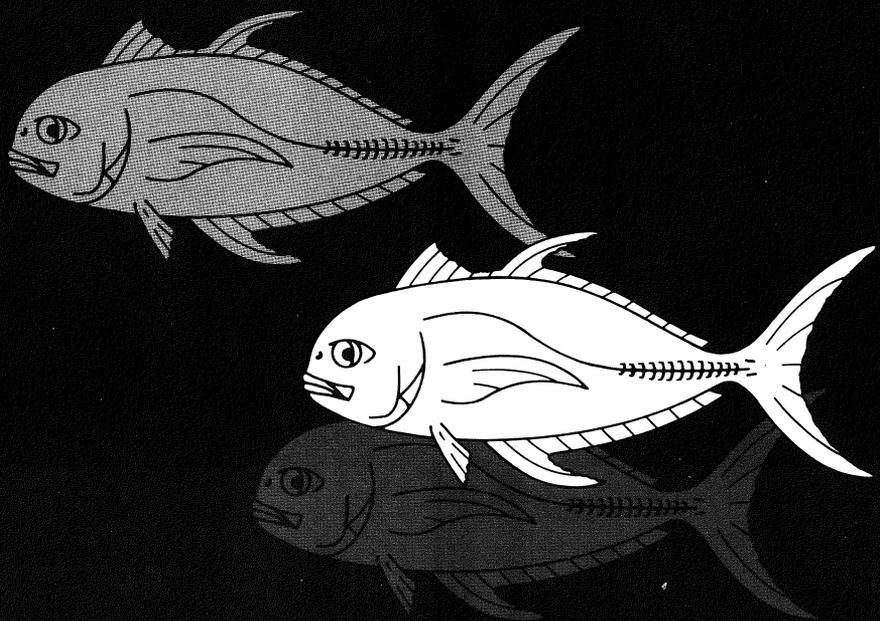


Ecology of Tropical Oceans



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Chapter 9

Dynamics of Tropical Fish Populations

OVERCOMING A MYTHOLOGY

Progress in understanding the dynamics of tropical fish populations has been hampered by the limited research capability of many tropical countries, which have relatively few marine scientists as well a general absence of long time series of catch, effort, and age composition data for their fisheries. Such data are available for many northern stocks, and have enabled analysis of the populations of paradigmatic species such as cod, plaice, and herring to have been carried to a high level of sophistication.

Thus, it is still difficult and sometimes impossible in the tropics to apply the principal concepts and methods that have emerged from the study and management of the great high-latitude fisheries. This problem is compounded because concepts and methods that are really perfectly applicable to tropical fish are often perceived to be irrelevant in the tropical context, and because of perceived fundamental differences between temperate and tropical fishes that are actually reflections of underlying quantitative differences in, for instance, rates of growth or mortality.

The lack of scientific capability in tropical countries, and how this constrains their access to the "Common Heritage of Mankind" in the seas, has been widely discussed in relation to the general development of the Third World (Goodwin and Nacht, 1986; Marr, 1982) as well as in works dealing with transfer of science and technology (Ziman, 1976) and we shall not enlarge on this problem here, except to note in passing that it seems to us that progress is now being made rather rapidly, and that the situation in the marine science programs of many tropical countries has much improved over the last 10 years or so.

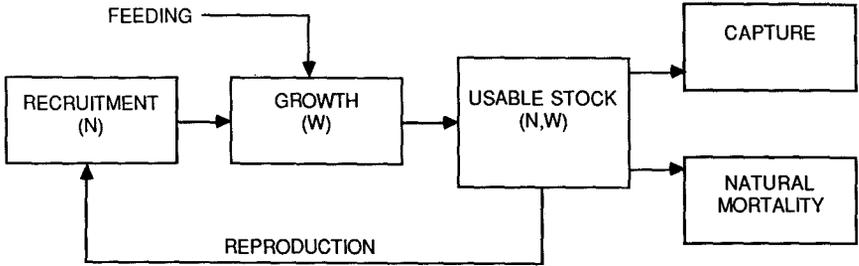


Fig. 9.1. Main factors investigated in fish population dynamics: : recruitment, growth (positive factors), capture and natural mortality (negative) and stock size. N, Numbers; W, weight. (From Pauly, 1982a, modified from Ricker, 1975.)

Because we believe that only a conscious attempt to deal with the multilayered mythology shrouding the dynamics of tropical fish populations can provide a base upon which progress will occur, dispelling this mythology will be the central theme of this chapter. So, in what follows, we shall attempt to separate what we believe are characteristic and basic features of tropical marine fish populations from features that have been attributed to them after only cursory analysis, based on hasty comparison with much better-known temperate fish populations. We shall review the nutrition, growth, mortality, reproduction, and recruitment of tropical fish populations, that is, those attributes that determine their potential yield to fisheries (Fig. 9.1).

GROWTH OF FISHES

One of the earliest scientific contributions on the age and growth of tropical fishes (Mohr, 1921) rationalized such studies in the following words:

In modern fisheries research, ageing of fishes is very important because . . . through age determination we have the means to identify the age composition of our fish population, and so it can be determined to what degree the various age classes are utilized by the fishery. Only an exact knowledge of the age of the fish allows inferences on the appropriateness or the need for management measures such as closed seasons or minimum sizes"

Mohr then went on to describe what she perceived (already then!) as the major problem of biological studies on tropical fish, namely "the suggestion, and later the dogma, that the scales of tropical fish should have no annual rings." This myth persisted widely among fishery biologists (including one of us) until the 1960s, and although, as we shall discuss below,

conditions do occur where tropical fishes do not seem to generate annual rings on their hard parts, such rings are now known to occur in scales, otoliths, and vertebrae of tropical fish under far too wide a range of conditions to be dismissed as exceptions that prove the rule.

Another related myth states that spawning in the tropics is continuous, and therefore analysis of the growth of tropical fish based on the study of length-frequency data must fail. Once again, although there have been some puzzling failures of length-frequency analysis to generate growth data, such as the case of *Ethmalosa dorsalis* in West Africa (Salzen, 1958), this technique is now widely and effectively applied to tropical fish populations.

In fact, as we shall discuss below, while spawning of tropical fish is often more protracted than that of temperate fish, it is usually concentrated in one or two periods each year. Also we must remember that it is not necessarily the fluctuations of spawning themselves that generate the peaks and troughs of length-frequency data. The same effect can be caused by the occurrence during larval and juvenile life of recruitment windows (Bakun *et al.*, 1982), which can vary seasonally even when egg production is constant. Later, we shall present several length-frequency data sets from typical tropical fish, all displaying well-structured peaks and troughs, and which can be rather simply analyzed using Petersen's method (Petersen, 1891), Modal Progression Analysis (George and Banerji, 1964), or computer-based modifications of earlier techniques (Pauly and David, 1981).

The final myth we shall attempt to dispel is the frequently repeated statement that tropical marine fish are not subject to growth oscillations, or seasonal variations in their rate of growth. Of course, growth checks in tropical freshwater fish are well known, and known to be caused by wet-dry season alternation in riverine or lacustrine environments. Models could therefore be derived to account for growth fluctuations in yield computations for tropical freshwater fisheries (e.g., Daget and Ecoutin, 1976). We shall emphasize in this chapter that the growth of tropical marine fish can also be significantly checked by seasonal changes in their environment, and that faulty concepts and analyses probably explain occasional failures to identify seasonal changes in growth rate in tropical marine fishes.

A Simple Model of Fish Growth

Many general models exist to describe and explain the growth of fish. Most of these have been formulated for cold-water fishes, and treat tropical forms as an exception (see, for example, Ursin, 1967). In this section

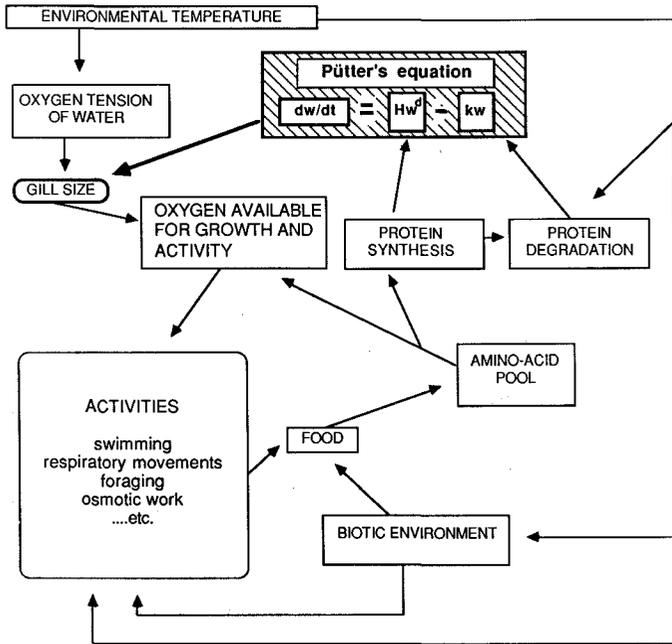


Fig. 9.2. Graphical model of fish growth with excretion process omitted, with emphasis on the limiting role for oxygen availability for protein synthesis. (Modified from Pauly, 1981.)

we propose a simple, general growth model which is applicable to fish of all latitudes.

Figure 9.2 presents a simple metabolic model of fish growth from which various forms of the well-known von Bertalanffy equation can be derived (von Bertalanffy, 1938; Pauly, 1981) and which accommodates, among other things, the tendency for tropical fish or warm water biota in general to remain smaller (i.e., to reach smaller asymptotic sizes) than their temperate counterparts.

This model is based on the following elementary observations (Pauly, 1981):

1. Fish are aerobic heterotrophs that need oxygen both for maintenance and for the synthesis of new body substances.
2. Oxygen cannot be stored by fish in more than insignificant quantities.
3. Oxygen enters the body of fish through a surface (gills, or gills + body surface) which on geometric grounds cannot grow as fast as body volume (weight) and hence oxygen demand.

From these three observations it follows that factors such as elevated temperature or stress (Selye, 1980), which increase routine metabolism, will decrease the amount of oxygen available per unit time for growth (Fig. 9.2). Such factors must lead, given species-specific anatomical constraints, to a reduction of the largest size reached by the oldest animals of a given population (Fig. 9.3).

The version of the von Bertalanffy growth model used here can be derived also from the formulation

$$\begin{array}{l} \text{Oxygen} \\ \text{available} \\ \text{for} \\ \text{growth} \end{array} = \begin{array}{l} \text{Oxygen supplied} \\ \text{through the} \\ \text{gills and other} \\ \text{body surfaces} \end{array} - \begin{array}{l} \text{Oxygen needed by} \\ \text{entire fish} \\ \text{for maintenance and} \\ \text{other activities} \end{array} \quad (9.1)$$

It should be noted in interpreting this formulation that the oxygen consumption of fish, as measured experimentally (e.g., Scholander *et al.*, 1953), is the oxygen available to the tissues of the fish and not its whole-organism oxygen demand, as is frequently assumed.

Equation (9.1) leads, since synthesis of body substance is oxygen dependent, to the better-known equation of Pütter (1920)

$$dw/dt = Hw^d - kw \quad (9.2)$$

where dw/dt is the growth rate, H the rate of synthesis of body substance, k a constant related to body oxygen requirements, w the body weight, and

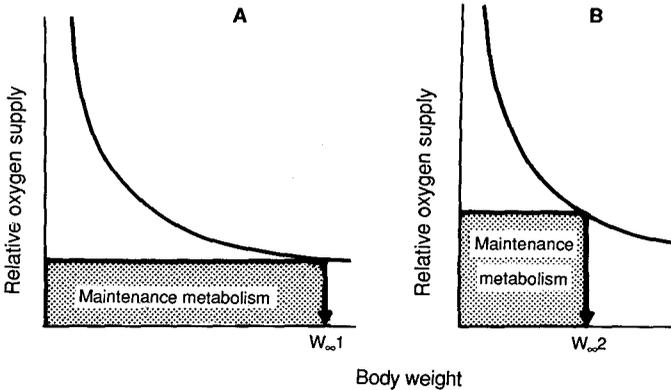


Fig. 9.3. Relationship between oxygen supply per unit of body weight (i.e., gill surface area per unit body weight) and the body weight of growing fish. Note that in A growth in weight must cease when, at W_{∞} , O_2 supply is equal to maintenance requirements and that for B any factor increasing maintenance requirements (elevated ambient temperature, reduced food availability, stress, etc.) will tend to reduce the weight at which O_2 supply becomes limiting to further growth and hence reduces W_{∞} . (From Pauly, 1984.)

d an exponent smaller than unity and often set equal to $2/3$ (Bertalanffy, 1938; Pauly, 1981). Equation (9.2) can be integrated to the von Bertalanffy growth formula (VBGF), often used to model the growth of tropical fishes

$$L_t = L_\infty (1 - e^{-K(t-t_0)}) \quad (9.3)$$

where L_t is the length of fish at age t , L_∞ is the average length of fish of the stock in question would reach if they were to live indefinitely, K is a constant equal to $1/3$ of k in Eq. (9.2) and t_0 is the (usually negative) age the fish would have at zero length in the unlikely case that adult growth patterns also applied to newly hatched fish, so that t_0 is usually only a convenience parameter. The corresponding equation for growth in weight is

$$W_t = L_\infty (1 - e^{-K(t-t_0)})^3 \quad (9.4)$$

where W_t and W_∞ are the weights corresponding to L_t and L_∞ , respectively. Other versions of the VBGF exist, but the two versions presented here are sufficient to support the following discussion.

The model in Eqs. (9.1, 9.2) and Fig. 9.2 implies that factors which increase oxygen demand will lead to an increase in the parameter K of the VBGF, and a reduction of its parameters L_∞ or W_∞ . For a given species, this leads to a near constancy of the parameter ϕ' , defined by

$$\phi' = \log_{10} K + 2 \log_{10} L_\infty \quad (9.5)$$

and of the parameter ϕ , defined by

$$\phi = \log_{10} K + 2/3 \log_{10} W_\infty \quad (9.6)$$

To illustrate this, Fig. 9.4 shows the nearly normal, and rather narrow, frequency distributions of ϕ' values in various stocks of skipjack tuna (*Katsuwonus pelamis*).

Thus, while fitting of growth curves to empirical size-at-age data may lead in any given species to a wide range of growth parameter values (see Table 9.1), the underlying growth performance of the species in question can be captured by a single parameter based on the two growth parameters L_∞ and K and which, moreover, can be shown to be related to gill size, as required by a theory that links growth performance and oxygen supply (Fig. 9.5).

Seasonal growth oscillation of tropical fish can be expressed by a modified version of the VBGF of the form

$$L_t = L_\infty [(1 - \exp[-K(t-t_0)]) + [(CK/2\pi) \sin 2\pi(t-t_s)]] \quad (9.7)$$

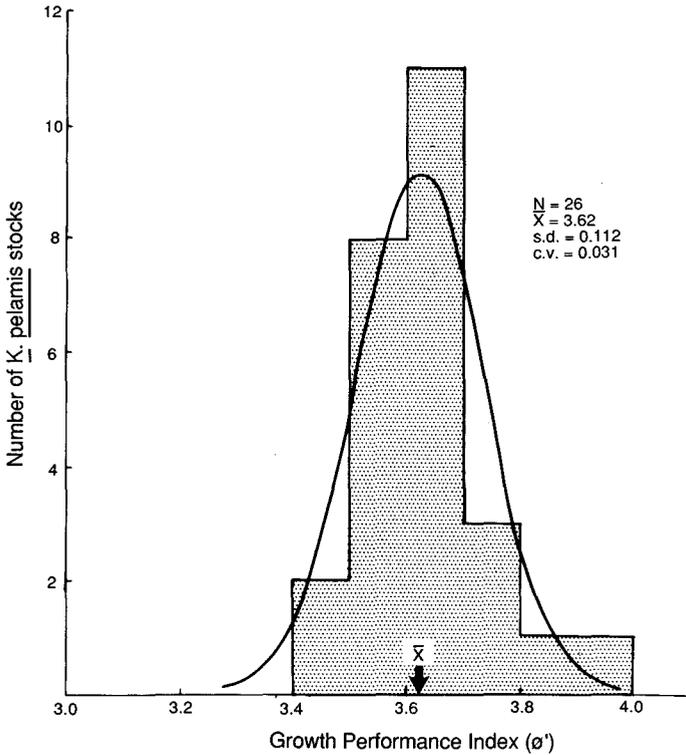


Fig. 9.4. Frequency distribution of ϕ' ($\log_{10} K + 2 \log_{10} L_{\infty}$) in 26 stocks of skipjack tuna (*K. pelamis*).

where L_t , t , L_{∞} , and K are defined as above, and where C and t_s are new parameters. The first of these parameters (C) expresses the amplitude of the seasonal growth oscillations (Fig. 9.6), and usually takes values ranging between 0 (no growth oscillations) and 1 (strong growth oscillations, generating one complete growth stop per year). The second parameter (t_s) fixes the start of a sinusoidal growth oscillation in relation to $t = 0$ and need not concern us further here.

The model and the seven equations presented in this section, along with Figs. 9.2 and 9.3, suffice to explain and illustrate the fundamental aspects of the growth of tropical fishes (and invertebrates, too, as we shall discuss in Chapter 10). We can therefore proceed to an examination of how this model can be applied in practice to analyzing the population biology of tropical sea fish.

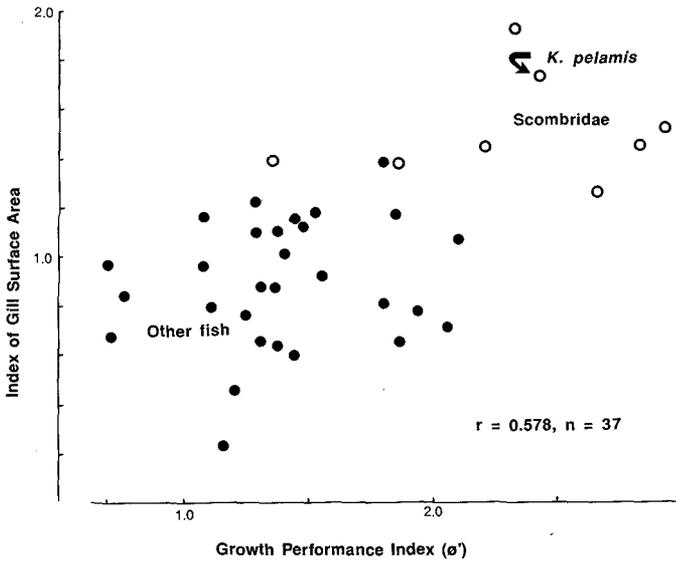


Fig. 9.5. Relationship between standardised gill surface area and the index of growth performance ϕ' ($\log_{10} K + 2 \log_{10} L_{\infty}$) in various marine fishes. (Source of data is Pauly, 1981, 1985a.)

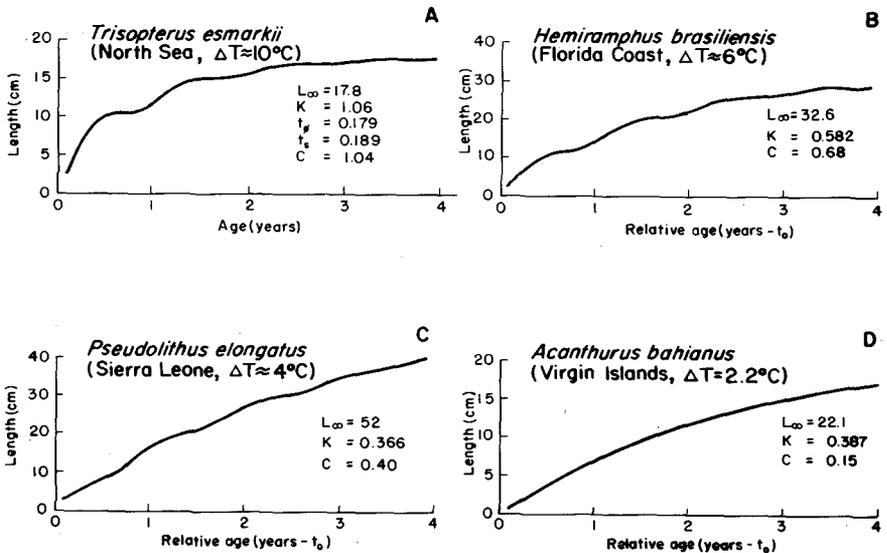


Fig. 9.6. Seasonally oscillating growth curves in four species of fishes. Note that variations are not visible in the *Acanthurus* curve although they significantly affected the growth rates of the tagged fish upon which the parameters of this curve are based (Pauly and Gaschütz, 1979; Gordon, 1977; Berkeley and Houde, 1978; Pauly and Ingles, 1981; Randall, 1962).

