2 Cohort analysis

Several methods are brought together under this heading. They deal with a method of sequential computation of fishing mortality and of population size for which Ricker (1975, p. 194) gives the background. Cadima (1978) reviewed the terminology used and the methods of calculation to be applied for the different types of available data. Generally speaking, if M is known or assumed, the fishing mortality at each age can be calculated if the catch by age class and the fishing mortality or the population in numbers at one age class is known.

Usually C_i, F_i and M (assumed to be constant) are known in the last time interval (the inverse method). If N_i is the number of individuals in the population at the beginning of the interval, N_i as the average number during the interval, and D_i as the total number of death in the interval, one can calculate

$$Z_i = F_i + M; \; S_i = e^{-Z_i}; \; \overline{N}_i = C_i/F_i; \; D_i = Z_i\overline{N}_i$$

$$N_i = D_i/(1-S_i) \text{ and}$$

$$C_{i-1}/N_i = F_{i-1}.(1-e^{-(F_{i-1}+M)})/(F_{i-1}+M).e^{-(F_{i-1} + M)}$$

This last equation, solved by successive iterations or by using Schumacher's (1970) tables, enables F_{i-1} to be obtained. The process can be repeated for each next younger age group, until the beginning of the catch sequence, the last value of N_i thus obtained being the recruitment value. This method can also be applied beginning with the first interval (direct method or prognosis).

The initial value of M must be obtained by other methods (tagging, variable effort methods, rough estimates) or taken from literature dealing with the same or related species. This presents a great difficulty in the penaeids since available values vary greatly according to the source of information.

The initial value of F can be obtained by tagging (Garcia, 1977 with Penaeus notialis) or any other suitable method.

Where there is uncertainty about the value of M or F, cohort analysis can still be carried out using different values for these parameters. The calculations are then facilitated by using currently available computer programmes such as COHORT written by Fox and available from La Jolla (California, USA). The inverse method is then usually preferred since every initial value of F leads to a solution. All F vectors thus derived are compatible with the corresponding catch vector and Jones (1961) showed that, for a given M, estimates of F converge quickly towards their true values. This method often allows elimination of the more improbable F values. It was employed, for example, by Marcille (1978) on shrimps in Madagascar.

Pope (1972) proposed a simplified cohort analysis method which was later on modified by Jones (1974) to enable direct application to catch data by size classes (annual catch by size, category, for example).

If one assigns the indices 1, 2, 3 to successive size groups, index 1 (one) defining the group for the smallest size, Jones (1974) shows that

$$N_1 = N_2 \left\{ \frac{L_\infty - L_1}{L_\infty - L_2} \right\}^{MK} + C_{1-2} \left\{ \frac{L_\infty - L_1}{L_\infty - L_2} \right\}^{M/2K}$$

where C_{1-2} is the catch in number of the individuals with size between L_1 and L_2. For greater facility this can be written as

$$N_1 = (N_2 . X_{1-2} + C_{1-2})^{X_{1-2}}$$

where

$$X_{1-2} = \left\{ \frac{L_\infty - L_1}{L_\infty - L_2} \right\}^{M/2K}$$

If N_{n-1}, the numbers at the lower limit of the group with the largest sizes is known, N_{n-2}, N_{n-3}, N_{n-4}, etc. can then be calculated successively.

The exploitation rate can be calculated by the relation of the catches to the number of deaths in the $(N_1 - N_2)$ interval

$$(F/Z)_{1-2} = C_{1-2} / (N_1 - N_2)$$

The survival rate and total mortality in the size interval are given by

$$S_{1-2}.\Delta t = e^{-Z_{1-2}.\Delta t} = N_2/N_1$$

where Δ_t is the time needed to grow from L_1 to L_2. Then

$$Z_{1-2}.\Delta t = -\log_e(S_{1-2}.\Delta t)$$
$$F_{1-2}.\Delta t = (F/Z)_{1-2} \cdot Z_{1-2}\Delta t$$

The values for total mortality for the time interval t can then be obtained by

$$Z_{1-2} = M_{1-2}/(1-(F/Z)_{1-2})$$

or again

$$Z_{1-2} = (Z_{1-2} \cdot \Delta t)/\Delta t$$

The rationale is the same if a value of $(F/Z)_{n-1,n}$ is available for the group of largest sizes. For example N_n, the number at the lower limit of the last size group can be derived from

$$N_n = D_{n-1,n} = C_{n-1,n}/(F/Z)_{n-1,n}$$

The calculation can then be pursued as previously. The following table summarizes the calculations made on a cohort of Penaeus semisulcatus in Kowait by Jones and Van Zalinge (M.S.).

1	2	3	4	5	6	7	8	9
Size category No/pound	Length interval (LC)	$\frac{L_\infty - L_1}{L_\infty - L_2} = A$	$X = A^{0,75}$	Numbers caught (10^6)	Numbers at beginning of the size intervals (10^6)	F/Z	F (annual)	Z (annual)
<< 15	40,5-L_{max}	-	-	0,63	1,26	(0,5) 1/	- .	-
16/20	36,2-40,5	1,617	1,434(1,117) 2/	0,63	2,28	0,62	6,3	10,2
21/25	33,2-36,2	1,268	1,195(1,117) 2/	0,98	3,94	0,59	5,6	9,5
26/30	30,9-33,2	1,159	1,117	1,78	6,91	0,60	5,8	9,7
31/35	29,1-30,9	1,109	1,081	1,89	10,11	0,59	5,6	9,5
36/40	27,6-29,1	1,080	1,060	2,00	13,47	0,59	5,7	9,6
41/50	25,3-27,6	1,116	1,086	3,18	19,33	0,54	4,6	8,5
51/70	22,1-25,3	1,141	1,104	2,96	26,81	0,40	2,6	6,5
71/110	18,5-22,1	1,142	1,104	1,30	34,15	0,18	0,8	4,7
111/140	11,2-18,5	1,255	1,185	2,81	51,31	0,16	0,8	4,7

1/ Starting value

2/ The value between brackets has been used by the authors instead of the computed one

It should be noted that Pope's (1972) original method was, according to the author, still valid for values as high as at least 0.3 for M and 1.2 for F.

7.5.3 Conclusions

The use of this type of method is for penaeids confronted with several difficulties.

(a) The size frequency histograms are difficult to divide into age groups by the usual methods. One is therefore often obliged to "chop" them into "age" segments using a growth curve (or different curves if there are seasonal growth variations). To limit the bias introduced by this procedure, it is preferable to select rather large age intervals (three monthly intervals for example), although this brings in its own risk of bias.

(b) Recruitment is often continuous and consists of a permanent inflow varying seasonally, of individuals of age t_r (in reality this age can vary slightly during the year). When only one annual generation is examined, the procedure outlined in section 7.5.1 and in Figure 55 can be used as a basis for the construction of a catch-by-age series.

However, in the most likely circumstances, the existence of seasonal variations in catchability, fishing effort and growth will make it preferable to use a subdivision into cohorts (for example on a three-monthly basis). The usual method of establishing catches by age would be to compile three-monthly size distributions of the catch, and to divide these into age groups of three months each (0-2, 3-5, etc.) so as to make a diagonal reconstitution of the catches by age (Fig. 57A). This procedure is in fact based on the assumption that either the recruitment occurs just at the beginning of the three monthly period - which is not the case -, or that it is constant with time, which cannot be the case when intervals smaller than one year are used, since seasonal variations in recruitment occur.

If available data allow a better procedure would be to compile and divide monthly histograms into monthly age groups and afterwards to construct catch vectors by three monthly age groups using the approach outline in Fig. 57B.

(c) It should finally be noted that observed variations in q (if f is known in each time interval) would be the resultant of variations related to the age and to the season. These two cannot be assessed separately.

(d) In view of the special characteristics of stocks with a short life-span and of the current lack of available experience on the subject, it is advisable to make cautious use of the methods discussed in this chapter and first to find out how far the basic assumptions are met. Profitable reference can be made in any case to the work of Agger, Boetius and Lassen (1971); Pope (1972, 1978) and Ulltang (1977).

(e) Where resources are composed of a multitude of small stocks, each more or less associated with coastal bays, as in Madagascar, migration from one bay to another is liable to introduce bias into the catch analyses for each stock separately. Ulltang (1977) and Aldenberg (1975) draw attention to this aspect of cohort analysis.

7.6 APPROXIMATIVE METHODS

Industry generally develops much quicker than research, and therefore the time factor becomes an essential component in the efficiency of research directed to resource management. The use of rapid methods for the evaluation of basic parameters was recommended in 1956 by Holt and the problem has been repeatedly underlined since, (Holt, 1962; Gulland, 1971; Joseph, 1972; Rikhter and Efanov, 1976; Pauly, 1979). The problem is especially acute for penaeids where stocks are most frequently found outside regions where advanced research potential is available and where information on the stocks and the fisheries is very scarce.

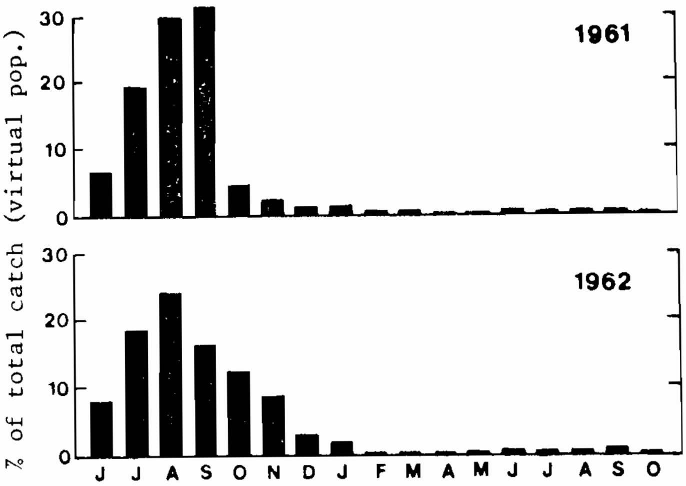


Fig. 56 Comparison of catches (in % of the virtual population) by month for the 1961 and 1962 year classes (from Neal 1967).

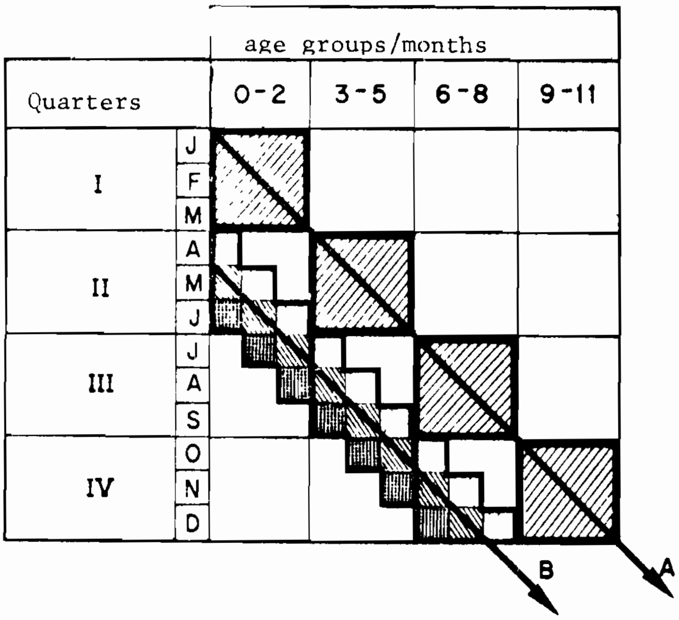


Fig. 57 Schematic diagram for the preparation of the catch vector.

A. Usual procedure implying that the recruitment occurs at the very beginning of each quarter, or is constant.

B. Procedure for continuous recruitment with seasonal variations.

Holt (1962) advocated comparative studies between the essential biological parameters (growth, mortality, maturation) within groups of species in order to identify the possible general laws, which could be used for the quick determination of parameters for species of the same group, little or not known at all. Beverton (1963) investigated this possibility for clupeids and noted the existence of some consistency in the relationships between these parameters. He concluded that a relation existed between growth and longevity (between average maximum age or natural mortality and K) and indicated that the maturation could even be more related to longevity than growth.

Despite the fact that the data on this matter are rather scarce for shrimps it has been felt necessary to include this aspect in this review and to give some relationships which could eventually be used with caution.

7.6.1 Relation between natural mortality, growth and life-span

Beverton and Holt (1959) and Holt (1960, 1962), demonstrated the relation between maximum age (T_{max} and L_{∞}) as well as between M and K for different groups of fish. Information on this type of relation does not exist for shrimps where data are still rare and scattered.

Tanaka (1960) quoted by Saville (1977) has given a relationship between maximum age and M which can be used to obtain a first approximation for M. This type of relation must be used cautiously and Beverton and Holt (1959) and Beverton (1963) emphasize that its statistical significance is limited because the accuracy of the data used is not known and the values obtained are in some cases certainly over or under estimates: the maximum age must be the average of maximal values obtained through a series of samples of identical size, which is practically never the case. In addition, the observed value of T_{max} depends on sampling intensity.

These considerations must be borne in mind, more particularly with regard to crustaceans for which, lacking a direct method of age determination, all assessments of maximum age (based on extrapolation of the growth curve to the average maximum size reached or on tagging) is uncertain. The reserves expressed by Knight (1968) regarding the biological significance of the calculated growth parameters and the divergent views of Kruger (1969), should be noted.

In spite of the limitations expressed, Beverton and Holt (1959) noted that K and M seem to be closely related. For penaeid shrimps, the high values of K (0.15 - 0.30/month, that is 1.8 to 3.6/year) lead one to the assumption that there is a high natural mortality, which is of course evident for these animals with a short life-span.

If the values of M and T compiled by these two authors (Fig. 58) as well as Tanaka's (1960) relation, reproduced by Saville (1977), are plotted, it can be noted:

- that the latter seems to underestimate the M values
- that for penaeids, with a maximum age of about two years, the order of magnitude of M would be from 2 to 3/year, that is 0.16 to 0.25/month as a first approximation. This estimate, even though very wide, can be compared with values taken from the literature which range from 0.04 to 2.2/month, that is 0.5 to 26/year. This indicates that certain values in the literature are clearly too high.

More recently Pauly (1978) showed a correlation between M, L_{∞}, K and T (average annual temperature at the surface) of the form

$$\log M = 0{,}1228 - 0{,}1912 \log L_{\infty} + 0{,}7845 \log K + 0{,}2391 \log T$$

$$\log M = -0{,}1091 - 0{,}1017 \log W_{\infty} + 0{,}5912 \log K + 0{,}3598 \log T$$

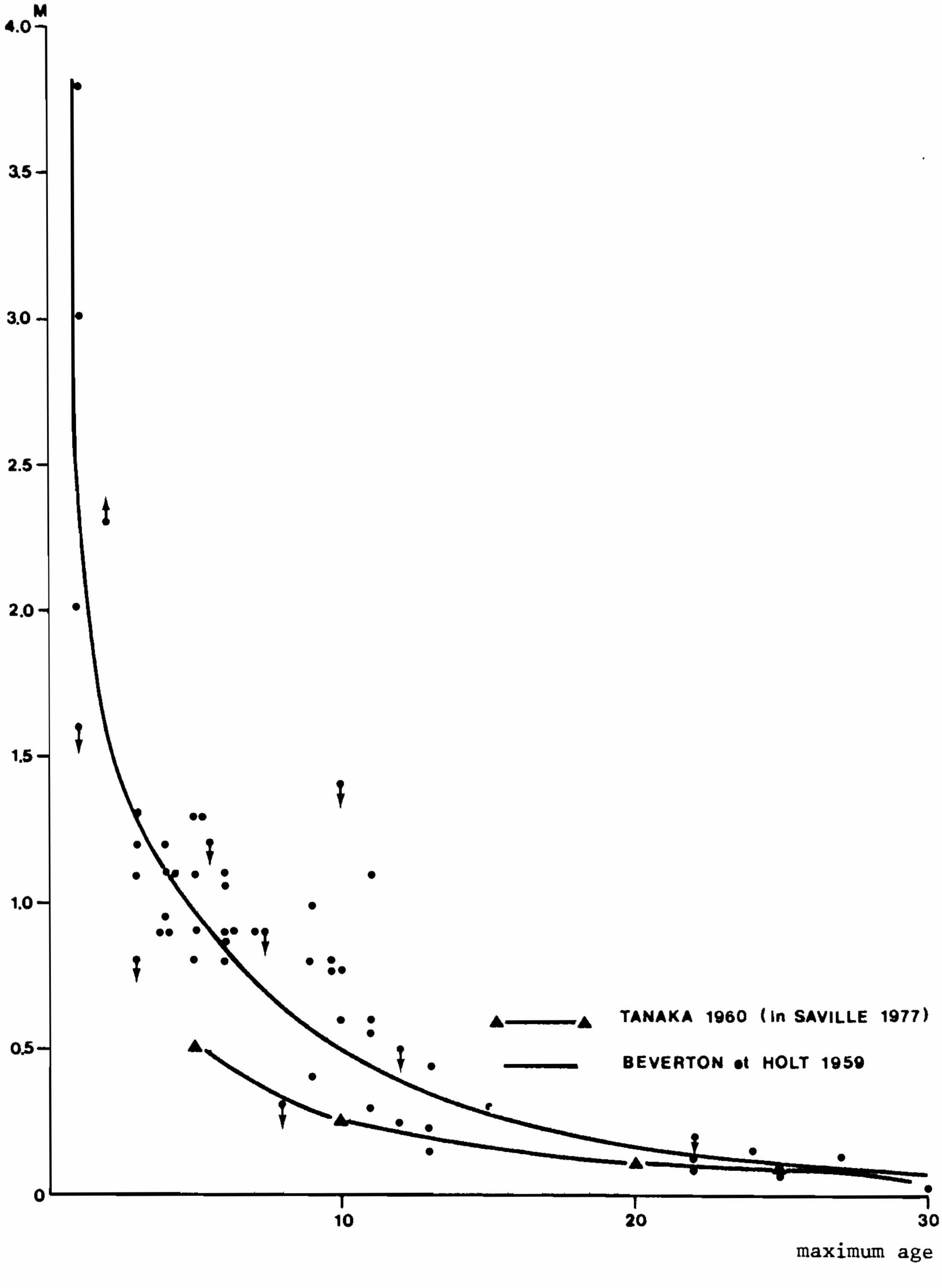


Fig. 58 Relation between maximum age and natural mortality. Data from Beverton and Holt (1959) and Tanaka (1960). The latter redrawn from Saville (1977).

L_∞ being expressed in total length in cm, W_∞ in grams and T being in degrees Centigrade. Applied to data for Penaeus notialis[1/] on the Ivory Coast ($K = 2.2$; $L_\infty = 20$ cm LT; $T = 24^\circ C$), this model enabled the calculation of $M = 2.8$/year, a value which is very close to that calculated by other methods ($M = 2.5$).

7.6.2 Relation between natural mortality and sexual maturity

Beverton and Holt (1959) investigated, without great success, a relation between longevity T_{max} and the L_m/L_∞ ratio where L_m is the size at first spawning. Holt (1962 noted that it was generally accepted that the L_m/L_∞ ratio was about 2/3 (average value 0.64 falling between maximal and minimal values of 0.3 and 0.9). In tropical zones a close average value of 0.58 ± 0.03 (at a 95% confidence level) was found (I.S.R.A./O.R.S.T.O.M., 1979).

Continuing investigations into this, as yet, little studied area of comparative dynamics, Rikhter and Efanov (1976) showed a close association between M and t_m or t_{m50}, t_m the age at first sexual maturity and t_{m50} the age when 50% of the population is mature, also called by Rikhter and Efanov "the age at massive maturation". They demonstrated a hyperbolic relation with the equation

$$M = 1{,}521/(t_{m50})^{0{,}720} - 0{,}155$$

With this empirical relation, it should be possible to establish orders of magnitude for M. It is unfortunately impossible to calculate the variance of the estimates.

As an example, Penaeus notialis on the Ivory Coast achieves first spawning at 7 months and 50% of the shrimps are mature at 10 months. The formula gives $M = 1.6$/year or 0.13/month. This value is given only as an indication since, as in figure 58, the relation used is hyperbolic and therefore has very little accuracy for young ages at maturation. It is nevertheless a further element which tends to show that natural mortality in penaeids is certainly high but not as high as certain earlier pioneering work would lead us to believe.

Rikhter and Efanov (1976) also suggested that the age of massive maturation could be taken to be equal to t_{opt}, the "optimum age" defined as the age at which the biomass of an age class is maximal. If this observation is confirmed, Beverton and Holt's (1966) equations for calculating L_{opt} for animals with isometric growth can be used directly to estimate M

$$L_{opt} = 3\,L_\infty/(3 + M/K)$$

The same applies to Kutty and Qasim's (1968) equation for non isometric growth

$$e^{Kt_{opt}} = (l_\infty - l_0)\,(nK+M)/ML_\infty$$

[1/] Data from Garcia, 1977 - females

and

$$e^{K(t_{opt} - t_o)} = (nK+M)/M$$

where t_o is the theoretical age when $l = o$, l_o is the size at age $t = o$ and n the power factor of the length/weight relationship.

7.6.3 Swept area method

The essential principle of the calculation of F by this method is given by Beverton and Holt (1956) and was used to assess the order of magnitude of F for shrimp stocks in the Tortugas region (Florida) (Berry, 1969) and by Mathews (1973) in Mexico. This method assumes that F is equal to the ratio of the total area swept by the fleet and the total area covered by the stock if the shrimps are uniformly distributed and all those present in the swept area are caught.

Berry estimated that the true opening of the trawl equalled only 70% of the head rope length; he then calculated the true trawled area, eliminating little visited zones, and assumed that all shrimps in front of the trawl opening were caught. According to Penn (1976) the method gives greatly overestimated values of F for *Penaeus latisulcatus* in Australia. This observation is confirmed by the work of Loesh *et al.*, (1976) who showed that the efficiency of a trawl on shallow bottoms is only 30 to 50%. Watson (1976) showed that the efficiency of an electric trawl when fishing shrimps, when they are buried in the bottom, had an efficiency of 35 to 55% when fishing during the day. Klima (1976) estimated the efficiency of shrimp trawls at 0.55 to 0.68 for trawls of 18 to 21 m (head rope length), and their efficiency for catching fish as 0.25.

One can make the following general observations:

(a) Shrimps are very rarely uniformly distributed. There is generally much heterogeneity in sizes, in ages and in density and fishing is not random but highly directed at the best shrimp densities with the aid of the try-net. It is advisable therefore, in order to take these factors into account, to divide the fishing zone into strata and to combine the values of F for each stratum, weighted by the densities in the strata to avoid an underestimation of the overall F (Beverton and Holt, 1956).

(b) It is often assumed that all shrimps in the path of the trawl are caught. This may be acceptable in Florida with *P. duorarum*, where fishing takes place exclusively at night. When fishing is carried out throughout the day, it is evident that the assumption is not valid since catchability varies with the hour of the day. Catchability is also subject to seasonal variations (Garcia, 1973, 1977; Penn, 1976) and is most probably never total. This bias tends to an overestimation of total mortality and is thus opposite to the effect of the bias mentioned in (a).

In view of these observations, F values obtained by this method must be treated cautiously.

7.6.4 Average age or average length methods

As Beverton and Holt (1956) have emphasized, economy of effort can be made in some cases by estimating mortality from "integral" properties of age compositions of the stock. For example the average age of shrimps in catches can be related to Z by the equation:

$$\hat{Z} = 1/(\bar{t} - t_c) \quad \text{(Holt, 1965)}$$

where $\bar{t}$ is the average age of the individuals of a size greater than t_c, the age at first capture.

When recruitment is continuous, as is most often the case with shrimps, Ssentongo and Larkin (1973) indicated that the non-biased estimate is

$$\hat{Z} = n/(\bar{t} - t_c)\,(n+1)$$

where n is the number of samples used to estimate t. The variance is given by

$$\text{Var } \hat{Z} = (n/(n+1)^2/n(\bar{t}-t_c)^2$$

When age is difficult to determine, as in the case of the crustaceans, the analysis of the average size of individuals in the stock and its change during exploitation, also enables an approximate assessment of mortality.

Beverton and Holt (1956) showed that if $\bar{l}$ is the average size of individuals of size greater than l_c (size at first capture) one can write

$$Z = K(L_\infty - \bar{l})/(\bar{l}-l_c)$$

This method, used by Banerji and George (1967) for *Metapenaeus dobsoni*, gave an average value of Z = 4.04/year or 0.34/month.

Ssentongo and Larkin (1973) give a derived method which allows the calculation of Z when recruitment is continuous, as is generally the case with coastal penaeids

$$Z = K.\ \frac{n}{n+1} \cdot \frac{1}{\bar{y} - y_c}$$

where $y = -\log_e \left(1 - \frac{\bar{l}t}{L_\infty}\right)$, $\bar{y}$ being the average of y in n samples

and $y_c = -\log_e \left(1 - \frac{lc}{L_\infty}\right)$

These methods, in spite of their sensitivity to small variations in l_c can give an order of magnitude for total mortality.

7.7 CONCLUSIONS

Estimation of mortality in penaeids is compounded by difficulties in obtaining reliable age composition and in the use of tags without introducing the risk of considerable bias. The comparative dynamics approach (Holt, 1962) is still difficult to use since the values available in the literature are scarce and scattered. The general relations between M and the maximum age, T_{max}, or M and the age at maturity t_m, are not precise for the shortest life-spans and only enable an approximate idea of the order of magnitude of M to be obtained.

The first marking experiments undertaken in the United States provided estimates of M which were so high that they made all mesh regulations practically useless. Results obtained later in various regions of the world led to the conclusion that the earlier values were certainly overestimates, probably because marking techniques and their analysis had not yet been completely mastered.

Even if there is an increasing tendency to accept that protection of the juveniles leads to better production, it nevertheless remains difficult to define an exact value for the mortalities and in particular for natural mortality, which is of primary importance in the models.

To give an example, some values found in the literature are given below .

It can be seen that the values found for M vary from 0.04 to 2.2 per month or 0.48 to 26.4/year. The lowest value obtained by Berry is probably an underestimate since the f value obtained by the swept area method is probably too high (see section 7.6.3). The large majority of the values fall between 0.10 and 0.45 per month. Since most were derived from tagging, they can be prone to errors by excess. This leads to annual values of M = 1.2 to 5.4. Cautious use of the methods proposed in sections 7.6.1 and 7.6.2 should enable elimination of the less probable values.

Finally, it should be noted that it is often accepted that the male mortality must be greater than female mortality because the former's growth ends more rapidly (Holt, 1960, 1962; Beverton and Holt, 1959; Beverton, 1963). Nevertheless for P. notialis, Garcia (1975) showed that the sex-ratio as a function of age is stable and close to 50%, which means that mortality is the same for both sexes (Fig. 34). This stability of the sex-ratio was also shown by Iversen, Jones and Idyll (1960).

SPECIES	AUTHORS	M/month	F/month	Z/month
P. duorarum	Kutkuhn (1966)	2,2	3,8	3,0 -6,0
	Berry (1967)	0,08-0,24	0,64-0,92	0,88-1,08
	Costello & Allen (1968)	0,32-0,44	0,12-0,28	0,44-0,72
	Berry (1969)	0,04-0,08	0,36	0,40-0,48
	Garcia (1977)	0,17-0,32	0,15-0,16	0,32-0,48
	Garcia (1979)	0,21	-	0,24-0,32*
P. setiferus	Klima & Benigno (1965)	0,32	0,24-0,76	0,96-1,08
	Klima (1974)	0,16-0,48	0,40-0,48	0,65-0.90
P. aztecus	Klima (1964)	0,84	0,24	1,08
P. indicus	Le Reste (1978)	0,21	0,27	0,48
	Marcille (1978)	0,15-0,25		
P. latisulcatus	Penn (1976)	0,05-0,13	0,04	0,09-0,16**
	Marcille (1978)	0,10-0,30		
Metapenaeus dobsoni	Banerji & George (1967)	-	-	0,34
Penaeus plebejus	Lucas (1974)	0,2 (adults) 0,88 (juv.)	0,88(adults) 0,16 (juv.)	0,28 1,04
Metapenaeus monoceros	Marcille (1978)	0,10-0,20		

* For various levels of effort

** Practically unexploited stock

8. VARIATIONS IN CATCHABILITY 1/

One of the conditions essential to the assessment or the management of resources is the acquisition of a good estimate of fishing effort.

In order to avoid bias the classic relationship

$F = qf$ must be satisfied

It follows therefore that any variation in q, either periodic or long term, involves, for a given nominal effort, a variation in the corresponding fishing mortality. In addition, the catch per unit effort c/f is often used as an index of abundance insofar as the equally classical relation

$c/f = qD$ is accepted

where D is the density (abundance per unit area). The result is that every variation in q is accompanied by an "apparent" variation in density. For these reasons it appeared useful to the authors to examine the different known types of variations of q and their consequences in shrimp stocks, even at the cost of some repetitions.

To facilitate the description the following types of variations will be distinguished: diel, tidal, lunar, seasonal, spatial, age specific and interannual. The distinction between some of them is sometimes arbitrary; it is clear that for these very short lived animals which stay about one year in the fishery there is an overlap between seasonal, spatial and age specific variations since they are closely related to the development of the cohorts in time and space.