TABLE 9.1. Estimates of the Growth Parameter (K) in Skipjack Tuna of a Range of Fork Length (FL), with Computed Values of the Growth Performance Parameter ϕ' ^a

Area	FL (cm)	K (y^{-1})	ϕ'	Source
Hawaii	84.60	1.16	3.92	Uchiyama and Struhsaker, 1981
Hawaii	85.10	0.95	3.84	Brock, 1954
Eastern tropical Pacific	85.10	0.44	3.50	Schaefer, 1961
Hawaii	82.30	0.77	3.72	Rothschild, 1967
Pacific Ocean 10°N 100°W	80.50	0.63	3.61	Joseph and Calkins, 1969
North of Madagascar	62.30	0.98	3.58	Marcille and Stequert, 1976
Central Pacific	102.00	0.55	3.76	Uchiyama and Struhsaker, 1981
Hawaii	92.40	0.47	3.60	Uchiyama and Struhsaker, 1981
Eastern Pacific	142.50	0.29	3.77	Uchiyama and Struhsaker, 1981
Eastern Pacific	72.90	0.83	3.64	Joseph and Calkins, 1969
Eastern Pacific	107.50	0.41	3.68	Joseph and Calkins, 1969
Eastern Pacific	88.10	0.43	3.52	Joseph and Calkins, 1969
Papua New Guinea	65.47	0.95	3.61	Josse <i>et al.</i> , 1979
Papua New Guinea	74.80	0.52	3.46	Wankowski, 1981
Papua New Guinea	65.00	0.92	3.59	Kerney, 1974
Philippines (southern)	84.50	0.51	3.56	White, 1982
Philippines (southern)	82.20	0.48	3.51	Tandog, 1984
Hawaii	101.10	0.39	3.60	Skillman, 1981
Taiwan	103.60	0.30	3.51	Chi and Yang, 1973
Taiwan	103.80	0.43	3.67	Chi and Yang, 1973
Eastern Pacific	79.06	0.64	3.60	Josse <i>et al.</i> , 1979
Western Pacific	61.30	1.25	3.67	Sibert <i>et al.</i> , 1983
Eastern Pacific	75.50	0.77	3.64	Sibert <i>et al.</i> , 1983
East tropical Atlantic Ocean	80.00	0.60	3.58	Bard and Antoine, 1983
Vanuatu, western Pacific (1)	60.00	0.75	3.43	Brouard <i>et al.</i> , 1984
Vanuatu, western Pacific (2)	62.00	1.10	3.63	Brouard <i>et al.</i> , 1984

^a Sources of data as indicated.

Diel Growth Variation and Daily Otolith Rings

It was realized during the 1960s and 1970s that the main outlines of fish growth could be determined for many tropical stocks by analysis of seasonal growth rings on otoliths (Bayagbona *et al.*, 1963; Poinard and Troadec, 1966) as well as by size-frequency analysis, thus finally dispelling the myth that Mohr (1921) had written about nearly half a century earlier. Further progress in the study of fish growth then awaited the observation of Panella (1971) that the very fine striations within otoliths, previously described but not correctly interpreted by Hickling (1931), were often laid down daily. Figure 9.7 illustrates daily and other rings in the otoliths of a number of tropical fish species. Diel growth striations,

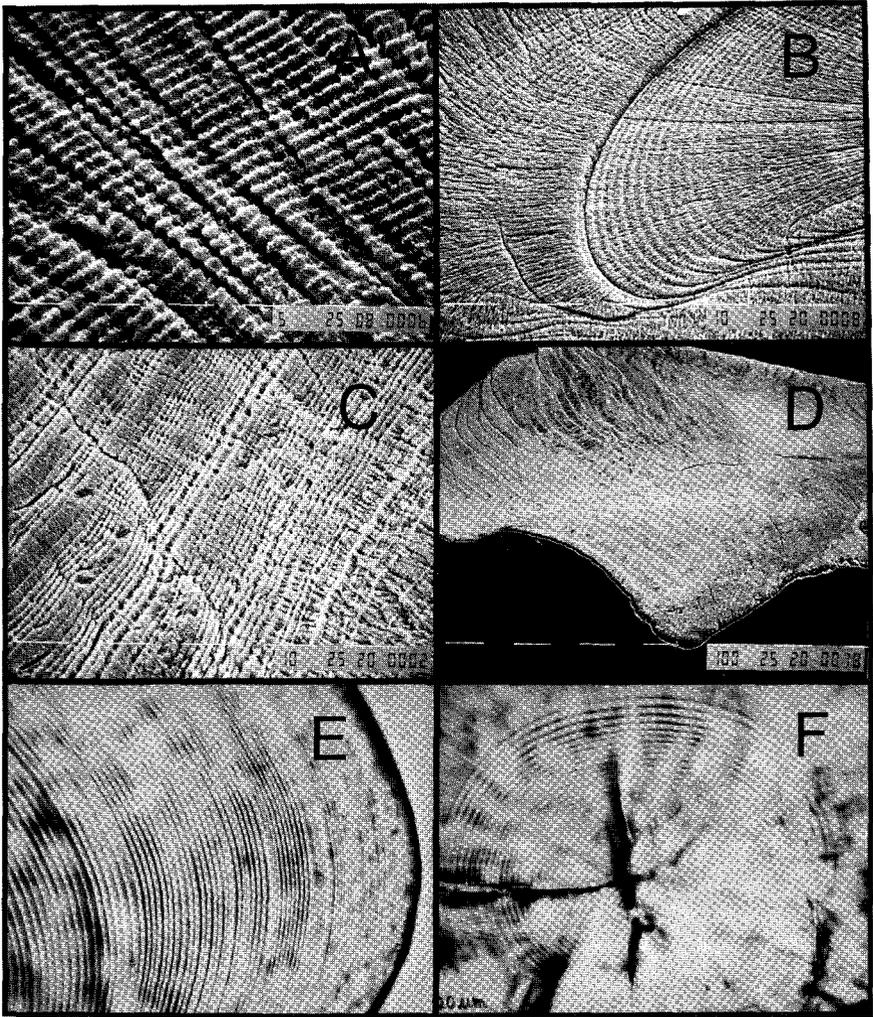


Fig. 9.7. Daily, seasonal, and annual rings in the otoliths of tropical fish. (A) *Pomadasys argenteus* (Kuwait) 56 cm SL, very regular daily growth increments on sagitta; (B) *Scarus sexvittatus* (Australia) 24.5 cm SL, transition at end of larval stage; (C) *Pomadasys argenteus*, shows irregular, possibly tidal, spacing of increments; (D) *Stegastes* sp. (Australia) 13 cm SL, annual zones in sectioned sagitta; (E) *Scarus iserti* (Australia) 6 cm SL, daily rings of early larval period; (F) *Hyporhamphus unifasciatus* (Virgin Islands) 10 cm SL, extremely regular daily rings. A–D are scanning electron micrographs, E–F are light micrographs. Size of scale bars in μm indicated by left-hand number. (Photos by E. B. Brothers, EFS Consultants.)

presumably representing physiological changes driven by the solar or tidal cycles, had previously been observed in the skeletons of both living and fossil corals and molluscs. With their recognition in fish otoliths by Panella, it finally became possible not only to settle long-standing controversies about the growth rates of a number of important commercial species (Shubnikov, 1976), but also to probe more deeply into the fundamental factors that affect fish growth in all latitudes.

For example, it became possible to estimate the duration of the larval stage of coral reef fishes, to assess the relationships between repeated spawning or tidal cycles and growth, and even to age long-lived tropical fish which do not display annual rings (Ralston, 1985). One topic which has received little attention, however, is the cause for the occurrence of daily, or primary rings in virtually all fish species so far investigated (Gjøsaeter *et al.*, 1984). Attempts have been made to argue that temperature (Brothers, 1981) or endogenous rhythms cause such rings, but the explanations so far advanced fail to explain their ubiquitous nature, as is apparent from the recent review of diel rings by Jones (1986).

Proceeding from the growth model proposed in the previous section it seems probable that daily growth rings in the otolith of fish (and in the analogous organs of invertebrates) are simply the consequence of diurnal changes in activity levels, and concomitant changes in the oxygen budget of the tissues. Such a model for the origin of diel striations in invertebrates has been proposed by Lutz and Rhoads (1974) and there is abundant circumstantial evidence to support the concept (e.g., Panella, 1974; Brothers and MacFarland, 1981). Thus, in diurnal fish, high levels of activity during feeding, sustained high-speed swimming to escape from predators, social displays, etc., will induce anaerobiosis and high levels of lactic acid in body tissues during daytime (Burggren and Cameron, 1980; Wardle, 1978). These conditions must occur also in the fluids surrounding the otoliths, and must result in alterations of the chemistry of the outermost layer of the otolith. At night, when diurnal fish are relatively quiescent, they will compensate for the residual oxygen debt they have incurred during the day, and resume growth based on amino acid stores built up during the daytime. Such a model provides a sufficient explanation for Brothers' (1981) observation that "the protein-rich portion of simple daily growth units is formed at night." This proposition could be confirmed if it were found that the pattern of protein-rich/protein-poor striations was inverted between day and night in nocturnal fish such as the Holocentridae.

This model represents a special case of the more general growth model presented in the previous section, which itself appears to explain a wide variety of otherwise unrelated phenomena, as will be discussed below. It

should be mentioned, however, that ageing by means of daily rings is a rather time-consuming and error-prone process, and also that the various counting techniques are still being refined (see, for example, Gjsaeter *et al.*, 1984). It is therefore at present of more use as a technique for special research projects, rather than in routine aging for fish stock management. The technique is also, of course, susceptible to the biasing of results that can be induced by improper sampling from the catch in exactly the same manner as for routine techniques of growth parameter estimation based on annual rings or length-frequency data.

Seasonal Growth Variations

Figure 9.6 shows seasonally varying growth curves in four fish populations in which estimated values of the parameter C (Eq. 9.7) varies significantly. This figure, as well as Fig. 9.8, shows that in fishes and invertebrates the value of C , the amplitude of seasonal changes in growth rate, is

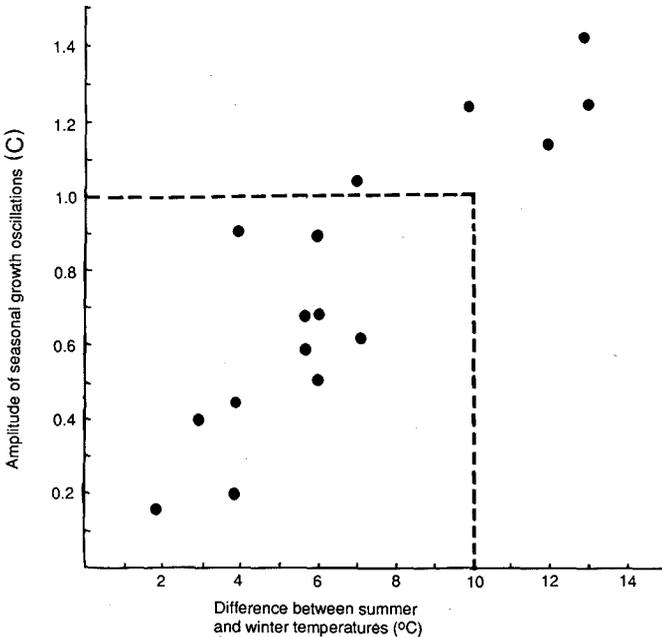


Fig. 9.8. Relations between the amplitude (C) of seasonal growth oscillations in fish, penaeid shrimp, and squid and the summer–winter temperature difference of their habitat. Values of $C = >1$ imply a period of no growth, not discussed here because it occurs only in tropical freshwater and high latitude habitats. (Modified from Pauly, 1985b.)

related to the range of change in water temperature between the warmer and cooler seasons. This relationship is not necessarily causal, and obviously it might be due to another factor, such as the availability of food, itself driven by temperature change. However, the fact that the value of C varies with temperature throughout the tropics as well as in temperate seas, for invertebrates as well as fish, and despite a diversity of specific life-history strategies, strongly suggests that temperature is the causative agent. This is strengthened by the fact that fish seem able to continue growing (i.e., have values of $C < 1$) within a range of $\Delta T = 10^\circ\text{C}$, which is approximately the range over which enzyme systems will usually function, although at temperature-dependent rates (Rose, 1967).

Given appropriate models and fitting methods, seasonal variation in growth rate can be detected in several different kinds of data sets, such as sizes-at-age, length frequencies, and size increments from tagging and recapture (Fig. 9.6). Indeed, sensitive analysis can show unequivocal seasonal growth variations in data sets previously used to demonstrate the absence of seasonal growth variability in tropical fish (Ingles and Pauly, 1981). Such findings reveal the interesting paradox that while growth of a species within a region is accelerated by higher seasonal temperatures, the ultimate size of adult fish is reduced in regions having higher sea water temperatures integrated over the whole year, a paradox fully compatible with the metabolic growth model presented here.

The discovery that significant seasonal growth oscillations are frequently encountered in tropical fish should lead to improved growth parameter estimates, as well as to improvement of some of the yield models used for managing tropical fisheries. This is probably another example of how the mythology surrounding tropical fish population studies has in the past prevented progress. The myth of continuous, rapid growth of tropical fish clearly prevented seasonal growth oscillations from being observed, even where they now appear obvious.

Seasonal Rings in the Hard Parts of Tropical Fishes

Given that growth varies seasonally in so many tropical fish species, it is not surprising that daily growth rings in otoliths themselves show seasonal changes that integrate into identifiable zones representing seasonal changes in growth rate. These zones usually represent a winter growth check in high-latitude fish, while in tropical fish they probably reflect growth checks that are caused by whatever are the principal seasonal changes in each habitat.

The occurrence of seasonal marks from which fish may be aged by routine techniques developed for high-latitude fisheries is of more signifi-

cance to practical fishery management than the occurrence of daily rings which are more time-consuming to count. However, most of the studies of growth marks in tropical fish over the last 15 years have concentrated on daily rings (see the references and lists of studies in Gjøsaeter *et al.*, 1984); the very simple techniques introduced by Bayagbona *et al.* (1963), Bayagbona (1966), Poinard and Troadec (1966), and LeGuen (1970, 1976) have been little exploited in tropical fishery management. These authors showed that the "burnt otolith" technique of Christensen (1964), which was developed to darken rings on otherwise hard-to-read otoliths from North Sea fish, gave extremely easily-read, brown, hyaline rings on the otoliths of several species of West African sciaenids. These protein-rich rings are laid down during periods of warmer water, and alternate with white opaque rings laid down during cooler seasons. Four rings are laid down each year in sciaenids on the coast of Zaire, corresponding to the two maxima and two minima that occur annually in the temperature regime in the eastern Gulf of Guinea. The physiological basis for these rings has not been directly established, though the influence of environmental temperature, feeding regime, and reproductive cycle—and hence the cycle of lipid sequestration in body fat—have been considered. A similar discussion of the nature of seasonal rings also made visible by the burnt otolith technique in the flatfish *Psettodes erumei* from the Gulf of Thailand has been given by Kühlmorgen-Hille (1976); in this fish, it is suggested that narrow, hyaline rings represent spawning checks.

Although usually found to be less reliable than otolith rings especially in older fish (O'Gorman *et al.*, 1987), scales have been found to bear seasonal rings in at least some groups of tropical-subtropical fish, and their presence or absence can give us clues with regards to the summer-winter temperature differences needed to induce readable annual rings in tropical fish (Fig. 9.9). The evidence presently available suggests that a seasonal temperature difference of $\Delta T = 4\text{--}5^\circ\text{C}$ may be necessary to induce readable annual rings in tropical fish, and that such rings may be therefore expected everywhere such differences occur. However, the existence of clear otolith rings on sciaenids in the Gulf of Guinea in habitats where ΔT can be less than this value suggests that other factors than temperature can also induce growth rings (and growth oscillations, see above) in tropical fish. It is to be expected that once the exploration of daily rings, and what they can tell us about growth in larval and juvenile fish, has run its course, examination of seasonal rings on otoliths and perhaps other hard parts will become a routine tool in tropical fishery management.

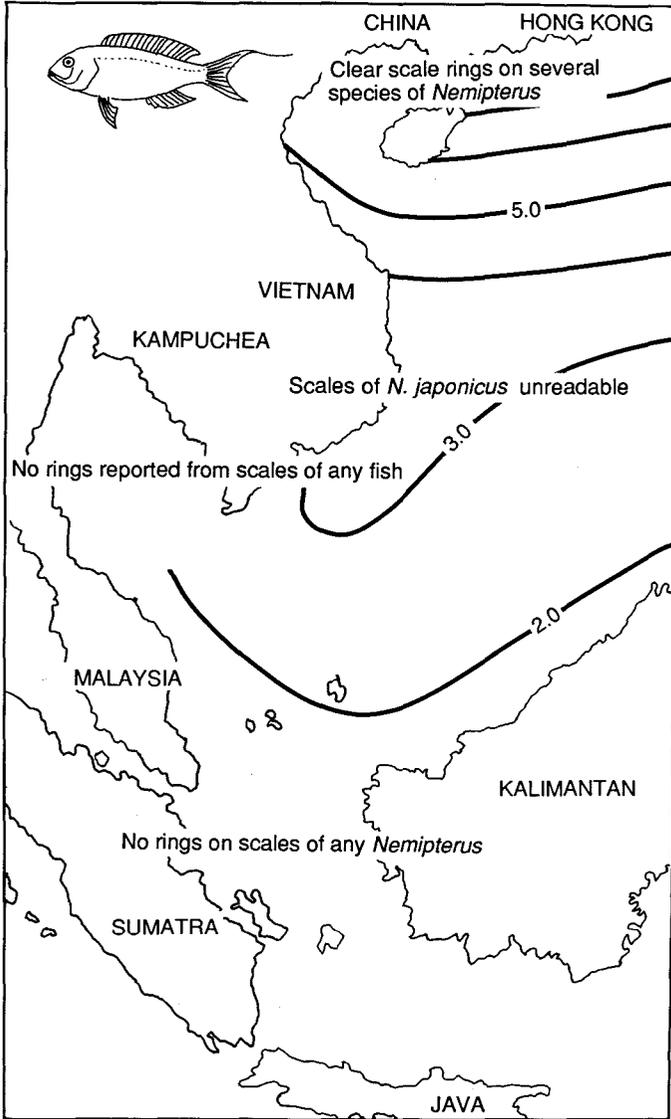


Fig. 9.9. Relationships between readability of scale rings in threadfin bream (*Nemipterus* spp.) and summer-winter temperature differences in °C (Eggleston, 1972; Chevey, 1934; Pauly, field obs.).

Length–Frequency Data and Fish Growth

Prior to the discovery of daily and seasonal rings in otoliths and scales, the analysis of length–frequency data was the only method that could be applied routinely to draw inferences on the growth of tropical fishes. Marking-recapture studies, and direct observation of captive fish, have been used in tropical fish research but have not yielded extensive and useful data. Because there is always some residual uncertainty in growth analysis based on a single technique, the use of length–frequency data will probably always be required alongside the reading of seasonal and diel growth checks on skeletal tissue and scales.

A great deal of confused terminology surrounds the use of length–frequency data in growth analysis and before discussing the available techniques it is necessary to clarify the terms we shall use. We shall restrict the term “Petersen’s method,” which is usually very loosely used, to the analysis of one length–frequency sample at a time. Such analysis consists of identification of class modes or means in the sample in question, using either a purely visual approach (Petersen, 1892), graphical techniques (Harding, 1949; Cassie, 1954; Bhattacharya, 1967), or computer-based methods of class separation (Abramson, 1970; Yong and Skillman, 1975). These techniques are reviewed in Everitt and Hand (1981). After the identification of class modes, the next step in Petersen’s technique is the subjective attribution of relative ages to the modal or mean lengths thus identified. This then enables the derivation of growth parameters from the identified mean lengths, and the relative ages attributed to them.

Petersen’s method for length frequency analysis is illustrated in Fig. 9.10a, which also illustrates what happens if the subjective attribution of relative ages goes wrong (which happens quite frequently, and is behind many of the statements that the VBGF is not suitable as a model for growth of this or that fish).

We shall use the term “Modal Progression Analysis” (MPA) for the method in which several length-frequency samples are plotted sequentially, and where the apparent shift of modes is used to infer growth. In MPA the identification of class modal or mean lengths is done as in Petersen’s method, after which subjective identification of modes perceived to belong to the same cohort of fish enables the tracing of growth curves, or computation of growth increments between modes. Growth parameters are then estimated from the growth curve traced by eye using a Ford–Walford plot, or from the computed growth increments using the method of Gulland and Holt (1959). Thus, in MPA, the critical issue is not the attribution of “ages” to the various group, as in the Petersen method,

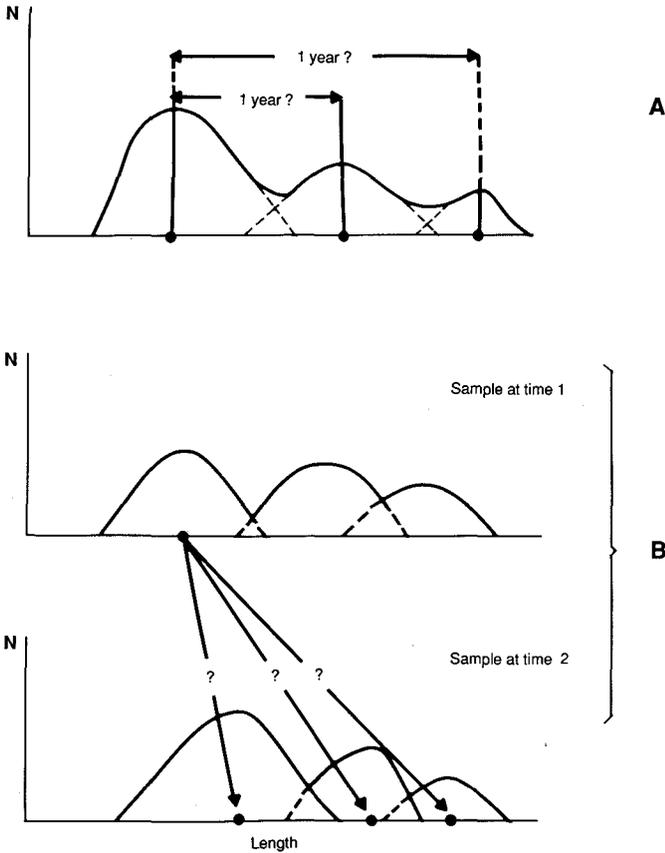


Fig. 9.10. Basic principles involved in traditional methods for length–frequency analysis. (A) Application of the Petersen method to a length–frequency sample; note that the time separating peaks must be assumed, a difficult task in species that may spawn several times annually. (B) Application of the modal class progression analysis to a set of two samples obtained at known times; note that the problem here is the proper identification of peaks to be interconnected (Pauly *et al.*, 1984b).

but the linking of peaks perceived to belong to the same cohort (Fig. 9.10b).

The subjective judgment required in the second steps of both of these methods and the large potential errors thus induced have prompted a search for ways of reformulating these two traditional methods so that improved solutions are obtained. Two major lines of inquiry have been followed:

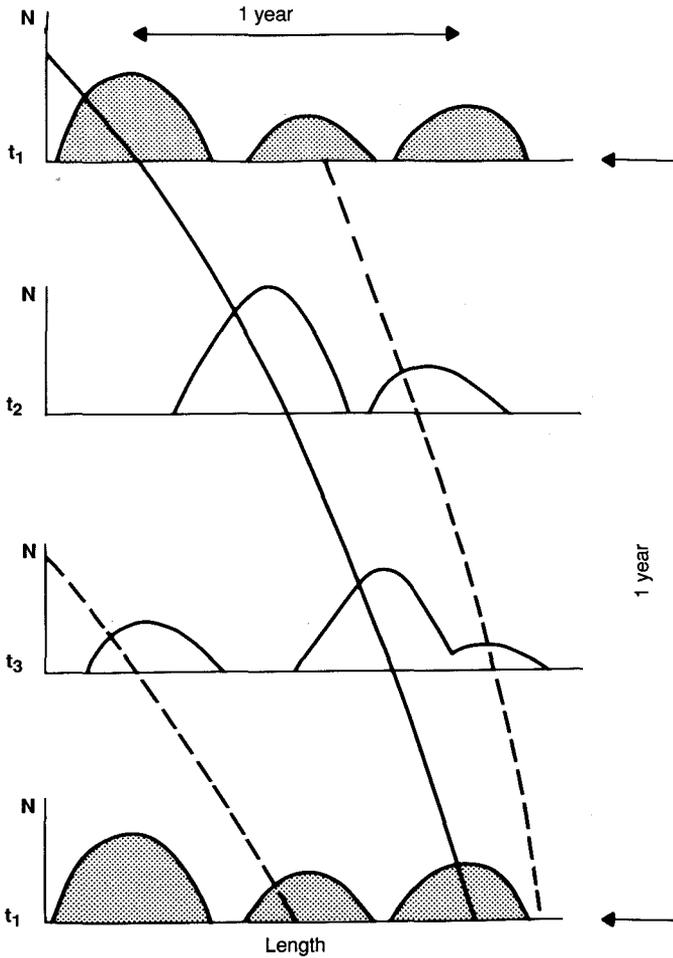


Fig. 9.11. An application of the "integrated method" to a hypothetical set of length-frequency samples. The attribution of a relative age to the third peak of sample t_1 is confirmed by the modal class progression which suggests a growth curve passing through the major peaks of samples t_1 , t_2 , and t_3 and through the third peak of t_1 repeated after 1 year. A smooth curve is thus achieved with more reliability than by the application of either of the two earlier methods (from Pauly *et al.*, 1984b).

1. Constraining possible solutions through the use of preselected growth functions, usually the VBGF and especially its seasonally oscillating formulation.
2. Combining the length-frequency data with other information, such as growth increment data from tagging-recapture experiments, or length-at-age data obtained from otolith analysis (Morgan, 1987).

Petersen's method and MPA can be integrated into a technique (Fig. 9.11) that can be implemented either using one single large sample, collected during a short period within a year, or a number of samples representing different periods of the year. However, in the latter case, seasonal growth oscillations (as defined and discussed above) must be considered explicitly lest some of the peaks in a set of data should be missed by the growth curve.

Moreover, whether one sample or several are analyzed, account must be taken of the possibility that two cohorts of unequal strength may be in the data, yet prior knowledge of this is usually not available. Finally, as in all analyses using length–frequency data, it must be recognized that such data tend to be biased by the fishing gear used to obtain them, so that they usually contain fewer small fish than really occur in the sampled population.

These various problems, which occur simultaneously in real-life situations, make paper-and-pencil methods, integrated or not, for the analysis of length–frequency data rather unreliable, and several computer-based methods have been developed that can objectively extract growth parameters and related information from length–frequency data, while accounting for seasonal growth, variable cohort strength, and gear selection.

The ELEFAN I and II software described by Pauly and David (1981) and Pauly (1982b) belong to this class of model, and have been implemented on microcomputers that are now widely available in tropical countries (Brey and Pauly, 1986; Saeger and Gayanilo, 1986). Alternative methods (Sparre, 1987) based on parametric statistics usually require access to a library of routines on mainframe computers, and are thus not so readily available to isolated researchers. Parametric techniques are also usually applicable only to length–frequency data that are weighted by a population abundance index, such as catch per unit of effort.

The following two examples of length–frequency analysis have been worked out with ELEFAN software to illustrate some of the practical problems in two very different tropical fisheries. In each example, the growth curves were fitted after taking account of incomplete recruitment of small fish through gear selection (Pauly, 1986a; Hampton and Majkowski, 1987).

Our first example is the analysis of growth during the period 1963–1965 of the Peruvian anchoveta (*Engraulis ringens*), whose biology was briefly discussed in Chapter 7. Though the temperature range off the Peruvian coast is relatively small ($\Delta T = 3\text{--}5^\circ\text{C}$), it is notable from Fig. 9.12 that lowest size-adjusted growth rates for *Engraulis ringens* occur during the period of lowest mixed-layer temperatures off Central Peru. The best growth curve for the main 1963 cohort was found to be one that oscillates seasonally, though not strongly ($C = 0.31$), with minimum growth rate in

September (Fig. 9.12). This cohort entered the fishery in October 1963 at a mean length of 7–8 cm and disappeared about 20 months later, in mid-1965. The growth of some cohorts preceding or succeeding the main cohort is also shown in Fig. 9.12. It will be noted that the assumption of annually repeated growth curves used in Fig. 9.11 is reasonable as far as this data set is concerned.

The second example provided here is the small West African croaker *Pseudotolithus elongatus* found in estuarine and inshore habitats from Senegal to northern Angola. Our analysis is based on length–frequency data for 1953–1954 in the Sierra Leone estuary. These data had been previously been analyzed using MPA, and had yielded a growth curve with parameters very similar to that shown in Fig. 9.6 (Longhurst, 1963, 1964b). Figure 9.13 shows an ELEFAN growth curve for the same data,

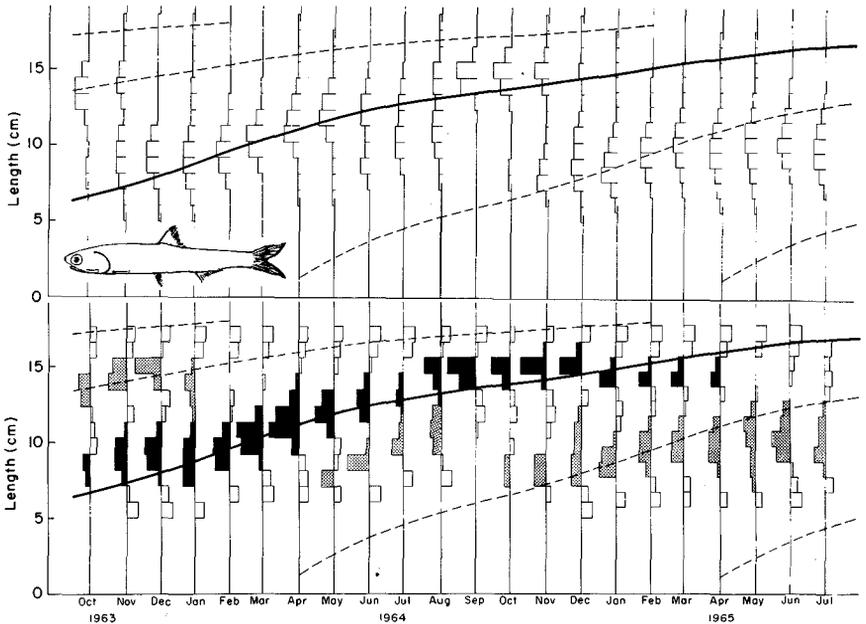


Fig. 9.12. Analysis of length–frequency data on the Peruvian anchovy (*Engraulis ringens*, northern/central) using the ELEFAN I program (Pauly and David, 1981). The upper graph shows the original length frequency data (courtesy, I. Tsukuyama, IMARPE) with superimposed growth curve. The lower graph shows the restructured length–frequency data, with peaks in black or grey and the troughs separating peaks as open histograms. The best curve ($L_{\infty} = 19.75$ cm, $K = 0.71$, $C = 0.31$, and Winter Point = 0.7, i.e., September) was found by varying the growth parameters until a maximum number of positive points were accumulated, and troughs avoided as much as consistent with a continuous curve.

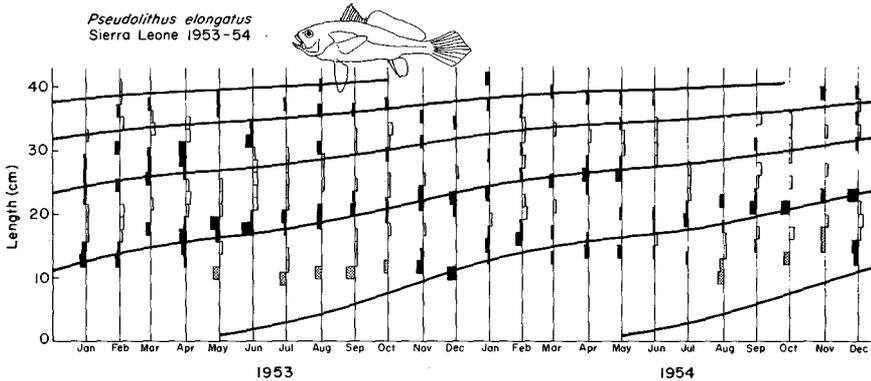


Fig. 9.13. Growth of "gwangwa" (*Pseudotolithus elongatus*) in the Sierra Leone estuary as estimated by the ELEFAN I program ($L_{\infty} = 52$ cm, $K = 0.366$, $C = 0.4$, $WP = 0.37$). (Based on data in Longhurst, 1964a.)

superimposed on the restructured length–frequency data to which the curve was actually fitted. These restructured data, a characteristic output of ELEFAN software, express the positions of the peaks and troughs in a length–frequency data set as positive and negative histograms, while the absolute values express how distinct a peak (or a trough) is. The curve itself is fitted by varying the parameters of an equation such as Eq. (9.7) until a maximum of positive points is accumulated, so that the curve passes through as many peaks as possible, while avoiding troughs.

It will be noted that the succession of size classes for *Pseudotolithus elongatus* is rather clear for the first 2–3 years, then becomes relatively difficult to follow, as is to be expected in a species in which the very oldest known individuals are less than 10 years (LeGuen, 1970) and in which the numbers of fish at age 4 are already only about 1% of those taken in commercial trawl samples (Longhurst, 1963). For this reason the fitting of the data to a given growth function (in this case, a seasonally oscillating VGBF) is helpful in identifying which sequence of peaks most probably belong to the same cohort.

These two examples will serve to illustrate the utility of length–frequency-based growth analysis in tropical fish, but special caution is appropriate concerning quality and quantity of the data needed for such analyses. In particular, users of these methods must be aware of their limitations, especially the possibility that because of behavioral features of the fish sampled, or bias of the sampling gear, they should not be applied (see contributions in Pauly and Morgan, 1987). A sufficient number of measurements, well distributed over time, is also obviously necessary for more than cursory analyses (see Table 9.2).

TABLE 9.2. Criteria for Assessing the Reliability of Length-Frequency Samples for Studying the Population Dynamics of Fish. Reliability, on a Scale of 0-5^a

Total sample size	Months over which sample is accumulated				
	1	2	4	6	12
1-99	0	0	0	0	0
100-499	0	0	1	2	2
500-999	1	1	2	3	4
1000-1499	1	2	3	4	5
1500-∞	2	3	4	5	5+

^a From Pauly (1984b), based on Munro (1980).

The analysis of sciaenid growth discussed above was based on measurements of 9847 individual fish, and additional special samples were obtained with small-meshed trawls properly to sample small fish that would have escaped through the standard survey gear; a similar study of *P. senegalensis* and *P. typus* off Nigeria was based on about 147,000 fish measured over a 3-year period. Such numbers are quite easy and cheap to obtain with a proper catch-sampling program and are self-regulating, in the sense that the data themselves, as they are accumulated, clearly demonstrate when a sufficient sample of fish has been measured to identify its major size classes.

Environmental Factors Affecting Growth

In a Darwinian world, not all members of a given population of fish or marine invertebrates are equal. Thus, given a scarcity of resources, or adverse environmental factors, environmental pressure will be experienced differently by different members of the population. Both specialized predators and more catholic carnivores take a proportionately higher number of less fit and hence vulnerable animals of a given prey species (Jones, 1982). In the marine environment, which offers relatively open connection between different subsystems, and especially so in the tropics where interactions may be more intense than in temperate systems (Robinson, 1978), such removal of vulnerable individuals should be rather intense, resulting in the evidence for environmental effects on fish growth being systematically and quite literally eaten away.

We have already discussed some of the ways in which environmental temperature may determine growth rates in marine fish, and in the last

section of this chapter we shall discuss the energetics of fish nutrition, and the manner in which energy deficits are avoided during feeding activities. However, a number of other factors may cause changes in growth rate, and we shall now discuss two of these—social interaction and water depth.

It is in the defense of a home territory, or in the maintenance of a stable pair-bond, that vertebrate social interactions are strongest, yet for marine fish the defense of space is important only in some families of reef fish, and it is among these that we should look for effects of social interactions on growth rates. In reef-dwelling species of *Amphiprion*, dominant females continually chase all males present in their habitat except one, with which a pair-bond is formed. This stress is sufficient to keep all unmated males in the habitat smaller than the large mated male. In the event that the pair-bond is broken by removal of the mated male, the female ceases to chase the unmated males, and these begin rapidly to grow until one of them can replace the missing large male (Allen, 1975; Fricke and Fricke, 1977). This is in line with Eq. (9.1), which implies that release from stress should indeed result in increased growth rate. Other examples of social interactions affecting growth rates of tropical fish are given in Keenleyside (1979).

Water depth as a factor is usually not discussed in connection to growth. Johannes (1981) noted that “an increase in mean size of fish with depth has often been noted by biologists, but no one as yet has come up with a generally accepted explanation for this trend.” The model of growth outlined in this chapter allows us to accept Johannes’ challenge and to comment on what is also known as Heincke’s Law, which states that in the North Sea the size of individual plaice depends on stock abundance and also on distance from the coast and depth (Heincke, 1913; Harden-Jones, 1968). In fact, all that is needed to explain the tendency for larger fish to occur in deeper water is to postulate that routine metabolism decreases in deeper water because of decreased water temperature, as is predicted by our simple growth model (Figs. 9.14a and 9.15).

MORTALITY OF TROPICAL MARINE FISHES

Some Definitions of Mortality

The rate of mortality is an important number in the management of fish populations and it can be quantified by several quite different and complementary techniques. One approach to quantifying natural mortality is to measure the abundance and food demand of major classes of predators

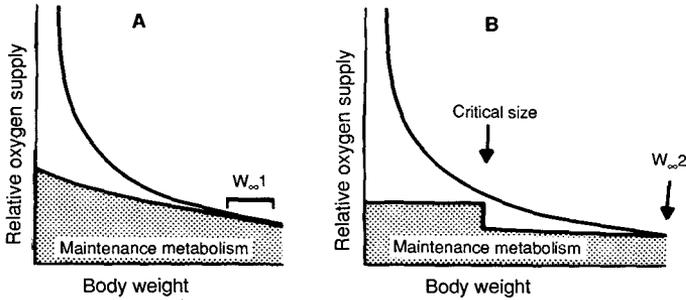


Fig. 9.14. Schematic representation of the effect on tissue oxygen supply available for growth of (A) gradual decline of maintenance metabolism achieved by migration to colder (deeper) water and (B) when a given abundant food item becomes available once a critical body size has been reached which renders the prey obtainable. A will lead to a growth curve with a long phase of steady growth, and B to a diphasic growth curve.

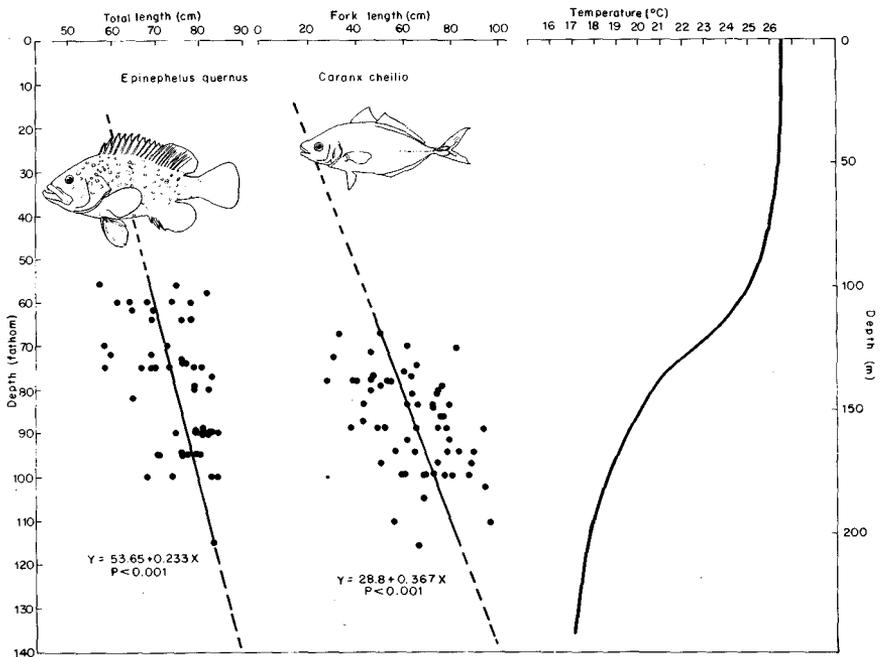


Fig. 9.15. Increase of average size in two species of reef fish as a function of depth and temperature at French Frigate Shoals, Hawaiian Islands (S. Ralston, 1981; J. J. Polovina, personal communication).

(Potts *et al.*, 1986) so as to draw inferences about their impact on the prey population, and we have discussed several examples of this approach in previous chapters. Provided satisfactory tagging techniques can be developed for the tropics (which is not always the case) classical release-recapture methods are available for transfer from temperate fisheries biology. The principal biological problems to be overcome before this method gives good results are to understand the size of the area over which individuals of the tagged stock are distributed and to use tags that cannot be shed and are readable after some months in the sea. This technique is perhaps most easily applied in lakes, lagoons, and other enclosed bodies of water where the landed catch is easily monitored.

Finally, one can infer mortalities, if certain assumptions about recruitment and growth can be made, from the size or age frequency distribution of fish sampled over a given period. We shall not dwell here on the methodological aspect of these approaches which are covered in general population dynamics texts (Gulland, 1983; Ricker, 1975; Pauly, 1984a). Rather we shall discuss the results of some studies that have led to the identification of specific features of the natural mortality of tropical marine fishes. We shall not discuss eggs and larvae, which are dealt with in another section of this chapter, nor fishing mortality except where fishing and natural mortalities interact. We shall express all mortality as instantaneous rates, defined by

$$N_t = N_0^{\text{exp}} - Mt \quad (9.8)$$

where N_0 is the number of fish at a given time, and N_t the number of fish still alive after time t , given a natural mortality rate M . In this equation, M can be replaced by total mortality (Z), defined as the sum of natural mortality (M) and fishing mortality (F). All mortality rates that we shall quote (and which have the dimension 1/time) are on the same annual basis as the parameter K of the VGBF.

In this general book, which is not devoted specifically to issues of fish stock assessment and fisheries management, we cannot deal in detail with the interactions between natural and fishing mortality. However, it is appropriate to mention here some implications of Fig. 9.16, illustrating Munro's concept of the interaction of F and M and based on studies of Jamaican reefs (Munro, 1983). This concept implies a high natural mortality in unexploited stocks and a partial replacement of natural by fishing mortality under exploitation, resulting from a higher rate of removal of predators than prey species. Evidence for the ubiquity of this phenomenon is beginning to emerge and would probably be accepted as conclusive, were it not for all the inherent difficulties in estimating M reliably in exploited stocks.

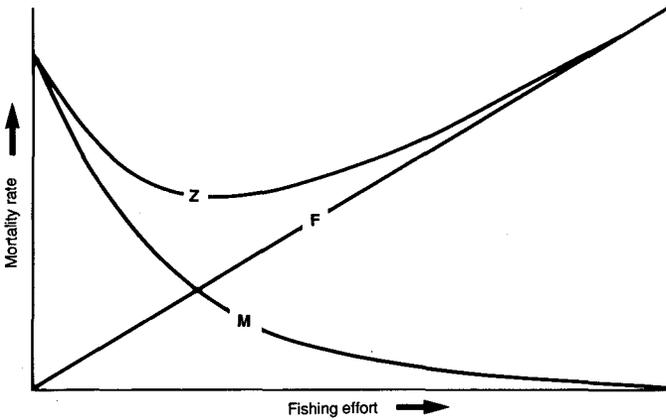


Fig. 9.16. Theoretical relationship between natural mortality rate (M), fishing mortality rate (F), and total mortality rate (Z) which will exist if natural mortality rates in an exploited community decline as a result of concurrent exploitation of predatory species. (From Munro, 1980.)