8.1 DIEL VARIATIONS

These have been mentioned in Chapter 2. Such variations have been demonstrated for many years by many authors since they are clearly shown by diel variations in yield. Shrimp in general are animals active at night and stay buried in the sediment during the day. Reflecting the activity rhythm, the yields are generally higher at night both at sea and in the estuaries and lagoons. It is not however always the case at sea and when yields are higher during the day it can be supposed that for reasons associated with light (and the transparency of the water) the shrimps lie resting on the bottom during the day and swim freely at night, particularly out of range of the trawls. The "apparent" activity rhythm is then the inverse of the true one.

These short term variations are "erased" by the use of average catch and effort data used to calculate an index of daily abundance. Garcia et al. (1973) studied this phenomenon in great detail in the Gulf of Guinea on various fishing grounds from Nigeria to Senegal at various seasons. They showed that in this region in which the water carries a high concentration of solid particles, the yields were more frequently at a maximum during the day but that some reversals of the "apparent" rhythm of activity occurred periodically, associated with seasonal changes in hydrological conditions (temperature and turbidity).

It will be seen later on that these seasonal modifications introduce seasonal variations in q.

8.2 TIDAL VARIATIONS

Variations related to the tide cycle are clearly evident when fishing for juveniles with fixed nets, where the catches are taken mostly during ebb tide. The catchability is liable to vary with the speed of the current; Yokel (1970) showed that if this speed went below 0.31 m/second the shrimps could swim out of the nets against the current. The seasonal variations in tidal currents and floods can also induce seasonal variations in catchability for this type of fishing.

1/ The word "catchability" is taken here in its broadest sense

8.3 LUNAR VARIATIONS

Practically all fishermen speak of variations related to lunar phases but at sea they are difficult to demonstrate unequivocally. Their existence however has been well demonstrated by certain authors (chapter 2). They are on the other hand very evident in lagoons or estuaries when fishing for migrating juveniles, where primary and secondary maxima of catch rates have been observed at new and full moon respectively.

8.4 SEASONAL VARIATIONS

These have long been known in practically all exploited stocks. Their study has, nevertheless, frequently been neglected since in classical fish population dynamics the use of average annual indices of abundance for the study of long-living species enables one to circumvent the difficulty of allowing for these variations.

However, the study of species with a short life-span, like shrimps, requires the use of a time interval smaller than the period of oscillation of the biological processes (one year). This necessity stresses the importance of studying the seasonal rhythm, the effect of which can no longer be cancelled out by the averaging effect of the use of an annual basic time interval.

There are many sources of seasonal variations of catchability. An inventory was attempted by Garcia (1977b) which will be repeated and completed here.

The main sources of variation are:

- the hydrological conditions and the behaviour
- the recruitment and selectivity patterns
- the variations of the numerical abundance
- the variations of the concentration of fishing on different species

8.4.1 Hydrological conditions and behaviour

8.4.1.1 Turbidity

It has been seen in the first section of this chapter that the diel variations in yield may give a correct or an inverted image of the activity rhythm of the shrimps. Garcia et al. (1973) have shown the occurrence of clear seasonal changes in the "apparent" rhythm of activity on various fishing grounds of the Gulf of Guinea. This rhythm shows a maximum during daytime when the water turbidity is high and at night when the turbidity is low.

These authors showed that the change from an "apparent" diurnal behaviour (maximum yields obtained during the day) to a nocturnal one (maximum yields obtained during the night) occurred with a simultaneous decrease in the apparent density, related to a decrease in catchability. They also indicated that seasons with a stable rhythm could be distinguished from seasons with an unstable one. It is probable that this instability may have an influence on the efficiency of fishing effort.

In a more recent work in the same region, Garcia (1978) showed by cohort analysis the existence of seasonal variations in catchability which are synchronous with variations in turbidity (Fig. 59).

Marcille (1978) in Madagascar also showed that during the dry season, the relative fishing power of some trawlers is increased (Fig. 24B) by the sudden showers which increase the turbidity of the coastal waters. These changes in catchability, which are related to changes in behaviour and especially in the vertical extension of the schools may affect differently the catches of trawls with different vertical openings. They, therefore, change the standardization relationships (see section 4.1.1.2).

8.4.1.2 The temperature

Contradictory suggestions on the influence of temperature on the catchability have been published. Garcia et al. (1973) have suggested that in Senegal the low winter temperatures (about 14-16°C) improve the catchability by suppressing any activity rhythm. The shrimps numbed by the cold will be equally catchable during the day and the night. On the contrary Penn (1976) in Australia related the observed increase in catchability to an increase in temperature.

8.4.1.3 The currents

The particular case of the migrating shrimps can be recalled here. When the juveniles leave lagoons or estuaries and when they are fished with fixed nets, the catch per hour fishing or per day depends not only on the true abundance of the shrimps in the estuary (itself depending on the seasonal reproduction cycle) but also on the volume of water filtered by the net per unit of fishing time. The catch will thus depend of the current speed and the catchability will be higher during the spring tides than during the slack tides. It will also be higher during the flood seasons than during the low water ones. For a more detailed analysis of the problem of evaluating fishing effort in this type of fishery reference could usefully be made to section 4.1.2.2.

8.4.2 Variations related with recruitment and selectivity

The variations of catchability of a cohort with its age, related to the selectivity of the fishing gears, are known. The function is in general sigmoid, symetrical or not. In the case of long living animals where the newly recruited year class represents only a small part of the exploited stock, the selectivity has no marked seasonal effect on the overall catchability of the population. In the case of short living animals such as shrimps, of which the life-span in the fishery is often less than 1 year, the age structure of the stock is subject to important seasonal variations related to the recruitment (Garcia, 1977). An illustration of this phenomenon and of its amplitude is given in Figure 77. For such stocks the combination of selectivity and recruitment processes may induce seasonal variations in the overall catchability of the population and especially an increase of q with the average age of the population until the selection process is completed for the annual generation considered.

8.4.3 Variations related with numerical abundance: for the same reasons as above, the abundance of the available stock (in numbers) is liable to seasonal variations, the amplitude of which will depend on the amplitude of the seasonal variations of recruitment. If it is considered that all the elementary recruitments within a year generate a theoretical year class, it is obvious that the proportion of this year class available to the fishery varies during the year. This implies that the proportion of the total annual year class caught by a unit of effort will vary during the year with a maximum just after the recruitment peak and a decrease until the beginning of the new recruitment cycle. These variations can be taken as variations in q (in its broadest sense) and a given effort will apply a different global fishing mortality according to the period of the year considered.

8.4.4 Changes in concentration indices

When the resource consists of different species and the effort is only globally known, the seasonal variations of the relative distribution of effort on the different species induces seasonal variations in specific catchability. It will be seen in sections 8.5 and 8.6 that changes in the concentration of effort on the different cohorts or age groups of one species induce spatial and age specific variations of q.

8.4.5 Conclusions

There are numerous sources of seasonal variations of the catchability (taken here in its broadest sense). Despite the fact that most of them have not been quantified, their direction can be qualitatively assessed. Those which are related to the dynamics of the population (numerical abundance and mean age) tend to counteract. Those which are related to hydrological conditions can either sum each other or counteract. The seasonal resultant of all these variations is difficult to define analytically. It can however be calculated from successive marking experiments or by cohort analysis (cf. chapter 6).

The consequences of these types of variations are the following:

- the variations of F with age are different for each elementary cohort which contributes to the annual generation,

- the total mortality applied to a stock by a given annual effort will depend on the seasonal distribution of the latter. The same holds true for the total catch and the yield per recruit,

- the result of a management measure, such as a closed fishing season, will essentially depend on its timing within the year.

These seasonal variations should therefore be taken into account as far as possible when using simulation techniques for determining the expected effect of differences in fishing, and of management measures.

8.5 SPATIAL VARIATIONS

For trawl fishing these are known and depend on the configuration of the bottom, its characteristics, presence of vegetation, strong currents, etc. The problem generally has been little studied because it is easy to circumvent by the use of average effort if the relative distribution of the effort on the species considered does not change with time (constant indices of concentration).

However, when the distribution is heterogeneous and the fishing is well directed, as is the case for shrimps because of the try net, the effort is generally concentrated on the greatest biomass (Fig. 60). The consequence is that if at each point the catchability is the same (since the proportion of the population present at this point and caught per unit of effort is the same) it is as a whole greater in zones of high abundance since the proportion of the total stock which is caught per unit effort is higher there. The result is that for any change in the distribution of effort on the biomass one will induce changes in the relation between F and f. To solve this problem, Beverton and Holt (1957, page 148) developed the concept of "overall effective fishing intensity".

Spatial variability in q is even more evident in artisanal fisheries, partly because of the morphology of the estuaries and partly because of the competition between fishing gear. In fact the quantity caught by fixed nets currently used in India and Africa depends on the time of setting the net and in particular on the water flow at the place of fishing. Since this flow is stronger in narrow areas, a greater yield is frequently observed in narrow passages (gullies, fjords, bridges, etc.). This moreover greatly complicates the regulation of fishing since the consequence of a reduction in the number of nets will vary according to the region involved; the total mortality will depend on the localization of the nets which are withdrawn and those which remain.

8.6 AGE-RELATED VARIATIONS

Variations related to selectivity and recruitment and to seasonal variations of the numerical abundance of the population have already been noted in sections 7.4.2 and 7.4.3.

In addition, it is necessary to emphasize that the consequence of the concentration of effort on higher abundances is the existence of variations of q with age. It was seen in the previous section (7.5) that fishing is concentrated in the most densely populated bathymetric and geographic strata (Fig. 60). Since a parallel stratification of size and age exists, there is consequently a concentration of effort on the main cohorts during the period when their biomass is greatest (Fig. 61).

8.7 INTERANNUAL VARIATIONS

The understanding of these variations is important in view of the use of annual effort data in production models (Schaeffer and Fox models for instance).

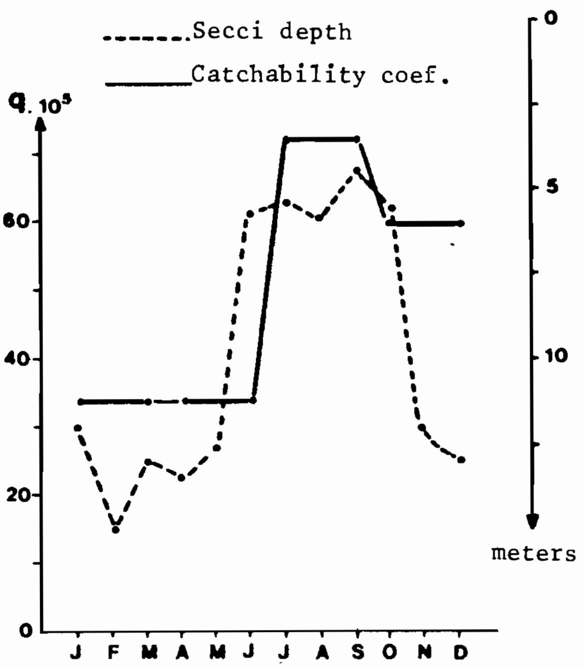


Fig. 59 Seasonal variations of the catchability coefficient and turbidity for *Penaeus notialis* (from Garcia, 1975)

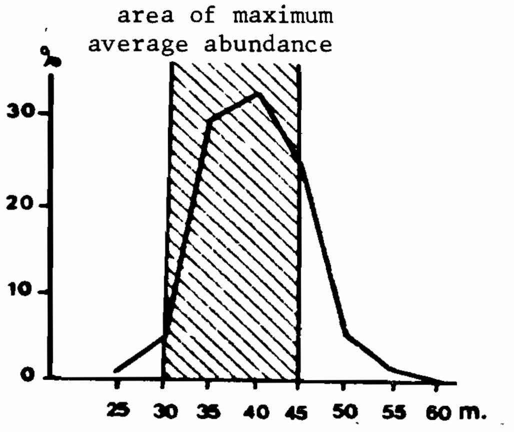


Fig. 60 Bathymetric distribution of the annual fishing effort and abundance in Ivory Coast (from Garcia, 1977)

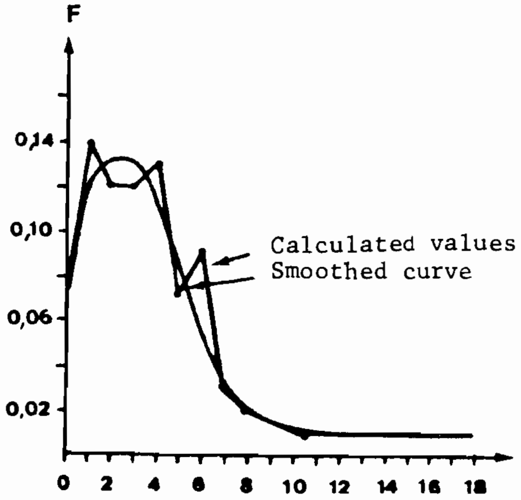


Fig. 61 Variations of F with age in *Penaeus notialis* (from Garcia, 1977)

8.7.1 Changes in seasonal distribution of effort

Because of the existence of seasonal variations of q, any change in the relative distribution of the effort within the year will induce a modification of the relationship between nominal annual effort and the related fishing mortality.

8.7.2 Changes in the target species

When many species are exploited together, it generally occurs that despite the fact that they are exploited more or less simultaneously, the fishing operations are more especially directed towards areas with the highest concentration of species giving the highest profit, and will be directed more and more towards secondary species when the abundance of the primary ones becomes lower and lower.

A similar phenomenon has been detected in Senegal where only one species of shrimp is exploited but where the transfer of effort occurs towards fish species which live on the shrimpgrounds or on neighbouring ones (Lhomme, pers.comm.).

In this situation, without a good measure of the true distribution of effort on the different species, the long term trend of effort for a given species will in general not be correctly evaluated and the decrease of abundance of the main target species will generally be overestimated. An example of a tentative solution for this problem in Australia is given by Hall and Penn (1979).

8.7.3 Changes in the ratio between searching time and fishing time

Hancock (1979) indicated that this phenomenon, well known for pelagic fisheries also occurs in fisheries for highly schooling shrimps like Penaeus merguiensis. If the shrimp abundance decreases over the years, this is accompanied by a decrease in the number of schools, and therefore by an increase of the searching time to the prejudice of the fishing time. The latter is therefore no longer sufficient to measure correctly the trends in fishing mortality, and it becomes essential to evaluate the time spent searching for the schools.

9. INTERANNUAL VARIATIONS IN ABUNDANCE AND PREDICTIVE MODELS

For animals such as penaeids with a short life-span, where the annual catch depends almost entirely on one year class recruited during the year, analysis of the interannual variations in abundance and the establishment of predictive models are essential for rational exploitation of the resources. In fact, the consequences of such variations for the efficacy of different potential management measures are important and will be discussed in the following chapters (11 and 12).

Firstly, we will briefly recall the different possible causes of variations in annual abundance and afterwards we will review the various correlations established for predictive purposes and their underlying mechanisms in penaeids. In this type of population, the most important variations are obviously linked to variations in annual recruitment, which because of the very small number of generations contributing to the catch are directly translated into practically proportional variations in total catch if the exploitation pattern remains stable. Variations in catchability are certainly partially responsible for seasonal variations of catches but, a priori, play a negligeable role in interannual variations.

Other causes of variation also exist which are associated with the particular population dynamics. Although these have as yet been little or not at all cited in the literature it seemed to us that they require inclusion for the sake of completeness of this review.

9.1 INTERANNUAL VARIATIONS IN ABUNDANCE

9.1.1 Nature of the variations

The industrial exploitation of penaeid shrimps is a recent event in most of the tropical regions of the world. The catches in the last 20 years have therefore varied enormously as a function of fishing effort, of the improvements made to the fishing power of the fleets and of the progressive development of exploitation strategy from single species fisheries (at the initiation of fishing) to multispecies fisheries (when the fishery is fully developed), etc. If one adds to this the fact that good series of fishery statistics, sufficiently complete and detailed to allow refined analysis, are seldom obtainable, one will understand that data which enable long-term studies of catch variability to be made are rare.

Thus, one of the first questions is: does the abundance of a shrimp stock vary independently of effort? The reply is ambiguous. According to certain authors there are important variations, according to others the abundance is stable. The stability of artisanal production in certain lagoons in the Ivory Coast over a number of years is an argument in favour of stable recruitment. On the other hand, there are important variations in the artisanal fisheries in Senegal (Le Reste, 1979). In addition, Boerema (1974) pointed out that variations in abundance at sea are small in Panama but great in the Middle East.

The divergent opinions can be partially related to the length of the time series available, and obviously short-term interannual variations (or "noise") must be differentiated from long-term variations (the "interannual signal"). When a short series of data is available, the "signal" is often masked by the development process of a fishery which is not yet stabilized and is therefore not apparent; it can be confused with variations related to fishing effort, thus completely biaising the c.p.u.e./effort relationship and the resulting assessment.

When, on the other hand, the available data allow (Fig. 63-66), the "interannual signal" is clearly distinguishable. It is tempting to look for the cause of this phenomenon in long-term climatic variations, as many authors have done, as we shall see later.

Such being the case the patterns of climatic variability are not identical in the equatorial zone and in the tropical or temperate ones. Therefore, it would not be surprising that the abundance of shrimp stocks in these regions is subject to different variations. For example, it can be seen in Fig. 63 that the "noise" on either side of the "signals" is much greater in Texas (±30% roughly, between 1930 and 1945) than in Louisiana (±15% roughly during the same period).

The example used is only an indication, without prejudgement on our part as to the true causes of this long and short-term variability. Our intention is only to draw attention to the different types of possible variations and their combinations since the consequences for the management and the development of an optimum exploitation strategy may be different. It would be useful to identify the different world stocks by their variability spectra (interannual signal amplitude and frequency, "noise" amplitude) but this is outside the scope of this review. We should also note however that all studies of this type should attempt to establish to what extent the "apparent" stability of the catches in a multispecies fishery reflects the ability of a fleet to maintain its total catch by adjusting its fishing strategy rather than the true stability of the underlying populations.

9.1.2 Variations in recruitment

The life cycle of most penaeids includes an important littoral stage the successful outcome of which is associated with various phenomenons.

9.1.2.1 Variations in spawning

There are few long-term studies which make it possible to examine this source of variation. We make reference here to the work of Lhomme (1979).

Fig. 62 shows the variation of the percentage of ripe females in the catches as a function of size from 1973 to 1977. The information in this curve is too integrated to allow an accurate analysis to be made, but the figure shows that the reproduction phenomenon varies and that for a given size the proportion of ripe individuals observed depends on the year.

Although it is not possible to calculate the statistical significance of the observed differences, it is clear that 1975 was an abnormal year for the two stocks at St. Louis and Roxo-Bissagos and that 1977 was distinctly abnormal for the latter.

We do not know to what extent these spawning anomalies affected the recruitment.

9.1.2.2 Survival and larval migration

After spawning, the resulting larvae must arrive in shallower zones where they will find the shelter necessary to their survival and growth. Obviously the opportunity to penetrate into the estuaries is closely linked to hydrological conditions (coastal currents, tidal currents, total water balance of the estuary, etc.).

Heavy rainfall and the resulting floods seem, according to the respective authors, to be a favourable factor since they increase the extent of the zone with a strong salinity gradient to which larvae might direct themselves - or unfavourable by simply hindering the entry of larvae into the estuary.

9.1.2.3 Survival in the estuaries

It is evident that it is at the larval level at sea and certainly in the estuaries that the essential factors operate which regulate the numbers of coastal penaeids. Many authors have suggested that heavy rainfalls and floods tended to favour survival and growth, on the one hand by increasing the surface of the available nursery areas (but for salt-requiring species this can have the opposite effect), and thereby reducing intra-species competition and on the other hand by increasing the productivity of the environment bringing in nutrients from the surroundings.

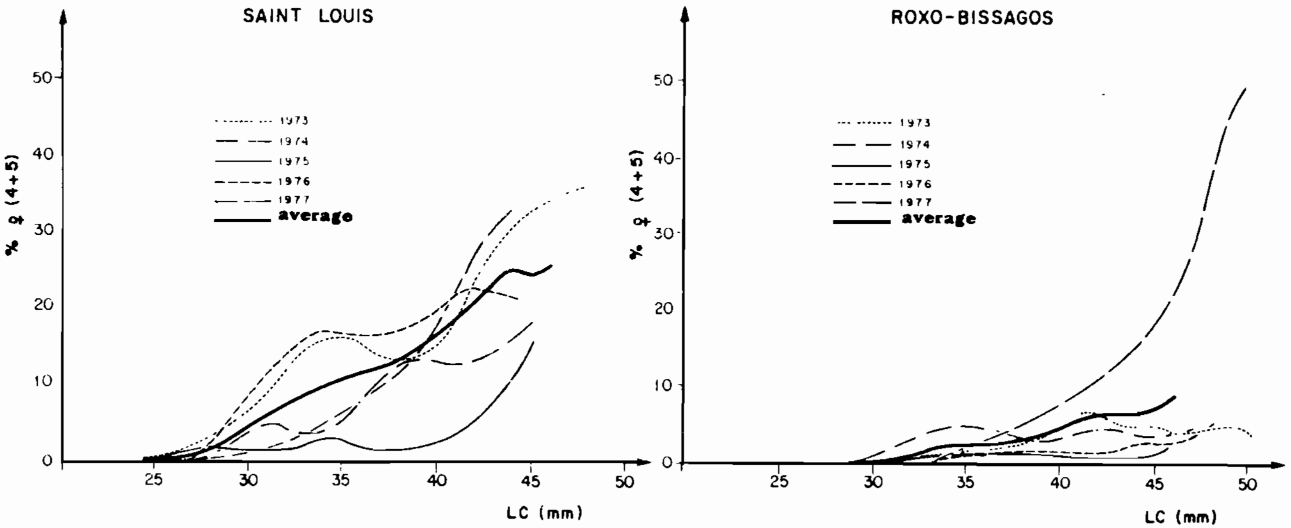


Fig. 62 Variations of the % of mature females with size for *Penaeus notialis* in Senegal (from Lhomme, 1976b)

9.1.3 Natural variations in size at first capture

These variations are essentially linked to interannual variations in the average size at migration of the young shrimp back to the sea.

The catchable biomass just before or during this migration depends on the number of recruited post-larvae, on their survival until migration, on their growth and thus on the prevailing temperatures and the length of stay in the estuary (Ford and St Amant, 1971; Le Reste, 1979). The latter author showed that the average size at migration varied considerably as a function of the ambient salinity, with consequent variations in catchable biomass (Fig. 66). It should not be forgotten that here fixed nets were used for fishing and that in fact any delay in migration results in a natural increase in the age at first capture in the estuary. The fact that there is a resulting increase in biomass would indicate a lower natural mortality than that calculated by many authors (cf. chapter 7).

It will be emphasized later (cf. chapter 10, section 1.2) the fact that these events have consequences at sea. Shrimps migrating late, at a greater size, have a recruitment curve which is displaced towards larger sizes, causing here again interannual variations in size at first capture at sea. Although the available data do not allow measurement of the effects of this variation on annual abundance, it is probable that they are not negligible.

9.1.4 Conclusions

There are many causes of interannual variations in abundance in penaeid stocks. Cause and effect relations are difficult to demonstrate even if they are sometimes a matter of plain common sense. It is possible that certain factors such as floods for example, might have a favourable effect here and an unfavourable one there, depending on their intensity (threshold effect) or the shape of the estuary (creek or lagoon, wide or narrow mouth).

Since these variations have been discovered in many regions, predictions from simple regression models have been attempted by considering the marine or estuarine stock as a "black box" which reacts to a given factor (rainfall, floods, annual temperature, etc.) to produce a certain biomass and thus a certain annual catch.

9.2 Predictive models

These are established by correlation from historical data with the intention of arriving at catch predictions. The principle is to demonstrate a sufficiently accurate quantitative relationship between abundance and a biological or climatological parameter in order to predict interannual variation in catch. To be useful, the model must allow an accurate prediction sufficiently in advance for the information to be usable.

For shrimps, the annual catch depends almost entirely on recruitment during the year and only short-term predictions can be made. In the long-term, only the general trend can be forecast if it is possible to associate it with a periodic climatological factor (solar activity for example).

Two types of model can be distinguished for shrimps according to whether the relations are established relative to a climatological factor (rain, floods, sunshine, solar activity) or to a biological factor (generally, the abundance of a previous stage of the life cycle).

9.2.1 Prediction from climatological data

9.2.1.1 Relation to floods and rainfall

Because of the importance of coastal zones in the shrimp life cycle and the major roles which coast-offshore gradients seem to play in the migration processes during development, the influence of continental discharges was the first to be studied. The results are contradictory since the demonstrated relations are either positive or negative, according to the cases which were examined.

In the U.S.A., as early as 1953, Hildebrand and Gunter (1953) and Gunter and Hildebrand (1954) showed for *P. setiferus* in Texas that there was a good relationship between total catch and the rainfall of the two previous years ($r = 0.66$) or during the current and two previous years ($r = 0.70$). The relation is significant at the 1 per cent level and the high catches are related to heavier rains.

The authors suggested a cause and effect relationship with the desalination of the coastal water, the observed lag-time possibly corresponding to the delay between the rains and their effect on the salinity of the water and then on the production of the shrimp stocks.

Several years later, Gunter and Edwards (1969) confirmed these results using longer time series (1927 to 1964) of the same species in the same region. Analysis of available data in Louisiana for the same species did not however demonstrate a relation between annual catches and the Mississippi outflows. Their logical conclusion was that brackishness was there always above the minimum threshold.

The same type of analysis was applied by the authors to *P. aztecus* in Texas and Louisiana and showed no significant relationship, suggesting that even with more data there would be a negative correlation; this result was considered logical for a species which is supposedly adapted to an area with low freshwater outputs and high salinity.

This problem has been more recently studied again by Barret and Gillespie (1973, 1975) who show that, in fact, there exists a negative correlation in Louisiana between river outflow in spring and catches of *P. aztecus*; and also between outflow in summer and catches of *P. setiferus* 1/. According to these two authors, excessive discharges in this region where the freshwater output is already important, would limit the available nurseries (with appropriate salinity) limiting the production and this explanation would be confirmed by the fact that *P. aztecus* production in Lousiana estuaries is higher when the salinity is higher in spring.

Freshwater outputs seem thus favourable to production in Texas and unfavourable in Louisiana for the same species, indicating therefore that the positive relationship between low salinity and production for *P. setiferus* might not be a linear function but could present a threshold beyond which it reverses.

More recently, Lhomme and Garcia (1981) also showed in Senegal that the anomalies in rainfall and stock abundance were positively correlated in the St. Louis fishing ground (with low freshwater input) and negatively correlated in Roxo-Bissagos where the freshwater output is much higher.

The work of Gunter and Edwards (1969) on *P. setiferus* also deserves additional comment. In fact, the comparison of the variations of annual catches in Lousiana and Texas shows quite good agreement between long-term variations (Fig. 63). As a result, while the previous paragraphs seem to indicate differences in reactions to freshwater outflow between these two stocks, it is still true that there exist nearly synchronous long-term variations which would imply the action of a common factor, probably of climatological origin.

1/ These results have been used by Griffin, Lacewell and Nichols (1976) to elaborate a production model taking into account the variations of total annual effort and the river discharges. The proposed empirical model is $Y = 3365\ D^{-0,5064}(1.0 - 0,994746^{E})$, where E is the fishing effort and D the annual discharge. In this model, the suggested possibility that the relationship between discharge and production might not be monotonous was not considered.

Synchronous variations have also been shown by Berry and Baxter (1969) for the annual catches of P. aztecus in the north western Gulf of Mexico (Fig. 64) but this synchronism could come from the occurrence of important migrations within the whole area (Barret and Gillespie, 1975, page 3).

It would have been interesting to know whether there was also any synchronism between the variations of two different species but the positive observation on this by Barret and Gillespie (1973) is contradicted by the same authors in 1975.

In Australia, Thompson (1956) had long since demonstrated a positive correlation between variations in rainfall and the annual catches of juveniles (1924 to 1941) without making any suggestions as to the underlying causes. In particular he observed a good correlation between the catch and the rainfall of the two previous years ($r = 0.76$), or the rains which fell 6 to 12 months before the fishing season. He also showed, over 6 years only (1948-1953) similar variations between the rainfall of one year and the catches of aduls at sea in the same region the following year.

This preliminary observation was confirmed by Ruello (1973), with a longer series of data (Fig. 65). He observed the best correlations with the rainfall of the previous year ($r = 0.64$) as well as those of the same year added to the previous year ($r = 0,69$). The river outflows also showed a good positive correlation.

The observation of Thompson (1956) of a positive correlation between rainfall and juvenile production in estuaries is in contradiction with the observations of Castello and Olinto Moller (1978) in Mexico, Le Reste (1979) in Senegal (Fig. 65) and Barret and Gillespie (1975) in Louisiana which have shown a negative correlation between rainfall and the estuarine production.

Again, the observations available from the literature indicate a negative or positive correlation depending on the area or the species.

Several hypotheses have been advanced to explain the observed phenomena: direct effect on fecundity, facilitation of larval migration by an increase in salinity gradients or detrimental effect of excessive discharges on the larval recruitment, effects on the habitat available in the estuaries and hence on competition, growth and survival, etc., several of these factors possibly acting together.