Straightforward methods for the estimation of Z (or M in unexploited stocks) use the mean length of fish in catch samples (Beverton and Holt, 1956) or length-converted catch curves (Pauly, 1984b) of which an example is provided in Chapter 10. The generally straight catch curves that are obtained when suitable data are analyzed suggest that the assumption of constant mortality rate implied in Eq. (9.8) is, in most cases, a reasonable one.

Relations between Growth Parameters, Temperature, and Natural Mortality

Beverton and Holt (1959) were the first to point out that in fishes there is a strong relationship between the parameter K of the VGBF, and M as defined above. Their inference was based on a data compilation which covered a narrow range of sizes, and very few tropical fish. For this reason, they failed to identify the equally strong relationship between M and temperature and the parameters L_{∞} or W_{∞} of the VGBF (Pauly, 1980a).

When we examine taxa that are relatively similar in size, and are drawn from habitats with similar temperatures, the ratio M/K holds almost constant, however. Thus, in the case of Serranidae and Lutjanidae, Ralston (1986) found that $M/K = 2$ (Fig. 9.17). We present in Chapter 10 another such relationship for sea urchins. Similar ratios could be derived for a

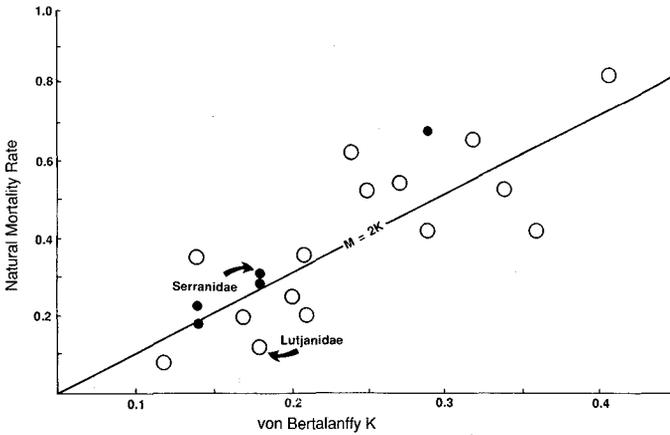


Fig. 9.17. Relationship between natural mortality (M) and the growth constant K in Serranidae and Lutjanidae; K is on an annual basis. (From Ralston, 1986.)

number of fishes covering different ranges of sizes and occupying different ranges of mean environmental temperature, using the compilation of data points in Pauly (1980a, 1985a), for instance.

Another generalization relevant to tropical fish is

$$\log_{10} M = 0.065 - 0.287 \log_{10} L_{\infty} + 0.604 \log_{10} K + 0.513 \log_{10} T \quad (9.9)$$

which expresses the relationship between M , L_{∞} (in cm), K , and mean habitat temperature ($^{\circ}\text{C}$). Equation (9.9) was derived from 175 specific data sets for fish ranging from 2 to 1226 cm, and for temperatures ranging from 3°C to 30°C (Pauly, 1980a, 1985a). This data set can also be used to establish a direct, significant relationship between M/K and mean environmental temperature, which results in

$$\log_e (M/K) = -0.22 + 0.30 \log_e T \quad (9.10)$$

Equations (9.9) and (9.10), which are both based on a very large data set, show unequivocally that the natural mortality of tropical fishes is markedly higher than that of cold water fishes, other things being equal. This finding has considerable theoretical implications because the species-specific mechanisms compensating for higher adult mortality, such as egg production and recruitment, must compensate these elevated mortalities in tropical species, while predation, which probably accounts for most of the natural mortality of fish, should bear more heavily on tropical than temperate species.

Additionally, hypotheses such as the utilization of r versus K reproduc-

tive strategies, placing emphasis on life-history strategies of individual fish species, may be incomplete since biological rates such as growth and reproductive output appear to be constrained by the basic geometry which limits relative growth of gills and gonads, and temperature which regulates metabolic and mortality rates. This point is discussed further below in relation to fish, and in Chapter 10 in relation to sea urchins and squids, but this book is not the place for a comprehensive reinterpretation of the published evidence. It is simply appropriate for us to discuss a few points to illustrate the implications of relatively constant ratios between VGBF parameters, mortality, and temperature.

We have suggested that tropical fishes should produce more eggs per unit time, other things being equal, than their temperate counterparts, and Fig. 9.18 provides evidence that this does in fact occur. Moreover, recent discoveries related to the spawning dynamics of clupeoids, notably *Engraulis mordax*, strongly suggest that previous approaches to estimating egg production in teleosts have seriously underestimated this process, particularly in serial spawners which are abundant among tropical fishes (Lasker, 1985; Breder and Rosen, 1966).

It is easy to document, at least for fish held under experimental conditions, that there is a positive relationship between food intake and temperature (Menzel, 1960; Kraljevic, 1984), and hence we infer a relationship between temperature and predation pressure. To demonstrate a positive effect of mean habitat temperature on mean food consumption of fish under natural conditions is more difficult, however, given the generally low precision of all estimates of food intake for fish swimming free in the ocean.

Our suggestion concerning the limited utility of analysis of life history strategies will probably be seen as contentious, given how a strong a role such analysis plays in the articulation of biological thought at the present time. However, while simulations of life history strategies may confirm that individuals in a given population maximize their fitness or reproductive output by, for instance, opting to remain small, the question must be asked, what is the cue for the adjustment of their growth rates, and their size at first reproduction so that maximum benefit accrues at the population level. Thorpe (1986) is one of the few authors to have perceived this problem. He writes,

the concept of a critical size at which a major developmental conversion . . . may occur begs the question of how the organism recognizes how large it is. It needs some reference standard.

The solution proposed below, in our section on the reproduction of tropical fishes, is based on Pauly (1985b) and is essentially the same as

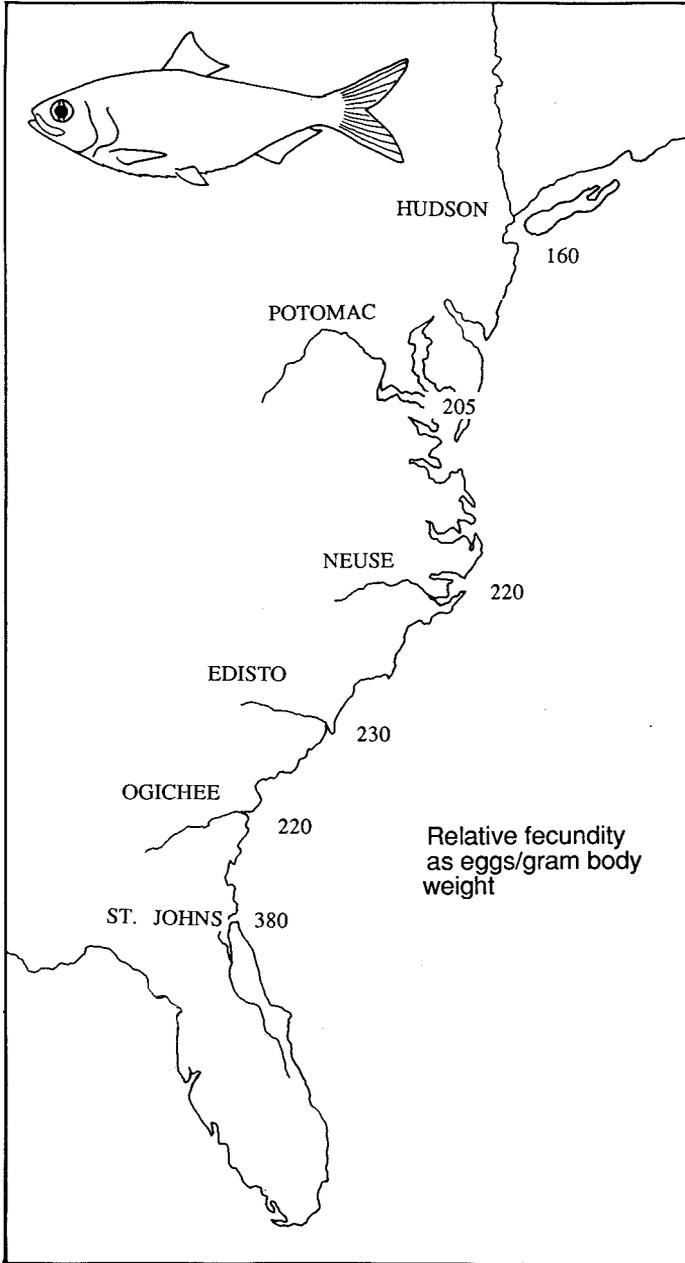


Fig. 9.18. Latitudinal trend of relative fecundity in anadromous shad *Alosa sapidissima* along the eastern coast of the United States. (Adapted from Davis, 1957.)

that proposed by Thorpe (1986). It contradicts much of the conventional view of the interrelationships between growth and reproduction, while being fully compatible, however, with the generalized growth model proposed earlier, and which provides the backbone of this chapter.

REPRODUCTION AND RECRUITMENT OF TROPICAL MARINE FISHES

Relationship between Growth and Reproduction

Instead of reviewing the very many observations that have accumulated of the patterns of recruitment in tropical marine fishes and presenting them as a compendium of tabular statements similar to those collected by Breder and Rosen (1969), we shall review one recently proposed hypothesis which seems to provide an explanation for a large class of observations concerning tropical fish reproduction.

Based on the metabolic growth model presented above, this hypothesis explains why fish should first spawn at a predictable size, or more precisely, at a predictable fraction of their asymptotic size (L_∞ or W_∞). Conceptually, three time scales can be defined for spawning and related processes.

1. A short time scale (seconds to days) for processes that occur just before shedding gametes (e.g., reproductive behavior, final maturation, etc).
2. A medium time scale (weeks to months) during which gonad maturation and spawning migrations take place, as triggered and influenced by environmental stimuli.
3. A long time scale (months to years) during which the age, and particularly the size (L_m or W_m), is determined at which a fish becomes sexually mature for the first time.

It is only scale (3) to which the hypothesis applies, the elements involved in (1) and (2) being adequately covered in the literature (e.g., Breder and Rosen, 1966) for fish inhabiting all latitudes.

The hypothesis itself is simple. To explain it, we return to Fig. 9.14 to observe that fishes at W_∞ have no surplus energy (expressed as no surplus oxygen) that could be devoted to the elaboration of gonads, and hence they must first spawn at some smaller size. Indeed, it is a trivial observation that the ratio L_m/L_∞ usually ranges between 0.4 and 0.9, is usually smaller in large fishes and higher in small fishes, and is remarkably constant within families comprising fish of approximately similar dimension (Beverton and Holt, 1959; Cushing, 1981).

The question might be posed: How do the physiological processes of individual fish “know” the value of their future L_∞ so that L_m can occur at the appropriate time? However, absurd questions lead to absurd answers, and we should probably rather ask if the relative constancy of the L_m/L_∞ ratio within fish taxa is due to the fact that both L_m and L_∞ are determined by the same process. It was suggested above that asymptotic size in fishes is determined mainly by the interactions between oxygen supply and demand, as mediated by species-specific gill surface area. It is suggested here that the basic mechanism outlined above determines size and hence also age at first maturity. All that is needed now is to postulate a genetically fixed threshold (i.e., a multiple of the routine metabolic level) below which one or more substances are produced that enable the brain of a fish to respond to environmental stimuli for reproduction.

Figure 9.19 illustrates this concept by contrasting two fish stocks of the same species, one living in a cool, food-rich water mass leading to high values of L_∞ and hence also high values of L_m , the other living in a food-limited, marginal, or warm-water habitat leading to low values of L_∞ and L_m . Figure 9.20 illustrates the method by which a preliminary estimate of the threshold level alluded to above was obtained. This figure shows that fishes, whether guppies, cod, or tuna, reach first maturity when their overall metabolic level (that is, active + maintenance metabolism) is about 1.4 times the level of their maintenance metabolism.

This hypothesis, which has a minimum of *ad hoc* assumptions and derived hypotheses, complements the explanation given above as to why

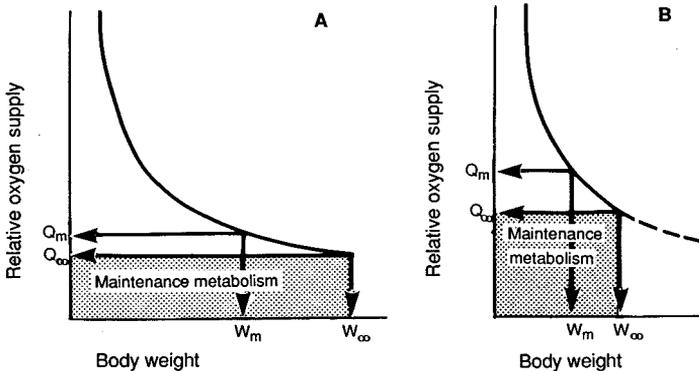


Fig. 9.19. Interrelationships between oxygen supply at maintenance level (Q_m), oxygen supply near first maturity (Q_∞), and the weight of fish. Note that the Q_m/Q_∞ ratio is constant for two different habitats one of which (A) is linked with large asymptotic size and a large size at first maturity, the other (B) being associated with the opposite situation. Note also that the constancy of Q_m/Q_∞ can only be imperfectly mirrored in the ratio L_m/L_∞ , which can be derived from W_∞ and W_m . (Modified from Pauly, 1984b.)

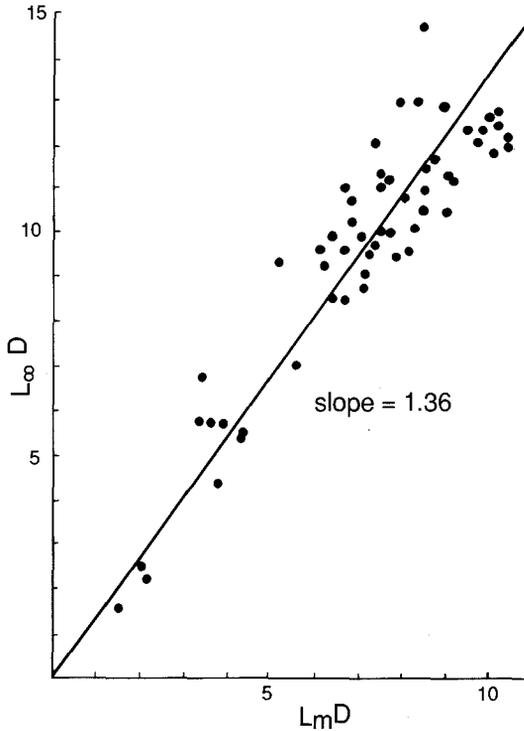


Fig. 9.20. Plot of asymptotic length (L_∞ , cm) raised to the power D on length at first maturity (L_m , cm) also raised to the power D in 56 species of fishes, ranging from guppies to tuna. The exponent D is equal to $b(1 - d)$, where b is the exponent of the length-weight relationship and d is the exponent of the relationship linking the body weight and the gill surface area of fishes. Note linearity of this plot, which suggests that fish reach first maturity when their total metabolism is equal to about 1.4 times their maintenance metabolism (Pauly, 1984b).

warm-water fish stay smaller than their cold-water counterparts with a mechanism explaining how size at maturity is adjusted to these smaller asymptotic sizes, without the need to postulate the operation of an absolute biological clock for the long-term time scale mentioned above. It also explains the abortive, or “trial run” maturations discussed by Hickling (1930) and Iles (1974) and is equally applicable to invertebrates as to fish.

Obviously, the relationship between L_m and L_∞ does not cover all aspects of the relationships between growth and reproduction, which can be rather complex and involve a variety of other relations, such as those between body weight and apparent fecundity, itself mediated by the relationship between body weight and gonad weight (Fig. 9.21). Other rela-

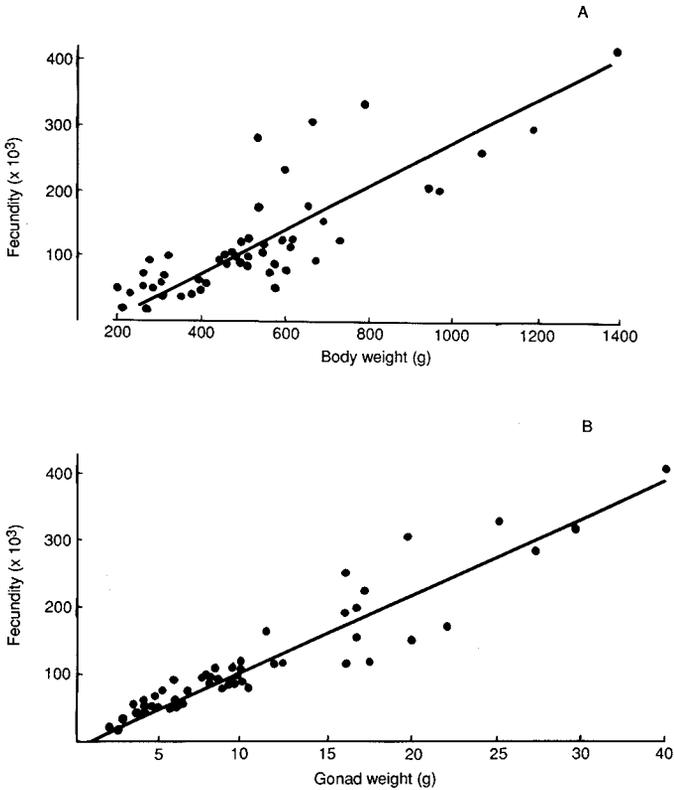


Fig. 9.21. Relationship between fecundity and (A) body weight or (B) gonad weight in *Pseudotolithus elongatus* off West Africa (Fontana and LeGuen, 1969).

tions between growth and reproduction are even more intricate, and may involve high fecundities that are mediated via reduction of egg size, which itself may be related to temperature-induced reduction of body size within and between different species of fish.

Egg size and fecundity also varies seasonally, as does the reproductive status of fish populations (Fig. 9.22), and knowledge of these seasonal changes is invaluable in understanding population biology. For this reason, great care must be given to the development and standardization of gonad maturity scales that are truly reflective of the peculiar features of tropical fishes, especially the rapid rematuration of spawned fish (Fig. 9.23).

Few of the generalizations thought to be relevant to tropical fishes have been as conceptually barren as the commonly held notion that tropical

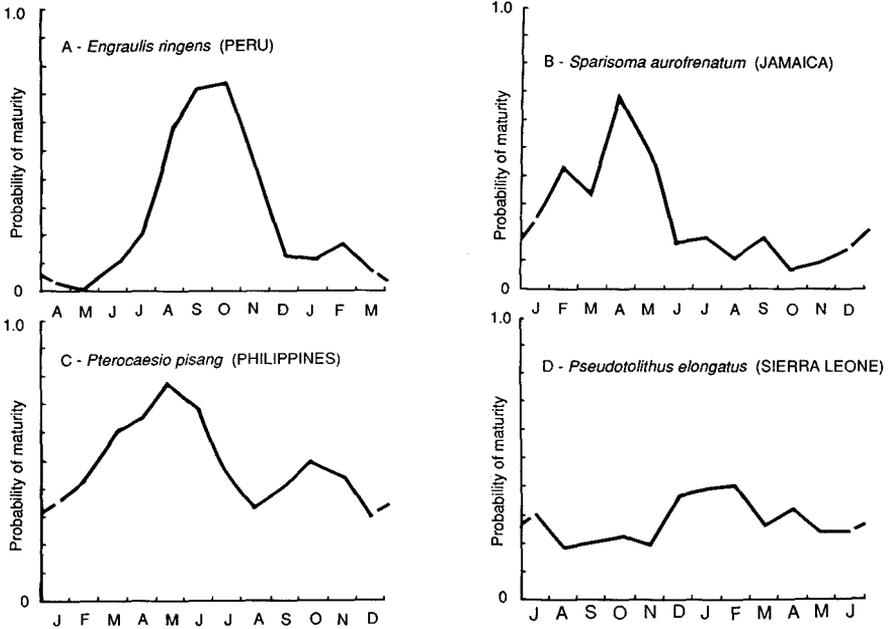


Fig. 9.22. Approximate probabilities for the adults of four tropical fishes to be ripe, or mature, by month, showing some reproductive activity throughout the year, but with seasonal peaks. (A, Average for 1966–1970, Jordan, 1980; B, Reeson, 1983; C, data adjusted from Cabanban, 1984; data from Longhurst, 1963).

fish reproduce throughout the year, or continuously. This view was probably prompted by the perennial luxuriance of some terrestrial habitats in the tropics, but is clearly incorrect because most tropical fishes do display a marked reproductive seasonality (Fig. 9.22), while many temperate fishes also have long spawning seasons, with at least some spawning through most of the year (Murphy, 1982). Thus, the difference between seasonality of spawning (and recruitment) between temperate and tropical fishes is really only a quantitative difference in the relative spread of the recruitment seasons.

The development time of marine fish eggs follows well-known physiological laws and is a negative function of water temperature. This can be expressed by the equation

$$\log_{10} D = 7.1 + 0.608 \log_{10} E_d - 4.09 \log_{10} (T + 26) \quad (9.11)$$

where D is the egg development time in days, E_d is egg diameter in mm, and T is the water temperature in °C. This equation is based on 140 sets of observations of spherical eggs of marine fish, ranging from 0.6 to 3.4 mm

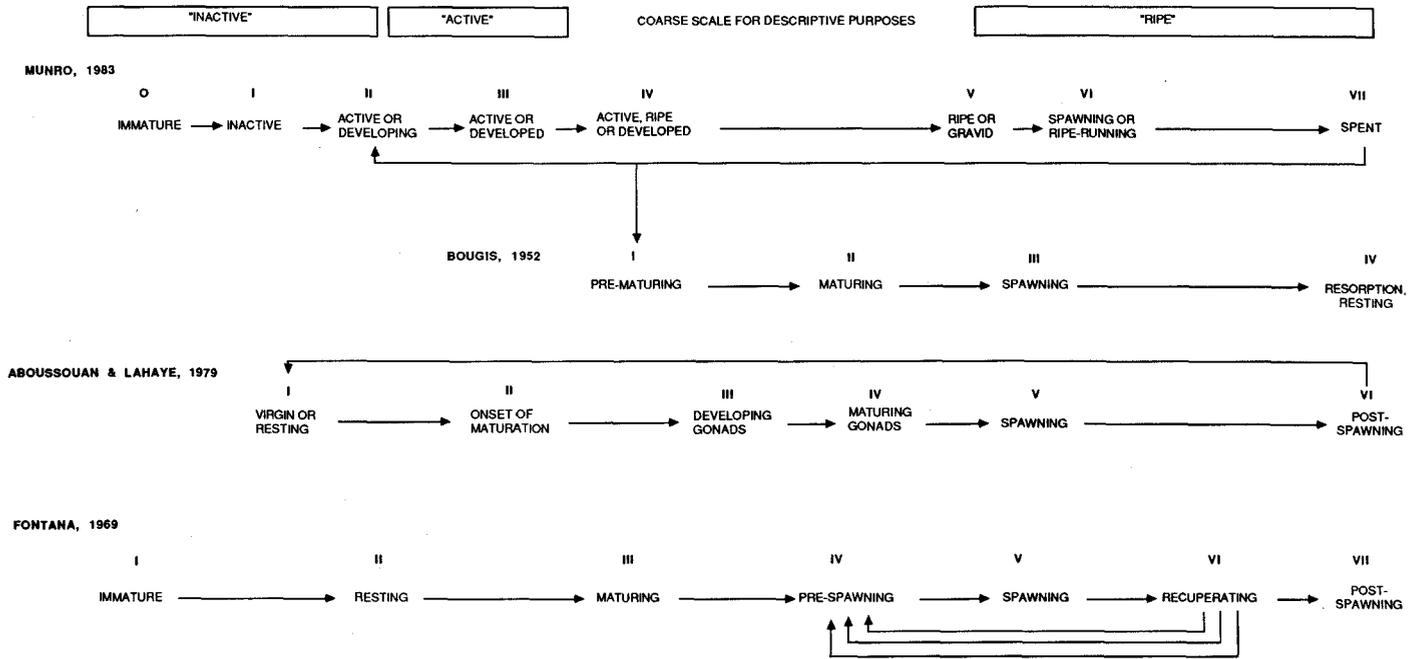


Fig. 9.23. Maturation scales proposed by various authors for tropical and subtropical fishes.

in diameter, at temperatures ranging from 3 to 30°C (Pauly and Pullin, 1987). Note that the slope (0.608) linking $\log_{10} D$ and $\log_{10} \phi$ shows that, for a given temperature, egg development time is not proportional to egg volume (which would require a slope of 3), nor to its surface (a slope of 2), nor yet to its radius (a slope of 1), but to a "physiologically effective radius," determined by an active transport system within the egg.

Equation (9.11) has, besides theoretical and anatomical implications, also some eminently practical consequences; biomass of temperate fish stocks are routinely determined by egg and larval surveys (Saville, 1977; Lasker, 1985), but these may be difficult or impossible to implement in tropical waters, since the eggs of tropical fish may occur too ephemerally in the plankton to be readily quantifiable. Off Sierra Leone, a search for the spawning grounds of the shad *Ethmalosa dorsalis* during normal working days proved quite fruitless, until it was discovered that the species spawned in the early evening, and that hatching was completed between 15 and 18 h later: thus, no eggs were available to survey during the afternoon (Bainbridge, 1961). In contrast, the eggs of the Peruvian anchoveta *Engraulis ringens* remain in the plankton for about 50 h before hatching and are available for semi-synoptic surveys to measure adult spawning stock size. This is one consequence of the differential effect of temperature of 27–28°C off Sierra Leone and 15–17°C off Peru at rather similar latitudes.

The Recruitment Problem

Aristotle was probably the first naturalist to write about recruitment, when he recorded that the fishermen of ancient Greece distinguished three size and age groups of tuna, which they called "auxids," "pelamides," and "thynni" or full-grown tuna (Hist. Anim. B. vi. c. 17). The fishermen were also reported to have observed that a scarcity of pelamides 1 year was followed by a failure of the fishery for thynni in the following year, which makes Aristotle's account the first ever on the still unresolved "recruitment problem."

Similar observations are available from medieval herring fisheries of Northern Europe, and stock availability (and hence recruitment) was one of the earliest preoccupations of nascent fishery biology in the late nineteenth century, but it is only since Ricker's seminal paper of 1954 that a clear-cut statement of this problem has been available: What is the relationship linking a parent stock to the number of its progeny entering the fishery as a result of each year's reproduction? For many years after its formulation by Ricker, environmental variability was neglected and research was almost entirely directed at attempts to derive an equation,

with parameters including coefficients for prerecruit mortality, to compile long time series of indices of parent stock size and of recruitment and force the former onto the latter.

Even if the neglect of environmental forcing used in this approach had been valid, much of the basic research done on recruitment in high latitudes could not have been relevant to tropical fisheries because for most tropical fish stocks sufficiently long time series may not be available, given the difficulties inherent in collecting reliable single-species statistics in multispecies, multigear fisheries (Bakun *et al.*, 1982). Moreover, the very notion of assuming that a single variable, parent stock, should be sufficient to explain between-year variability of recruitment is probably misleading (Fig. 9.24), especially since the demonstration that multivariate approaches (Csirke, 1980; Fig. 9.25) structured around key environmental variables (Fig. 9.26) can extract much more information from available data. The classical approach is in any case inappropriate for short-lived tropical species, which tend to have two, rather than only one, pulse of recruitment per year (Figs. 9.22 and 9.27) so that an approach using one data point per year would underutilize available information.

In fact, a whole new methodology for the utilization of within-year information on recruitment has recently been developed in conjunction with research on the recruitment of *Engraulis mordax* (Methot, 1984;

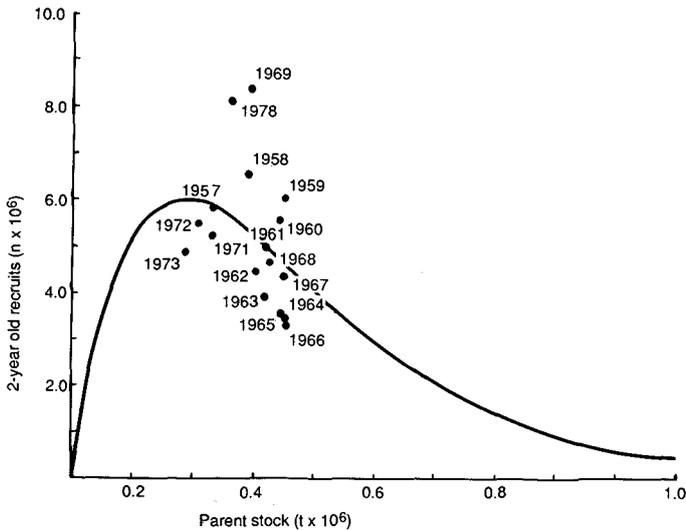


Fig. 9.24. Ricker curve fitted to the spawning stock biomass and recruits of southern bluefin tuna. Stock and recruit estimates by cohort analysis, showing how little of the variance is actually explained by this relationship (Murphy, 1982).

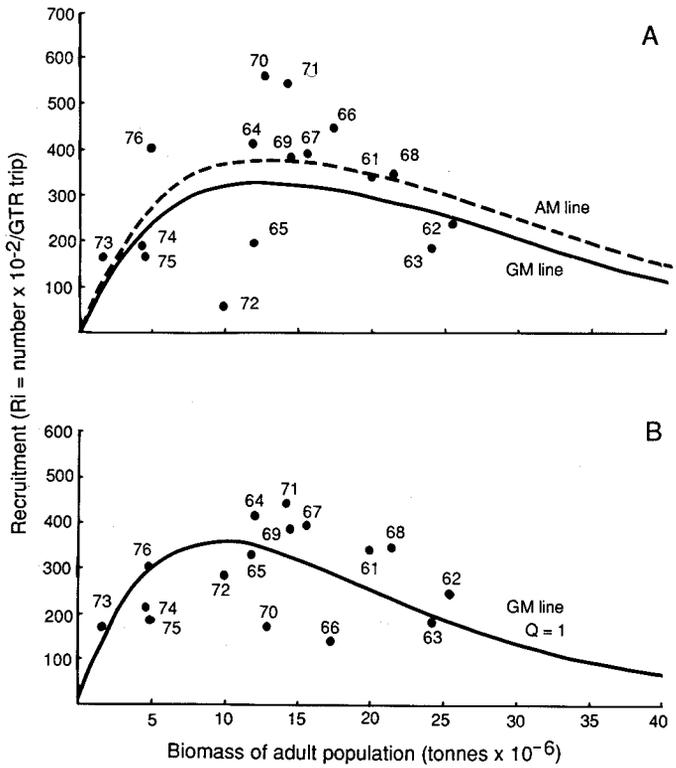


Fig. 9.25. Stock/recruitment relationship of Peruvian anchovy *Engraulis ringens* showing effect of incorporating an additional variable into the relationship. (A) Simple Ricker plot, showing rather bad fit and correspondingly low correlation of observed to expected recruitment (GM line, $r = 0.494$). (B) Plot of the residuals of a multivariate relationship involving recruitment, parent stock and concentration index Q related to occurrence of ENSO's, onto stock recruitment relationship, drawn for an average value of Q . This shows an improved fit with a correlation of observed to expected recruitment of $r = 0.893$. (Based on Csirke, 1980.)

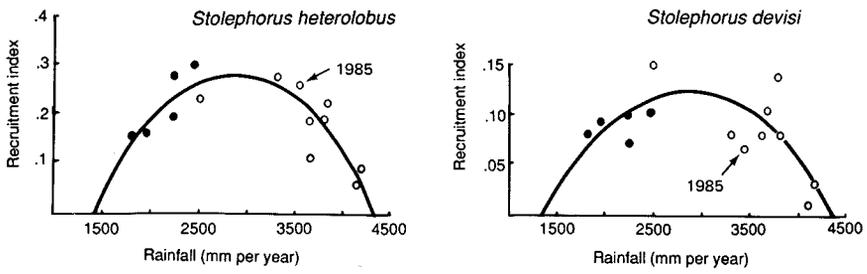
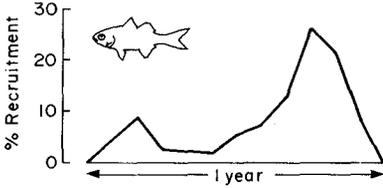
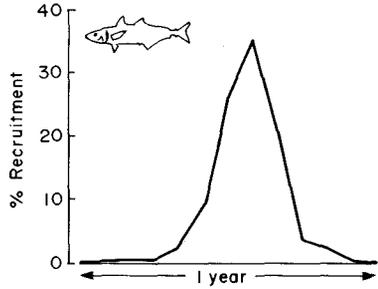


Fig. 9.26. Relationship between rainfall and recruitment in two tropical anchovy species. Recruitment is expressed as catch per effort for unit area of area fished in two regions off northern Papua New Guinea. Ysabel Passage shown as open circles, Cape Lambert as closed circles. The points for 1985 were added after parabolas were fitted (Dalzell, 1984a and personal communication).

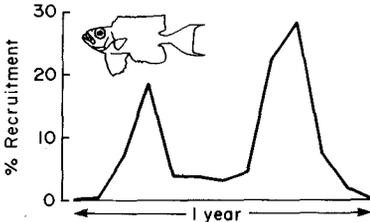
Ambassis gymnocephalus
(Centropomidae)
Manila Bay, 1978-1979



Decapterus macrosoma
(Carangidae)
Palawan, 1965



Priacanthus tayenus
(Priacanthidae)
Samar Sea, 1979-1980



Leiognathus blochii
(Leiognathidae)
Manila Bay, 1957

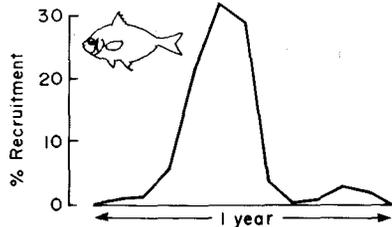


Fig. 9.27. Examples of recruitment patterns, based on backward projection of length-frequency data onto the time axis, of four species of Philippine fish. (From Ingles and Pauly, 1984.)

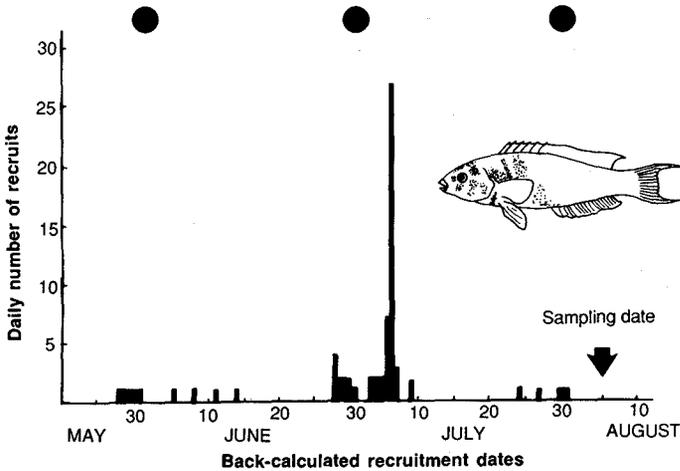


Fig. 9.28. Back-calculated settlement dates obtained by daily rings in the wrasse *Thalassoma bifasciatum* at San Blas Island, Panama (Victor, 1982.)

Lasker, 1985) which is potentially applicable to tropical fishes and which should lead to a whole array of new insights, as demonstrated by the successful application of aspects of this methodology to reef fishes such as *Thalassoma bifasciatum* and *Halichoeres bivittatus* by Victor (1982). Fine temporal resolution from the analysis of daily rings is a powerful tool in testing hypotheses on how recruitment is determined (Lasker, 1978; Fig. 9.28). On the other hand, detailed analysis of length–frequency data can only be performed at a coarser temporal scale. Thus, recruitment patterns obtained by projection of length–frequency data onto a time axis obtained with ELEFAN II software (Pauly, 1982b) can then be related to events on a similar temporal scale, such as the monsoon seasons (Pauly and Navaluna, 1983; see also Fig. 9.27).

In fact, the mechanisms beyond simplistic stock-recruitment relationships that determine recruitment in continental shelf fish remain enigmatic, are obviously diverse, and are now widely accepted as perhaps the principal determinant of abundance variability in most stocks. The environmental control of recruitment is perhaps the most important problem facing fisheries scientists today, and how it functions in tropical seas is very little known.

Any recruitment mechanism must, by definition, satisfy each of three simple criteria: larvae must (1) encounter adequate food supplies and (2) a tolerable level of predation to ensure survival of sufficient numbers to maintain the adult population, while (3) they must complete their larval life in a suitable location to enter the next stage in their life history. These criteria are usually found to be satisfied by a reproductive strategy that ensures that larvae are injected into the marine ecosystem at a suitable location and time. Since both spatial and temporal cues are subject to environmental variability, as are the conditions governing successful recruitment, a variety of reproductive strategies are utilized in all latitudes.

Reproductive strategies of fish form a continuous series whose end-members have been called (Lambert and Ware, 1984) the “big bang” and the “hedged bet” strategies, respectively; in the former, all individuals spawn more or less synchronously while, in the latter, serial spawning extends throughout a longer or shorter season. Generally, in temperate latitudes, pelagic spawners with small, fast-growing larvae adopt the big bang strategy while benthic spawners, with relatively slow-growing larvae, hedge their bets by producing many individual cohorts, spaced usually about 3 weeks apart. Synchronous spawners in temperate regions appear to use cues that enable them to spawn when suitable food occurs in maximum abundance, but predator swamping is an alternative and in some ways more attractive hypothesis to explain this reproductive behavior. Serial spawning, on the other hand, is usually interpreted as a means

of ensuring that at least one cohort shall encounter conditions that ensure good survival.

Can we transfer this analysis of reproductive strategies to the tropics? As we have already noted, most species of fish of tropical continental shelves have rather extended spawning seasons (Weber, 1976). Reviews of the reproductive cycles of several hundreds of fish species of many families from the coasts of India and western Pacific reveal spawning seasons extending over several months, and some tendency for reproductive quiescence during the seasons of strong monsoon winds (Table 9.3). This kind of reproductive cycle occurs also in tropical Atlantic continental shelf fish.

Detailed studies (Johannes, 1978) of the reproductive behavior patterns of demersal fish along tropical coasts with fringing reefs have revealed a variety of mechanisms clearly related to predator avoidance both by the spawning fish themselves and for their young larvae. The corals, hydroids, crustaceans, and small fish of the reef fauna are efficient at trapping zooplankton (and hence fish larvae) by a myriad of different techniques, and spawning reef fish tend to release their eggs in locations that ensure they will be carried offshore and held there long enough for local dissemination to occur at the end of the larval period.

Paradoxically, as we have already discussed, the larvae of many species of fish of open continental shelves have an opposite tendency—to seek enclosed coastal lagoons that will serve (in the same manner as for the penaeid prawns of the continental shelf) as nursery grounds. Though this is an essential factor in the life histories of many of the important commercial species on subtropical coasts, it is not yet clear to what extent it has the same importance on tropical coasts unencumbered with fringing reefs (see Chapter 7).

It is not unreasonable to generalize concerning the significance of these observations in terms of how environmental variability might affect recruitment success in the tropical seas. Two explanations suggest themselves for the general observation that spawning of continental shelf species occurs at times of low wind stress. First, this is when the water column is most likely to be well stratified and when layers of abundant planktonic food organisms will be available for the nourishment of fish larvae which, at least under some circumstances, are thought to be unable to obtain a sufficient energy return from searching for prey in a well-mixed water column where plankton is unstratified (Lasker, 1975). Second, during periods of quieter winds it is less likely that massive off-shelf advection of fish larvae would occur. At least under some circumstances this is thought to lead to poor recruitment in some species of continental shelf fish. Some organisms, such as larval rock lobsters and penaeid

TABLE 9.3. Spawning Periods of Some Fish Species Along the West Coast of India^a

Area	Species	Months											
		J	F	M	A	M	J	J	A	S	O	N	D
Bombay	<i>Psettodes erumei</i>										*****	*****	
Bombay	<i>Otolithus ruber</i>									*****	*****	*****	
Bombay	<i>Johnius dussumieri</i>	*****	*****						*****	*****	*****	*****	
Bombay	<i>Muraenesox talabonoides</i>				*****	*****					*****	*****	
Bombay	<i>Polynemus heptadactylus</i>				*****	*****	*****			*****	*****	*****	*****
Bombay	<i>Pseudosciaena diacanthus</i>						*****	*****	*****	*****	*****	*****	
Bombay	<i>Polydactylus indicus</i>				*****	*****	*****				*****	*****	*****
Bombay	<i>Polydactylus indicus</i>				*****	*****	*****						
Gulf of Kutch	Several spp.	*****	*****						*****	*****	*****		*****
Karwar	<i>Rastrelliger kanagartha</i>							*****	*****	*****	*****		
Karwar	<i>Sardinella longiceps</i>							*****	*****	*****	*****	*****	*****
Karwar	<i>Opiostopterus tardoore</i>		*****	*****	*****	*****	*****	*****	*****	*****			
Karwar	<i>Sardinella fimbriata</i>	*****	*****	*****									
Karwar	<i>Sardinella longiceps</i>	*****						*****	*****	*****	*****	*****	*****
Mangalore	<i>Nematalosa nasus</i>									*****	*****	*****	
Mangalore	<i>Anodontostoma chacunda</i>	*****	*****	*****							*****	*****	*****
Mangalore	<i>Otolithus argenteus</i>	*****									*****	*****	*****
Mangalore	<i>Saurida tumbil</i>	*****									*****	*****	*****
Mangalore	<i>Sardinella longiceps</i>						*****	*****	*****				
Mangalore	<i>Rastrelliger kanagartha</i>		*****	*****	*****	*****	*****	*****	*****	*****			
Cannanore	<i>Cynoglossus semifasciatus</i>											*****	
Calicut	<i>Trichiurus haumela</i>							*****	*****				
Calicut	<i>Sardinella longiceps</i>							*****	*****	*****	*****		
Calicut	<i>Sardinella longiceps</i>							*****	*****	*****	*****		
Calicut	<i>Leiognathus bindus</i>	*****	*****										*****
Calicut	<i>Caranx kalla</i>	*****					*****	*****					*****
Calicut	<i>Cynoglossus semifasciatus</i>	*****	*****	*****	*****	*****	*****	*****	*****	*****	*****	*****	*****
Calicut	<i>Thrissoles mystax</i>	*****	*****	*****	*****	*****	*****	*****	*****	*****	*****	*****	*****
Calicut	<i>Sardinella longiceps</i>							*****	*****	*****			
Cochin	<i>Rastrelliger kanagartha</i>		*****	*****	*****	*****	*****	*****	*****	*****	*****	*****	
Cochin	<i>Sardinella fimbriata</i>							*****	*****	*****	*****	*****	
	Total per month	11	9	9	10	10	14	15	16	18	14	11	11

^a From Weber (1976).

prawns, have developed ontogenetic or diel vertical migration patterns that interact with differential current vectors at different depths in the water column to achieve transport that will maintain them in region where survival is likely to be high (Rothlisberg *et al.*, 1983). In the open ocean, Taylor columns and leeward gyres may act to maintain populations of pelagic larvae near islands of sea-mounts so that sufficient numbers are able to recruit demersal or coastal pelagic populations (Bakun, 1986).