The apparent synchronization of the long-term variations in a wide part of the Gulf of Mexico would suggest the effect of climatological factors acting on a wide scale by a mechanism difficult to analyze because of the complexity of the ecosystem and the life cycles concerned.

Most of the advanced hypotheses assume that the climatological factors affect the number of recruits. As has already been said, some factors such as river floods, may be beneficial or not and one can assume that the relationship is perhaps a non-linear one, the production being enhanced up to a given threshold, depending on local conditions, and limited beyond it.

A rather different mechanism involving salinity induced natural variation of sizes at first capture can be advocated from the results obtained by Le Reste (1979). This author studied variations in production of a large artisanal fishery in Casamance (Senegal), an estuary which is hypersaline for part of the year. He showed that the increase in the average annual size of shrimps caught, recorded since the beginning of the Sahelian draught, was associated with the increase of the salinity in the estuary. He also showed that in dry years, when the size at migration (and therefore at first capture) is large, catches are high and vice versa. The salinity of the Casamance estuary, which is mostly fed from underground water, depends on rainfall from previous years and Le Reste showed a good negative correlation between the catches of one year and the rainfall of the previous years. This is interpreted as the influence of salinity on the length of stay in the estuary, an explanation advanced and sustained by Garcia (1977) for the Ivory Coast and Nigeria. The more extended stay in the estuary would increase the age at first capture and the catchable biomass through the interaction of growth and mortality. The use of the correlation as a predictive model has enabled good agreement between observed and calculated catches to be obtained (Fig. 66). The quality and reliability of the prediction must be tested in future years.

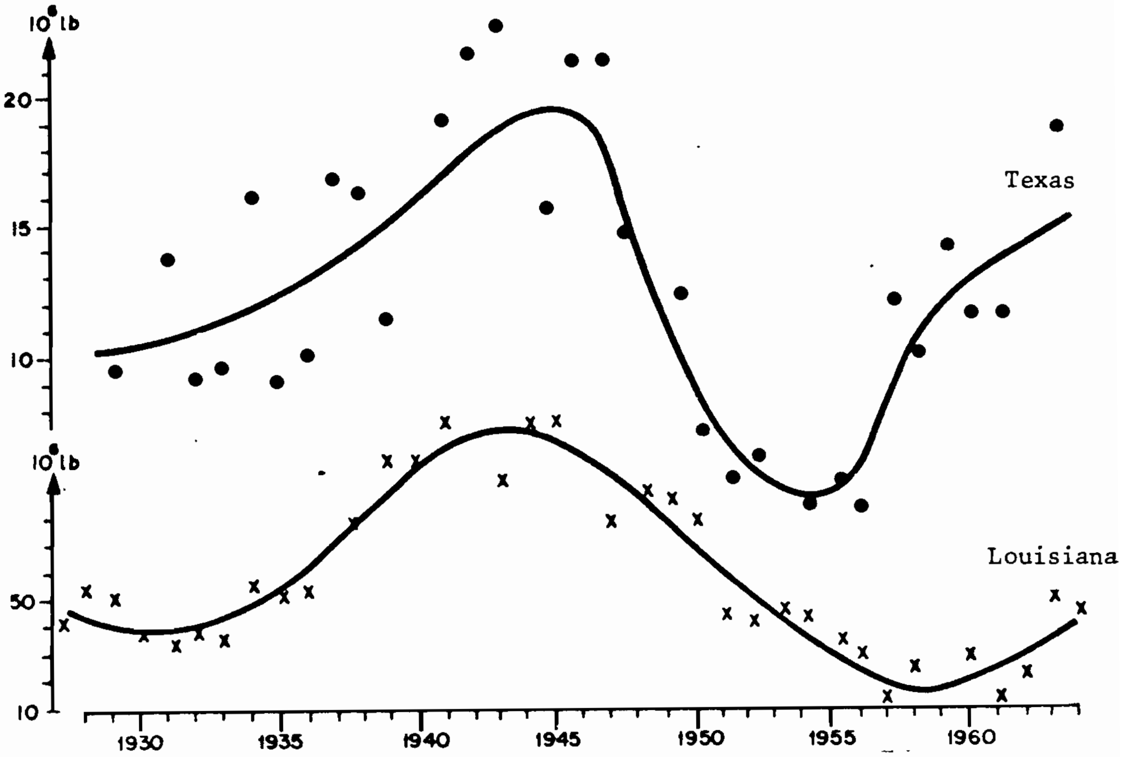


Fig. 63 Long-term variations of landings of *Penaeus setiferus* in Texas (●●) and Louisiana (xx) - Data from Gunter and Edwards, 1969.

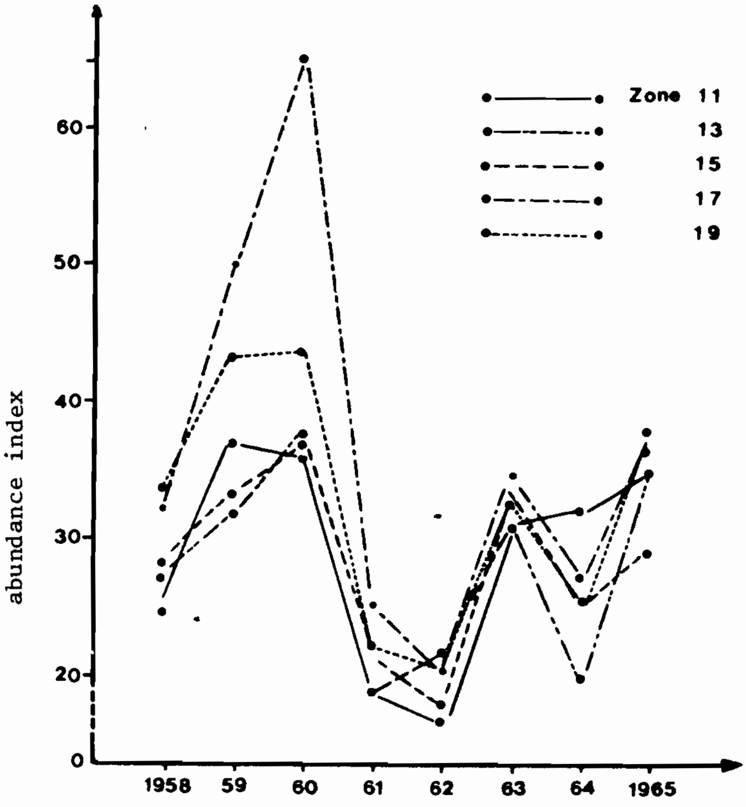


Fig. 64 Interannual variations of catches in different statistical divisions in North and North-West Gulf of Mexico, from Alabama to Mexico (from Berry and Baxter, 1969)

Lastly, it should be noted that certain authors have tried to link catches with a certain time lag, to rainfall month by month. The correlation is generally excellent since it links two seasonal factors, but cannot be used for prediction of annual catches.

9.2.1.2 Relation with temperature

Williams (1969) showed, in the United States, a relation between the temperature characteristic of the year and the shrimp abundance expressed as catch per unit effort. The introduction of a time lag did not noticeably improve the relation. When he grouped the data from Georgia, the Carolinas and Texas, catches were higher during the warmer years. The author noted however that although these relations were still apparent, they were less good if the different regions were considered separately.

This relation in fact does not seem to be of use in predicting with good accuracy interannual variations in each region separately and is only significant at the level of the whole southeast coast of the United States; it is only in this way that the range of the annual thermal values is sufficiently large to allow a morpho-edaphic type of relationship to emerge, showing in fact that the overall shrimp potential of a region is related to its annual thermal profile (Fig. 67). This is easily understood when it is recognized that the essential growth and reproductive mechanisms of these tropical animals are temperature dependent. The author has moreover pointed out that the data along the regression line are in fact arranged in a latitudinal order. These observations should be taken in conjunction with those of Turner (1967) expressed in the following section.

A relation of a different type was established in Texas by Baxter (1969) showing that there was a connection between the date of the peak annual juvenile migration seawards and the air temperature in April of the same year (Fig. 68). This prediction could be useful in determining accurately the period in which sampling should be made so as to determine an index of abundance for migrating juveniles. Along the same line, a work undertaken in Louisiana (Barret and Gillespie, 1973, 1975) indicates that the catch of *P. aztecus* in the estuary in May depended on the temperature in April.

9.2.1.3 Relation with latitude

Turner (1977) showed that there was, on a world scale, a connection between production (Y) and latitude (x in degrees) of the form

$$Y = 159.2^{-0,070(x)}$$

9.2.1.4 Relation with solar activity

Although there have been no such studies on penaeid shrimp, it is interesting to note that Driver (1979) showed good correlation between the production of *Crangon crangon* (a carid shrimp) and the rhythm of solar activity. A previous study showed that predictions could be made 1 to 2 years in advance based on rainfall measurements and air temperatures. Since interannual variations in climate have well established links with solar activity, the author tried and succeeded in obtaining good correlations ($r = 0.86$) with an 11 year periodicity.

9.2.1.5 Relation to the area of intertidal zones

Turner (1977) also showed that the catches in lagoons within a region were associated with the area of intertidal zones. He accepted nevertheless that this relation could simply be a consequence of the relation between estuarine production and the size of the sea/estuary "interface". In the same way Barret and Gillespie (1973, 1975) showed a relationship between the interannual variation of the estuarine area adequate for shrimp life (salinity above 10 p.p.m.) and catch.

9.2.1.6 Conclusions

There are sufficient indications to show that annual shrimp production varies from one year to the other in relation to large scale climatological factors. One can assume that there is an underlying cause and effect relation, which however, will remain very difficult to prove because the mechanisms are certainly complex and involve the modification by the climatic conditions, of several parameters (fecundity, post-larval recruitment, age at migration, growth and survival, catchability).

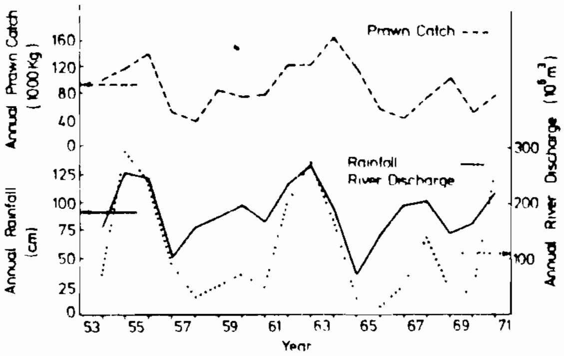


Fig. 65 Annual fluctuations in *Metapenaeus macleayi* catch, rainfall and river discharge (from Ruello, 1973)

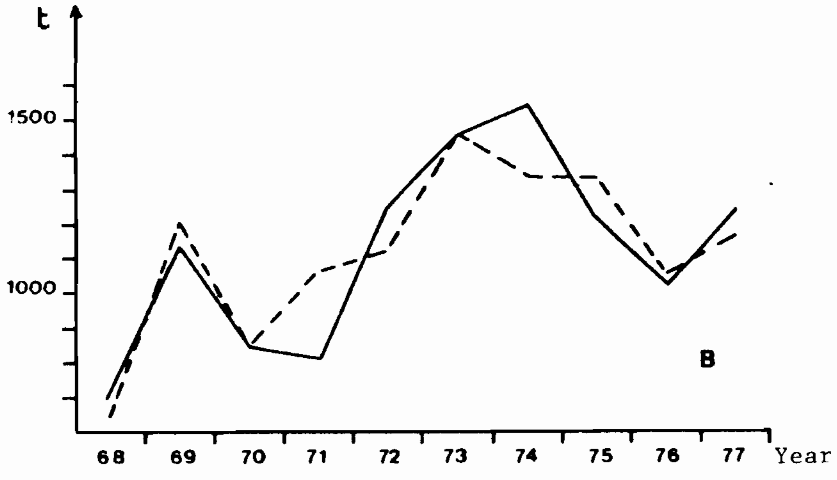


Fig. 66 Observed (--) and calculated (—) catches in the artisanal fishery of Casamance (Senegal) (from Le Reste, 1979)

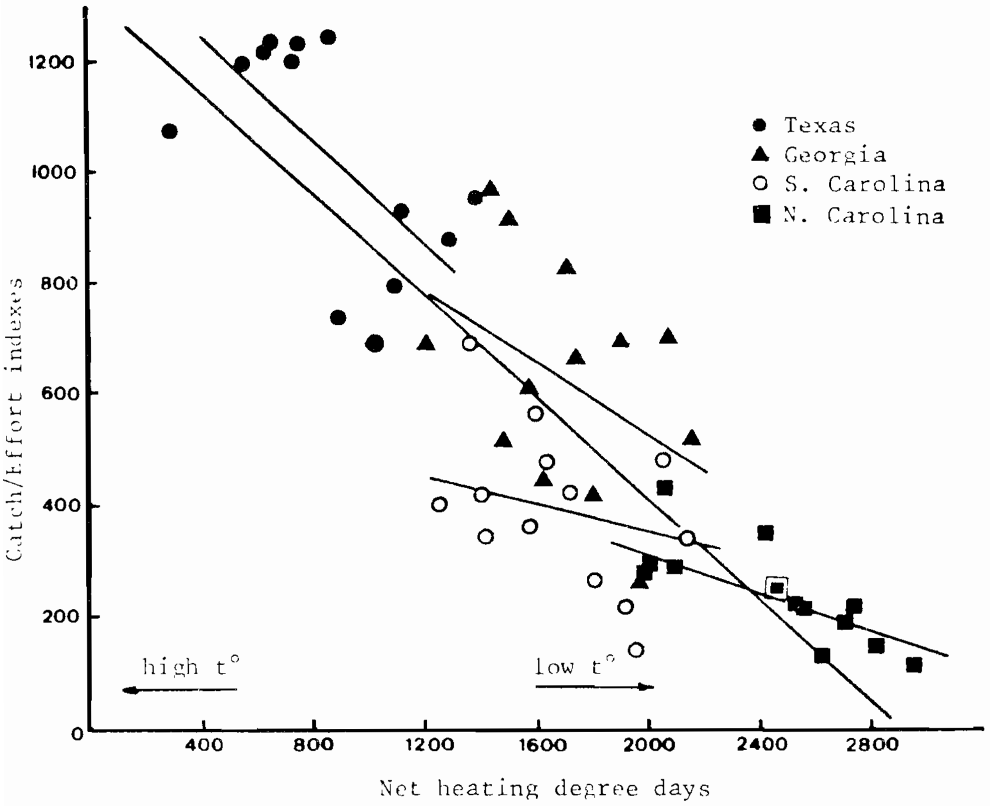


Fig. 67 Relationship between yearly thermal balance and catch rates (from Williams, 1969)

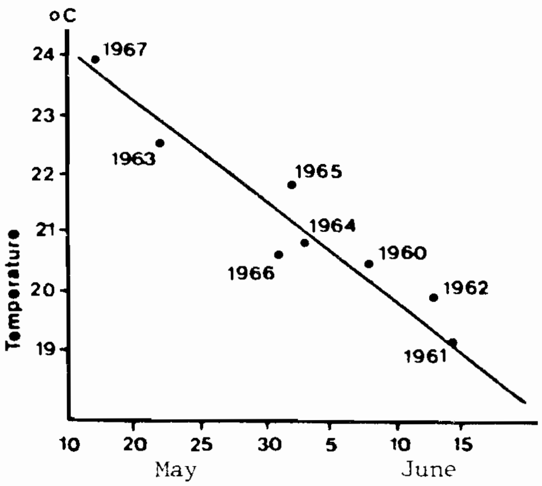


Fig. 68 Relationship between the temperature in April in Galveston, and the date of maximum abundance of juveniles in the bay (from Baxter, 1969)

The climatological parameters which have been measured, whether rainfall, river discharges, annual thermal profile, or solar activity, can in the end only be overall indicators of climatological variations affecting many other parameters (hours of sunshine and hence primary production and photoperiodicity, salinity, chronology or relative length of seasons, displacements of fronts, position or strength of currents and undercurrents) which are all also liable to influence the biological production of the shrimp stocks.

Finally, however, it is not necessary to understand all the mechanisms in order to use an empirical relation as a predictive tool if the diagnostic accuracy is judged to be sufficient. It is obvious for this purpose that the above relationships have been established. It should however be emphasized that, according to Marr (1972), this type of relation is often only precise in extreme conditions and that when conditions are average, the strongest variance is often linked to biotic factors (competition, etc.). It follows therefore that a given parameter can only be sufficiently informative in zones where it is a limiting factor and that hence only abnormal years can be forecast with sufficient precision.

Since the relation is not necessarily a linear one, forecasts should not be based on extrapolation outside the range of the observations.

9.3 FORECASTS BASED ON EARLIER STAGES OF THE LIFE CYCLE

The shrimp life cycles goes through several stages, post-larval, juvenile, adult, two of which correspond to a migration where the shrimps are concentrated and sampling is easier. Since the sixties, many studies have attempted to show the relation between the abundance in an early stage and in a later, exploited stage, in order to obtain an index of pre-recruitment and a simple predictive model.

9.3.1 The relation between adult abundance and abundance of their larval and post-larval progeny

According to Neal (1975) it has not been possible to show any connection. He suggests that this indicates that the variability at the larval and post-larval stage is related essentially to the environment. The present authors are not aware of any direct observations on this matter. It is however true that reproduction is subject to strong variation from one year to the next (section 9.1.2.1).

9.3.2 The relation between larval abundance at sea and abundance of adults of the same generation

Again, according to Neal (1975), no relation has been observed. It should be noted that the main obstacle for these studies lies in obtaining a sufficiently accurate index of larval abundance at sea at a reasonable cost. The problems arise on the one hand from the characteristics of the distribution of the plankton (cf. chapter 2) and on the other from the rapid development (with high larval mortality) through the many successive larval stages which are a feature of penaeid development. In fact, at any given moment, the abundance of a certain stage (protozoea for example) depends on the spawning intensity and also on the time elapsed between spawning and sampling because of the permanent "migration" into and out of the stage considered and on the larval mortality.

9.3.3 The relation between post-larval and subsequent juvenile or adult abundance

Where enough data is available on the variations of abundance of two successive stages within a year, it is possible to find a relation between the respective peaks of abundance (Fig. 69). Then, when a long series of abundances at various developmental stages are available for many years, the respective indices of abundance can be calculated and their correlation, if significant, can be used as a predictive tool (Fig. 70).

Baxter (1963) at the conclusion of a 3-year study on P. aztecus in Texas showed good correlation between seasonal variations of abundance in post-larvae, juveniles and adults in lagoons. He suggested that prediction might be possible but that only a detailed study could confirm this (Fig. 69).

Later, Berry and Baxter (1969), after seven years of studies in the same region noted the absence of a useful relationship between post-larval abundance and bait or commercial catch. They suggested that sampling by the Renfro net (cf. section2.3.24) should be re-examined.

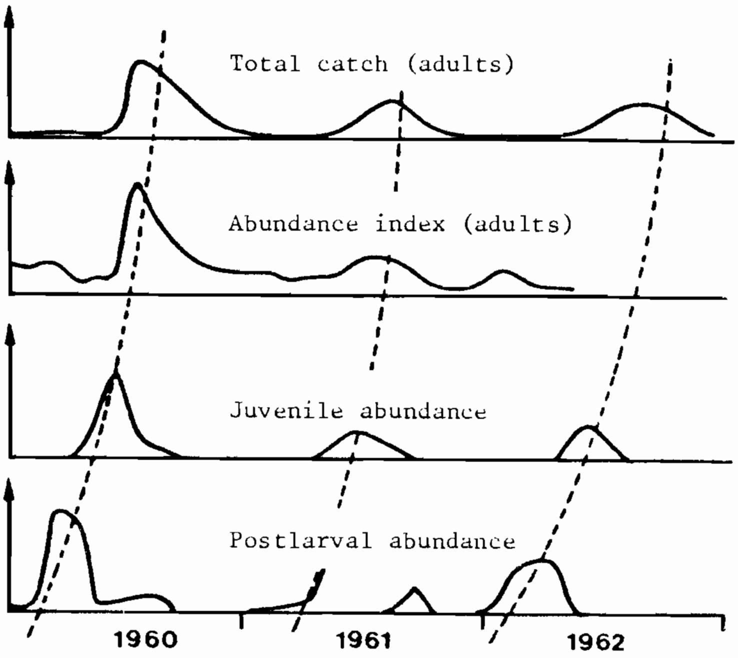


Fig. 69 Relation between seasonal variations of abundance indexes of postlarvae, juveniles and adults (simplified from Baxter, 1963)

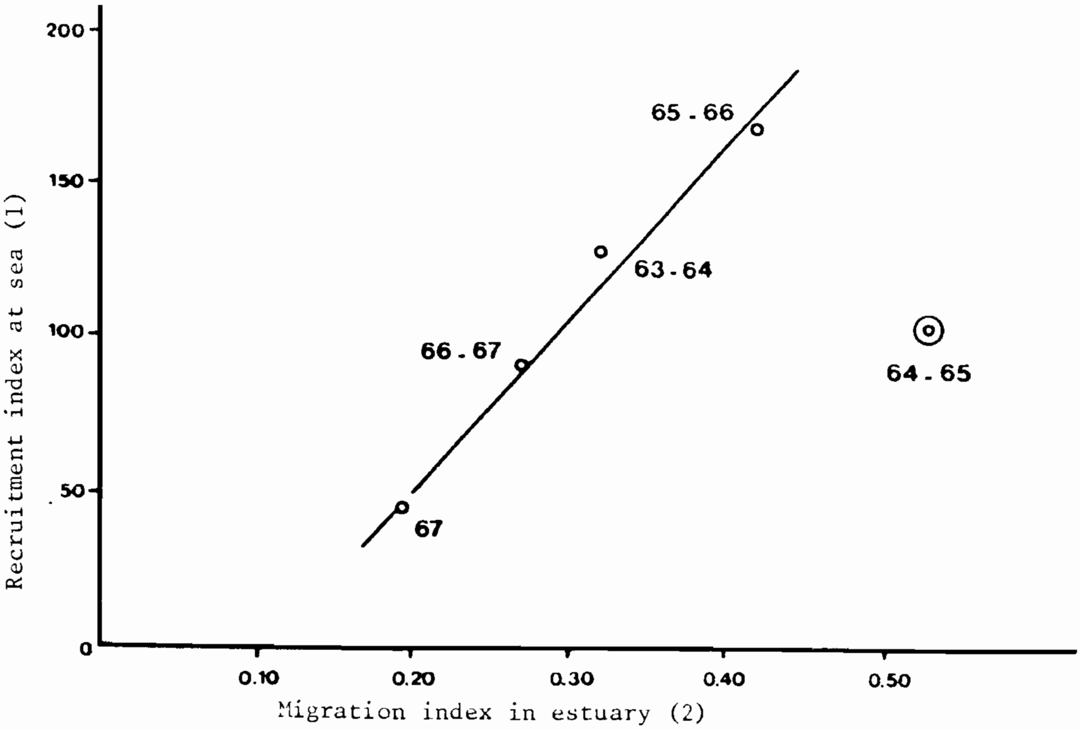


Fig. 70 Relationship between migration and recruitment (modified from Yokel, 1969):

1. Average sub-adult catch per day (68/lb and over)
2. Annual migrating sub-adults abundance index (Nb/revolution)

The results are corroborated by those of St. Amant et al., (1965) who showed that in Louisiana there was no good relation between post-larval and juvenile abundance. This would indicate that the production depended heavily on larval survival in the estuaries and that there was a considerable regulation of the numbers in the population at that stage.

Subrahmanyam (1966) and Subrahmanyam and Rao (1970) showed that, for two successive years, post-larval abundance and catches varied in the same direction. However, these studies were made over periods which were too short to assess the quantitative value of the relation. The same applied to the two-year work of Christmas et al. (1966), which results are however confirmed by Christmas et al. (1976) who obtained over a three-year period a prediction valid at about 10%.

Still more recently, during a two-year study, Roessler and Rehrer (1975) showed good correlation between the seasonal variations in post-larval abundance in the Everglades and the recruitment index of sub-adults at sea. The high correlation observed (r = 0,78) is normal since it is established between two seasonal factors.

In fact, apart from Berry and Baxter's work there are, to our knowledge, no other well-founded examples extending over a sufficiently long period, and the question of the practical usefulness of post-larval abundance indices for predicting juvenile or adult abundance remains without a definite answer. In fact, the answer could well vary with the ecosystem considered.

9.3.4 The relation between juvenile abundance and abundance of the adult stock at sea

Yokel et al. (1969) and Yokel (1969) showed with P. duorarum in Florida that if seasonal variations in size at migration (implying different time lags) were taken into account, there was good correlation between indices of numerical abundance for migrating juveniles and those of young recruits on the fishing grounds (Fig. 70). The fishing yields on juveniles could thus be used as indices of pre-recruitment. Berry and Baxter (1969) on P. aztecus of Texas, have shown that there was a good correlation between the catches of juveniles in the bait shrimp fishery (from 25 April to 31 August and the catch of adults at sea (between July and September). Caillouet and Baxter (1973) gave equations of the relationships obtained for Texas and Lousiana. In Texas there is an excellent correlation (r = 0.85) for P. aztecus if the annual catch at sea is related with the juvenile abundance index in Galveston Bay (from 25 April to 12 June) and a mediocre one (r = 0.28) if this catch is related with the annual estuarine catch. The correlation is fair (r = 0.58) with the same kind of data for P. setiferus. In Louisiana the correlation between the annual estuarine and marine catch is excellent for P. aztecus (r = 0.73) and P. setiferus (r = 0.86), which has been confirmed by Barrett and Gillespie (1975).

9.3.5 Conclusions

When an attempt is made to relate the shrimp catches at sea to the abundance of one of the preceding stages of the life cycle, it seems that only migrating sub-adults can give a useful short-term prediction index (about 3 months in advance). The usefulness of the post-larval indices still needs to be confirmed with a longer series of data.

The optimistic conclusions of Berry and Baxter (1969, p. 797) on the possible use of post-larval abundance for prediction purposes, if the sampling can be improved, have neither really confirmed or contradicted since no other work of similar importance has been undertaken. Because of the relatively high cost of obtaining such data, in comparison with the data obtained from fisheries on juveniles, it is not certain that such a programme of work could be implemented and followed routinely in the future.

10. RECRUITMENT AND SELECTION

The life of an exploited species can be schematically divided into two principal elements, a non-available phase and an exploited phase. In the first we can put the period from spawning to the arrival on the fishing grounds and in the second the period from this to the end of shrimp life. For practical reasons, in constructing a fishery model with the aim of assessing resources or defining optimal conditions of exploitation only the second phase is taken into account since the information coming from the previous phase is reduced to the number of individuals surviving at the end of it; that is the recruitment. When such information is not available, recruitment is assumed to be constant; when it is available, seasonal and year to year variations in this parameter are taken into consideration and make an important contribution to the model.

The process by which an age group integrates itself for the first time into the exploitable stock is also known as "recruitment". This is a more or less progressive event which is a function of age (or size).

The presence of an age group in the fishing zone does not necessarily mean that they are catchable by the means of exploitation employed and the process by which they enter into the exploited phase is known as selection. When the two processes, recruitment and selection, occur in overlapping size intervals, the entry process into the exploited phase would eventually be their resultant.

In this chapter, first the recruitment and then the selection curves will be examined. Thereafter, the relation between stock and recruitment will be discussed.

10.1 RECRUITMENT

10.1.1 Recruitment and the life cycle

The first phase in the life of coastal penaeids takes place at sea during a period of three weeks to one month (at the larval stage), and thereafter in the coastal zones, in bays, estuaries, in mangrove swamps which are rich in food, or in submerged vegetation (during the juvenile and sub-adult stage). As their development progresses the shrimps migrate towards greater and greater depths. When the areas of distribution of juveniles and adults are clearly separated geographically, a true migration seawards occurs after which spawning takes place. Some penaeids spawn nevertheless in the estuaries (cf. chapter 2).

This is the process by which recruitment occurs, that is the mechanism by which the shrimps enter into the operating zones of various fisheries. They will then enter into the exploited phase by a process which is rather similar, in many aspects, to the selection one (cf. section 10.2).

Since the types of exploitation (and the operational zones of the various gears) are extremely diversified, there are in fact several successive recruitment phases:

- when the shrimps leave the nursery edges and become accessible to artisanal fisheries;

- when they reach the large bays where they are accessible to small trawlers;

- during migration, when they are caught by fixed nets;

- when they reach the sea and are caught by industrial trawlers.

The entry processes into the different fisheries is associated with the development stage of the shrimps. If recruitment is defined as the probability of a shrimp of a given size to be found in the fishing area this probability can be expressed for shrimps of each size as the percentage of shrimps at that size in the total population (at sea and in the lagoons) that is present in that area. If the percentages are plotted against size a recruitment curve will be obtained.

(a) Recruitment in artisanal fisheries

Although curves of this type have never been calculated for the estuarine exploitation phases, it can be readily supposed that they are unimodal and similar to those observed for gill nets (see Gulland, for example). In fact, the percentage liable to be caught increases at first as the size increases and the shrimps become available, passes through a maximum and then decreases with the migration of the larger shrimp towards the next type of exploitation. The data existing on this subject are however, to our knowledge, practically nil, in spite of the importance of this phenomenon for building exploitation models for the estuarine phase.

(b) Recruitment in the sea

The recruitment phase from the estuaries seawards is better known and section 2.3.4 can be referred to for a summary of information on seasonal variations of this phenomenon. These are important and provide basic data for simulation models (chapter 11). In most cases shrimps are recruited all year round and more or less important seasonal variations occur. They can be demonstrated through variations in abundance of migrating shrimps (cf. sections 2.3.4.2.3 and 2.3.4.3) or through the abundance of juveniles caught by trawlers at sea (Fig. 6). It is likely that recruitment occurs when a given stage of development is reached or when unfavourable conditions in the estuary compel it. The age at which it occurs is therefore variable, depending on environmental conditions.

For the large penaeids this age is about 2.5-4 months (Kutkhun, 1966, for P. duorarum; Garcia, 1970, 1977 and Galois, 1975, for P. notialis; Baxter, 1967 for P. aztecus; Le Reste, 1971, 1973 for P. indicus, etc.).

10.1.2 The recruitment curve at sea

The information generally sought is the size (and age) at recruitment (l_r, t_r). This is obtained by drawing the recruitment curve, showing for each size the percentage of the total population present on the fishing ground (Fig. 72). Although theoretically the curve can take various forms it is most frequently sigmoid. The average size at recruitment l_r is that for which the total percentage of individuals of a size less than l_r already recruited is equal to the percentage of individuals of a size greater than l_r not yet recruited. When the curve is symmetrical it is generally assumed that $l_r = l_{r50}$, the size at which 50% of the individuals of that size were recruited.

By its nature, the curve is difficult to define since the necessary quantitative information is very difficult to obtain and for this reason, to our knowledge, no such data concerning penaeids can be found in the literature. However, an approximation can be made: if it is known that shrimps of a size less than, say 26 mm (LC) are almost never found at sea and that shrimps of of size greater than 26 mm (LC) are never found in estuaries, the recruitment curve has two firm points for 0 and 100 per cent. Between these two points the recruitment curve can be approximated by a sigmoid curve or a straight line. The latter solution was chosen, for example, by Lhomme (1978) for Penaeus notialis in Senegal. The sigmoid curve can be approximated by a cumulative frequency distribution curve of the sizes of shrimp during migration, when this is known.

It is necessary to remember that size at migration (and hence at recruitment) varies seasonally and from year to year, depending on hydrological conditions (cf. 2.3.4.2.4) and that this phenomenon is responsible of natural changes in size at first capture in some artisanal fisheries. The case of P. notialis in Casamance (Senegal) is especially clear. The mean recruitment size varies from 24.3 mm (LC) in periods of normal rainfall (Lhomme, 1978) to 30 mm (LC) in dry years. This variation is equivalent to a modification in the vector of the fishing mortality as a function of age which consequences for the annual catch are not negligible (cf. 9.2.1.1).

10.1.3 The stock-recruitment relationship

This relation, which is usually understood to be the relation between the number of spawners in a population and the number of their genitors, is of extreme importance for constructing models of exploited stocks. It can, according to the species, be an asymptotic curve (as described by Beverton and Holt for North Sea flatfish), dome-shaped (the classical Ricker curve that is found for salmon) or practically linear (as demonstrated by Cushing, 1971, 1973, for Clupeids). The form of the curve determines the resistance of a stock to exploitation since it describes to what extent the stock's reproductive potential 1/ will be influenced, or even improved (in the case of a dome-shaped curve) by exploitation.

There are no shrimp stocks, even those which have been heavily exploited, for which it can be shown with certainty that the recruitment has been affected by the exploitation of adults, except perhaps recently in the gulf between Iran and the Arabian peninsula (Van Zalinge, pers. comm.). This leads one to suppose that the curve is of the Beverton and Holt type for which the reproductive potential remains constant even for large decreases in the parent population. This is anyway what was suggested by Neal (1975) and Le Reste and Marcille (1973) in the U.S.A. and Madagascar respectively.

There is more generally a tendency to assume that the recruitment is not linked to the abundance of the spawners within the normal range of exploitation levels and that it seems to be more influenced by environmental conditions (cf. chapter 9) or by the deterioration of the estuarine conditions (cf. section 12.4.1.3).

It has been mentioned in the previous chapter that the magnitude of the shrimp recruitment probably depends to a large extent on the hydrological conditions and their repercussions on the reproduction, the survival of the larvae during their migration towards the estuaries, as well as on their growth, on competition, and on the duration of the stay in the coastal area (lagoons, etc.). It will be shown later on (cf. section 12.4.1.3.3) that the annual production of certain stocks also appears to have been clearly affected by the destruction of the coastal biotopes by human activities (Doi et al., 1973). All these elements show that there is a strong effect on recruitment in the estuarine phase, which may be the cause that no relation between the stock and its recruitment has been observed. Gunter (1966) already made the suggestion that the exploitation could not affect the renewal of the stock, and drew attention to the fact that after the nearly total destruction of the shrimp resources of the Atlantic coast of the United States by the cold winter of 1940, the catches in autumn 1941 were normal. This indicated that there the few survivors were sufficient to repopulate the stock 2/.

Bakun and Parrish (1981) indicated that if the nurseries have a limited and relatively constant biological capacity, the Beverton and Holt type relationship is the most likely one. It would seem that this observation would well apply to the coastal penaeid shrimps, albeit understood that the biological capacity of the estuaries is only "relatively" constant and varies with the climatological conditions. Because these variations are important it would be necessary, e.g. in the case where floods are the decisive factor, to adopt not one stock-recruitment relationship but a family of curves corresponding to the various possible values of the floods.

For practical purposes, however, if there is no clear relationship between the stock and the recruitment within a range of reasonable levels of exploitation, such relationship can be wholly neglected and recruitment can be considered to depend on the environment only. This conclusion, even if not clearly expressed, underlies all the applications of predictive models based on the relation between the production and the climatological conditions (cf. chapter 9).

It may be noted that Abramson and Tomlinson (1972) and Geibel and Heiman (1976) also concluded that there was no useful stock-recruitment relationship in the pandalid shrimp of California, even though the biology of these species and in particular the constraints of their recruitment are completely different.

1/ Taken here to mean the potential of a stock to reconstitute or reproduce its biomass from one year to the next

2/ It is however probable that the harmful effects of a cold wave on an ecosystem are not of the same nature as the selective over-exploitation of one species in this ecosystem, especially if one considers the predator-prey relationships

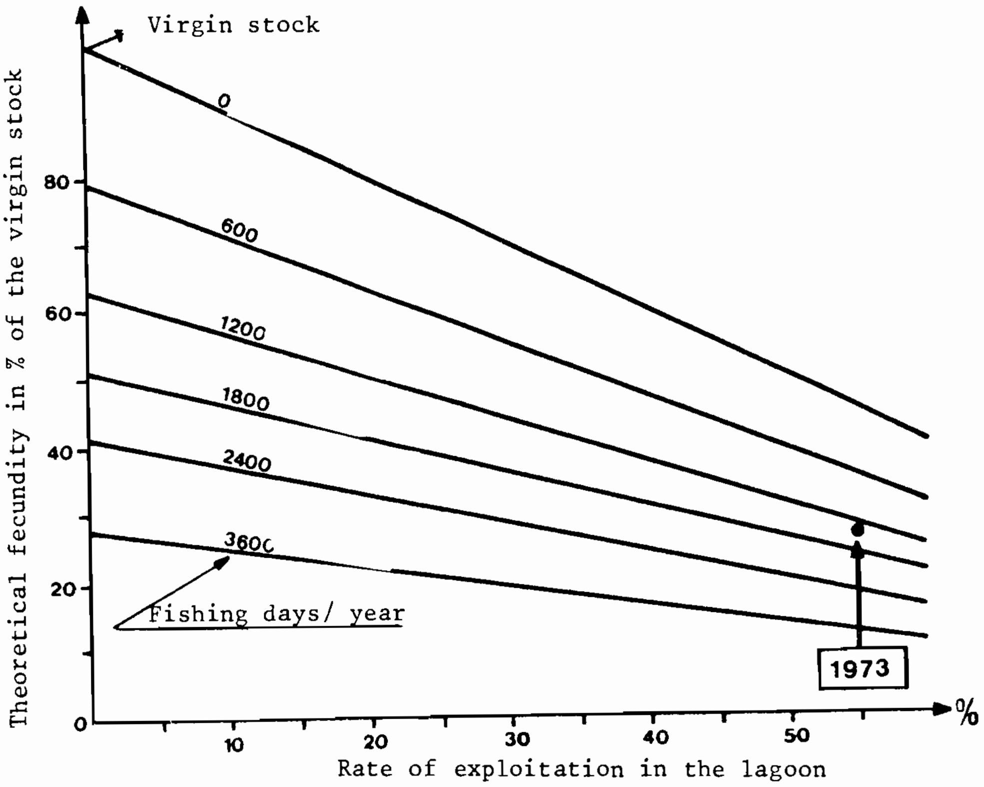


Fig. 71 Variation of the theoretical fecundity with the exploitation rate in the lagoon rate in the lagoons (in %) and the effort at sea (from 0 to 3600 fishing days 3600 fishing days per year) for *Peneaus notialis* in Ivory-coast. (from Garcia 1978). The situation in 1973 is indicated.

The hypothesis of a recruitment relatively independant of the stock would be contradicted by Cushing's observations (1973) who relates the shape of the stock-recruitment relationship to the average individual fecundity of a stock. The partial individual fecundity of the big peneaids varies with age between about 100 000 and 500 000 eggs. The average partial fecundity would be about 200 000. The exact number of eggs layed is however not known (despite the fact that according to Penn, 1980, there are few degenerate eggs in natural conditions) because a shrimp spawns many times a year and its total individual fecundity is unknown. This fecundity is however certainly more than 200 000. It should be therefore guessed on this basis that the stock-recruitment relationship of penaeids is of the Ricker's dome-shaped type typical of high fecundity animals. Beverton and Holt (1957) have moreover related the shape of this curve to cannibalism, which is a very characteristic behaviour of reared shrimps during moulting periods.

The above speculations do not hide the fact that the form of the stock-recruitment relationship is completely unknown.

However, penaeid shrimps are nearly always heavily exploited, and the size at first capture is below, and often much below, the size at first sexual maturity. This is particularly the case if there is an artisanal or semi-industrial fishery for juveniles. In such cases, the reproduction potential of the stock is greatly reduced and even if the stock-recruitment relationship is unknown, it is possible that the stock declines to a level where great prudence is required.

The concept of theoretical fecundity per recruit (Le Guen, 1971) is here of interest because, expressed in a value relative to that of the virgin stock, it allows one to study the reduction of the reproduction potential as the result of exploitation for different levels of fishing mortality.

Fig. 71 gives an example for the stock of _P. notialis_ in Ivory Coast.

10.2 SELECTIVITY

Selection is the process through which recruited shrimps enter progressively into the exploited phase. To differentiate this process from the selection of a target species or a target age group by preferential application of fishing effort the term "retention" might be preferable. The rate of retention of a fish of a given size is the probability that it is retained by the trawl, when it has met and entered it.

It is expressed by the percentage of fish of each size group retained in the trawl cod-end. The phenomenon is in fact of the same type as recruitment and is shown by a more or less symmetrical sigmoid curve. This curve is generally obtained by determining the size-frequency distribution of shrimp held in the trawl and comparing this with the distribution of the total population entering the trawl. The data are usually obtained from fishing experiments with the double cod-end method, or from fishing with two different trawls, either simultaneously or alternatively; one is selective and the other is assumed to retain all shrimp encountered. The information looked for is the average age of selection (t_s) which is often also the average age of entry into the catch (or age at first capture t_c) when there is no interference with the recruitment process (cf. section 10.3). In practice, a retention curve as a function of size is used and the size l_s is defined as the point at which the number of fish retained by the trawl of size less than l_s, is equal to the number of fish released with a size greater than l_s. If the percentages retained at each length are defined as Y_i, and the upper limit of the first size interval where a value of 100% is obtained as l_{n+1}, and if the class interval is equal to unity, one has

$$l_s = l_{n+1} - \Sigma Y_i$$

when the curve is symmetrical, l_s is equal to l_{s50}, the size at which 50% of the individuals are retained.

It is generally assumed that the relation between l_s, the average selection or retention length, and the mesh size (m) is linear and has the form $l_s = b.m$, where b is the selection coefficient.

Some information available on this subject is given on figure 74 where the sizes of the shrimps are expressed either in carapace length or total length depending on the reference considered. Some variability is shown in the relationship probably due to some differences in the morphology of the species concerned, to the conditions of the different experiments (type of trawl and twine) and to the use of either l_s or l_{s50} to define the average selection size. It should be noted that the catch probability for a given mesh and particularly the value of l_s depends on the trawling time (Berry and Hervey, 1965) because of progressive clogging. This implies that the curves should be determined for a trawling time equal to the average in professional fishing.

Additional information on selectivity studies and in particular on their practical aspects can be found in the manuals of Beverton and Holt, Ricker, Gulland and in ICNAF (1963) and Pope (1975).

According to Gulland (1972) the selectivity curves for shrimp are not sufficiently defined to justify regulations for mesh size. Mistakidis (1958) also points out that selectivity is not "perfect" for prawns and that the trawls always retain, independent of mesh size, a proportion of the juveniles. The percentage however decreases as the mesh size used increased; Kurk et al. (1965) confirmed that well defined selectivity curves exist for the prawns In penaeids mesh regulation seems to be a usable method for management purposes according to the work of Roelofs (1950) and of Berry and Hervey (1965) on Penaeus aztecus, Regan et al. (1957) on P. duorarum, Simpson and Perez (1975) and Lhomme (1978) on P. notialis; Gorman (in Hynd, 1973, species not given); Aoyama (1973) on P. orientalis and Lluch (1975) on P. vannamei and P. californiensis. All these studies were made on large-sized species but George et al. (1974) and Garcia and Lhomme (1977) studied the selectivity of nets fixed to posts in estuaries (Fig. 75) for juveniles fishing. The results show that even for juveniles the mesh size is liable to exert selection on the sizes caught. It should be noted that the fixed nets are used off the bottom and that there is little clogging (except in rainy seasons when the vegetal detritus are abundant). It is probable on the other hand, that the large amount of these detritus, empty shells, etc. on the bottom, must interfere with the selectivity of the trawls used in small bays and close to nurseries. However, Simpson and Perez (1975) showed that escape through the body of the trawl net could be considerable.

It is interesting to compare the selection coefficients of different species obtained by different authors.

Author	Species	Selection factor	
		Carapace length	Total length
Aoyama (1973)	P. orientalis	0,40	
Lhomme (1979)	P. notialis	0,37 - 0,52	2,0 à 2,6 1/
Regan et al. (1957)	P. duorarum	0,35 - 0,37	
Lluch (1975)	Penaeus spp.		2 à 2,4 2/
Kurk et al. (1965)	Crangon crangon		2,15

1/ Conversion made by the authors using the Garcia (1970) ratio LC/LT

2/ Calculations made by the authors from published figures

Nearly all these values refer to the large penaeids of the genus Penaeus and it is not certain that they would apply to other species.

It should be noted however that the value obtained for the small prawn C. crangon is in the range observed for the penaeids. This leads one to hope that the above values could be generally applied to all shrimps which have the usual shape but supplementary experiments would be necessary for confirmation.

If one considers the straight lines which limit the scatter of points on figure 74 and an average line (all drawn by eye) the following approximate values would be obtained for the selection factor

$b \simeq 1{,}90 \pm 0{,}40$ if the sizes are in total length

$b \simeq 0{,}40 \pm 0{,}10$ if they are in carapace length

Such a generalization would be of interest because it would allow one to obtain approximate values of selection length for a lot of species which have not yet been investigated.

10.3 THE RECRUITMENT CURVE

The traditionally important information for evaluation models is t_c, the age at first capture (corresponding to a size l_c). When recruitment and selection are sufficiently distinct and recruitment is completed when selection begins, the former can be ignored in marine stock management. If otherwise, the resultant curve obtained by multiplying the percentage of recruitment by the percentage of retention for each individual size must be calculated (Fig. 72). The same procedure used for the calculation of l_s also can be used for the calculation of l_c (and thus t_c). If the resultant curve can be considered as symmetrical, l_{c50} would also be a good approximation of l_c.

The use of the concept of size (or age) at first capture implies that the recruitment (selection) situation is similar to that of a "knife-edge", that is that the percentage recruited is nil at lengths below this size and equal to 100 beyond it. With this approximation the calculations can be simplified and the yield per recruit tables of Beverton and Holt (1964) used.

For penaeids, however, this approach cannot be entirely satisfactory if the size (and age) range in which selection occurs covers too great a part of the exploited phase.

In the example in Fig. 72, it can be seen that the interval goes from 15 mm (LC) to about 45 mm (LC). Inasmuch as few females and practically no males reach this size this means that the selection interval covers practically the whole exploitable life of the shrimp.

In these conditions simplification of the recruitment curve into a "knife-edge" curve and the hypothesis that 100% of the shrimps are recruited at size l_c is liable to give an appreciable source of bias.

The biologist must judge to what degree the recruitment curve can be taken as a "knife-edge". When this approximation does not appear acceptable a linear approximation might be preferable (Beverton and Holt, 1957, page 77) by taking the ascending part of the selection curve to be a straight line. A step-wise approximation could also be used in which the catch probability (expressed as a percentage) is taken to be constant for each age (Fig. 76). This approach gives a better picture of the situation under examination but practically excludes the use of yield tables, making it necessary to use more complicated computation procedures (Ricker's model for instance).

10.4 CALCULATION OF THE CONSEQUENCES OF CHANGING THE MESH SIZE

There are numerous methods for making this calculation and the choice depends on the available data. The results of most direct interest to fishermen are on the one hand the immediate effects of the regulations and on the other hand the expected long-term effects under the new exploitation system. Beverton and Holt (1957) showed, using an elegant method, how the population develops with time after the introduction of a change in mesh size. Allen (1953), Holt (1961, 1969), Jones (1974) and Cadima (1977) proposed simple methods of calculation which require a minimum of data.

10.4.1 Calculation of the immediate effects

The general principle is the following. Knowing the annual distribution of the size frequencies in the catch obtained with the current mesh size, the selection curve of this mesh, as well as that of the new one that is proposed to be applied, the immediate effects of the mesh change can be calculated. In particular, if for a given size, the percentages retained by the old and the new mesh are respectively r_1 and r_k and if C_1 is the catch in number using the old mesh, the catch in number with the new mesh size C_k can be calculated using the equation

$$C_k = C_1 r_1 / r_k$$

This will be the catch immediately after the changeover when the population structure is still the one which prevailed under the old system of exploitation.

If the average individual weight is known for each size the numerical catch can be converted to catch by weight and the total caught under the old exploitation system and just after the change in mesh size will be

$$Y_1 = \Sigma\ C_1 \bar{\omega} \quad \text{and} \quad Y_k = \Sigma\ C_k \bar{\omega}$$

The immediate result in weight of the new regulation will relatively to the catch in the former situation then be expressed by

$$L = (Y_1 - Y_k)/Y_1$$

In the case of penaeids, it is obvious that the use of an annual size distribution to calculate an "immediate" effect has no sense. For animals with a short life-span and rapid growth, the population consists practically of a single age class, is never in equilibrium and has seasonal variations in the age and size structure. Fig. 77 gives, as an example, variations in average size on the Arabian shelf.

The size distribution of the total annual catches is thus quite theoretical and gives a virtual image of an "annual" population which never exists in fact. In addition the "long-term" effects of the regulation will be obtained in the same year that the new mesh size came into force and the principle that the population "immediately" after the mesh changeover stays identical cannot be adopted except for a period of one or two months at the most. This would imply that the calculations of immediate effects of a change in mesh size should be done, at best, not with the annual size frequency distribution but with the distribution corresponding to the month or the two months following the date proposed for the change. However, the practical value of the results is probably less than limited.

The computation of the exact transitory effects of the change in mesh size, from the date of its implementation to the new equilibrium situation can be done more rigorously by the simulation techniques, using for instance Ricker's model (cf. chapter 11) provided that data are available on growth, natural and fishing mortality, and on the annual recruitment cycle with their seasonal variations. One wonders however if the calculated results on immediate and transitory effects of the mesh change has any predictive practical value since penaeid stocks are highly dynamic and sometimes display great interannual variability in recruitment (see section 9.1.2).

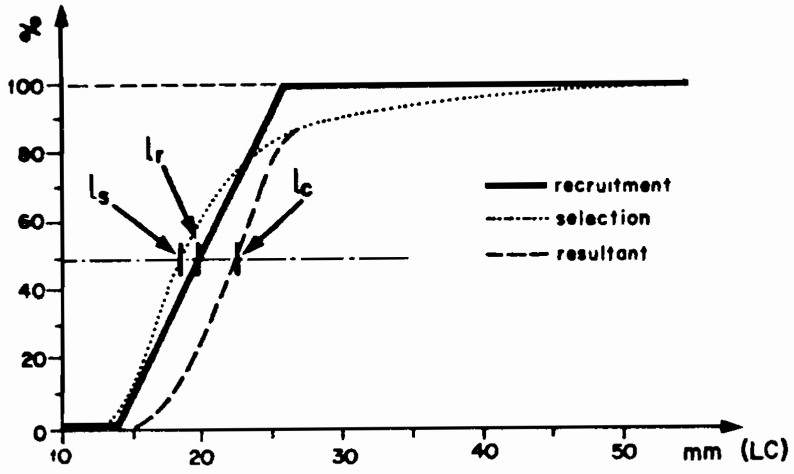


Fig. 72 Recruitment curve (linear approximation), selection ogives for the 25 mm (bar) mesh size, and resultant curve for *Penaeus notialis* in Senegal (from Lhomme, 1978)

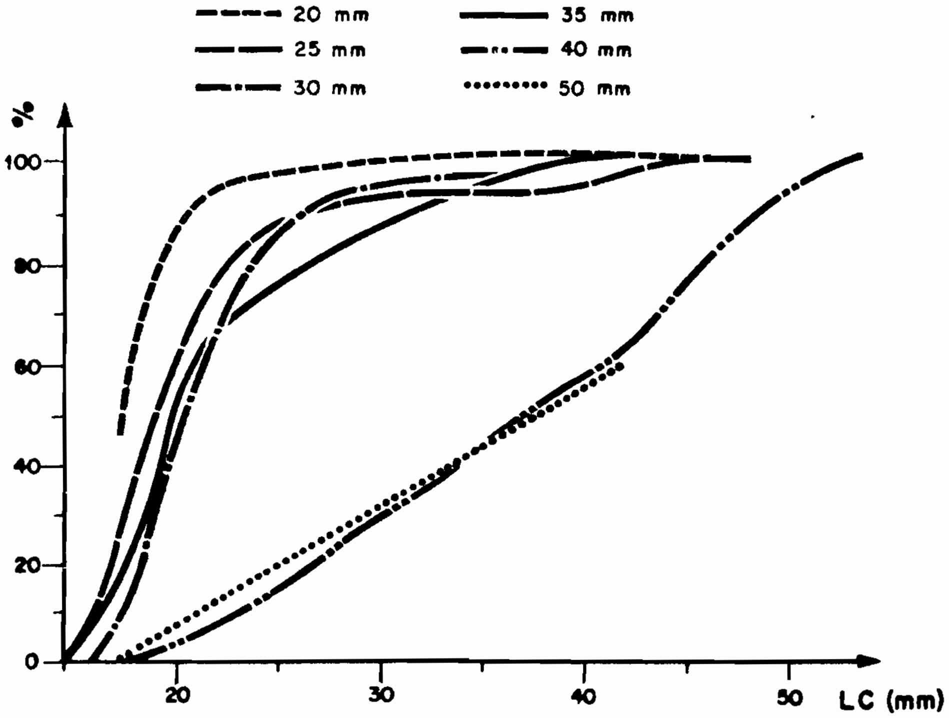


Fig. 73 Selectivity ogives for the 25 to 50 mm (bar) meshes for *Penaeus notialis* (from Lhomme, 1978)

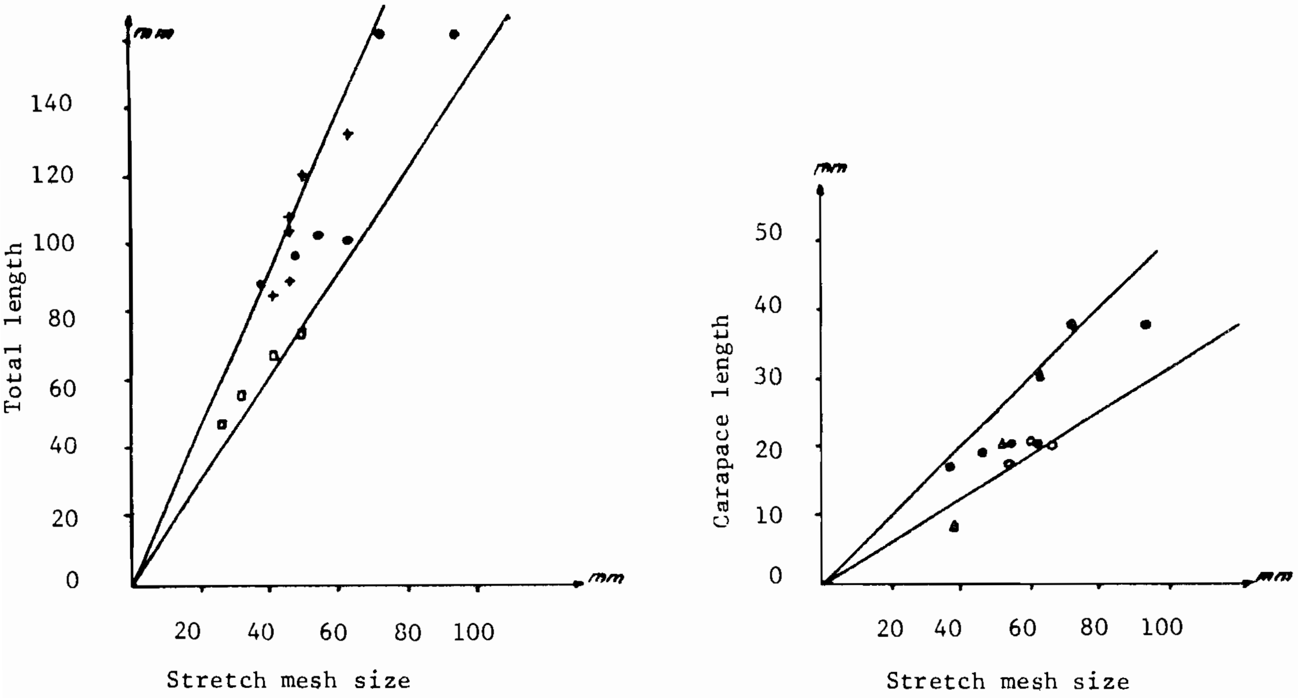


Fig. 74 Relation between mesh size and mean selection length for different species of shrimps:
● *P. notialis* (Lhomme, 1977)
□ *P. indicus* (George et al., 1974)
+ *P. vannamei/P. californiensis* (Lluch, 1975)
△ *P. orientalis* (Aoyama, 1973)
○ *P. duorarum* (Regan et al., 1957)

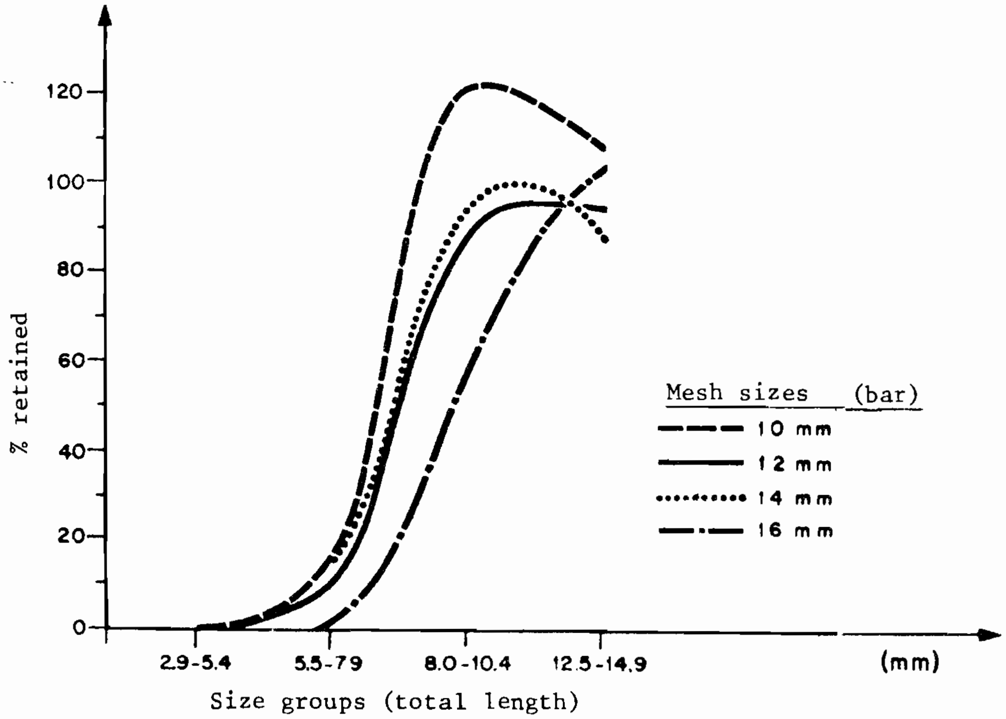


Fig. 75 Selectivity curves for the stake-nets used in Ebriē lagoon (from Garcia and Lhomme, 1977)

It is important on the other hand to know the long-term result of the new exploitation regime, a result that would in any case be quickly obtained (about six months after the mesh changeover if this occurred just before the main reecruitment.