Because the relevant factors do not lend themselves to simple quantification, it is not yet possible statistically to isolate the causal relationships between timing of reproductive processes and the factors leading to recruitment level. In many cases, it seems as if more than one purpose is served by a reproductive strategy and only in some extreme cases is it obvious which one is the principal: The extreme cases of synchronous spawning are more likely to be related to predator swamping than to achieving simultaneity with a food source, or avoiding transport away from juvenile nursery areas. At the other extreme, the serial spawning that occurs in so many species of continental shelf species throughout a relatively long season is more likely to be a mechanism that maximizes the utilization of planktonic food for larvae (which itself has a relatively long season of abundance on tropical continental shelves) and enhances the probability that at least some of the many larval cohorts will have a high rate of survival.

What level of variability in recruitment in tropical species is driven by the action of environmental variability on these different reproductive strategies? There is far less information on recruitment-driven changes in stock size in any tropical fisheries than in temperate fisheries where year-class structure of populations is a routine measurement in stock management. It is usually not clear whether the variability which is observed in relative abundance is caused by differences in year-class (or cohort) strength or if it is an effect of different settlement or migration patterns. The apparent abundance of pomacentrids at several locations on the Great Barrier, between years and over a 4-year period, varies by a factor of $\times 2-9$, but this is probably an effect of settlement patchiness, not overall recruitment variability (Williams, 1983). In the same region, statistical analysis of relative settlement of labrid larvae on seven reefs showed that abundance did not covary between reefs or between years, nor yet between closely related species (Eckert, 1984).

We should also note here that analysis of age or length-based catch curves, especially for demersal stocks, normally provide estimates of total mortality that are compatible with expectations for natural and fishing mortality, and therefore that recruitment to the stocks represented in

these catch curves must have been fairly constant, since constant recruitment is one of the necessary conditions for catch curves to be straight, and for their slope to provide reasonable estimates of total mortality (see Ingles and Pauly, 1984, for a large number of catch curves from typical tropical stocks). Thus, at least as far as demersal stocks are concerned, it does seem that recruitment fluctuations are either relatively small or damped by density-dependent mortality at the juvenile stage, or both.

FOOD AND FEEDING OF TROPICAL MARINE FISHES

Food provides energy, but there is also an energy cost in capturing, processing, and defending it, and these are the topics analyzed by optimum foraging theory (Mittelbach, 1981; Tricas, 1986). If fish, as they grow larger, gradually get access to food with a higher relative energy content, or if they become more efficient at capturing their food, the cost line in Fig. 9.14 will gradually decline, and enable them to grow to a larger size than might have been originally predicted. If these same fish, however, also move into deeper water as they grow, this effect will not be distinguishable from the effects on their metabolism of lower temperatures. If, on the other hand, such a transition from energy-poorer to energy-richer food should be very rapid (Fig. 9.14), this may result in the second growth phase noted by various authors, a phenomenon one might call "second wind" or "deuxième souffle" growth.

Two lines of inquiry are open for the study of the food and feeding habits of tropical fish. One is to accept complexity, and to try to track it in ever increasing details. The other is to attempt to relate to food and feeding of fish as an energy flow to a quantity that can be parameterized, such as biomass per unit time (Longhurst, 1984). It is obvious that these two lines of inquiry have between them a middle ground in which the complexity of the trophic relationships of fish can be somehow reduced by intermediate models, and thus made accessible to holistic modeling.

Analyzing food intake from stomach contents or underwater observation is usually the first step that to be performed when studying the food of fish. As we did in the previous chapter, species can then be assigned to broad classes (planktivore, piscivore, omnivores, etc.) or to finer groupings based on the detailed taxonomics of the ingested prey and cluster analysis of the intake data (Table 9.4).

Such studies usually provide few deep insights, beyond confirming that fish have catholic tastes and illustrating the now well-known rule that larger vertebrate predators habitually take larger prey (Fig. 9.29). Most such studies fail to report absolute prey size related to predator size or

TABLE 9.4. Some Examples of Major Studies on the Food and Feeding Habits of Tropical Marine Fish

Topic	# Stomachs examined	Method	Remarks	Source
Tropical flatfish	N.A.	Various	Relations between food anatomy, and behavior	de Groot, 1971, 1973
Indian sea fish	N.A.	Various	Energetics of feeding, review of Indian studies	Qasim, 1972
Gulf of Guinea: 71 consshelf species, 26 estuarine species	28,320	% Occurrence	3 Years standard data allows study of dynamics of feeding	Longhurst, 1957b, 1960b
Caribbean reef fish (212 species)	5,226	% Volume of contents	Description of each species ("Citation Classic")	Randall, 1967, 1985
Jamaica reef fish	N.A.	Various	Descriptive, reviews of relevant literature	Munro, 1983
<i>Saurida</i> spp., Indian coasts	2,940	Various	Compares items in stomachs with their abundance in sea	Rao, 1981
Coastal fishes, south Gulf of Mexico	N.A.	Various	Describes linkages between different habitats	Yáñez-Arancibia, 1985
Shelf fishes, on Venezuelan shelf	>10,000	Various	Descriptive, identifies primary prey species	Penchaszadeh and Salaya, 1984
Reef fishes, on the Hawaiian coast	1,547	% Volume, occurrence, and much visual observation	Descriptive, emphasizes precise trophic role of each studied species on the reef	Hobson, 1974
Yellowfin, skipjack tuna, in eastern Pacific	6,080	% Volume % Occurrence	Descriptive account, stratified by 14 areas, 3 size classes	Alverson, 1963

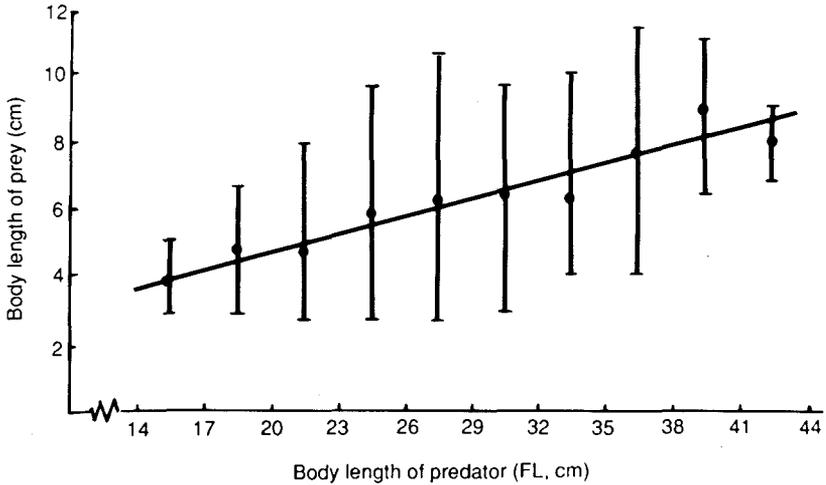


Fig. 9.29. Relationship between the body length of a bar jack (*Caranx ruber*) and of its prey, which is mainly labrids, scarids, and shrimps, on the Cuban continental shelf. (Modified from Siebert and Popova, 1982.)

prey weights, and do not enable absolute energy flow be computed. Most studies, instead, report ingested prey in the form of individual counts, or as percentage occurrence of stomach contents. MacDonald and Green (1983) have shown conclusively that these various available (and hotly debated) methods all give essentially the same results, as was also noted by Longhurst much earlier (1957b).

Even more important is the fact that stomach contents do not by themselves necessarily rank prey according to the fundamental feeding preferences of the fish, nor of the absolute or long-term relative abundances of their prey in the environment. Rather, stomach contents are a simple function of local prey availability and suitability, this latter often simply being a function of size and the predator's previous experience with that prey (Ursin, 1973; Fig. 9.29).

A complementary approach that has led to considerable insights on the food and feeding habits of tropical marine fishes is analysis of their comparative anatomy and physiology, combined with stomach content studies. Thus, for example, the mouths, teeth, eyes, and other body structures of different species of tropical flatfish (Pleuronectoidea) have been related to details of their behavior and their feeding habits by de Groot (1971, 1973), while the prey spectrum of different reef fishes have been related to their degree of evolutionary development by Hobson (1974).

The specialized feeding habits of the cichlid *Sarotherodon me-*

TABLE 9.5. Comparison of Feeding-Related Features of *Sarotherodon melanotheron* (Cichlidae) and *Mugil cephalus* (Mugilidae)^a

Feature	<i>S. melanotheron</i>	<i>M. cephalus</i>
Feeding behavior	Picks up sediment, and swallows after some sorting in mouth	Skims off surface layer of deposits, and filters ingested material
Gill rakers	Absent	Present
Gut/body length ratio at 8 cm length	About 7 : 1	About 3 : 1
Gut clearance rate	3 per day	5 per day
Food item/sediment ratio in stomach contents	2 : 1	100 : 1

^a From Pauly (1976) and Odum (1970).

lanotheron and the mullet *Mugil cephalus*, both of which utilize the organic fraction of the soft mud deposited in coastal lagoons is made possible by a number of characteristic anatomical and behavioral adaptations (Table 9.5) of the kind we refer to, and these enable them to concentrate this fraction by a factor of 2 for *S. melanotheron* and 100 for *M. cephalus*.

An interesting approach to holistic analysis of the nutrition of fish, illustrated by the work of Elliott and Person (1978), involves estimation of only two parameters, mean weight of stomach contents over time and gastric evacuation rate. Given certain assumptions, the product of these two parameters provides the rate of food consumption of the fish for which the parameters have been estimated. This approach was applied to tropical fish (Table 9.6) by Olson and Boggs (1986).

TABLE 9.6. Estimated Food Consumption per Unit Biomass in Some Selected Fish Populations

Species	Daily	Annual
<i>Epinephalus tawina</i> ^a	0.64	2.34
<i>Epinephalus guttatus</i> ^a	0.76	2.78
<i>Sparus auratus</i> ^a	0.88	3.22
<i>Acanthopagrus cuvieri</i> ^a	0.64	2.33
<i>Gadus morhua</i> (60–100 cm) ^b	0.80	2.92
<i>Thunnus albacares</i> ^c	3.90	14.24

^a Pauly and Palomares (1985).

^b Daan (1973).

^c From Olson and Boggs (1986) based on Elliott and Person (1978).

Finally, we propose a model for food consumption of natural fish population that is intended to be consistent with the key equations presented in this chapter. It uses gross food conversion efficiency, (K_1) as its starting point. This quantity, defined as

$$K_1 = (\text{growth increment/food ingested}) \quad (9.12)$$

and which can easily be determined by feeding experimentally (Menzel 1960), can be expressed as a function of body weight

$$K_1 = 1 - (W/W_\infty)^\beta \quad (9.13)$$

where W_∞ is the weight of a fish after cessation of growth, and whose conversion efficiency is therefore zero (Figs. 9.3 and 9.30). Note that this model can be derived from Eq. (9.1) and that it explains the decrease of K_1 with size as the result of a lack of oxygen for growth (Silvert and Pauly, 1987; also see Figs. 9.2 and 9.3).

Various manipulations involving Eqs. (9.4) and (9.8), and incorporation of an equation for biomass per recruit (Beverton and Holt, 1957) lead finally to a compact model for estimating the food of a fish population per unit of its biomass, i.e.,

$$\frac{Q}{B} = \frac{3K \int_{t_r}^{\infty} \frac{(1 - e^{-Kr_1})^2 \cdot e^{-(Kr_1 + Zr_3)}}{1 - (1 - e^{-Kr_1})^{3\beta}}}{\left(\frac{1}{Z} - \frac{3e^{Kr_2}}{Z + K} + \frac{3e^{-2Kr_2}}{Z + 2K} - \frac{e^{-3Kr_2}}{Z + 3K}\right)} \quad (9.14)$$

where $r_1 = t - t_0$; $r_2 = t - t_r$ and $r_3 = t - t_r$, t_r is the age of the youngest fish considered, K , t_0 , and Z are as defined above, and β is the exponent in Eq. (9.13) and the slope in graphs such as Fig. 9.30.

Table 9.6 presents some results obtained with the application of variants of this model, to three warm-water demersal species, as compared with results obtained for cod using a more conventional approach.

This chapter differs from the rest of our book. In it we have tried to present a comprehensive model of fish population biology that has largely been assembled from the studies of the second author. Because some new concepts are introduced, a brief overview of the whole model is perhaps in order in closing this chapter.

What are the key elements of the theory proposed here? They can be summarized as five statements in simple language, as follows:

1. Fish morphology and the physics of oxygen solution and diffusion work together to limit the oxygen available to the tissues of any growing fish, whatever its environment, and whatever evolutionary or behavioral measures it may take to maximize its oxygen availability.

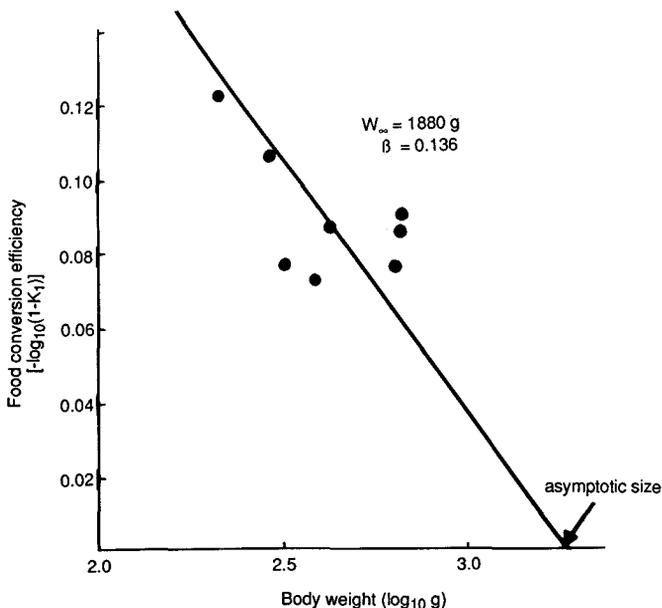


Fig. 9.30. Relationship of food conversion efficiency to body weight in red hind *Epinephalus guttatus*. (From Pauly, 1986b, based on Menzel, 1960, and Thompson and Munro, 1983.)

2. Thus, factors affecting O₂ consumption must limit not only the growth rate of fishes, but also their ultimate size, and any model of the dynamics of fish growth, and the distribution of their maximum sizes in space and time that cannot accommodate this effect must be fundamentally unsatisfactory.

3. Because of the limits thus placed on growth rates, natural mortality rates of fishes are constrained, for any combination of growth parameters, to a rather narrow and broadly predictable range of values.

4. Fishes do not stop growing because they start elaborating gonads; rather they initiate gonad maturation when their growth rate and metabolic rate drops below a predictable threshold.

5. Because the food conversion efficiency of a fish species diminishes with size, models that include growth as a linear function of food consumption will usually be unsatisfactory, and will suggest variations of growth rate of a magnitude that does not occur in nature.

Each of these five statements is open to refutation so that the model is "scientific" in the (trivial) Popperian sense. More interesting is to ask

why this model is offered only in the mid-1980s, rather than 20 years earlier when all of its constituent elements had become available (von Bertalanffy, 1951; Beverton and Holt, 1959; Beverton, 1963; Taylor, 1958, 1962; Gray, 1954). Possibly, the large amount of detailed information on the paradigmatic, high-latitude fishes alluded to above (cod, herring, salmon, etc.) is precisely what prevented workers in high-latitude areas from deriving rules applicable to the whole range of fish species that actually occurs in the oceans. Working in the tropics, on the other hand, forces one to seek much wider patterns and their possible causes, empirical relationships of the type advocated by authors such as Parker and Larkin (1959), or Roff (1980) being simply impossible to establish for more than a handful of species. Whether the model presented here is accepted or not will not depend only on whether propositions 1–5 pass independent experimental tests, however.

An occupational hazard of tropical biologists has been to hear their models described as “rubbish, may apply in the tropics, but not here,” as one thankfully anonymous reviewer described some of the research described in this chapter. We suggest that what may apply in the tropics may also come to be found to be very important “here” because, as we should not forget, most basic life forms of fish and aquatic invertebrates evolved in environments resembling the present-day tropics, and radiated from there to more marginal habitats in higher latitudes.

Chapter 10

Population Biology of Large Marine Invertebrates

In this chapter we have chosen to illustrate, using three representative groups as examples, how techniques developed for fish population dynamics can be applied to the population biology of invertebrates. Our reason for making this point explicitly is that, somewhat like the mythology surrounding tropical fish growth rates, it is easy to believe that the basic biology of invertebrates is so different from fish that population analysis techniques relevant to fish must be inappropriate for invertebrates (e.g., Juanico, 1983). It is our intention to illustrate the extent to which models of population growth and decay are independent of the phylum to which the modeled population belongs. Echinoids, penaeid shrimps, and cephalopods are the products of separate lines of evolutionary development and each possess fundamentally different morphology and physiology, yet (as we shall show) their populations are amenable to analysis by population models formulated for fish stock management purposes. Tropical invertebrate populations are increasingly coming under heavy exploitation and their rational management will require the careful application of such models. Further, the dynamics of natural population interactions within ecosystems may be studied by techniques specifically developed to analyze the interaction between fishermen and fish and, fortunately, this is increasingly recognized to be the case. The growth of organisms as diverse as giant mud-clams in Sierra Leone estuaries (Okera, 1976), prawns off Australia (Rothlisberg *et al.*, 1985a), and rock lobsters off Cuba (Cruz *et al.*, 1981) have been analyzed by fish population models. In this chapter, we shall also try to point out some attributes of tropical invertebrates that cannot be accommodated in unmodified fish population models.

LIFE-HISTORY STRATEGIES OF SEA URCHINS

Although collected for direct human consumption of their gonads in a number of countries, sea urchins (Echinoidea, Echinodermata) are economically important mainly because of their impact as grazers of algae that are cultivated or harvested commercially (Doty, 1973; Gomez *et al.*, 1983). For the same reason, their ecological importance in structuring macrophyte-based littoral ecosystems is also considerable, and grazing by sea urchins may affect the whole structure of shallow-water tropical ecosystems (Hay, 1984a,b) as well as temperate ones (e.g., Mann, 1977). Sea urchin population biology has thus received considerable attention in recent years (Jangoux and Lawrence, 1983), especially with regard to what controls their recruitment (Ebert, 1983; Bacolod and Dy, 1986) and the rapid growth and decline of their populations.

One approach to understanding the dynamics of sea urchin populations has been through comparative studies of the parameters of their growth (Fig. 10.1) and mortality, such as the work of Ebert (1975) on postlarval echinoids of several species. Figure 10.2 shows a plot of values for M on their corresponding values of K , based on the sea urchin data in Table 10.1. This shows clearly that sea urchins exhibit a close relationship between K and M , and that this relationship is similar to the one discussed for fish in Chapter 9.

This suggests that other relationships reported for fish, such as the inverse correlation between K and asymptotic size, should also hold for sea urchins. But Ebert (1975) concluded that no correlation (or else a positive correlation) exists for sea urchins between asymptotic size and K , whereas in fish this correlation is negative. However, the sea urchins used by Ebert ranged only from 1.7 to 11.0 cm, or less than one order of magnitude in dimension. Where inverse relationship between K and asymptotic size have been found for fish populations, this has involved either analyzing a very wide range of sizes in different taxa or comparing several stocks of the same species (Beverton and Holt, 1959; Pauly, 1980a). And, as expected, we find that analysis of growth parameters in different stocks of a single species of tropical sea urchin (*Diadema antiillarum*) does indeed lead to the anticipated inverse relationship between K and asymptotic size having a slope almost exactly equal to the mean slope reported for fishes (Fig. 10.3), and used to derive the growth performance index ϕ' (Eq. 9.5).

Ebert also suggested that tropical species of sea urchins have a significant inverse relationship between asymptotic size K or M and the upper limits of inshore occurrence (Table 10.1), so that tropical sea urchins increase in size, growth rate, and mortality rate downward from the surf

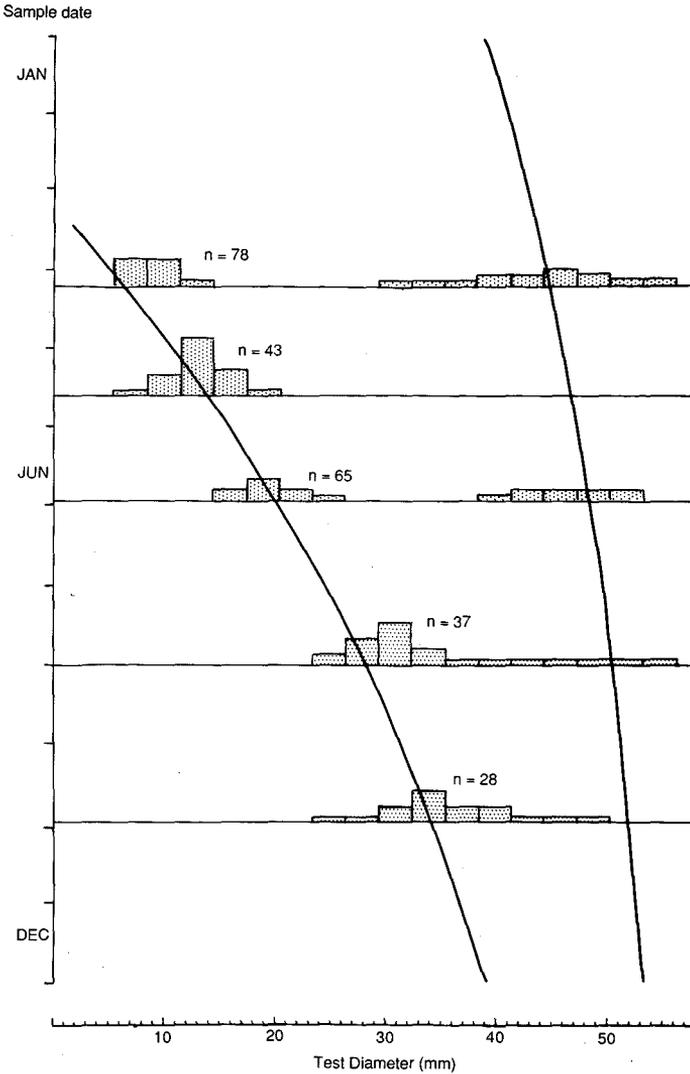


Fig. 10.1. Growth of the sea urchin *Diadema antillarum*, based on the size–frequency data in Bauer (1976) analyzed with the ELEFAN I program (see also Table 10.9).

zone. He suggested that individual urchins living in the surf zone survive longer, on the average, because subtidal individuals, which live in a less stressful environment, are able to expend fewer resources on maintenance and more on growth in size and for reproduction.

The metabolic growth model presented in Chapter 9 explains why sea

TABLE 10.1. Population Parameters of Tropical Sea Urchins Ranked by Upper Limit of Preferred Depths

	Depth rank ^b	Species	L_{∞} ^c	$K(1/y)$	$M(1/y)$	ϕ' ^d
1 ^a	1	<i>Colobocentrus atratus</i>	3.00	0.45	0.33	0.61
2	4.5	<i>Eucidarus tribuloides</i>	5.27	0.67	0.43	1.27
3	6.5	<i>Tripneustes ventricosus</i>	9.00	1.24	0.95	2.00
4	6.5	<i>Echinotrix diadema</i>	9.00	0.82	0.64	1.82
5	8	<i>Diadema antillarum</i>	7.56	1.18	1.30	1.83
6	8	<i>Diadema antillarum</i>	5.80	1.22	1.90	1.61
7	8	<i>Diadema antillarum</i>	5.85 ^e	1.35 ^e	2.07 ^f	1.66
8 ^g	8	<i>Diadema antillarum</i>	3.87	4.14	—	1.79
9 ^g	8	<i>Diadema antillarum</i>	3.91	4.31	—	1.82

^a 1–6 from Ebert (1975), 8–9 computed by method of Gulland and Holt (1959) and growth curves of Bauer (1982).

^b Depth ranks: surf zone = 1, subtidal = 8.

^c L_{∞} is test diameter, cm.

^d $\phi' = \log_{10} K + 2 \log_{10} L_{\infty}$.

^e Estimated by ELEFAN I (based on data in Bauer, 1976).

^f Length-converted catch curve based on Fig. 10.1.

^g 8–9 are possibly stressed laboratory animals.

urchins living in the surf zone should remain smaller than those living in the less stressful subtidal. However, that their K (and hence M) should be the lowest on record is indeed puzzling but most probably will prove to be a consequence of some aspect of the detailed ecology of a sessile, grazing organism in the intertidal ecosystem. This may be a good example of the occasional need to modify fish population models because of some distinctly unfishlike aspect of the ecology or physiology of a group of invertebrates.

A further example of how a theoretical population model may be incapable of tracking actual population numbers is the case of a major population crash, due to some cause not normally accommodated in population models, such as a pollutant, or a pandemic pathogen. The sea urchin *Diadema antillarum*, which ranges from Florida to Surinam (Bauer, 1980), has been studied by several authors, notably Scoffin *et al.* (1980) and Hay (1984a,b), and shown to be a major factor affecting community structure in tropical neritic ecosystems. *Diadema* reaches densities of >50 individuals per square meter and erodes calcium from reef rock while grazing algal turf, eats live coral, and is a highly competitive herbivore able to cause large areas of barren rock, in the same way as kelp beds are turned into "urchin barrens" by the North Atlantic urchin *Strongylocentrotus*.

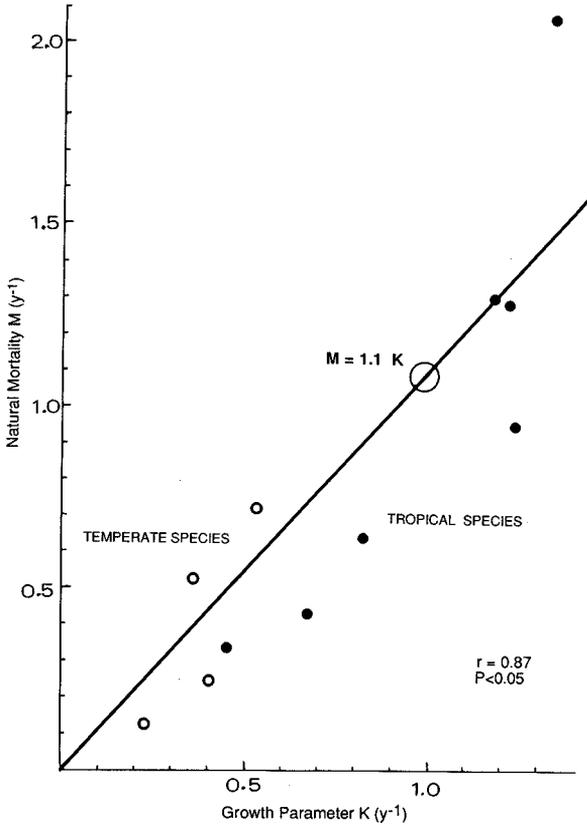


Fig. 10.2. Relationship between the growth parameter K and natural mortality estimates (M) (see also Table 10.1) in sea urchins. (Based on data in Ebert, 1975.)

In the 12 months following January 1983, populations of *D. antillarum* throughout the Caribbean were reduced to about 1% of their former abundance by the spread of a pathogen from an initial infection near Panama (Lessios *et al.*, 1984a). The timing of the infection is entirely consistent with the spread of a pathogenic organism by the current systems of the Caribbean (Gordon, 1969), and it is safe to assume that this was a phenomenon similar to the population crashes of *Strongylocentrotus* through infection with an amoeboid pathogen (*Paramoeba*) that occur in years only when water temperatures are anomalously high (Scheibling and Stevenson, 1984). One cannot help noting that the spread of the pathogen through the Caribbean occurred in the months of maximum warm SST anomalies in the eastern Pacific related to the 1982–1983 El Niño–South-

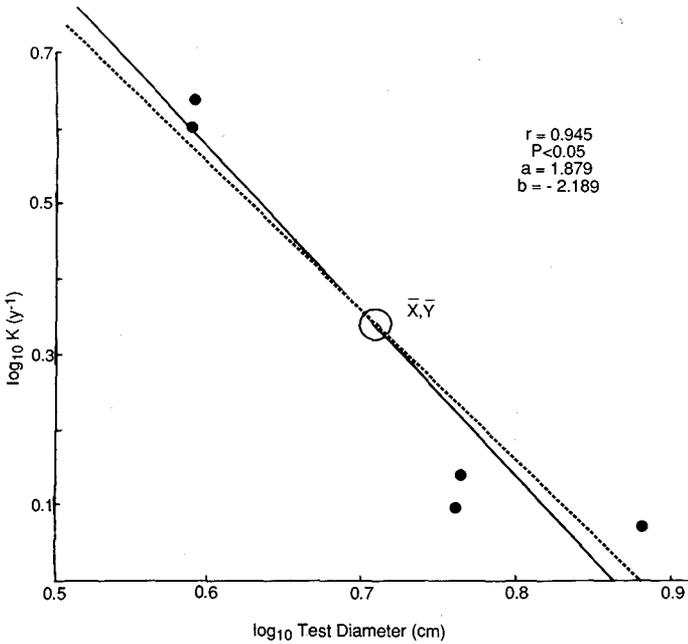


Fig. 10.3. Relationship between K and asymptotic size for S set of these growth parameters in the sea urchin *Diadema antillarum*, based on Table 10.1. Note how these data (solid line) match with the relationship expected on theoretical grounds (dashed line), as explained in the text.

ern Oscillation (ENSO) event, and when there was some evidence of warm anomalies also in the tropical western Atlantic.

It can be predicted that communities previously structured by grazing *D. antillarum* will, for several years, show different abundance and distribution of algae. Lessios *et al.* (1984b) also expected that the sudden decline in the availability of *Diadema* probably increased the predation pressure on the few individuals that survived the disease, and on other species of predators.

This prediction was confirmed by the switch during 1983 of the queen triggerfish *Balistes vetula* from a diet consisting predominantly of *D. antillarum* to one mainly of crustaceans (Fig. 10.4). Thus, what previously appeared to be a specialized predator (Reinthal *et al.*, 1984) is in fact a generalist, with a wide ethological repertoire (Fricke, 1975), which enables it to handle and utilize a large number of preys, and which concentrates on a difficult prey (*D. antillarum* in this case) only if its high abundance is sufficient to offset (in terms of net energy yields) the relatively high cost of handling it.

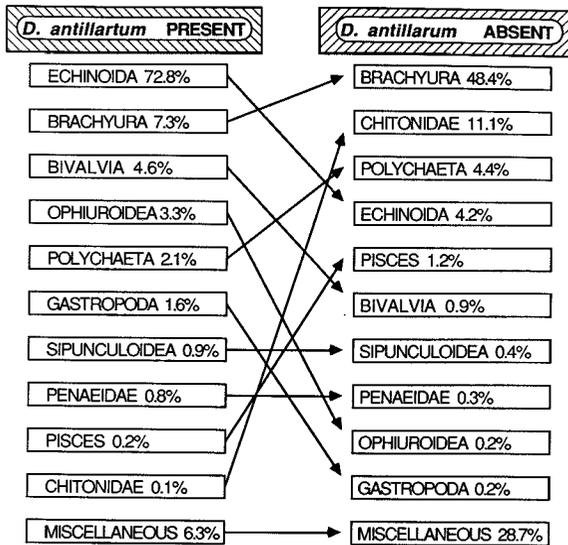


Fig. 10.4. Food composition, by volume, of the queen triggerfish, *Balistes vetula* in the presence of *Diadema antillarum* based on 95 specimens from the Virgin Islands, and absence based on 23 specimens from Belize (Randall, 1967; Reinthal *et al.*, 1984).

There is no known case of pathogenic fish mortality of this scope, and practical fish population models usually accommodate fish disease only as an unexceptional and stochastic element within *M*, the natural mortality parameter. This is an example of how some detailed aspects of invertebrate biology may require some revision to fish population models prior to their application in the management of invertebrates.

RECRUITMENT OF PENAEID SHRIMPS

Importance of Tropical Resources

Because of their economic importance to some tropical nations (Table 10.2), shrimps of the family Penaeidae have been much studied, and many aspects of their biology and numerical population dynamics have been clarified in recent years (Gulland, 1971; Holthuis, 1980; Garcia and LeReste, 1981; International Development & Research Council, 1982; Rothlisberg *et al.*, 1985a; Yáñez-Arancibia, 1984). The application of fish models to shrimp population dynamics has now become routine, and the FAO manual published by Garcia and LeReste (1981) is an excellent entry

TABLE 10.2. Nominal Global Catches of Shrimps

"Top twenty" countries, total shrimp catches					
Country	t y ⁻¹	How reported	Country	t y ⁻¹	How reported
India	214,980	All as "Natant decapods"	Brazil	50,660	All as "Natant decapods"
China	185,790	90% are <i>Acetes</i>	Vietnam	49,100	All as "Natant decapods"
Thailand	173,967	11% <i>Sergestes</i> , rest <i>Penaeus</i>	Greenland	41,243	<i>Pandalus borealis</i>
Indonesia	129,610	71% Reported as penaeids	Ecuador	36,600	All as "Natant decapods"
USA	119,906	89% Penaeids, 9% <i>Pandalus</i>	Korea	36,424	47% are <i>Acetes</i> , 9% penaeids
Malaysia	76,475	16% Sergestids, rest penaeids	USSR	29,394	<i>Crangon</i> spp.
Norway	75,035	<i>Pandalus jordani</i>	Pakistan	27,502	All reported as penaeids
Mexico	65,586	All as "Natant decapods"	Australia	20,814	All as "Natant decapods"
Japan	61,943	8% Penaeids	Argentina	19,289	<i>Artemisia</i> , <i>Pleoticus</i>
Philippines	55,748	47% Sergestids, 53% penaeids	Panama	13,491	91% as penaeids

 Tropical shrimp catches by species, as reported

<i>P. aztecus</i>	64,034	<i>Metapenaeus</i> spp.	46,240
<i>P. merguensis</i>	59,454	<i>M. joinieri</i>	1,386
<i>P. californiensis</i>	598	<i>P. longirostris</i>	6,424
<i>P. duorarum</i>	14,007	<i>P. atlantica</i>	122
<i>P. japonicus</i>	6,576	Atlantic sea-bobs	1,954
<i>P. monodon</i>	20,755	<i>Artemisia</i> spp.	314
<i>P. chinensis</i>	18,346	Pacific sea-bobs	10,677
<i>P. kerathurus</i>	10,666		
<i>P. semisulcatus</i>	1,806	<i>P. edwardsianus</i>	510
<i>P. setiferus</i>	30,064	<i>Pleoticus, Sicyonia</i>	20,603
<i>P. brevirostris</i>	2,311		
<i>P. latisulcatus</i>	1,208	<i>Sergestes, Acetes</i>	57,776
<i>P. notialis</i>	5,950		
<i>Penaeus</i> spp. (includes above species)	265,963	“Natantia”	1,753,339
Total			2,354,843
Temperate shrimp catches			
<i>Palaemon</i> spp.	2,977		
<i>Crangon</i> spp.	56,999		
<i>Pandalus borealis</i>	147,944		
Other pandalids	32,580		
“Natantia”	24,875		
Total			265,375
All shrimps			2,620,218

^a Data rearranged from FAO landing statistics for 1983. Data as tonnes.

into this field. Measurement of effort, the use of tagging techniques, the calculation of growth, fecundity, and mortality, the relationship between parameters of the von Bertalanffy growth equation (VGBF), the analysis of the stock-recruitment relationship, and consideration of optimal exploitation levels can now all be handled for penaeids by techniques developed for fish models.

Many tropical countries are expected to increase their shrimp exports through intensification of the present fisheries and the development of aquaculture (New and Rabanal, 1985; Lawrence, 1985). However, besides market saturation effects (Palomares, 1985), the feasibility of these plans will depend both on the availability of wild stocks of shrimp to support increased fishing pressure, and on whether shrimp farming will modify coastal wetland habitat so as to destroy more wild stock potential than is gained by output from the farms (as is already the case in Ecuador) to the extent that almost half of the mangrove area was converted to shrimp ponds by 1985, and it is projected that almost all will be converted by 1990 (Terchunian *et al.*, 1986). Conversion at a comparable rate is also occurring in Bangladesh (Quader *et al.*, 1986) where the Sunderbans, the largest mangrove area (59×10^4 ha) remaining anywhere, is undergoing rapid conversion.

This problem therefore makes shrimp recruitment models of peculiar importance today. We examine recruitment in detail, because it is here that the special biology of penaeids may cause some aspects of fish recruitment models to become irrelevant.

Parental Stock Biomass as a Factor Affecting Recruitment

For young shrimp to be recruited to a stock, there must be some parents to produce viable eggs so that at least one point (the origin) of the stock-recruitment relationship will always be known. Sharp and Csirke (1983) have criticized both the fish stock-recruitment models involving computation of one point per year, with subsequent fitting of a single curve of the Ricker (1954) or Beverton and Holt (1959) type, and also the more flexible model of Shepherd (1982).

Garcia (1983) has made the same comments for the application of such models to shrimp. Figure 10.5 (left side of figure) gives several apparent stock-recruitment relationships in shrimps from various areas that seem to imply a relatively linear relationship between parent stock size and subsequent recruitment. However, Garcia questions whether the apparent relationship parallels the stock-recruit relationship in fish, citing the strong serial correlation between stock and recruitment inherent in a fishery based on very short-lived species, and the impossibility that the sim-

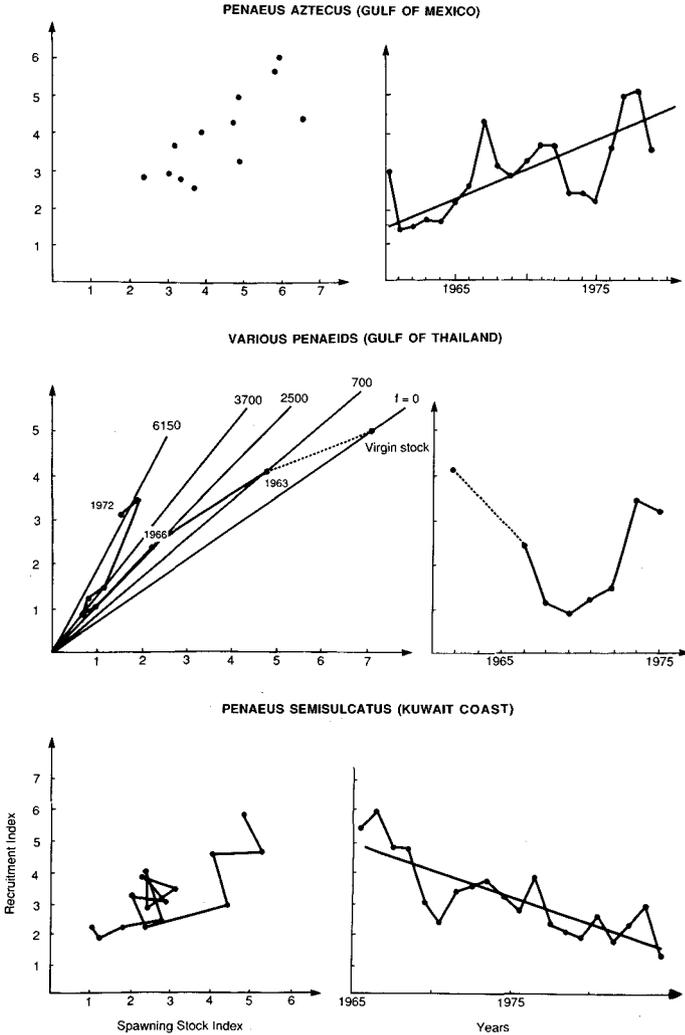


Fig. 10.5. Stock-recruitment relationships and temporal trends of recruitment in some penaeid shrimp stocks (Garcia, 1983; Mathews, 1985).

ple relationship should be linear over such a wide range of fishing effort. The temporal trends (right side of Fig. 10.5) on the other hand, are real, and they describe three different processes in the shrimp stocks in question: (1) A trend toward increased recruitment in *P. aztecus*, for which an explanation is wanting; (2) an initial decrease, subsequently followed by an increase in the stock-size of Gulf of Thailand shrimp, attributed to

decreased predation on pre-recruit shrimp as the biomass of small fish species decreased (Pauly, 1982c, 1984c); (3) a steadily decreasing stock-size of Kuwait shrimps, attributed to a steady loss of intertidal area for the juveniles in the Gulf region (see below). It is most important to know if these observed changes in stock size are, in fact, due to recruitment being modified in some way by environmental modification, or by a feedback mechanism inherent in a linear stock–recruitment relationship.

Seasonal Fluctuations in Recruitment

Penaeid shrimps are short-lived, recruitment occurring to the coastal populations as little as 4 months after spawning. Thus, within-year events that are often neglected in population models for fish with a greater longevity must be considered explicitly when formulating shrimp population models. It is essential, for instance, to accommodate seasonally fluctuating growth rates in such models, because totally erroneous inferences may be drawn on life cycles and relative cohort strength if this is not explicitly done (Garcia and LeReste, 1981; Pauly, 1985b; Garcia, 1985).

We have already described in Chapter 4 the essentials of penaeid life cycles. Figure 10.6 illustrates, as a special case, the life cycle of *Metapenaeus affinis* in Kuwait waters, along with some features of its environment. The figure illustrates that growth oscillates seasonally, that spawning occurs in two pulses per year, one being of shorter duration, and that recruitment consequently occurs as two cohorts, one smaller than the other.

Detailed investigation of the interaction between oceanographic, physi-

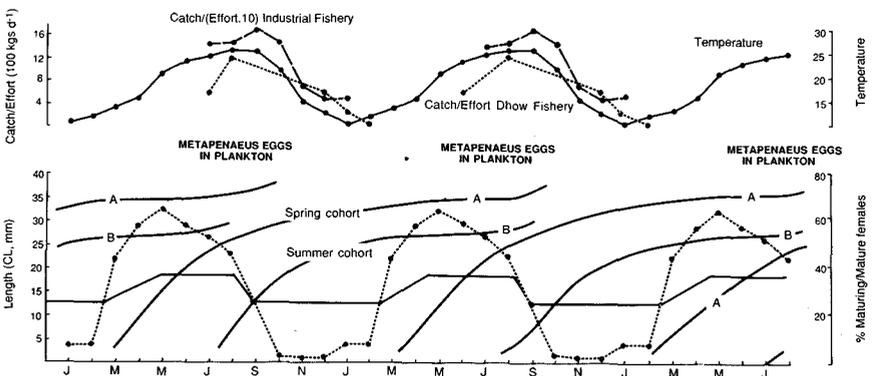


Fig. 10.6. Summary of main features of the life-history cycle of *Metapenaeus affinis* in Kuwait waters (Mathews *et al.*, 1987b).

ological, and behavioral processes has shown why *P. merguensis* has two recruitment events per year in the Gulf of Carpentaria (Rothlisberg *et al.*, 1985b). These studies suggest that *P. merguensis* in the Gulf of Carpentaria may be maladapted to its environment, which is not surprising since the Gulf is a Quaternary feature, about 5000 years old, while penaeid shrimp species are, in some cases, unchanged morphologically since the Cretaceous (Burokowsky, 1970). *P. merguensis* in the Gulf of Carpentaria produces the bulk of its eggs during the season least appropriate for larval survival, while its major cohort is recruited from a minor spawning event each year.