10.4.2 Calculation of long-term effects

The long-term benefits of the mesh change depend on the number of individuals released by the new mesh C_k (and which were formerly caught by the old mesh), on their growth, natural mortality and exploitation rate. The catch by weight under the new exploitation system (Y_2) relative to the theoretical catch just after the mesh change (Y_k) can be calculated (Cadima, 1977) by: 1/

$$Y_r/Y_k = e^{FT} \quad \text{from Holt (1958)}$$

with $T = (t_{c2} - t_{c1})$ where t_{c1} and t_{c2} are the ages at first capture with the old and new mesh size respectively or again

$$Y_r/Y_k = 1 + E\ (C_1 - C_k)\, e^{-MT*})/C_k \quad \text{from Gulland (1961)}$$

where $T*$ is equal to $(t_{c2} - \bar{t}_r)$, $\bar{t}_r$ being the average age of fish released by the new mesh;

or again

$$Y_r/Y_k = (C_1/C_k)^E = e^{E.\log_e(C_1/C_k)} \quad \text{Cadima (1977)}$$

Because $(Y_2/Y_1) = (Y_2/Y_k)(Y_k/Y_1)$ and Y_1 and Y_k are obtained as in section 10.4.1, the ratio (Y_2/Y_1) can be calculated and is the estimation of the long-term effect of the change in mesh size.

The application of these methods implies that recruitment is knife-edge, and that the size composition of the catch before the mesh change is known, as well as M, E and T^* (Gulland's method), F and T (Holt's method) and E (Cadima's method). The latter thus requires the least amount of basic data.

If the hypothesis of constant mortality with age beyond t_c does not seem too realistic, especially if the selection curve covers too great a part of the animal's life-span to assume "knife-edge" recruitment (or, in other words, if a large part of the catches are made within the selection range), Holt's formula will overestimate the true change while the other two will underestimate the results by weight, but not in numbers (Gulland, 1961).

When the necessary data are available (L_∞, L_{c1}, L_{c2}, K, M, F), Beverton and Holt's (1964) tables can of course also be used to calculate the indices of yields per recruit corresponding to the two exploitation regimes examined and a comparison can be made. If the selection curve is taken as a stepwise function, the life-span of the shrimp can then be divided into a few periods inside which Z is considered as a constant. The calculations can then be made with the help of yield tables, the total yield per recruit being equal to the sum of the partial yields. The calculation process is shown in the tables (Beverton and Holt, 1964, page 7). The calculations can also be made simply with the same data by using Ricker's formulations (1958, 1975) for calculating the yield per recruit, or even simpler, by adopting the approximative method of Thompson and Bell (in Ricker, 1975). These last two methods have the advantage of not requiring representation of growth by von Bertalanffy's model, and, above all, allow the expression of the results of mesh change in monetary terms by simply replacing the age-weight key by the age-value key in the calculation.

In the same way, variations in theoretical fecundity per recruit caused by the change in mesh size can be estimated.

1/ Using Cadima's notation. This concept of a transitory period is completely theoretical here as was emphasized in the preceding section but it is used to calculate Y_2

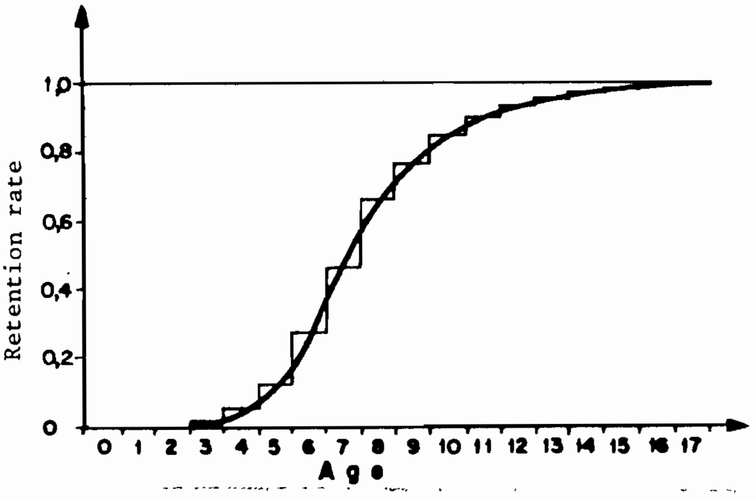


Fig. 76 Approximation of the selection agive by a step-wise function

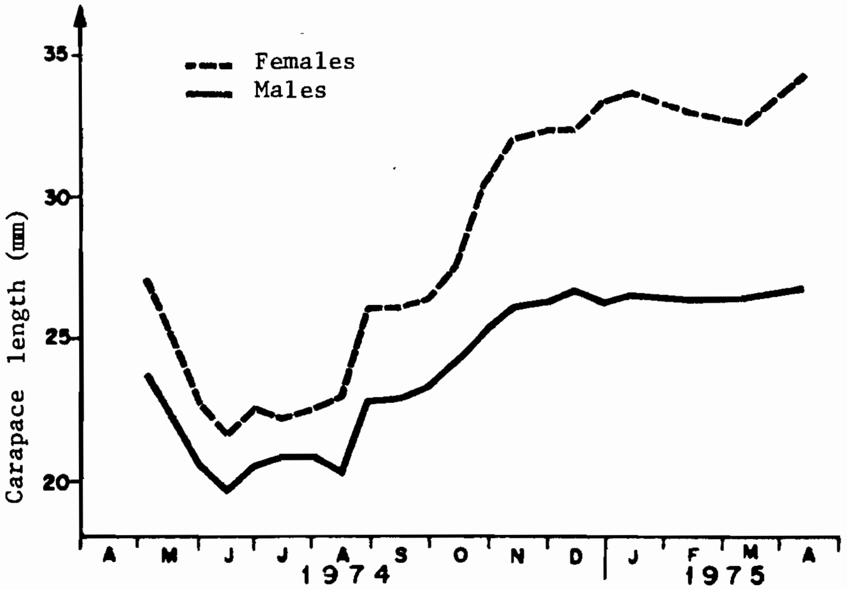


Fig. 77 Seasonal variations of the average size of *Penaeus semisulcatus* (males and females) in Saudi Arabia (from Price and Jones, 1975)

An example of the calculation by Ricker's method will be found in Ricker (1975, page 245). An example of the use of Thompson and Bell's method is given in Appendix I at the end of this chapter with a review of the main equations used. In fact, data on variations in fishing mortality with age are very rare for the penaeids: as we saw in chapter 7 they are difficult to separate from seasonal variations.

A cohort analysis made on catch vectors by size classes (Jones' 1976 method), which is reviewed in section 7.6.2, enables one to obtain a fishing mortality vector as a function of size. In this work the author shows that thereafter the effects of a modification of effort and/or mesh size can be calculated. Jones (1979) applied the method to the Norway lobster (Nephrops sp.) and his method as well as the main equations used, are reproduced as an example in Appendix II at the end of this chapter.

It should finally be noted that the calculations can be made more accurately with the help of simulation techniques. They are based on the same principles but they can only be easily carried out by computer. They allow in addition the use of growth and mortality data, information on recruitment levels and a seasonal variation in the basic parameters (catchability, effort, recruitment).

10.5 CONCLUSIONS

The study of selectivity of fishing gear and the determination of specific selection curves gives results which can be used directly in fishery management. These results are relatively easy to obtain from techniques which are simple to use. Data are nevertheless very scarce for penaeids and intensified studies on selectivity will be required, particularly for multi-specific shrimps stocks which consist of species with very different average sizes.

Although the long-term effect of a mesh change can be easily calculated approximately, a detailed analysis of events during the transition period requires the use of more elaborate methods, the principles of which are simple but which need much more data.

The usefulness of mesh size regulations as a management tool will be treated in chapter 12.

APPENDIX I

Calculation of the effect of a change of mesh size using Thompson and Bell's (1934) calculation method

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Age	S_1	F_{t_1}	Z_{t_1}	Popul. in nb N_{t_1}	Nb deaths D_{t_1}	Catch (Nb) C_{t_1}	Individual weight W_{t_1}	Catch in weight Y_{t_2}	S_2	F_{t_2}	Z_{t_2}	N_{t_2}	D_{t_2}	C_{t_2}	Y_{t_2}
2,5	0	0	0,3	1000	259	0	5	0	0	0	0,3	1000	259	0	0
3,5	0,5	0,15	0,45	741	269	90	10	900	0	0	0,3	741	192	0	0
4,5	1,0	0,3	0,60	472	213	106	20	2120	0	0	0,3	549	142	0	0
5,5	1,0	0,3	0,60	259	117	58	28	1624	0,5	0,15	0,45	407	148	49	1372
6,5	1,0	0,3	0,60	142	64	32	35	1120	1,0	0,3	0,60	259	117	58	2030
7,5	1,0	0,3	0,60	78	35	17	40	680	1,0	0,3	0,60	142	64	32	1280
8,5	1,0	0,3	0,60	43	20	10	45	450	1,0	0,3	0,60	78	35	17	765
9,5	1,0	0,3	0,60	23	10	5	48	240	1,0	0,3	0,60	43	20	10	480
10,5	1,0	0,3	0,60	13	6	3	50	150	1,0	0,3	0,60	23	10	5	250
11,5	1,0	0,3	0,60	7	3	1,5	52	78	1,0	0,3	0,60	13	6	3	156
12,5	1,0	0,3	0,60	4	2	1	53	53	1,0	0,3	0,60	7	3	2	106
Total							7415								6439

Columns 2 and 10 = Selectivity curves for the old mesh size (S_1) and the new (S_2)

3 and 11: F_t = F base x S_1 or F base x S_2, F base = 0.30/month

4 and 12: $Z_t = F_t + M_t$, M_t = Cte = 0.3/month

5 and 13: $N_t = N_{t-1} e^{-Zt}$, 1 000 recruits at 2 years

6 and 14: $D_t = N_{t+1} - N_t$

7 and 15: $C_t = D_t \cdot F_t/Z_t$ 9 and 16 $Y_t = C_t \cdot W_t$

Result of mesh change = (6 349 - 7 415)/7 415 = 13.9%

APPENDIX II

Calculation of the effect of an increase in effort (of 40%) and in mesh size (of 20 mm) on the yield per recruit on the Norway lobster (from Jones, 1979)

1 Length (mm)	2 N x W (kg)	3 F_1DT	4 S_1	5 S_2	6 F_2DT	7 F_1DT-F_2DT	8 $\Sigma(7)$	9 exp. (8)	10 $\frac{S_2}{S_1}$ (9)	11 (2)x(10)
10-15	1	0	0.0019	0	0	0	0	1.0000	0	0
15-20	480	0.0085	0.1170	0.0039	0	0.0085	0.0041	1.0041	0.0035	16
20-25	8 714	0.0792	0.6950	0.1038	0.0166	0.0626	0.0395	1.0403	0.1554	1 354
25-30	47 126	0.2943	0.9864	0.0557	0.2321	0.0622	0.1019	1.1073	0.6238	29 400
30-35	89 290	0.5323	1.0	0.9382	0.6992	- 0.1669	0.0495	1.0508	0.9858	88 022
35-40	88 170	0.6520	1.0	0.9984	0.9113	- 0.2593	- 0.1636	0.8491	0.8477	74 745
40-45	69 660	0.7647	1.0	1.0	1.0706	- 0.3059	- 0.4462	0.6401	0.6401	44 589
45-50	48 750	0.9828	1.0	1.0	1.3759	- 0.3931	- 0.7957	0.4513	0.4513	22 011
50-55	24 830	1.2130	1.0	1.0	1.6982	- 0.4852	- 1.235	0.2908	0.2908	7 221
55-60	9 829	1.7580	1.0	1.0	2.4612	- 0.7032	- 1.829	0.1606	0.1606	1 579
60-65	1 343	1.0780	1.0	1.0	1.5092	- 0.4312	- 2.396	0.0911	0.0911	122
65-70	508	1.0780	1.0	1.0	1.5092	- 0.4312	- 2.828	0.0591	0.0591	30
Total	388 701									269 109

APPENDIX II (Cont'd)

1. Basic data

Column 2: N = numbers caught by size class

W = individual average weight

Catch by weight with exploitation system 1 = 388 701

Column 3: The F vector by size interval DT in exploitation system 1 (mesh size 70 mm) obtained by cohort analysis according to Jones's method (1974)

Columns 4 and 5: Proportions retained for each size by mesh sizes of 70 mm (S_1) and 90 mm (S_2).

2. Calculations

Column 6: F vector in exploitation system 2 (mesh size 90 mm and effort x 1.4)

$F_2DT = (1 + x/100)S_2\ (F_1DT)/S_1)$ where x is the expected increase of effort in %. For example for the size class 25-30 mm:

$$F_2DT = 1.4\ .\ 0.5557\ .\ 0.2943/0.9854 = 0.2321$$

Column 7: Differences between F_1DT and F_2DT

Column 8: Sum of differences $\Sigma\ (F_1DT - F_2DT)$ up to the median point of the interval considered, that is 0.1019 = 0.85 + 0.0626 + (0.0622/2)

Column 9: $e^{\Sigma(F_1DT - F_2DT)}$

Column 10: $\frac{S_2}{S_1}\ .\ e^{\Sigma(F_1DT + F_2DT)}$

Column 11: $\frac{S_2NW}{S_1}\ .\ e^{\Sigma(F_1DT - F_2DT)} = 269{,}109$

3. Final result

The new catch is: $(1 + x/100) \left\{ \Sigma\frac{S_2NW}{S_1}\ .\ e^{\Sigma(F_1DT - F_2DT)} \right\} = 376{,}33$

and the final result is equal to: $\frac{(376{,}33 - 388{,}70)}{388{,}70} = 3{,}1\ \%$

11. RESOURCE ASSESSMENT AND DEFINITION OF OPTIMAL EXPLOITATION CONDITIONS

The preceding chapters aimed at reviewing the information required for resource assessment and the definition of optimal exploitation conditions (biological data, fishing statistics, population parameters, etc.). These data, on which the final quality of the assessments and the diagnosis largely depend are used in models which have not been specially designed for penaeids but on the contrary are generally used for tropical and nontropical fish.

Global models (or production models), analytical models (yield per recruit, simulation techniques) and approximative methods (from biomass estimates by comparison, etc.) can be distinguished. Rather than dwell on the mathematical formulation and the biological justification of the models, which are well covered in basic texts, we will examine the hypotheses implicit in these models and the justification for their use in the particular case of the penaeids. An interesting discussion for the more general case of the invertebrates will be found in Hancock (1979).

11.1 PRODUCTION MODELS

Schaefer's (1954) model and its derivatives (Fox, 1970; Pela and Tomlinson, 1969) are comparable to those used for the study of the predator-prey relations. They consider the stock as an entity for which the abundance depends on the predation action exerted by man. If the biomass is expressed as the catch per unit effort and predation by man by the fishing effort, a linear or non-linear negative relationship is generally observed between these two quantities. The relation between the total catch (equal to the surplus production) and the effort is a curve, which may be parabolic, and passes through a maximum at an intermediate abundance level.

The analysis of these relations allows the maximum sustainable yield (MSY) and the corresponding effort level (F_{MSY}) to be calculated. These models also form the basis for fishery management by catch quotas or effort limitation. Their general use implies certain hypotheses, which are commonly accepted, although it is sometimes known that they are not realistic. It is interesting to review them here to see how far they are applicable to penaeids.

11.1.1 Hypotheses proper to the models

Here the work of Pella and Tomlinson (1969) and Fox (1974) will be referred to.

(a) Determinism of the models. The production mechanisms are generally considered as deterministic processes. All variations in annual production other than those due to variations in fishing effort are ignored. For penaeids, production variations have been noted, which are probably of a climatological nature. However, the annual variations seem to have an amplitude which varies considerably according to the stocks examined. For those stocks where variation is such that the relation between c.p.u.e. and effort is completely masked, the model is evidently not applicable since it is too inaccurate (Geibel and Heimann, 1976). For others, the annual variations seem to be small but there may be long term periodic trends linked to fluctuations in climate. Here the danger lies mostly in the use of too short a series of data which may lead to false conclusions in the assessment. In either of the two cases, the model cannot be used for a management policy based on catch quotas, since the stock performance in one year does not enable one to predict those performances of the following years when supplementary data are lacking.

(b) Equilibrium conditions. It is assumed that to each effort level corresponds a stable state of the demographic population composition. This supposes that at each instant, the principal factor controlling stock size is fishing effort. It should be noted that when numerous neighbouring small stocks exist and the fleets can move from one stock to another it sometimes happens that it is stock abundance which controls the effort level and not the opposite. The c.p.u.e./effort relation does not in this case give the required picture of the stock development as an effect of fishing mortality. An example of this type of phenomenon can be found in the Gulf of Exmouth in Australia (FAO/CPOI, 1973).

(c) Single populations. It is often assumed that only one stock exists or else that the total of the stocks examined act as a single entity; the interaction between stocks is then deliberately disregarded. Fox (1974) showed the importance of the rate of mixing between stocks for the validity of overall assessments made on a group of stocks together. The problem is particularly acute when the resource is made up of a large number of small stocks with little known or unknown interrelationships as in Madagascar (see Marcille, 1978), and for stocks where the data do not permit a distinction to be made between neighbouring stocks (Fig. 78).

(d) Stable stock characteristics. It is assumed that the production depends on the biomass of the stock considered as a whole, or in other words that production and catch are independent of the demographic stock composition. It is obvious that in reality exploitation of a stock induces a rejuvenation and modifies its production characteristics. This aspect may lead to the inclusion in only one model of data which, in fact, follow different ones (Daget and Le Guen, 1974; Fox, 1974). In addition it should be noted that, in penaeids, the exploited "stock", its theoretical "biomass" and its age composition as reflected, for example, in annual catches never exist as such. At the annual level, only a virtual image of the population is obtained at best since a penaeid stock consisting of a single age class and has an extremely dynamic nature as the biomass, average age, fertility, etc. vary considerably throughout the year. This fact takes us far from the basic conditions of Schaefer's model. In penaeids, an additional difficulty is that the fishery at sea takes place on a stock with an annual production which depends a good deal on the catches of the juveniles in the estuaries by the more or less artisanal fisheries. A change in the rate of this exploitation will falsify the c.p.u.e./effort relationship at sea by modifying recruitment independently of the parent stock and the level of effort at sea.

11.1.2 Hypotheses concerning the data

(a) Constant catchability. This is one of the most sensitive points of this type of model. The catch is always rather well defined (although progressive changes in the discard practices could be a source of bias) and the effort is taken to obey the equation F = qf over the whole period studied. Reference to section 4.1.1.2 shows that there are many identified sources of bias for shrimps (changes in the duration of effective daily fishing time, changes in daily or seasonal distribution of fishing effort, improvements in the gear efficiency, etc.).

The definition of the effort applied to each species in a multispecific fishery is another great difficulty. When there are no accurate data, the overall effort is employed though the true distribution by species is very likely to be subject to progressive changes in time, associated with relative variations in abundance of the species examined. An example of an attempted solution to this problem is given by Hall and Penn (1979) for the Shark Bay (Australia) shrimp fishery.

Hancock (1979) has in fact pointed out that for shrimps, such as Penaeus merguiensis, with very marked schooling behaviour, the concept of "searching time" must, in some way, be included (as is the case for pelagic species) when determining the fishing effort, since a decrease in stock size causes a change in the proportion of searching time and trawling time.

(b) No time lags. It is assumed that the stock reacts to all variations in effort by reaching its equilibrium state immediately. This is an aspect which is all the more liable to cause distortion if the species has a long life-span, if the age at first capture is high and if the fishing effort variations are large.

This problem, which was deliberately disregarded in Schaefer's approach (1954, 1957) and Pela and Tomlinson (1969), is partially solved by the way in which Gulland (1969), Le Guen and Wise (1967), Fox (1974) and Walter (1975) approached the problem. Equilibrium conditions are approximated by relating the annual catch to the effort in the current and preceding years, combined in different ways by different authors.

Since penaeid stocks are generally composed of a single annual year-class, it can be taken that there is no time-lag. When there are important seasonal variations in recruitment, the data can be refined by not considering calendar years but rather biological years, beginning with the time of recruitment, thus practically corresponding to the catches made on one generation.

11.1.3 Conclusions.

During the review of different hypotheses implicit in production models, objections have been raised which tend to limit their application to penaeids. Neverthess, because of a frequent lack of detailed, more appropriate information, production models have often been used (FAO/UN, 1961; Boerema, 1969; Joseph, 1971; Cadima et al., 1972; Marcille, 1972, Marcille and Stequert, 1974;Garcia and Lhomme, 1977, 1979; Marcille, 1978). The use of this model by Griffin and collaborators (1973) in the Gulf of Mexico fisheries has been criticized by Eldridge (1974). Klima and Parrak (1978) have however used it again in the same region.

An example of the application of the model to the El Salvador fisheries is given in Fig. 78.

The quality of the assessment of the potential yield will be largely dependent on the quality of the annual catch data, and that of the exploitation level will depend on the true stability of the relation between F and f during the development of the fishery.

The assessment obtained with this model will be the more valid the longer the series of data on which it is based. Since shrimp production is liable to climate-associated variations, there is a danger with assessments based on short periods of compounding confusion between climate-associated variations and those due to effort, which could lead to a false assessment (Hancock, 1975 gives an example).

The drawback of this type of model is that it is impossible to integrate the data on estuarine fishing of juveniles with those from the sea fishery for adults. Very often, because of lack of data, only the sea fishery is taken into account (implicitly assuming that the level of artisanal fishing has not changed over the whole observation period). An integration of the data of the two types of fishery was attempted by adding the annual artisanal and industrial catches and calculating the consequent total effort by dividing the resulting total catch by the c.p.u.e. of the trawlers at sea (FAO, 1973). This method in fact can only be strictly applied when the age-compositions of the catches of the two fisheries are identical,which is not the case here. The effort thus calculated underestimates in fact the fishing mortality that it should represent.

The last but not the least of the defects of production models is that they do not enable prediction of the consequences of changes in fishing mortality as a function of age, e.g. by mesh regulations, closed seasons, etc. Their application as management tools is considered in the following chapter where their advantages and disadvantages will be discussed.

11.2 ANALYTICAL MODELS

As already mentioned several times, penaeid shrimps are generally exploited at two different stages of their life cycle (juvenile and adult) by two fisheries which are often very different from the socio-economic point of view. The production from each exploited phase may theoretically depend on the exploitation level in the other. It is desirable to try to optimize the total of the two fisheries, and to develop models which allow one to resolve this problem (it should be noted that although juvenile exploitation has a direct effect on the adult stock production, the opposite has not yet been demonstrated).

11.2.1 Yield per recruit models. The life cycle of a cohort is divided into two parts. The first, which extends from hatching to recruitment, is generally little known and difficult to put in an equation since the parameters are difficult to estimate. The second which extends from recruitment to the end of the life in the exploitable phase can be expressed as a model if the growth and mortality parameters are known. Since recruitment is most often unknown, the results are expressed as a relative value, as yield per recruit.

The two most often used models are those of Beverton and Holt (1957) and Ricker (1958). The first is mathematically more elegant but the second is more flexible and enables an easier representation of the reality especially since the use of computers is becoming more general (Paulik and Bayliff, 1967). Thompson and Bell's model (1934 and in Ricker, 1975) has been less employed although its principle is quite close to that of Ricker since it is based on the division of the life cycle into short time periods where the parameters are taken as constant. Berry adopted this model for *Penaeus duorarum* in Florida (in Lindner, 1966).

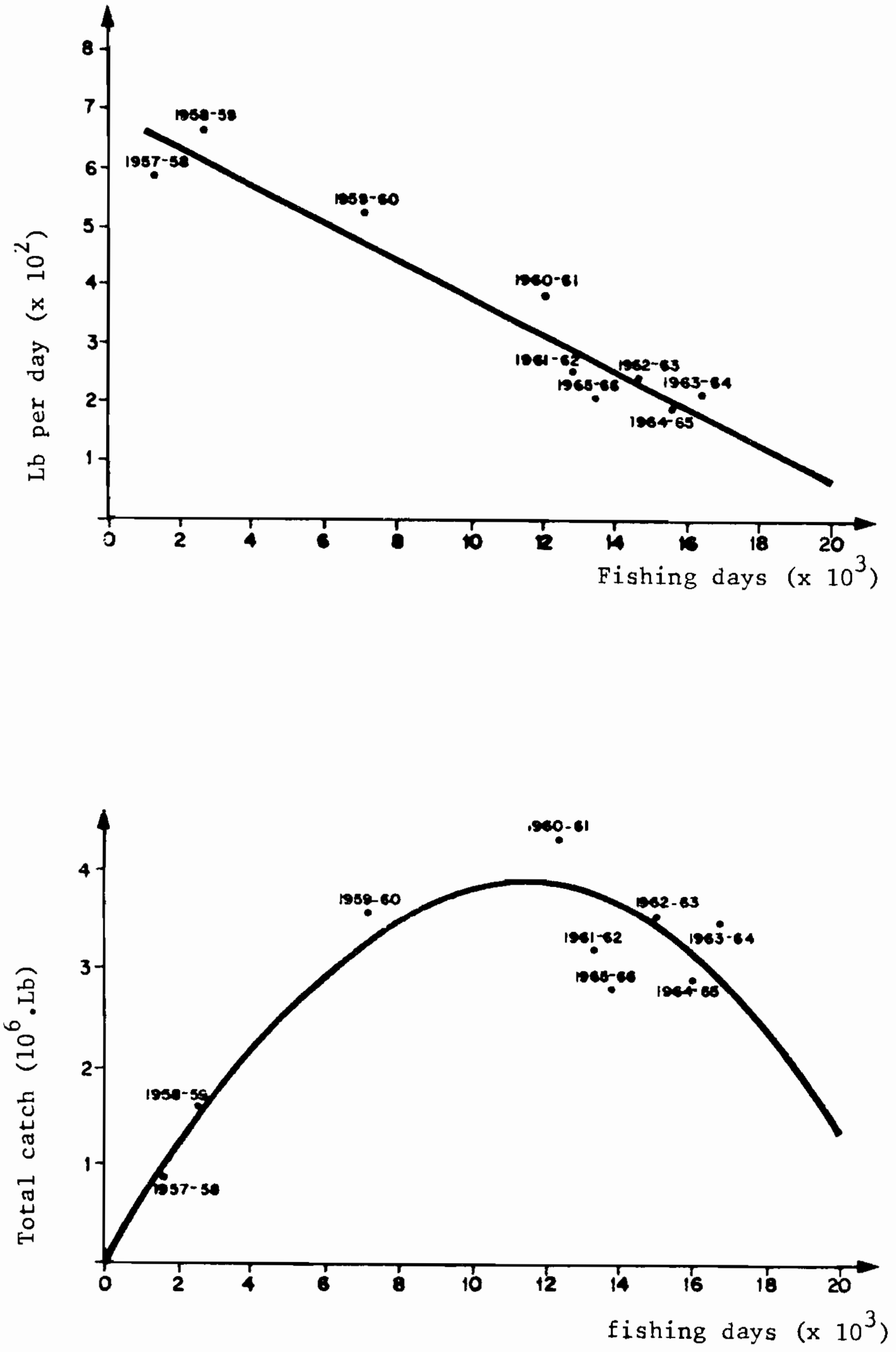


Fig. 78 Application of the Schaefer model to penaeid shrimp stock of El Salvador (it consists of a mixture of *P. occidentalis*, *P. vannamei*, *P. stylirostris*) - (from Ellis, 1968)

The basic hypotheses for these models are the following:

(a) Constant biological parameters. In the simplest versions the growth and natural mortality rates are assumed to be constant from one year to the next and independent of the exploitation level and thus of the stock density (density independent factors). Beverton and Holt's model assumes in addition that M and F do not vary with age. In reality variations can be taken into account by dividing the cohort life into segments in which the parameters are constant (cf. Beverton and Holt, 1966). The latter can be functions of density or environment, but at the cost of extreme complexity in the calculations.

The idea of yield per recruit allows one to avoid the problem of the often unknown stock-recruitment relationship·Unfortunately the application of this concept sometimes leads to consider the relation between total catch and effort to be the same as that between yield per recruit and effort, which is only the case if annual recruitment is constant and independent of the stock size.

(b) Model determinism. Although all parameters of the models can theoretically be considered to have random variability, this possibility is rarely used and the parameters are generally considered to be fixed and identical for all the individuals of a cohort.

(c) Equilibrium conditions. Most frequently in applying yield per recruit models, it is assumed that the stock is in equilibrium and that all conditions are stable. In this case the total annual production of all age classes present in the fishery together is equal to the production of a single year class throughout the exploited phase. The time variable used in the catch equations is usually the year for the long-lived fish. In the case of the short-lived shrimps this time variable has to be taken as much smaller than a year, and the month or the week is often used (in growth, mortality or recruitment studies) and the seasonal variations of the population parameters have to be taken into account.

Recruitment is a continuous function of time but as a first approximation it can be assumed that there are 12 monthly cohorts of unequal size. The yield of each cohort will depend on its seasonal growth pattern (linked to the hatching date) and on the exploitation (associated with seasonal variations in q and f). The overall production of the 12 cohorts e.g. the annual production of a whole year class, will depend then on the overall recruitment level of that year and on the seasonal variations in fishing effort, all other factors and their variations being taken as fixed.

Adopting an equilibrium hypothesis for penaeids thus implies stability from year to year of all seasonal variation patterns and particularly those of exploitation. As a consequence, the application of a simple yield per recruit model assumes that the complex production mechanism of 12 monthly cohorts during one year can be approximated by the production of a theoretical ideal year class having "average" dynamic parameters. The quality of the results will depend much on the representativity of the latter.

(d) Conclusions. If the necessary data are available (constant or age-specific natural and fishing mortality, growth, size at recruitment and selectivity) one can calculate the yield per recruit and the theoretical fecundity per recruit (Le Guen, 1971) as a function of fishing mortality and age at first capture. The means to predict the consequences of fishery management by control of effort, mesh regulations, establishment of closed areas, etc. can thus be obtained.

However, for penaeids these models do not enable seasonal variations (of growth, recruitment, catchability, etc.) to be readily taken into account; thus the exact consequences of a change in seasonal distribution of effort (e.g. by closed seasons) on the "average" fishing mortality as a function of age, and on overall production cannot be forecast. The simulation techniques that are the subject of the next section will allow us to solve the problem.

Models of this type have been used in the Gulf of Mexico by Kutkhun 1/ (1966) and Berry (1967)

1/ It should be noted that the values used by this author for natural mortality, obtained by tagging, are probably too high (cf. 7.7) for shrimps from the Tortugas (Florida). The results obtained by the latter are shown in figures 79 and 80. A preliminary study was made with a Thompson and Bell model (Lindner, 1966).

Ricker's and Thompson and Bell's models also allow the calculation of the theoretical fecundity per recruit (a concept introduced by Le Guen, 1971) and particularly its change as a function of F and l_c, by integrating into the model fertility data as a function of age (Fig. 81). The usefulness of this theoretical information was discussed in section 10.1.3. Expressed as a relative value with respect to the theoretical fertility of the virgin stock it is an index of the decrease of the spawning potential as an effect of fishing.

To allow better adapted management, the consequences of a management measure must be expressed not only in terms of production by weight (absolute or per recruit) but also in economic terms: catch value, costs, marginal products, etc. (cf. following chapter).

Yield per recruit models can be used for this purpose (Fig. 79B). Kutkhun (1966) for example replaced the equation of the growth in weight in Beverton and Holt's model by an equation in value. This expedient allowed him to express his results in value per recruit.

The more flexible Thompson and Bell and Ricker models lend themselves particularly well to this application since it is not necessary to adopt any mathematical model, particularly that of von Bertalanffy, to represent the relation between value and age and it is easy to use simply the observed values (Fig. 81).

11.2.2 Simulation techniques. These are increasingly widespread since the popularization of computers and help to overcome certain constraints imposed by the previous models. As the yield per recruit models, simulation techniques most often use an analytical approach.

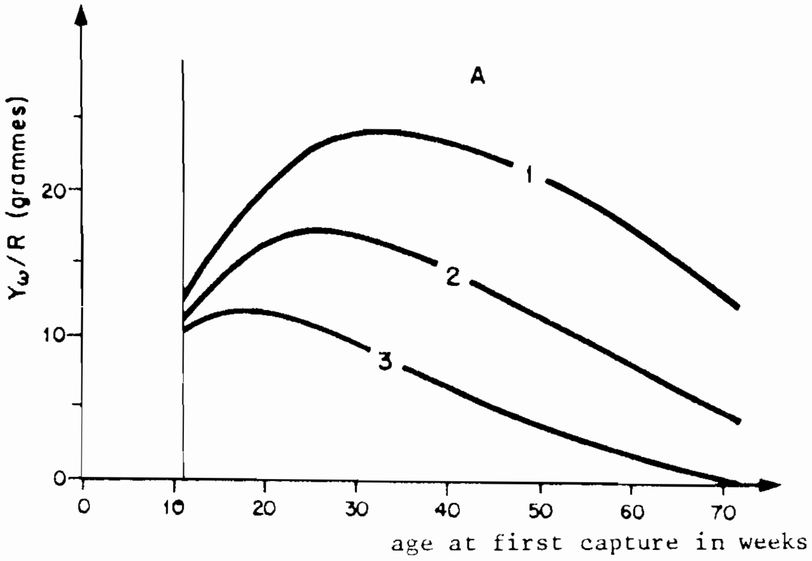
When the data exist, they allow a closer approach to reality than the simple yield per recruit models. A shrimp year class, for example, can be subdivided in 12 monthly cohorts of unequal size, thus reproducing the seasonal migration and recruitment pattern. Each cohort can follow its own seasonal pattern of growth and mortality as a function of age. Since there is a differential growth between the sexes (which implies that ages at first capture and biomass development are somewhat different) the sexes will be considered separately. In spite of the complicated calculations, the basic formulae are identical as before and the results have the same character. If the seasonal variations in recruitment are known only as relative values (monthly percentages of the total annual number of recruits for instance) the production for a given total annual number of recruits (1 000 for example) can be calculated. The results will in fact be of similar nature to those in the previous sections and are subject to the same restrictions, associated with the fact that the true stock-recruitment relationship is not known.

If one has the means of estimating the absolute value of the annual recruitment, the simulation can be more complete and the calculated results (monthly and annual total catch, catch per unit effort, size and age composition, seasonal variations in abundance, etc.) can be compared with the data observed in the past. If the reconstruction of past events is satisfactory, it is taken that the model can be used as a means to forecast the consequences of various possible management schemes.

The introduction into the simulation of a stock-recruitment relationship allows a "self generating" model to be constructed. For penaeid shrimps however, this relation is unknown and its relevance is open to question (cf. section 10.1.3).

Since the parameters used for simulation are only estimates, a study of the sensitivity of the simulation to variations in different parameters is recommended. This procedure allows one to demonstrate which are the most "sensitive" parameters which control the quality of the results, on which later research effort must concentrate.

It should be remembered that simulation with parameters obtained from cohort analysis must automatically give a good agreement of the simulated and observed results, but this agreement is trivial and is no proof of the proper representativity of the model.



1. F=0,193 M=0,024
2. F=0,227 M=0,039
3. F=0,160 M=0,061

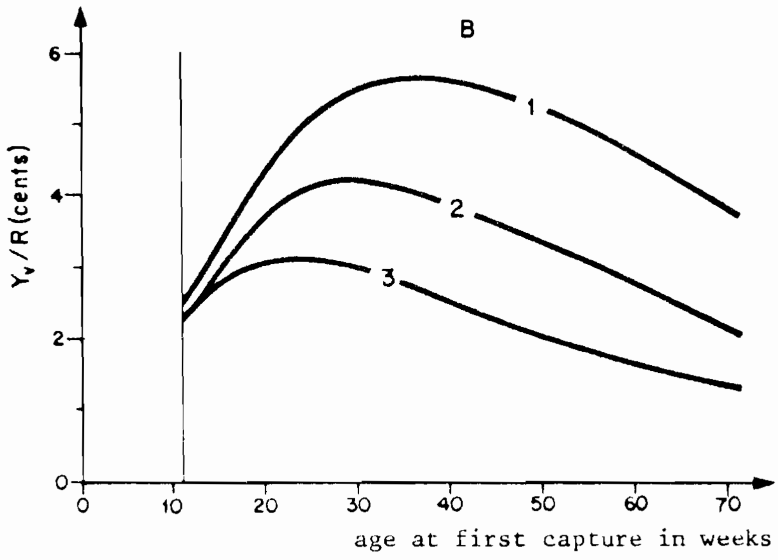


Fig. 79 Variations of the yield per recruit in weight (A) and value (B) as a function of the age at first capture for different sets of values for F and M (in weeks); *Penaeus duorarum*, Florida (from Berry, 1967)

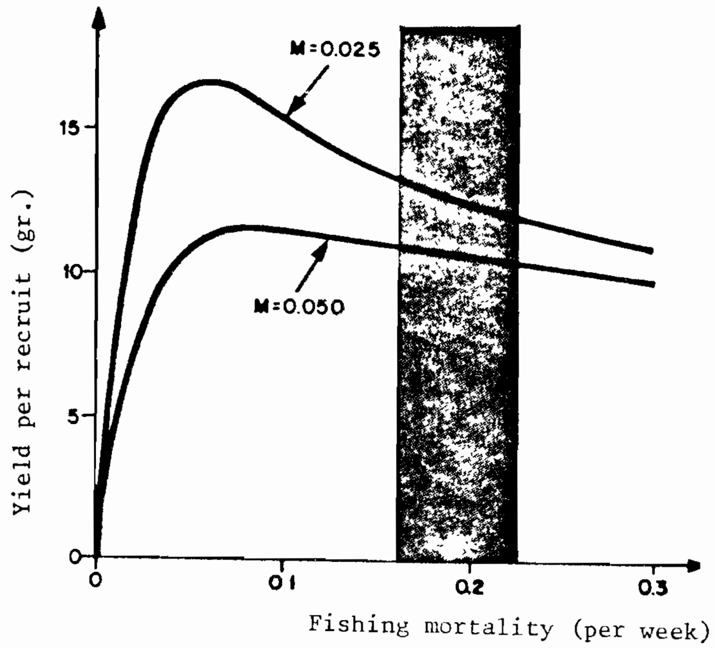


Fig. 80 Variation of the yield per recruit (in weight) as a function of F for two values of M (per week) from Berry, 1967)

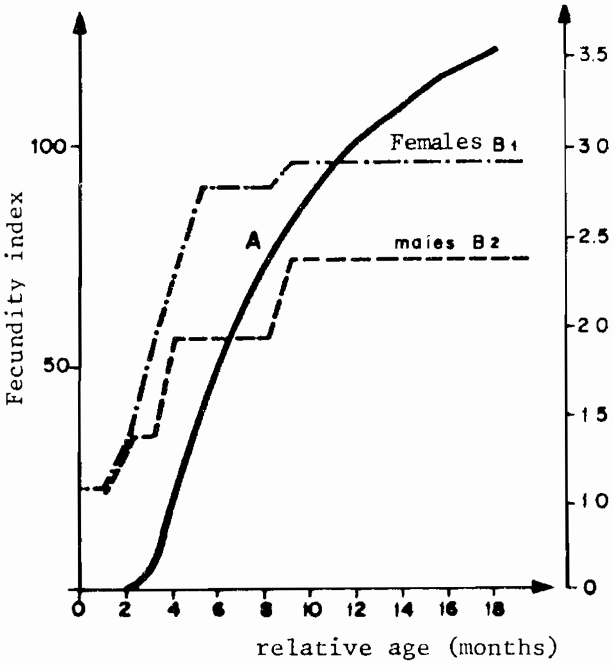


Fig. 81 Variations of the fecundity (A) and price (B) indexes as a function of the "relative" age in *Penaeus notialis* (from Garcia, 1977)

Simulation techniques have been applied for example by Abramson and Tomlinson (1972) to prawns (Pandalus sp.) and are beginning to be used for the penaeids (Lluch (1975); Garcia (1977, 1978); Garcia and Ndiaye (1977); Blomo et al. (1979); Grant and Griffin (1979); Clark and Kirkwood (1979)).

For penaeids they have the advantage of allowing the integration into a single model of juvenile and adult exploitation to assess the overall results of an integrated management programme (Fig. 82). Examples can be found in Garcia (1978) and Grant and Griffin (1979). The diagram of the bio-economic model established by this author is given as an example (Fig. 83).

They also allow the construction of models for determining the optimal strategy for exploitation of several independent stocks. In this way Clark and Kirkwood (1979) in Australia made simulation studies of the development of a fishery with free entry which included two different types of boat and exploited two stocks composed of species of different economic interest, so as to define the optimum time-space allocation of effort and the best fleet composition.

For animals with a short life-span, seasonal variations in population structure, biomass, number and spawning potential are important. Simulation of these variations is of great interest for the understanding of biological mechanisms. Garcia (1977) thus simulated the theoretical seasonal variations of the number of "adult" females (with a size greater than that of first maturity) in a population and showed the importance of this phenomenon to the interpretation of seasonal variations in spawning.

In reality the only limit to the application of simulation models is the availability and the quality of the data and one must always be cautious not to go too far from reality by requiring from models more than the basic data warrant.

11.3 APPROXIMATE METHODS OF RESOURCE EVALUATION

The developments in resource exploitation are generally more rapid than those of the research potential which has the task of supplying administrators with the scientific basis of rational management. There is therefore always a risk that accurate but too late scientific information allows only in fact a "post mortem" diagnosis.

It will be emphasized in the following chapter that it is preferable to manage a resource from the beginning of its development without waiting for unregulated exploitation to lead to a crisis situation which becomes difficult to resolve.

Quoting from Troadec (1977) "When the development of a fishery is to be followed, accuracy, precision and opportunity are three interdependent qualities of varying importance during the development of a fishery". When there is overemphasis on the search for greater precision, the increase in the required information "and thus cost and delay in its acquisition grow more rapidly than the precision derived, and it can be understood that precision might be antagonistic to accuracy and above all, to opportunity".

Approximative methods can be used for the assessment of basic parameters, an aspect which has been studied in chapter 7, or for a first appraisal of the exploitation potentials and levels. A summary of the possibilities can be found in Saetersdal (1973) or Troadec (1977) and we will only take up here those aspects which can be applied to penaeids with some hope of success.

11.3.1 Relation between biomass obtained by fishing surveys and potential

This method implies knowledge of a stock biomass, obtainable through trawling surveys.

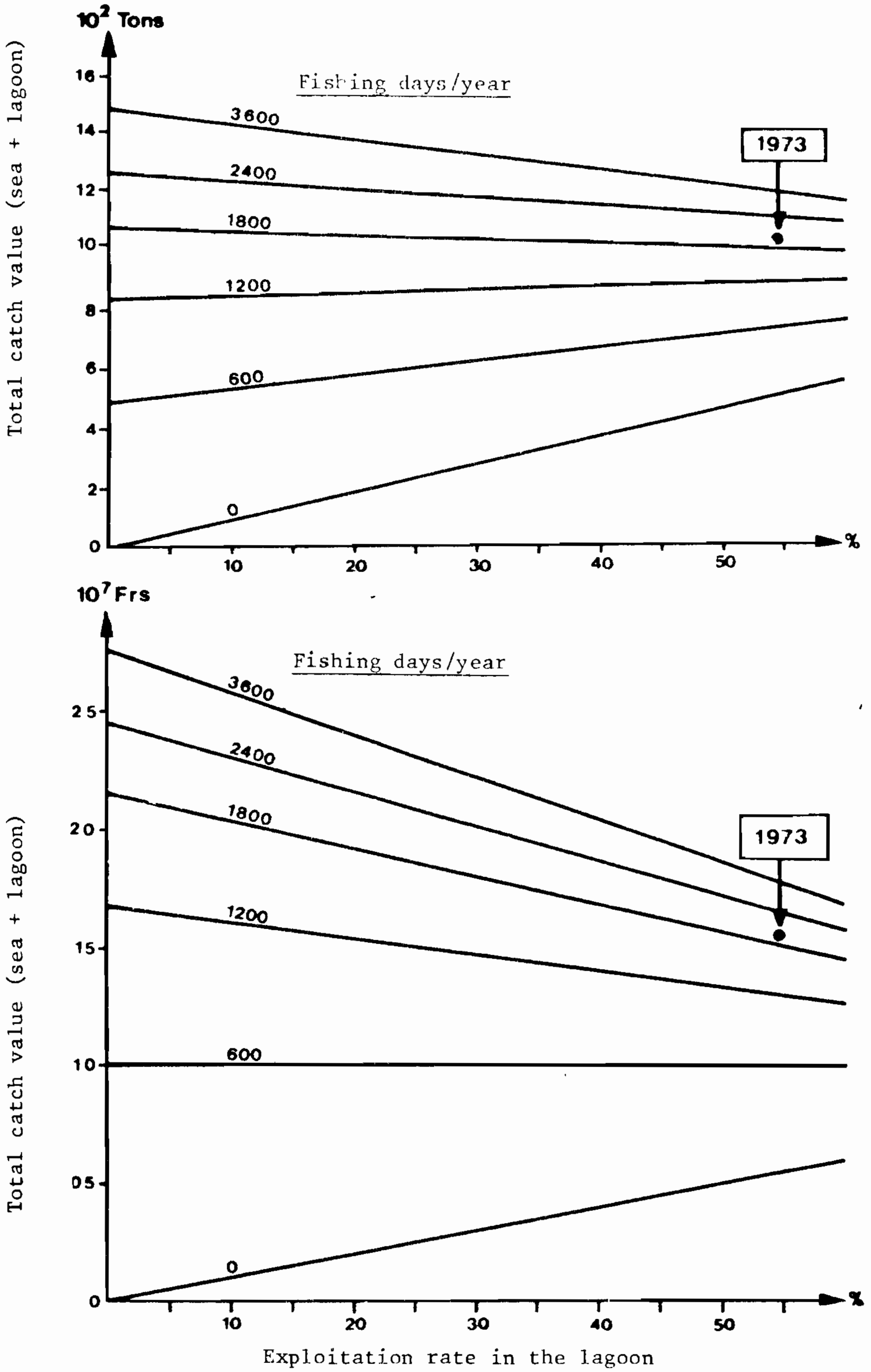


Fig. 82 Variation of the total catch (sea + lagoon) in weight and value as a function of the exploitation rate in the lagoon and the annual level of effort at sea, for *Penaeus notialis* in Ivory Coast. The situation in 1973 is indicated. (from Garcia, 1978).

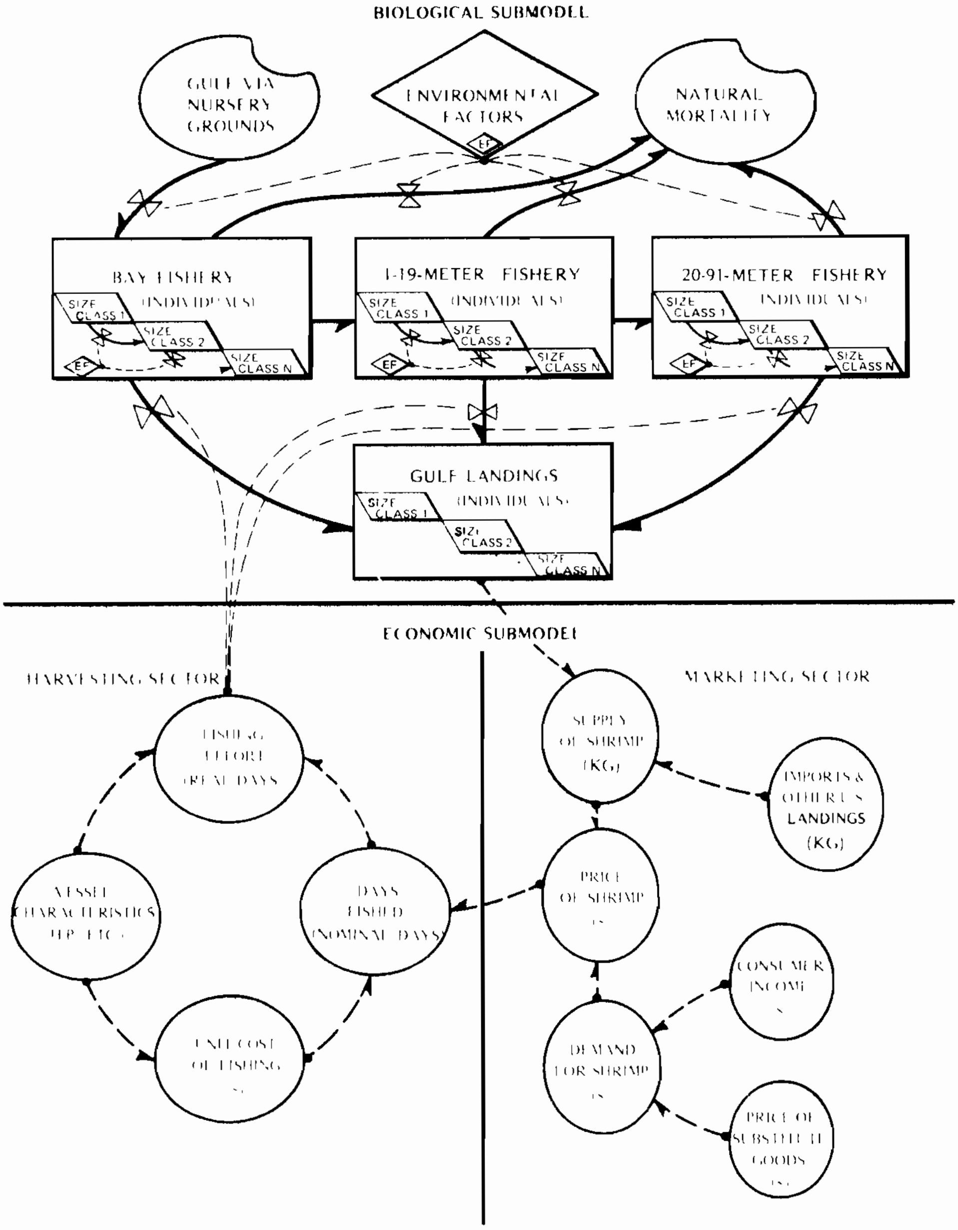


Fig. 83 Flow diagram of a conceptual bioeconomic model for the Gulf of Mexico shrimp fishery. Symbols follow Forrester (1961) - (from Grant and Griffin, 1979)

11.3.1.1 Remarks on the surveys

These can provide good preliminary assessments. Interesting species can be identified as well as their distribution and their relative abundance. If properly planned they enable assessment of the stock biomass if the true efficiency of the trawl is known, which, it must be admitted, is rather rare. If it must be assumed, because of lack of accurate data, that the trawl efficiency is complete and that all the fish present in the path of the trawl are caught, the calculated biomass must be considered as a minimum estimate since, as emphasized in section 7.7.3 this hypothesis is probably not realistic and the efficiency could well be closer to 0.5 than 1.0. There are many basic documents on survey theory: Alverson and Pereyra (1969), Alverson (1971), Mackett (1975), Holden and Raitt (1974); Gulland (1975) and Ulltang (1977), etc. and these will not be reviewed. It should only be noted that when surveys are repeated regularly with standard techniques over several years, they provide a tool for monitoring the state of the resources. The index of abundance obtained by a research vessel can replace the catch per unit effort of the fleet when the data of the commercial fishery do not have the required quality, and when the fleet and the research boat are truly exploiting the same population.

It should also be noted that the average catch rate obtained by a research vessel during a well-designed random survey of a virgin stock cannot be compared to the catch rate of a fishing vessel operating commercially since the distribution of the respective efforts is probably different, the professional fishery selecting the richest strata. If comparison is required, a selection of the trawl stations with the best yield can correct the error, but in excess, since the yield thus calculated will be greater than the average obtained by the units of a shrimp fleet competing in the same zone.

In fact the calculated catch rate from selection of the best zones on a virgin stock approaches the theoretical index of abundance at $F = 0$ (in a production model) and it should be noted that the value can be very different (above all for animals of short life-span) from the average obtained later on by the well developed fishery. Lindner (1971) noted that though the catch rates obtained on virgin stocks in the Gulf of Mexico reached 2 tonnes of shrimp tails per day in 1936 they were no more than 450 kg/day in 1946. Garcia (unpublished) has also noted during the initiation of a fishery in the Ivory Coast very high catch rates reaching on certain days 700 kg/hour and a very rapid drop in the first months of regular exploitation. The present yields, at a level close to that of the optimum exploitation, are 30 kg/hour.

11.3.1.2 Application of survey results to the assessment of potential yield or the exploitation level

When an assessment of the biomass B_o of a virgin stock is available, Gulland (1970a) showed that if it is assumed that the resource obeys Schaeffer's model and that at maximum production level natural and fishing mortality are close (M close to F_{max}) 1/ and since the biomass at this level (B_{max}) is equal to $Bo/2$, the classical expression $C_{max} = F_{max}.B_{max}$ becomes

$$C_{max} \# M.B_{max} \# M.B_o/2 \# 0.5\, M\, B_o \# XMB_o$$

where M can be obtained according to one of the approximative methods shown in chapter 7. The coefficient X, fixed above at 0.5 can be improved by taking into account the dynamic characteristics of the species examined, in particular l_c/l_{oo} and M/K. One can then put

$$X = \frac{Y_{max}}{M.B_o} = \frac{F_{max}.\ B_{max}}{M.B_o} = \frac{F_{max}}{M} \cdot \frac{B_{max}}{B_o}$$

1/ Hypothesis suggested by Tiurin (1962) and already adopted by Alverson and Pereyra (1969). The biological data on which it is based is not available.

If the case of a constant recruitment model is taken, tables IV of Beverton and Holt (1964) give

$$(Y'/F)_{E\max} / (Y'/F)_0$$

equal to $B_{\max}/B_0$ and the corresponding $(F_{\max}/M)$ for each value of M/K and l_c/l_∞.

For penaeids the most probable values of M (see chapter 7) and of K give a M/K ratio which falls between 1 and 2 while l_c/l_∞ is close to 0.4-0.5 for the fishery at sea. Referring to Gulland's (1970a) table 1, this gives values of X which fall between 0.32 and 0.44. It should be noted that as a first approximation the error made by using X = 0.5 is certainly lower than the errors in the estimated value of the biomass itself. It should also be noted that the calculation gives maximum yield estimates of the order of magnitude of the virgin biomass when M is greater than 3.0 on an annual basis (or 0.25/month). It is interesting to note as a result that for exploitation levels which are unknown but which run from 0 to $E_{\max}$ the possible range of values of potential yield falls approximately between B (for E = 0) and MB (for $E = E_{\max}$).

One is faced with a great difficulty when the biomass assessment is made on an already exploited stock. The previous simple equations cannot be applied. If the annual catch is known for the year i when the survey is done, the expression $C_i = F_i \cdot B_i$ and thus $C_i/B_i = F_i$ can again be used and this value of F_i can be compared with an estimate of M for the species under examination. If F_i is close to M it could be considered that the total catch could hardly be increased. On the other hand, if F_i is clearly lower than M, it must be possible to multiply the current effort by M/F_i to approach the maximum sustainable yield level. The latter cannot be so calculated but it can be deduced from the yield curves that the increase in catch will be lower than the increase in effort, that is, $C_{\max}$ will be lower than $C_i \cdot M/F_i$.

It can also be deduced that $C_{\max}$ will be between B and MB according to the exploitation rate exerted by the fishery at the time of the survey.

11.3.1.3 Observations on the method

This section must include some important observations. The first concerns biomass assessment. The important figure is the average annual value. We know that for short-lived animals such as the penaeids the biomass is subject to great seasonal variations and the average biomass and its confidence limits must therefore be determined from repeated observations during a full annual cycle. In addition the possible catch of a given stock will depend on seasonal variations in effort. These comments, when added to the previous observations on the difficulties in evaluating the true efficiency of trawls used to determine the shrimp density, show that the values obtained both for the biomass and for the catch potential must be considered as very first approximations to be used prudently and with adequate safeguards.

The second observation touches the fundamental basis of the method which assumes that at a maximum level of production M is close to F. This theorem is discussed by Francis (1974) who showed that it can only be accepted in the case that recruitment is independent of stock density (the Beverton and Holt type of "stock-recruitment" relationship).

It was shown in chapter 9 that the stock-recruitment relationship for penaeids was unknown but that there was a tendency to consider recruitment to be independent of the parental stock. If this is confirmed, the application of the approximative formula $C_{\max} = X.M.B_0$ will be thus fully justified for the penaeids.

11.3.2 Assessment from productivity indices

It is always tempting to reduce the necessary time and information for assessment of potential yield in a region by comparing it to another well known region for which productivity and ecological characteristics are analogous.

11.3.2.1 Morphoedaphic indices

As used in lake systems and rivers, these allow from simple morphoedaphic characteristics (concentration of dissolved solids, average lake depth, length of the water course, area of the supplying watershed), calculation of production (in kg/ha/year for example) in systems within similar climatological conditions and subject to similar exploitation levels. A detailed review of the hypotheses on which the use of these indices is based can be found in Ryder *et al*. (1974) and an example for African rivers in Welcomme (1976).

The diversification of the marine environment and the complexity of their study does not yet allow generalization of such indices. In Cushing (1969) can be found an example of the difficulties present in calculating fisheries potential in upwelling zones from planktonic productivity data.

The evident association of penaeid shrimp with mangrove swamps was studied by MacNae (1974) in the Indian Ocean. The catch varied from 1.3 to 10.6 ton/km^2 of mangrove according to the region. This scatter of values is not surprising when it is realized that the same species appears to be closely attached to the mangroves in a given region but also to be plentiful elsewhere in non-mangrove areas. It should be noted for example that penaeid juveniles can be found on pure sandy shores (in Japan) in association with marine phanerogams (in the Gulf of Mexico, in Kuweit) or in the mangroves (in Malaysia, India and West Africa). Moreover in the same region, closely related genera (*Penaeus* or *Parapenaeopsis* for example) have different requirements.

The only common link is that observed everywhere between penaeid juveniles and the sea-continent interface. For instance, Turner (1977) showed, within a region, a link between estuarine shrimp production and the area of the intertidal zones.

Shrimp production evidently depends also on many interacting factors such as temperature, rainfall and river deposits, spawning, growth, size of the estuary and the adult distribution zone, etc. It is clear that there is a latitudinal gradient for these parameters and that the hot and humid zones are also those where there are heavy alluvial deposits and where there are plentiful lagoons, deltas and sandy bottoms in which growth is rapid and spawning continuous. Turner (1977) thus showed that at world level there was good correlation between the shrimp production (Y) of a region (in Kg/ha/year) and the latitude in degrees (X), of the form

$$Y = 159e^{-0.070(X)}$$

This relationship alone already accounts for 55% of the observed variance, which is important. It is interesting from the theoretical point of view but of little practical value since, although the variance around the curve was not given, the observed value of Y for a given latitude varied from 1 to 10, a "precision" which is grossly inadequate for even an approximate assessment of the potential of a region.

It should finally be noted that in these studies standardized indices for the biological production should be used (e.g. potentials and maximum sustainable yields), and not the annual catches which would introduce an extra variability.

11.3.2.2 Direct production comparisons

The relation existing between the area of the known fishing grounds and their maximum sustainable yield can also be studied in a given region for use as a tool for the prediction of the production of less well-known resources. Garcia and Lhomme (1979) and Lhomme (1980) noted that on several grounds off the West African coast where the pink shrimp (*P. notialis*) is found, the maximum average productivity potential (M.S.Y./square mile/year) only varied from 1.6 (at the extreme northern limit of the distribution of the species) to 4.5 t/sq.mi/year. It is interesting to compare these values with those obtained in the Indian Ocean (FAO/CPOI, 1973). If the available information is examined from Mozambique to Thailand, including Australia, the "optimal" catches vary from 1.7 to 3.8 t/sq.mi/year, the average value being 2.4 t/sq.mi/year. The extreme values only vary by a factor of 2 or 3.

The use of such simple indices should allow to evaluate the order of magnitude of the potential of a stock, if the area of distribution is known. This approach was used, for example, by Garcia and Lhomme (1979) on the West African coast.

Nevertheless there are evident difficulties associated with the use of such an approach which are as follows: although the areas of exploited stocks are not always known and are often inaccurate, those for non-exploited stocks are liable to be even more difficult to define. Sedimentological maps can be used as a basis if the regional bionomy is known but the evident relative adaptability of shrimps to different types of sediments makes it too risky to define the demarcation of the grounds on the basis of this information only.

The true maximum average stock production will ultimately be greatly influenced by the spatial distribution of the annual fishing effort on the different species, on the artisanal fishing levels, and on the discards which vary with species, regions, type of exploitation and markets. In reality, in the few cases where it has been calculated, the total catch (artisanal for juveniles plus industrial for adults together shows little sensitivity to reasonable variations in the exploitation rate of juveniles (see section 12.5).

In spite of all the sources of error, the results about productivity from 15 stocks examined were sufficiently similar for it to be possible to give some value to this method. Of course the results must be considered provisional and must be checked either by trawl survey before the beginning of the exploitation (see previous sections) or by classical assessment techniques, applied from the start of the exploitation.

The approach proposed here for a very approximate assessment of the potential has also been suggested by Boerema (1974) to evaluate the level which the effort should not surpass. He pointed out that it can be assumed that the mortality per unit of fishing intensity applied by a standard trawler is the same for all species with equivalent behaviour (and, it could be added, for similar latitudes). If in addition these species have closely related biological properties (K, L_∞, M, fertility, etc.) the maximum production level should be obtained for equivalent fishing intensities.

This obviously approximate method enables the order of magnitude of the effort which should not be exceeded to be fixed from the beginning of an exploitation, and thus, to limit the number of licenses to a reasonable level. Such a measure, applied in 1968 in the Ivory Coast, by comparing its fishing grounds with those of Senegal and Florida enabled the number of authorized boats to be limited to 10 although the number of applications reached 32 (Garcia, unpublished). Much later, the results of an analytical study by simulation, based on several years of research, confirmed these measures (Garcia, 1977).

11.3.3 Conclusions

The need to provide, in many cases, a rapid preliminary diagnosis so as to avoid regrettable overinvestment argues the (cautious) use of simple, rapid and cheap methods to obtain information. The results obtained must however be considered to be inaccurate and very tentative, to give only orders of magnitude and to be aimed at avoiding gross management errors. Their use should only be the first step of a research programme aimed at better knowledge of the resource and its reactions to exploitation so as to improve the diagnosis and to provide elements for more sophisticated management when necessary.

12. RESOURCE MANAGEMENT 1/

Penaeid shrimps are one of the world's most profitable resources. Their very high price and strong demand in the market of the richer countries (United States, Japan, Europe) give strong incentives to the development of shrimp fisheries. Many developing countries wish to draw on such resources for their requirements in foreign exchange and hence all the conditions are present for the fishing effort to reach excessive levels in the absence of regulatory measures, which means overinvestment, excessive production costs, no economic return, and even perhaps an overall reduction of the value of the total catches.

Management of this type of fishery from the first stages of development seems therefore to be an important factor to obtain a balanced development and optimal profitability. In this respect, it is advisable to identify the management objectives so as to decide on the most suitable methods. Although the available data are not always as complete as one would wish, an extraordinary amount of information has accumulated since Boerema (in FAO/UN, 1961) and Gunter's (1966) pioneering work on shrimp fishery management.

12.1 MANAGEMENT PRINCIPLES

Whichever model gives the best representation of the relation between the production of a shrimp stock and the fishing effort (see previous chapter) the generally observed relation is the following: when the effort increases the catch increases also, at first almost proportionally. However, the catch very soon increases at a lesser rate than the effort, with the result that there is a progressive decrease in the catch per unit effort (Fig. 78). Since exploitation costs are approximately proportional to the applied effort, the curve linking the gross value of the catch to the exploitation costs will be of the form shown in Fig. 84a. At point B the value of the catch is maximum; at A the value is equal to the cost of fishing profitability being zero. Other economic indices are shown in Fig. 84b: the marginal yield (the net value added to the catch by an increase in cost of one unit), indicated by the slope of the total value curve in Fig. 84a and the net economic rent which is the difference between the value of the catch and the costs. These curves, obviously, only have meaning for a fishery considered as a whole and are not valid when a single fishing unit or a fishing company is considered.

If there is no management the fishery will develop as far as point A and even beyond if the net negative economic product is compensated by direct (subsidies, preferential loans) or indirect government aids (custom-free concessions, reduced fuel prices, etc.). In the prevailing world situation and as a consequence of the forthcoming new law of the sea (important unused fishing potential searching for action areas), it is obvious that a profitable fishery can develop very rapidly and there is a danger that fisheries might develop beyond the level of optimum fishing before proper management has been implemented because of inevitable delays in the decision making process. Lacking other possibilities the fishery might stabilize at D where only running costs are covered (fuel, personnel insurance) and where the exploitation means are degradated because of lack of amortization.

1/ The theme of this chapter is drawn mainly from the work of Gulland (1969a,1972 and 1977) and Troadec (1978).

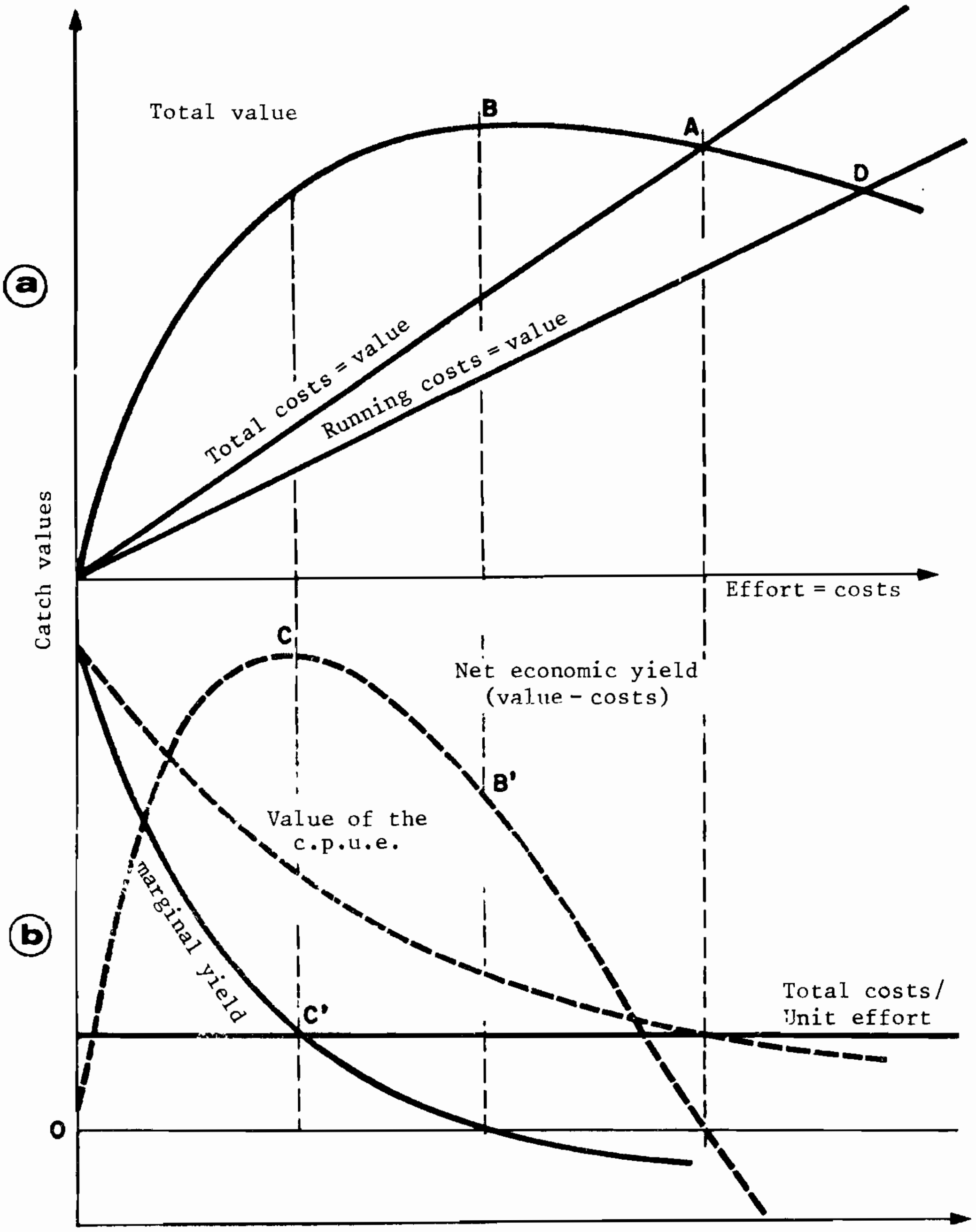


Fig. 84 a) Relation between effort and catch value showing the equilibrium position of a fishery without any management

b) Effects in changes in effort on the cpue value, marginal yield and net economic yield (from Gulland, 1972)

The shrimp fishing industry in the United States is an excellent example of inefficiently managed fisheries. According to Neal (1975) this fishery is in a state of "economic overfishing". There are too many boats and too much personnel and although the catch might be stabilized, the income per fisherman decreases. The industry is now undergoing many economic analyses (Griffin and Beatie (1978); Griffin et al. (1976); Blomo et al. (1978); Griffin and Nichols (1976); Griffin and Jones (1975); Rounsefell (1975); Greenfield (1975)). The last author, in an analysis of the economic crisis afflicting the fleet, blamed the rises in fuel costs for triggering the crises. He observed that the marginal yield has been decreasing for a long time but that it always remained more than one might expect in other alternative fisheries. The continuous rise in shrimp prices has allowed an inflationary movement to take place in the fishery and Rounsefell (1975) observed that each good year was followed by an upswing in new boats construction. In 1974 the overall net economic rent for all boat types was negative but the fleet continued operations because the incomes were greater than the running costs. This situation could be a short-term expedient but could not continue for long because the economic potential was degradating.

This is why Rounsefell, in criticizing the existing regulations asked for the urgent application of a system of limited entry together with a significant reduction in boat numbers. Once arrived at this point of development it is obvious that the crisis cannot be solved without some socio-economic shocks.

As a general rule, it is certain that in very many cases the net economic rent would be appreciably increased by reducing fishing effort (to a level lower than that which produces maximal catch value (B, B') where the marginal yield is nil. At point C, the marginal yield is equal to the cost of the unit of effort which produces it. At this point the total net economic rent is at a maximum. A difficulty lies in the fact that different countries exploiting the same resources will have different economic optima. There are, of course, other management objectives (better use of labour, better distribution of profits, etc.) but according to Gulland (1972), point C is generally not far from the optimum which would allow different requirements to be satisfied.

It should be remembered that in this type of economic analysis, the cost of intended management measures (cost of the limitations and their control, etc.) must be added to the production costs.

With respect to this theoretical, simplified scheme, management must be planned with some fundamental principles in mind:

a) It is preferable to intervene very early during the development of a fishery. In fact it is much easier to slow down expansion when that seems necessary than to reduce exploitation levels when the situation is catastrophic, since the short-term social and economic consequences are then so disastrous that the application of a management programme would be extremely painful.

b) Management must not just be considered as a restrictive and coercive process, but as an integrated activity which supports development of a fishery from its inception (financial incentives, loans, scientific surveying, technological improvement programmes, creation of infrastructures) by monitoring both the development and its consequences (following the state of the resources, assessment of potential), and establishing regulatory mechanisms (quotas, licenses, etc.) when useful. It is desirable to have the legislative and technical mechanisms for putting a break on the fishery well established before their use becomes necessary.

c) A well managed fishery creates a large net economic rent (the difference between catch values and fishing costs). It is very important to decide at the administrative level the use to which this surplus will be put, since it can reach levels which bear little relation to the incomes of other professions and thus may create some tensions. Such a decision will allow the definition of the legislative provisions necessary for the transfer of the revenues (to developing other fishing activities, to the state treasury, etc.).

d) Successful management is based on a clear definition of the objectives, on the availability of adequate data (biological, socio-economic and political) to enable the identification of various possible alternatives and on the establishment of a permanent consultation mechanism between the administration, the research and the exploitation, through which available information will be translated into decisions, the consequences of such decisions followed-up and the results used by feedback to improve or redefine the management strategy.

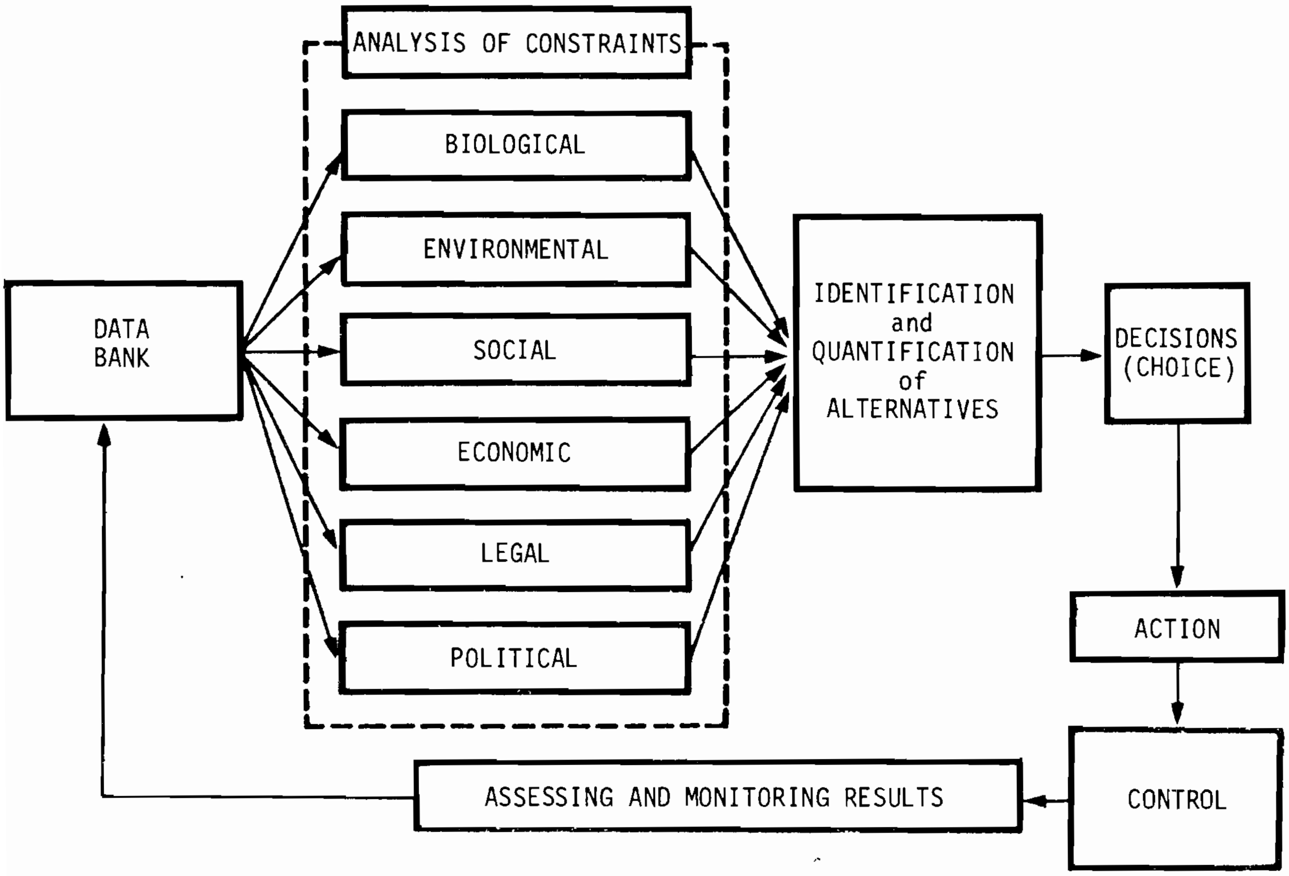


Fig. 85 Elementary mechanism of management (modified from Etzold and Christmas, 1977)

A general outline of this type of mechanism is given in Figure 85. A good example of the definition of objectives and of concrete proposals for a regional coordinating mechanism is given in Etzold and Christmas (1977).

12.2 MANAGEMENT OBJECTIVES

Efficient management policy is based on clear definition of the desired objectives and the establishment of a framework which will allow the application of the necessary measures. The various theoretically possible objectives for a shrimp fishery are the following:

a) Long-term conservation of resources

b) Maximization of physical yield

c) Maximization of the total value of the catch or of foreign currency income

d) Maximization of net economic rent

e) Decrease in production costs (fuel consumption for example)

f) Improvement in the economic and social conditions of labour by better employment opportunities or better redistribution of profits

g) Better exploitation of secondary species (too frequently discarded and thus representing considerable waste)

h) Improvement in trawler profitability by reducing the number of juvenile fish destroyed by the shrimpers.

In practice, the management policy will be defined in each particular case in the light of scientific knowledge and the immediate objectives, bearing in mind that the required data (biological and economic) are rarely completely available, sufficiently precise, or even reliable.

12.3 MAXIMUM SUSTAINABLE YIELD (MSY) AS A MANAGEMENT OBJECTIVE

The apparent simplicity of the production model concept (chapter 11) has led to its very intensive use during the last twenty-five years by most organizations concerned with management. This model has been used for penaeids and will probably continue to be for some time, for want of a better alternative. The adequacy of the model to show the relation between stock size and exploitation level has been discussed in the previous chapter. Here we will examine only the value of the MSY as a management tool.

The idea of maximum sustainable yield (MSY) is based on a simple model which:

a) describes the biological characteristics of a total stock in a manner comprehensible to everybody;

b) gives a scale of values for a fishery. The MSY represents the "best" situation which would be approached and all efforts beyond the level giving MSY are prohibited;

c) provides a slogan easily adopted by scientists, administrators and fishermen.

However, as Gulland (1969) reminds us, "It is doubtful if the achievement of maximum sustainable yield should be the objective of management except in very special circumstances".

Since then, many authors have amassed criticisms of all kinds to this concept (Christy and Scott, 1965; Larkin, 1977; Gulland, 1969, 1977, 1978; Sissenwine, 1978, etc.).

12.3.1 <u>Biological arguments</u>

Attempting to achieve MSY presents several serious obstacles:

a) Decrease of reproductive potential

It leads to the search for exploitation close to the ideal situation where the mean age in the catch approaches the optimal age (where the cohort biomass is at a maximum). Since this age (t_{opt}) is very near to the age of first maturity (t_m) the reproductive potential suffers, the parental stock is reduced to young individuals, fertility and egg quality diminish and the risk of catastrophy increases (Larkin, 1977).

b) Genetic impoverishment

It causes the disappearance of the less resilient elements of the population which results in genetic impoverishment of the stock. According to Larkin (1977) it is doubtless that many substocks have already disappeared.

c) Multispecific stocks

MSY is inadequate for multispecific stocks since the maximum for several stocks with different resilience cannot be obtained at the same time, and the sum of the MSYs of each species as calculated would be greater than the combined MSY which could be really achieved. In so far as it is assumed that the production of a population is more stable than its components, it would seem preferable to calculate an overall MSY, from the catches of all species together in order to avoid this overestimation.

d) Criticism of the equilibrium idea

The very idea of equilibrium (stability) inherent in the MSY (maximum "sustainable" yield) concept is challenged since variations in the annual recruitments and thus, inevitably, in production occur. Forced attempts to achieve MSY during a bad recruitment sequence might lead to dangerous stock instability.

There is a tendency to assume that sustained effort at the F_{msy} level will enable, on the average, the maximum attainable mean catch to be obtained since the annual yield would fluctuate through natural causes on either side of the MSY. According to Doubleday (1976) and Sissenwine (1978) this is not true and the maximum average yield (MAY) is lower than MSY, all the more when natural variability is high.

All attempts to reach MSY therefore leads to overexploitation. On the other hand, fixing F at the F_{MSY} level results in a maximum average yield which is, in the long run, lower than the MSY.

Sissenwine (1978) pointed out that when there were annual fluctuations in production (which is true for penaeids) an annual adjustment in the rate of exploitation would lead to an increase in the maximum average yields obtainable over an extended period.

In discussing the idea of maximum sustainable yield, Sissenwine came to the conclusion that the only magnitude which corresponded to the letter of the term was the quantity that would be caught whatever the interannual variations in biomass, and it is thus the lowest predictable production on the average. In practice this implies poor use of good production years, but for species with a very short life-span (penaeids, cephalopods, etc.) and with very variable and unpredictable production, this technique could, according to the author be the only feasible one if the annual objective could not be adjusted according to the recruitment indices otherwise obtained. Gulland and Boerema (1973) suggested that when annual production is independent of parental abundance (which may be true of penaeids where annual variations in production seem to mask possible connections with parental stock abundance) it is enough to keep F at the level which is considered as optimum on the yield per recruit curve (F_{max} or $F_{0.1}$).

12.3.2 Technical arguments

a) The value of statistics

The simplicity of the model is based on the need for elementary fishery statistics for its specific applications. Larkin (1977) recalls that official statistics are incomplete and largely imprecise although statisticians would say that they are more precise than accurate. This is true for penaeids for which, because of the lack of good quality statistics, the data on yield and effort distribution by species and by unit stock are imprecise, the estimate of effort often approximative, and the data on artisanal fishing most often lacking.

b) Regression methods

Sissenwine (1978) criticises the use of regression of the c.p.u.e. on the fishing effort when the latter is determined by dividing the catch by the c.p.u.e. and when, in addition, smoothing by moving averages is applied to an effort series so as to take account of time lags as, for instance in Gulland's (1969) method. This confounds the independent variable (c.p.u.e.) and the dependent variable which, in this case, is in reality the effort, and introduces a significant correlation even for series of catch and c.p.u.e. figures taken at random.

c) Limited value for management

Apart from the considerations already listed, one of the other handicaps of the concept of MSY is its unsuitability for predicting the consequences of changes in the seasonal or age-specific fishing mortality vector, and thus for predicting the results of a change in mesh size, of a closed season, or of an increase in artisanal fishing effort on juveniles.

12.3.3 Socio-economic arguments

Since 1965, Christy and Scott have emphasized the inability of MSY to take social (employment, recreation, etc.) or economic (costs, returns, profits, etc.) factors into account.

12.3.4 Conclusions

The difficulties of using the maximum sustainable yield (MSY) or the maximum average yield (MAY) concepts as an objective for management must be acknowledged. The achievement of the physical maximum in catch (in weight or value) is not a justifiable objective since it is difficult to reach and can only be approached at the expense of some danger to reproduction and resource stability (although this risk might be limited for shrimps) and through undue cost increases which cannot be justified by the increase in catches. Alternative proposals to MSY are nevertheless rare and lack precision: the definition of Roedel's (1975) optimum sustainable yield, (OSY), concept emphasizes the scope of the problem. In fact this new concept is thus defined:

> "A deliberate melding of biological, economic, social and political values, designed to produce the maximum benefit to society from stocks that are sought for human use, taking into account the effect of harvesting on dependant or associated species".

In reality, as Sissenwine (1978) pointed out, the OSY is in practice based essentially on MSY modified by various constraints (economic, social, etc.) and Larkin's (1977) "epitaph for the concept of maximum sustainable yields" seems premature.

The MSY still appears therefore to be a quantity which is useful to define. It represents a constraint which should be identified and not exceeded unless there are compelling reasons to do so, but is not necessarily the objective to be achieved. It seems therefore useful to define as a management objective a point to the left of the MSY on the curve (Fig. 84a).

Gulland and Boerema (1973) proposed a definition of the "optimum" effort level on a yield per recruit curve as a function of F by the criterion $F_{0.1}$, defined as the point where the yield per recruit curve (or the tangent to the curve) has a slope equal to 10% of the slope of the tangent at the origin, that is, where the marginal yield becomes only 10% of the theoretical marginal yield of the virgin stock. This criterion allows an appreciable reduction in costs for small loss in total catch, and an increase in net economic rent as well as a great improvement in reproductive potential.

By analogy, in a general production model the optimum exploitation level f_{opt} can be defined empirically as that where the marginal catch (increase in catch for a supplementary unit of effort) falls below 10% of the cpue obtained from the stock at the very beginning of exploitation.

12.4 MANAGEMENT METHODS 1/

These can be classified into two groups, which are however not entirely distinct: methods to regulate the sizes caught and those which regulate fishing effort.

12.4.1 Regulation of sizes caught

All the methods which can be considered under this heading result in a decrease in the mortality of the young fish in the hope of improving production to the extent that the potential gains through growth of the survivors will largely compensate for losses by natural death. This can be obtained either by regulating mesh sizes, by establishing a minimum size of the fish landed, by closing or regulating exploitation in nurseries, or by closed seasons during migration seawards.

Since these measures exert no influence on the size of the fleet, they cannot exclude that, in the long-term, investments and costs do become excessive.

12.4.1.1 Regulation of mesh size

According to Lindner (1965) the increase in mesh size needed to arrive at an appreciable increase in the size of the shrimp caught would be such that the immediate losses would be unacceptable even if a small long-term benefit could be expected. This statement, which applies only to shrimps, is confirmed by Lhomme (1979) who noted that mesh sizes of 20 to 35 mm (bar size) give selection curves which are practically overlapping but clearly separable from curves derived from mesh sizes of 40 and 50 mm (Fig. 73).

According to Gulland (1972) regulation of mesh size is not effective for penaeids because the selection process is not very efficient (because of the presence of the rostrum and appendages which may hinder passage through the mesh. Boerema (1974) indicated that the "mesh regulation would not be very effective for regulating the shrimp size, due to the very wide selection range of trawl meshes for shrimp" (cf. 10.2 and 10.4.2). According to this author the enforcement of this regulation would have to be complemented by a legislation on minimum legal size for the shrimp caught which in turn would only prevent their sale but not their destruction by the nets.

However, according to Hynd (1973), Garcia and Lhomme (1977) 2/, Garcia et al. (1979), Lhomme (1979), such a regulation may be useful and the latter authors gave the following arguments:

- Since shrimps have a short life-span and rapid growth the possible annual increase would be obtained before the completion of the first annual cycle.
- Increasing mesh size leads to an increase in age and individual average weight and price per kilogramme (which depends on the individual average weight). The possible increase in value would be proportionally greater than the increase in tonnage.

1/ An inventory of the methods used in various countries is available in an FAO document (1973) for the Indian Ocean and in a work by Calder et al., 1974 (for the United States)

2/ See section 10.2 for additional reference

- Mesh size now in use by all shrimpers results in catching larger quantities of non marketable small fish which are now discarded (several tons/day/boat off the African coast). These fish are mostly juveniles and their intensive destruction seriously endangers recruitment of species exploited by other fisheries. Even a small increase in mesh size (for which benefits in terms of shrimp production have still to be assessed) may be beneficial for coastal trawling fisheries.

The problem of regulating mesh size becomes difficult when fishing is carried out simultaneously on shrimp species of different optimal sizes. Adjusting mesh to the optimum for the most profitable stocks (generally the larger species) leads to under exploitation of secondary ones.

In the same way it should be noted that the selectivity of traps, bamboo weirs and other types of estuarine devices can also be modified to allow juveniles to escape by increasing the gap size between the bamboo laths from which the barriers and the traps are made (Le Reste and Marcille, 1973).

In order to achieve integrated management of the exploitation of demersal stocks, not only should one consider the different shrimp species caught together but also the fish bycatch (of which only the most valuable specimens are kept for the definition of the optimum mesh size. This management should also take into account the effect of the shrimp trawls on the fish resources exploited by fish trawlers (massive destruction of juveniles).

There are mesh size regulations in most countries (in Australia, according to Ruello since 1880) but fishermen often get round the law in the following ways:

- by using a different mesh to the official one
- by lining the trawl cod-end outside or inside with a finer mesh
- simply by superimposing two layers of the legal mesh size for the cod-end with the result that the apertures are about half the original mesh size
- by attaching a very heavy weight to the end of the cod-end so as to obtain maximum stretching of the net, thus decreasing the openings.

It is important to note that when intensive recruitment takes place over a limited period, a seasonal closed fishing period just before recruitment produces an effect which is very similar to that of controlling mesh size (for the shrimp species concerned only, of course).

12.4.1.2 Minimum landing size

This regulation is intended:

- to make it inattractive to fish in areas where the little shrimps are too abundant
- to decrease the temptation to evade mesh regulations.

The specialists agree that this has proved to be an inefficient method when used alone. It obliges fishermen to discard the young shrimps caught. Precious time is lost in sorting the catch and in any case the young shrimps, because of their fragility, are dead when discarded and the effect on resource conservation is nil. In the few cases where this measure has been applied it was for practical commercial reasons (processing difficulties, limited markets) and under dealers' pressure rather than for serious biological reasons. Rounsefell (1975) pointed out that in certain estuarine zones of the Gulf of Mexico discards reach 80% of the catches. This example is enough to show the worthlessness of the method when applied alone.

12.4.1.3 Nursery management and protection

The very first stage of rapid growth of shrimp takes place in the estuaries in the intertidal zone, in vegetation or mangrove swamps, and protection of this phase comes under conservation of the habitat (see section 12.4.1.3 a).

a) Fishing prohibition

When young shrimps reach somewhat greater depths they are liable to be caught, first by artisanal fishing (push nets, traps, etc.) then, when the depth is sufficient, by motorized trawling. The areas populated by shrimps which are smaller than the authorized size at first capture should therefore be permanently closed to all types of fishing.

The protection would be strengthened if this rule were accompanied by a law requiring a minimum commercial size. In developing countries however, the law can be circumvented since small dried or smoked shrimps, sometimes powdered, are used as a condiment and are sold through traditional channels which are difficult to control.

b) Management of the environment

Nurseries should also be protected from such indirect injury as pollution. The location of the areas where juveniles are concentrated should be taken into account when choosing sites of polluting industries, urban development, etc. The biological rehabilitation of habitats which have been degraded is a management measure which can give good results. On the other hand, the destruction of aquatic vegetation by "artisanal" trawling may also cause an appreciable drop in production.

Artificial modification of river courses (for irrigation, by antisalt dams, etc.) is also liable to affect the biotic capacity and thus recruitment in certain nurseries.

Intensive dredging of entrances to lagoons changes the salinity distribution in the estuaries and can possibly have important consequences (changes in species composition , lowered abundance). On the other hand, operations for the regulation of water levels in swamp to promote sea-estuary exchanges can be such that the entry of larvae into the zones needed for growth is improved and stock production thus increased. Management of natural zones and even the construction of artificial intertidal zones (Kurata, 1979) has been proposed so as to decrease predation and thus improve larval survival (Kurata, 1972).

c) Stock enhancement by larval seeding

This technique is mostly practised in Japan and is a by-product of aquaculture. The relative ease with which shrimps can be cultivated to the postlarval stage and the difficulties or raising them economically to commercial size has led certain laboratories to examine seriously the possibilities of supplementing shrimp spawning with an artificial supply of cultivated postlarval or juveniles.

This is a difficult approach and practical results do not seem easy to demonstrate. Doi *et al.* (1972) have developed a methodology enabling the evolution of populations to be followed so that the effect of seeding a wild stock can be assessed quantitatively and he emphasizes the major difficulties of such attempts. Kurata (1972) has listed the conditions essential to successful seeding and emphasized that certain principles involved are incompatible. According to Hiroko (1973) there are only a few biological proofs of the advantages produced with this technique and Doi *et al.* (1973) showed that in the Seto inland sea, where such experiments were conducted, the shrimp production was inversely proportional to the size of the intertidal zone which had been contaminated by human activities (Fig. 86). According to Doi the loss is 6 tons/sq.km of the natural zone destroyed and the result shows that it is an illusion to seek improvement in one way by artificially enhancing recruitment which has been destroyed in another way, that is by pollution or degradation of the nurseries.

However, a study by Hasegawa *et al.* (1975), pointed out that the recapture rate of "seedlings" by fishermen can reach 42% and that the operation can be profitable if the techniques for introducing the young shrimps are improved. Definitive results of this management technique still need to be demonstrated and further studies seem to be required before its efficiency can be assessed.

12.4.1.4 Closed seasons in estuaries

Except in marginal zones of the habitat, the greater part of the trawlable depths of a bay are populated by shrimps of which the size varies with the seasons. Because shrimps require protection up to a certain size, it is necessary to prohibit fishing until the size limit is reached.

The "ideal" closed season can, on average, be fixed from experimental data. However, the dynamics of the cohorts vary appreciably from one year to the other, depending on the date of the beginning of the season of spawning and larval recruitment in the estuaries as well as on the combination of temperature and salinity during the nursery period (Ford and St Amant, 1971). Since fishermen have great reservations about such a closure, it may often be necessary to decide every year on precise opening and closing dates which depend on the development of the shrimp population as established from continuous sampling during the critical period. The development of the shrimp biomass is an extremely dynamic process and according to Ruello (1973) the advantages gained by flexible management justify the necessary supplementary research costs. The opening date is calculated by extrapolation of the data collected during the preceding weeks and corresponds to the date at which a certain percentage (50 or 75% for example) of the population exceeds the adopted minimum size limit. A theoretical example is shown in Fig. 87. Such a method is used in the United States (Ford and St Amant, 1971; Ingle, 1956, 1960) and in Australia (Ruello, 1975).

The establishment of closed areas or closed seasons results in delaying the age of first capture to come closer to the optimum age, thus increasing the available average biomass and the total yield. When several species coexist in an estuary, the application of this principle is more complex, especially when the spawning seasons are different. Examples are given by Ford and St Amant (1971) and Eldridge and Goldstein (1977) proposed schemes which could be used when two species are involved.

12.4.1.5 Closed seasons at sea

Sea fishing could be closed at the moment of most intense recruitment. In this way the exploitation of concentrations of juveniles with rapid growth which have not reached the size of sexual maturity can be avoided. This closed season could be coordinated with the closed season in the estuaries if such exists. Work undertaken in the Ivory Coast (Garcia, 1977) shows that the expected results are very dependent on the pattern of the marine seasonal variations in catchability. Grant and Griffin (1979) studied the consequences of such closures on the catches in the Gulf of Mexico.

The economic side of these closed seasons must be considered before the decision to apply them is made. In fact, a short closed season (1 month) can be put to advantage by boat owners for repairs (always assuming that repair yards can take the whole fleet in the same month). A longer period can be costly if boats have no other possible activity and must cease operations. The economic advantages in this case, may be wasted because the fixed costs have still to be borne during the closure period.

There are however often possibilities of alternative activities eventually making slight adaptations in the equipment, which indeed are often undertaken by fishermen in periods of low yields. Thus, for example in the Ivory Coast in the cold season, part of the effort is diverted to coastal or deepwater shrimps which are neglected for the rest of the year. On the Southeast coast of the United States shrimpers look for fish out of the shrimping season (lutjanidae, serranidae, sparidae, pomadasidae) or fish for crabs, oysters, clams or deepwater shrimp (Mc Kenzie, 1974).

12.4.2 Control of fishing effort

Management of this kind results in cost reduction and often in increases in the catch and its value. Two kinds of regulations can be considered; those which aim at limiting individual fishing efficiency and those which seek to limit fleet capacity.

a) Limitation of fishing efficiency

These measures are rarely applied to shrimping operation at sea where innovation is the rule and where the change from classical trawling to double rig and then to TWIN equipment (see section 3.2) has allowed a continuous improvement in fishing efficiency. Decreasing the fleet efficiency adds to the costs of fishing and Gulland (1972) concluded that such measures can only be justified economically if they serve to avoid the destruction of juveniles (shrimps or associated species). Thus in some estuaries

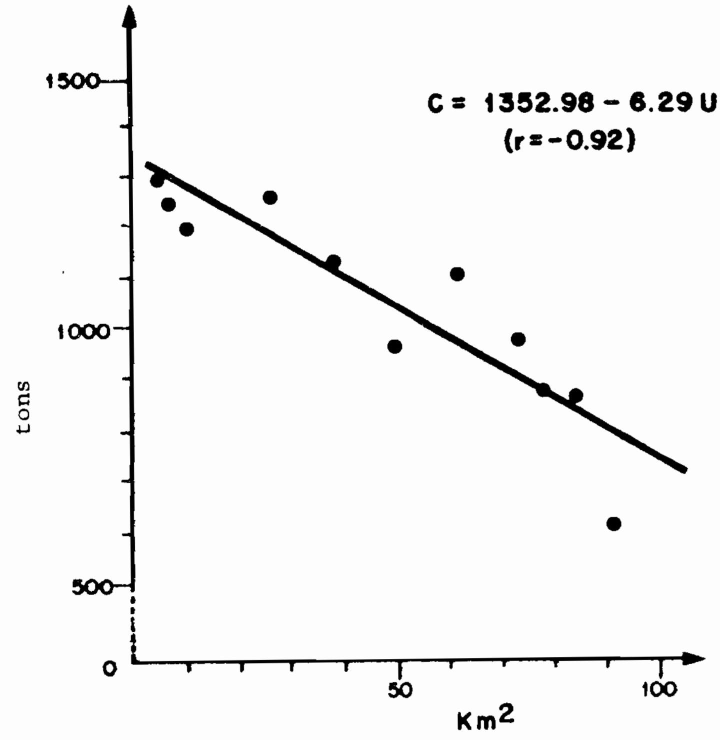


Fig. 86 Influence of the cumulated area of reclaimed land on annual shrimp (*Penaeus japonicus*) catches in the Seto inland Sea (from Doi et al. 1973)

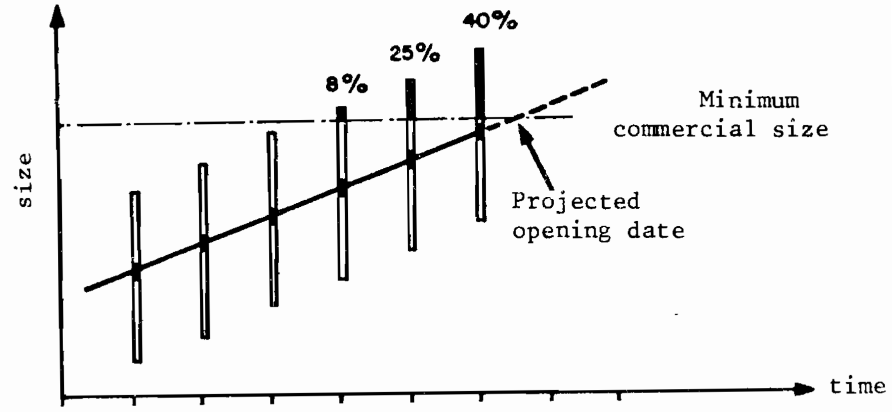


Fig. 87 Schematic diagram for the determination of the opening day of the fishery in the estuaries (adapted from Ford and St. Amant. 1971)

the size of the nets is limited as is the case in Australia since 1965 (Ruello, 1975). In addition, dragnets towed in shallow waters are forbidden in certain estuarine zones of Senegal. Artisanal fisheries using fixed nets, are a particular problem. The overall efficiency of this fishery depends on the position of the nets the efficiency of which varies according to the location and is especially high in passages and gullies (see chapter 8.5). The need to allow a certain amount of escape and thus a better distribution of financial returns along the migration route could justify the establishment of regulations on position and number of nets used. Prohibition of the use of efficient equipment could also be justified if it serves to give protection to a class of fishermen which does not have the means to invest in costly equipment. Trawling in lagoons could thus be forbidden so as to leave the benefits to the artisanal fishermen using fixed nets. It should however be remembered that the success of measures aimed at limiting the efficiency of the fishing nets is often challenged since the effective fishing power depends on many factors associated with the gear, the boat, and the effort distribution etc. which frequently enables fishermen to continue to increase efficiency by the use of a non-limited factor.

12.4.2.2 Effort (or yield) quota

Certain closed seasons also seem to be an indirect costly and inefficient way of limiting fleet efficiency. This is the case for example when fishing is discontinued when the effort or the catch has reached a certain level. This measure lowers running costs (in fuel) but if it is not accompanied by a fleet limitation, it is generally not enough to hinder long-term over-investment.

It has been said that when dealing with animals with a short life-span such as penaeid shrimps, cephalopods and perhaps some tropical fish species 1/, regulation by annual catch quota can be found inadequate. In fact, each fisherman, in trying to achieve a growing share of the overall quota tends to increase his fishing power, and especially to concentrate his operations earlier and earlier after recruitment. The same total catch would thus be composed of an increasingly greater number of increasingly younger juveniles which would cause a parallel increase in fishing mortality for the same total catch. In such a situation, regulation will not achieve the expected result, that is to keep the exploitation rate at the desired level. It might even have a harmful effect at the economics level. Nothing in fact hinders investments from seriously exceeding the level which would normally be necessary if the fishing operations were uniformaly distributed over the whole year. The annual effort could be better distributed by establishing quotas for the short periods (quarterly for example) so chosen as to give a better distribution of exploitation throughout the annual cycle. Such regulations would always however be more difficult to apply.

At the operational level, establishing catch quotas to control fishing mortality also assumes that the responsible management authority should be informed within short time of the catches being actually made. The difficulty that coastal countries experience in ascertaining the species composition and weight of the catches made by various fleets operating in their exclusive economic zones (difficulty in sampling their artisanal fisheries and control the activities and performances of foreign boats operating under licence) argue in favour of employing effort limitation.

12.4.2.3 Limitation of the access to fisheries

None of the measures recommended above can by itself alone avoid overexploitation. At the most the state of stocks can be improved and profitability temporarily increased. Very quickly, however, this improvement will encourage shipowners to invest in supplementary efforts which, through the action of the mechanisms already described at the beginning of the chapter, will waste any profits that the regulation might have produced (Pearse, 1980).

Regulation of the level of exploitation by directly controlling the catching power of a fleet, for example by limiting the number of boats or nets, avoids such difficulties. It not only prevents biological overexploitation of stocks but also, and this is not the least of the advantages, allows the exploitation costs to be minimized. In addition, if the effort needed to obtain the expected optimum exploitation level is overestimated, such a regulation will not involve the same damage which would arise from regulation by catch quota, if the maximum average yield has been overestimated (Walter, 1976).

1/ Where the bulk of the catch is made on the recruitment of the year

In view of the short life-span of tropical shrimps and of the fact that year to year variations in abundance are much greater than variations in catchability and because this method provides a possibility of controlling both the catches and the costs of exploitation, preference should be given to the regulation of exploitation inputs (boats, gears).

This can, for example, be done by limiting the number of boats in national fleets as well as the number of licenses granted to foreign boats in countries where foreign fishing takes place (such licenses must obviously state the limits of the size and other characteristics which affect the fishing powers of the boats as well as the type of gear and the permitted species).

Limitation of the number of fishing units is simple to apply, especially when applied early in the fishery, but control of exploitation rates by limiting fishing effort also involves the estimation and monitoring of the performances of different boat classes and, above all, the increases in efficiency that will certainly follow from technical innovations (increase in fishing power) or from improvements in the space-time distribution of fishing operations (improvement in the overall catchability coefficient). In principle, the catch rate of each boat class in each fishery can be determined from observation of the performance of a sample of boats. This possibility can appreciably simplify data collection. The latter is in any case indispensable for a periodic assessment of the gains in efficiency in order to determine the overall number of licenses required. Log books, which must be kept as a condition to obtain a licence, can be an excellent source of data for monitoring the fleet activity.

The introduction of a management system by licensing has both advantages and disadvantages. One of the essential aspects is that the regulation shall result in substantial profits to be shared among license holders, which adds considerably to the value of the licenses. According to Olsen (1975) this bonus reaches US$ 20 000 to 30 000 in Southern Australia.

This phenomenon may create some tension when the returns become much greater than those obtained from other trades (Haysom, 1975) as well as considerable pressure from outside from those who want to have access to the fishery.

Introduction of a high license fee will allow the administration to recuperate part of the surplus value created by management and will discourage further applications for licenses. According to Gulland (1978) the establishment of a license fee which becomes gradually higher as the optimum fishing effort level is approached must progressively discourage further applications since both the fishermen and the administration will reach the same conclusions regarding fishery profit levels. The potential value of a license can be used to stimulate exploitation of less frequented zones or species (by making exploratory fishing or landing a certain tonnage of fish of certain species a condition for obtaining a license) or to encourage the establishment of infrastructures ashore. Hancock (1975) noted that the exploitation of distant stocks was encouraged in Australia by limiting, a priori, access to such stocks thus creating a quasi monopoly for the pioneering companies.

On the other hand, according to Bowen (1975) the security given by a licensing system hinders the search for new fishing grounds, creates frustrating situations of near monopoly and artificially increases the value of licensed boats, creates an awkward discrimination against outside fishermen and allow inefficient fishing units to survive. Gulland (1972) also noted that the system could discourage technical advances though Hancock (1975) observed that this was not so in Australia where the fishing technique had always developed rapidly.

It should be noted that when there are several neighbouring stocks the granting of licenses for a given stock must be accompanied by the obligation to exploit this stock during a certain number of months annually.

Haysom (1975), in summarizing the results of an experiment on the limitation of entry into the Moreton Bay fishery (Australia), emphasized that the establishment of such a system for an already exploited stock gives many social and economic problems (especially if the stock was overexploited) and that the decision to grant licenses must be based on an adequate socio-economic analysis.

Since the problem of direct effort limitation is a general one and examples for penaeids are still rare (although this technique has been used in Australia since 1960, according to Meany, 1978) this section has been deliberately limited to setting out some ideas. For more examples and further development of the subject the work of Stokes (1979), for example, can be consulted.

12.4.2.4 Optimum distribution of effort on multiple resources

When the resource comprises a pattern of geographically distinct stocks composed of the same species, or of different species with different economic value and different abundance, it might be supposed that there is a strategy of distribution of effort on the resource which would allow the fleet to optimize the returns produced by the stock. Garrod (1973) for example pointed out that "under certain circumstances determined by the variability of a particular resource complex, a density-dependent regime of exploitation may be a more efficient method of exploitation of a given array of resources". An excellent example is given by Clayden (1972) for the North Atlantic cod-fishing complex.

For penaeids the exploited complex can be a group of more or less independent small adult stocks distributed along the total length of the coast, as in Madagascar (Marcille, 1978); the exploitation was first successively developed for the different elements as and when they were discovered and now all are exploited simultaneously. Another example can be found in Senegal where two independent stocks of Penaeus notialis exist (St. Louis and Roxo Bissagos). The first has a smaller potential, is closer to the main port and shows distinct seasonal variations in abundance. The second has much higher potential, is farther from the main port and shows practically stable abundance throughout the year. The fishing effort applied to the northern stock was at first very seasonal and when the yields were comparatively too low all the effort from the first was transferred to the second stock which was fished all year round. With the increase in the overall effort and the consequent decrease in yields on the second stock, fishing became less and less seasonal in the first one. The seasonal transfer of effort from one stock to the other is now very limited and two different fleets have in fact developed with different horse-powers and fish preservation characteristics. This development came about naturally and it can be assumed that it is the result of the fisherman searching empirically for some maximum return.

The problem becomes still more complicated if the diversification of this fishery since 1961 is taken into account. The shrimpers now sometimes look also for other species (flatfish, sciaenidae, pomadasydae, brotulae, etc.) either exclusively during certain trips, or in combination with shrimp fishing. Since the characteristics of the exploited stocks are very different there are certainly strategies which allow optimization of the returns (which the fishermen practice empirically) while at the same time maintaining the perennial nature of the stock (which is the responsibility of the administration).

Another and final example is found in the Ivory Coast where, since 1974-75, shrimpers exploiting P. notialis have begun to be interested in less sought after species such as Parapenaeus longirostris and even Parapenaeopsis atlantica which are abundant on the slopes and in river mouths respectively. The seasonal distribution of the effort on the three species is determined empirically as a function of the potential value of the catches at a given moment and also as a function of market demand.

Although this line of research will certainly be one of the most important over the next ten years, as far as the consequences for management are concerned, little work has yet been carried out on penaeids. Marcille (1978) has approached the question for stocks on the West Coast of Madagascar and has constructed a simple simulation model based on the equations of the production models of each stock attempting to find for each overall effort level the distribution which allows the highest total catch. He showed that the catches theoretically possible were 20% greater than those obtained by the fishery during its previous development.

It is obvious that economic parameters (steaming time, fuel costs, proximity of a landing port, value of species caught) play a major role in determining the optimum strategy. Whereas they were taken into account in a simplified way by Marcille, they are an important element of the simulation model devised by Clark and Kirkwood (1979) in Australia to optimize the development of a shrimp fishery with free entry, with two types of boats and two species of different values, by calculating the optimum space-time allocation of effort and the best composition of the fleet.

It should be noted that whether simultaneous exploitation of two geographically distinct resources of the same species, or two different species with a similar distribution in space but different catchabilities and values, are considered the problem raised is about the same. In both cases an optimum distribution scheme of fishing mortality exists, whatever the optimization criterion used.

We can only give a brief reminder here of one of the most important aspects of resource management in tropical zones. If the data for each elementary stock of the exploited complex are available and if these elements are thought not to interact, the search for an optimum theoretical strategy can be a relatively simple process. It will be much more difficult if the stocks considered do interact.

In all cases, the implementation of a management system to apply such an optimum strategy will certainly not be easy.

12.5 DISCUSSION

There are many available methods for the management of penaeids. Which one will be applicable will depend on the scientific knowledge available, the socio-economic constraints and the objectives sought.

Management should be an integrated process during the development of a fishery from the promotion of its start on to the definition of optimum management schemes, surveillance and monitoring of the state of the resource.

It is also an integrated process insofar as management must not be limited to the catching process only. It has been noted that the profit obtained by a limited access to the fishery can be used to create an infrastructure ashore. At the same time the worry to avoid overinvestment may lead to optimizing the number of processing plants and organizing the trade outlets. (A road network for example would help to promote the artisanal fishery by widening the market and, eventually, opening up an export market.)

Management must moreover take into account interactions with other fisheries (destruction of juvenile fish by shrimpers for example). The potential high rent of shrimp fishing can make it an instrument for developing little exploited zones. Fishing which began with shrimp can later be progressively diversified to include fish (by making it obligatory, for example, for each authorized fishing boat to land a certain tonnage of fish, if necessary by suitably adapting the boat).

Finally, one of the chief management problems in shrimp fisheries involves the conflicts between juvenile and adult exploitation. The first requires more or less sophisticated gear, from the cast net to the small trawler, and catches young individuals before their sexual maturity and optimum size. The second catches sub-adults and adults on an industrial scale. The two socio-economic systems involved are generally very different. Fishing in very shallow waters (less than 5 m) takes the shrimp while they are in full growth, even before the estuarine phase of the life cycle is completed. This juvenile exploitation causes an appreciable reduction in the recruitment to the marine stock. It can in fact be assumed that at the age when shrimps migrate the greatest part of the natural mortality (which takes place especially at the larval stage) has already occurred. Because of this, the decrease in number of the potential recruitment by the artisanal fishery on juveniles will be followed by a directly proportional decrease in the potential catch at sea (by weight). It is therefore evident that the maximum average yield at sea would be achieved by total elimination of artisanal fishing. Because of the social importance of this type of fishing it is no less evident that complete elimination would be difficult to justify. It should on the contrary be theoretically possible to suppress sea fishing and only retain artisanal fishing. However this extreme solution may be not desirable from the economic point of view.

The study of the relation between total yield (sea plus lagoon, in tonnage and value) and the various combinations of exploitation level in the two types of fishery is complex and requires the use of simulation techniques. A study of this kind carried out by Garcia (1977) on the Ivory Coast stocks of

Penaeus notialis showed (Fig. 82) that at exploitation rates at sea close to the maximum (which is now the rule almost everywhere), variations in lagoon exploitation rates from 0 to 50% have only a slight influence on total yield (in weight), but cause a significant beneficial change in value (from 12 to 40%). This result may not necessarily be generalized to all stocks of similar population dynamic characteristics. It depends greatly, in fact, on the changes of catchability with age and on seasonal variations in catchability linked to local hydrological conditions.

Grant and Griffin (1979) did a similar work more extensive on the economic aspects. They also concluded that variations in exploitation rates on juveniles did not influence total yield.

Other criteria, such as the respective cost of investments, including those in foreign currency, per ton of estuarine catch and of fishing at sea, the respective cost of exploitation, amount of employment created in rural or urban zones, the distribution of profits arising from fishing in different social and professional categories, etc. should also be considered, so as to determine a rational scheme of exploitation of the shrimp stocks (Troadec, 1978). McGoodwin (1979) gave for the Pacific Coast of Mexico a good example of the disastrous results, for the artisanal sector, of a shrimp fishery management programme based on simple economic considerations which completely discounted the social aspects by imposing a severe reduction in a traditional small-scale fishery.

Finally, shrimp exploitation management should also take into account the geographical coordination of management programmes.

When the resource is composed of shrimps which complete practically their whole life cycle in the estuary, as for example Metapenaeus mackleyi, each stock probably constitutes a distinct unit which can be managed separately.

When, on the other hand, the resource consists of the more classical shrimp species migrating from estuaries to sometimes very distant marine fishing grounds, the definition of unit stocks is perhaps more complicated. Mixtures can in fact occur by adult migration from one small bay to another (as in Madagascar). Then resource management must take the total of the interrelated sub-stocks into account and attempt to harmonize the regulations and to obtain the optimal time-space distribution of fishing effort (see section 12.4.2.4).

A resource may also belong to two different countries. Although penaeid migrations are generally limited at sea, they can nevertheless lead to such a situation (between the United States and Mexico, the Ivory Coast and Liberia or Senegal and Guinea Bissau) when the simple dispersion process or the seasonal migrations lead the shrimp to cross the political boundaries. The Roxo-Bissagos shrimp stock is an interesting example where a large part of the nurseries is in Senegal (where the artisanal fishing is extremely important) while the adult stock occurs for the great part in Guinea Bissau). The classical problem of conflicts between artisanal and industrial fishing is here still more complex since the two exploitation systems belong to countries whose economic interests do not necessarily coincide.

The situation is very similar when the resource belongs to federal states of the same country which have their own jurisdiction (Australia, United States). The definition of some agreed upon regional management system is then required. Good examples can be found in work carried out by Etzold and Christmas (1977) for the Gulf of Mexico and Eldrige and Goldstein (1977) for the Southeast coast of the United States.

The management of virgin stocks is a particular problem and although there are probably not many left, it is worthwhile to remember the action sequence proposed by Gulland (1972) and adopted for certain Australian stocks (Hancock, 1975).

1. To make a first approximate assessment of the potential and the maximum number of boats to be authorized, based on surface area of the resource and a comparison with other stocks in comparable zones.

2. To issue a number of licenses below this maximum and to require the provision of detailed statistics (fishing logbooks) as one of the obligatory conditions to granting a license.

3. To follow the activities of such boats for 2 or 3 years (the length of the probationary period could be associated with stock stability).

4. At the end of this period, to reassess the maximum and to correct the number of licenses if necessary, while at the same time remaining below the new maximum [1]. Hancock (1979) suggested that only 'conditional' licenses with no guarantees of renewal should be granted and that these should be subject to reappraisals of the state of the stock.

5. To make a study of boat profitability.

6. To calculate net returns and if very large, to decide on their use (payment of fishing rights, obligations to land fish, creation of employment by installing shore processing plants, etc.).

7. Steps 3 to 6 can be repeated periodically.

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[1] The danger of an assessment based on a too short a series of data, when variations in abundance can be foreseen should be noted with Hancock (1975). The assignment of natural trends in c.p.u.e. to exploitation effect leads to false assessment of potential.

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M-43
ISBN 92-5-101069-2