The example of *Penaeus merguensis* in the Gulf of Carpentaria confirms that the bimodal recruitment pattern is very basic to penaeids, since it is maintained under such apparently anomalous conditions, and the situation illustrated in Fig. 10.7 is probably valid for most species of penaeids: Their populations, at any one time, consist of two partly overlapping cohorts arising from the spring and autumn spawning peaks. Rothlisberg and his colleagues believe that for each cohort of *P. merguensis* in the Gulf of Carpentaria, it is the first spawning event that produces the more eggs, the second representing the effort of only a small number of survivors. Garcia (1985), however, believes that the normal generation interval, the period between massive reproduction of parent to massive reproduction of progeny generation, is 1 year in *Penaeus*, based on his observations of *P. notialis* = *duorarum* in the Gulf of Guinea, and on theoretical grounds. Garcia allows two cohorts each year but does not believe that a major spawning event occurs at the end of the first 6 months of life.

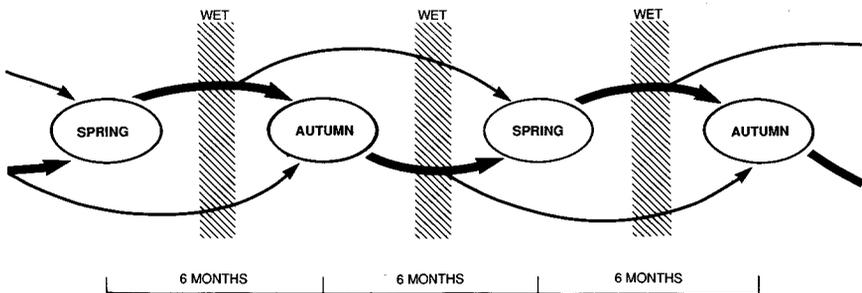


Fig. 10.7. "Interlocking" of cohorts in penaeid shrimp populations as illustrated by a generalization of life cycles in *P. merguensis* throughout the Indo-Pacific (Rothlisberg *et al.*, 1985b).

Link between Coastal Wetlands and Recruitment

MacNae (1974) was among the first to suggest the existence of a causal link between the area of mangrove forests and the yield of adjacent shrimp fisheries, which are generally proportional to recruitment, given the strong exploitation they are usually subjected to and the short life span of penaeids. This idea was expanded in the form of correlative studies by Martsubroto and Naamin (1977) and Turner (1977), and the empirical relationships they obtained have been widely used for practical purposes, such as for environmental impact assessment studies, and by ecologists as illustrative of the general relationships between coastal organisms and the tidal wetlands.

Although such relationship can be expanded to account for more predictors of shrimp yields than intertidal vegetation area alone, e.g., latitude (Turner, 1977), they can also be viewed as a conceptual cul-de-sac because they do not tell us which attributes of vegetated intertidal areas are causal. More importantly, these simple relationships have one very basic constraint: They cannot model those areas that have very large shrimp catches, but relatively small areas of intertidal vegetation, such as the coast of northwest India and Pakistan.

As we have indicated in Chapter 4, there are penaeids that require brackish habitats for their juvenile development and those that do not. Off northwest India, at least two of the principal species in the shrimp stocks (*Metapenaeus affinis* and *Parapenaeopsis stylifera*) do not use estuarine regions for their juvenile development, so that their presence must modify any simple relationship between shrimp production and area of adjacent coastal wetland.

In fact there is no certainty that such a relationship is causal even when it can be demonstrated to exist; it seems just as likely that causation is through the general level of productivity of the continental shelf sustained by terrestrial organic material borne by rivers. In fact, it is noteworthy that the region of the tropical seas that produces the greatest biomass of shrimp is also that which receives the greatest discharges of terrestrial organic material, as a simple comparison of Fig. 2.1 with Table 10.2 will verify.

Various relationships have in fact been reported between shrimp catches, and rainfall or rate of river discharge, notably on the West African (Garcia and LeReste, 1981), East African (da Silva, 1986) and Australian coasts (Fig. 10.8). In some cases these relationships indicate that moderate rainfall and/or river discharge increases recruitment, while very strong rainfall decreases recruitment. Such dome-shaped relationships may imply that fresh water input of the right magnitude may, in a given

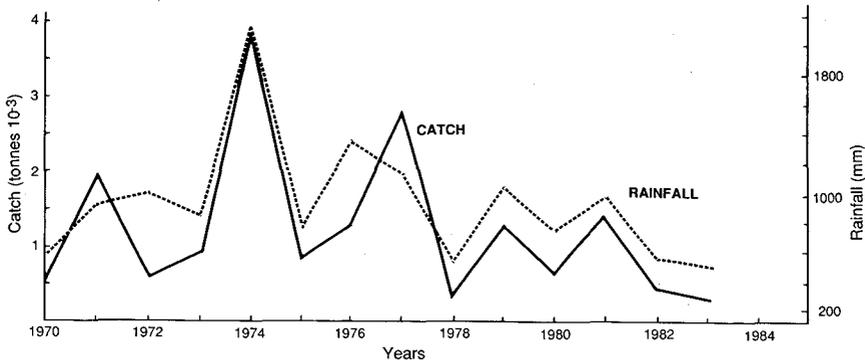


Fig. 10.8. Catch of *Penaeus merguensis* and rainfall for the Karumba region of the southeastern Gulf of Carpentaria, Australia, 1970–1983 (Staples, 1985).

inshore system, maintain water of appropriate salinity in lagoons, estuaries, and other coastal systems where juvenile shrimp occur, while reduced or excessive freshwater inputs lead to the coastal system becoming limnic or fully marine, respectively. As Browder and Moore (1981) point out, juvenile shrimp require the matching of two sets of variables for good survival: a static set related to the benthic environment and a dynamic set related to water conditions. Match or mismatch of the two sets can determine survival or failure of estuarine juvenile stocks. Staples (1985) describes the complex factors determining emigration of juvenile *P. merguensis* in the Gulf of Carpentaria as a function of river discharge. The proportion of the juvenile population that emigrates increases with increasing river discharge, though the size of the emigrants falls. Years of lowest rainfall are those in which only a few, large juveniles emigrate. Staples finds that the relationship between rainfall and recruitment shown in Fig. 10.7 depends not on the absolute size of the juvenile stock, but the proportion of it which emigrates.

Synthesis: Modeling Shrimp Recruitment

The various elements mentioned above, which have all been shown to affect shrimp recruitment, are but a few of those that have been hypothesized to have such effects and models have been formulated that attempt simultaneously to incorporate a number of these effects (Staples, 1985) and that may even include the added complexity of a fishery (Grant *et al.*, 1981). These models are variously successful, but some have a rather low predictive capability, especially where the economic vagaries of a fishery

intervene. Predictive success probably requires very profound understanding of the biology of the species concerned, as well as of the economic background driving the fishery. The simple relationship between rainfall and shrimp catches shown in Fig. 10.8 has some predictive capability, and has been formulated as a mathematical multistage model described also by Staples (1985). This incorporates adult spawning stock, juvenile stock, and rainfall, and it is predictive of emigrants and the resulting adult catches sufficiently closely to be of use at least in long-term fishery management planning.

SQUIDS AS COMPONENTS OF TROPICAL MULTISPECIES SYSTEMS

Application of Fish Models to Squid Populations

Squids (Cephalopoda, Teuthoidea) are important components of tropical marine ecosystems, both neritic and oceanic, although the true magnitude of their biomass and level of production has become apparent on a world-wide basis only with the extension of the Japanese squid fisheries beyond the northwestern Pacific Ocean (Sato and Hatanaka, 1983; Worms, 1983; Lange and Sissenwine, 1983; Voss, 1983). Another phenomenon that has recently attracted scientific attention is the explosive growth of cephalopod populations after the reduction of the associated fish component of their ecosystem; this has occurred in the Gulf of Thailand and off Mauretania (Ritrasaga, 1976; Pauly, 1979; Boonyubol and Pramokchutima, 1982; Caddy, 1983). Squid inhabit a variety of habitats (Packard, 1972; Brandt, 1983; Boyle, 1983; also Fig. 10.9). We deal here only with neritic and shelf species occurring in the tropics and subtropics.

Because of their unusual interest to neurophysiologists and ethologists, the majority of the scientific literature on cephalopods is of little relevance to their population biology. Indeed, the preoccupation of most squid biologists with giant nerve fibers and ethology has led to the suggestion that "squids are not fish and that few principles of fish biology apply to these molluscs" (Juanico, 1983). On the contrary, we wish to suggest that most principles of fish population biology do apply to squids. In the following section, we shall discuss the role of squids in some tropical ecosystems through the application of fish population models.

Since major research programs devoted to the study of squid populations are relatively recent in origin, knowledge of the life cycle of individual species is often lacking, as can be seen clearly from the level of information available in the 22 species reviews presented by Boyle (1983).

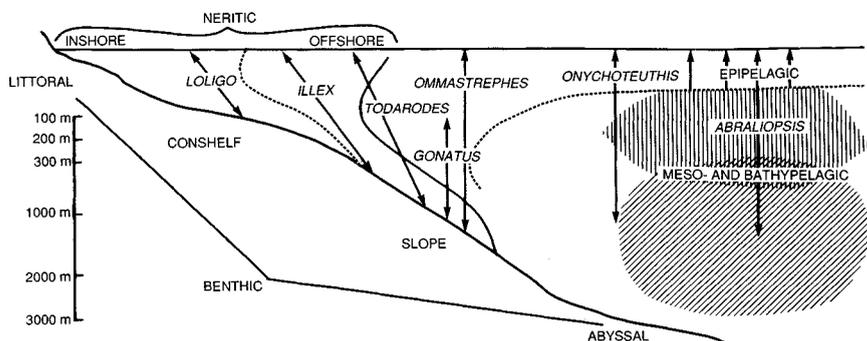


Fig. 10.9. The depth distribution of decapods in the major regions of the sea (Packard, 1972; Clarke and Lu, 1975; Roper and Young, 1975; Arnold, 1979).

However, the available evidence on growth, mortality, and other parameters of the population dynamics of squids is sufficient to suggest that they can be accommodated within fish population models (Pauly, 1985b). For example, Table 10.3 presents data for the maximum size of various species of squids in different parts of their range, and strongly suggests that squids conform to metabolic growth models for fish (Chapter 9), so that L_{\max} for squid is a negative function of temperature. Further confirmation of the metabolic growth model can be provided by within-species comparisons of the same parameters as functions of temperature (Table 10.4).

Squids grow rapidly, and their growth is a function of temperature. Consequently, experimental and observational studies have produced inconsistent (and contradictory) growth models, including apparently linear growth in small species in the absence of food limitation, cyclic growth related to environmental temperature, sigmoid and asymptotic growth, and even exponential growth throughout life. Growth has been measured by analysis of daily growth rings in statoliths, experiments in tanks, and length–frequency analysis.

However, these seemingly contradictory statements about the growth of cephalopods can be resolved within a basic asymptotic growth pattern with superimposed seasonal growth oscillations. This conforms to a von Bertalanffy growth model modified to include a constant expressing the amplitude C of the growth oscillations (Pauly, 1985b, and Chapter 9). Figure 10.10 shows how length–frequency data for the tropical squid *Sepioteuthis lessoniana* can be analyzed quite simply with techniques developed for fish growth models, thus rendering superfluous the often complex schemes proposed by some authors to describe squid growth.

Figure 10.11 compares the growth parameters of a number of squid

TABLE 10.3. Maximum Size of Species of Squid in Relation to Water Temperature as Indicated by Latitude^a

	<i>Sepio- teuthis lessoniana</i>		<i>Illex coindetii</i>	<i>Illex illecebrosus</i>				<i>Todarodes sagittarius</i>		<i>Nototo- darus sloani</i>		<i>Dosidicus gigas</i>	
	cm	kg	male cm	male cm	kg	female cm	kg	male cm	female cm	cm	kg	cm	kg
High north latitude	36	1.4	37	31	1.6	27	0.4	49	64	—	—	—	—
Low latitudes	33	1.2	26	20	0.2	18	0.1	32	37	32	0.6	100	18.8
High south latitudes	—	—	—	—	—	—	—	—	—	42	1.8	150	62.0

^a Mantle lengths and weights from Roper *et al.*, (1984). *D. gigas* weights from Ehrhardt *et al.*, 1983.

TABLE 10.4. Evidence for Applicability to *Loligo pealei* of a Fish Growth Model Which Gives a Limiting Role to O₂ Supply to Tissues

Observation	Interpretation
Largest specimens in coldest parts of range	Table 10.3 for other squids, and see Chapter 9 for fish.
Maturation occurs at smaller sizes in warmer parts of range	As occurs in fish, see Chapter 9
Gill filaments grow relatively faster in warm parts of range	As required to elevate standard metabolism in warm, low O ₂ water
Males have more gill filaments than females	Males reach 50 cm, females only 40 cm, off New England (Roper <i>et al.</i> , 1984)
<i>L. pealei</i> has relatively larger gills than <i>L. roperi</i>	<i>L. pealei</i> is larger species even when they co-occur

^a All information extracted from Cohen (1976).

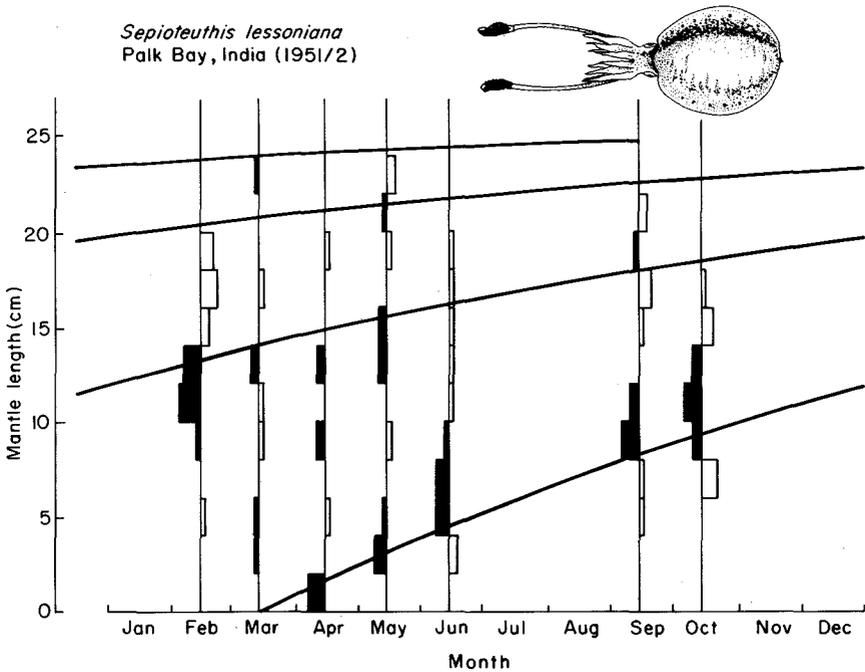


Fig. 10.10. Growth of the Palk Bay squid *Sepioteuthis lessoniana* based on length frequency data (in Rao, 1954) and the ELEFAN I program.

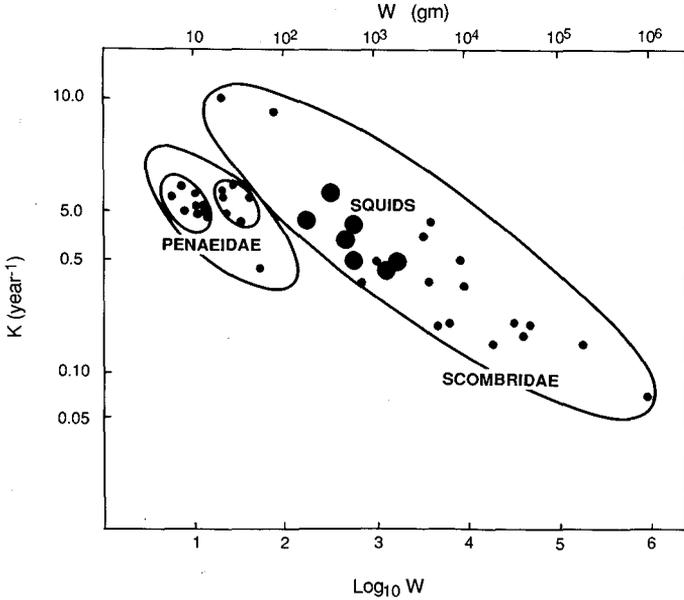


Fig. 10.11. Comparison of the growth performance of some squids with fast-growing fish (Scombridae) and other invertebrates (penaeid shrimps) by means of an auximetric grid, which leads to the conclusion that squids have as rapid growth as their pelagic competitors. (Data from Pauly, 1985a,b.)

species with those of penaeid shrimps and scombroid fish. As can be seen from this auximetric grid, the growth parameters of squids place them in the same league as the fast-growing, high-metabolism mackerel-like fishes, with which they share their pelagic habitats. Moreover, as Fig. 10.12 shows, the migration patterns for an oceanic squid, *Dosidicus gigas* of the eastern Pacific, show that it uses its environment very much in the same manner as large pelagic predatory teleosts, of which it is an evolutionary convergent ecological equivalent.

Analysis of mortality in cephalopods is not simple. There is excellent evidence that many, perhaps most, species of cephalopods undergo mortality in the same pattern as Pacific salmon, including a terminal, post-spawning mortality of both sexes. This is not a usual pattern of mortality for marine fish, and the application of fish population models must be sensitive to this difference. Spawning stress has been noted in many cephalopods as producing thin and watery flesh, damaged epithelium, opaque pupils, a cessation of feeding, and lack of germ cells in gonads. Of the 22 species synopses presented in Boyle (1983) of midge squid to octopuses, the 17 that include information on mortality describe some aspect of postspawning mortality.

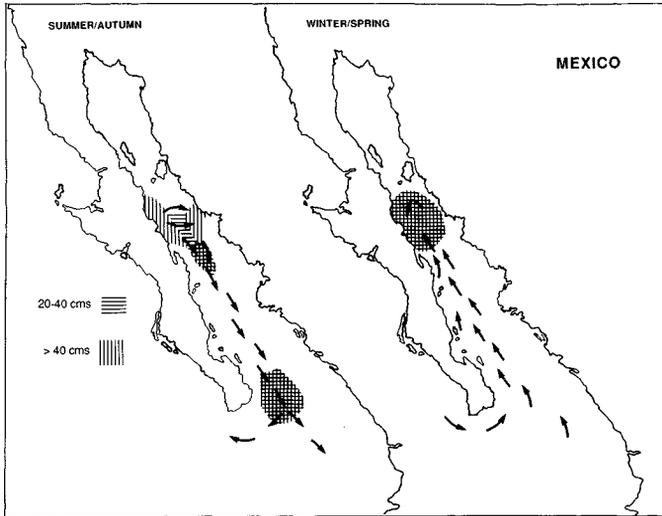


Fig. 10.12. Tentative migration scheme for giant squid *Dosidicus gigas* off Baja California (Ehrhardt *et al.*, 1983).

However, cephalopod mortality is not as simple as this might seem to imply. First, because natural mortality must occur at some rate throughout life, it is only a small percentage of larvae that recruit, and of recruits that survive to die in terminal postspawning mortality. Second, because there is evidence in some species that some individuals survive their first spawning and undergo serial spawning with mortality only at the end of the process. Thus, Bakhayoko (1980) describes complex migrations by *Sepia officinalis* off Senegal which include a return of some females to a second spawning event; Boyle (1983) includes data suggesting that *Loligo vulgaris* of the North Atlantic behaves in the same manner, and Juanico (1983) believes that *Doryteuthis plei* of the Caribbean is another multiple spawner.

Pauly (1985b) presented length-converted catch curves for *Loligo pealei* of the Gulf of Mexico, and *Ommastrephes* off Japan, which apparently include no evidence of terminal postspawning mortality, though the same kind of plot for *Dosidicus gigas* seems to do so.

Figure 10.13 shows a similar plot for the tropical neritic squid *Sepioteuthis lessoniana* from southern India, which seems to show no evidence of a terminal postspawning mortality though Rao (1954) noted many of the symptoms of spawning stress in this species in Palk Bay where, he says, females have mostly empty stomachs during the breeding season in addition to being stressed in other ways. It seems likely that the

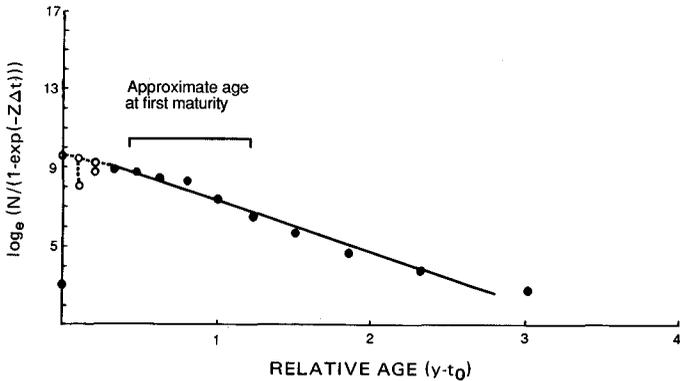


Fig. 10.13. Length-converted catch-curve for the squid *Sepioteuthis lessoniana* off southern India, with an estimated value of $Z = 2.56$ (data from Fig. 10.11).

Palk Bay squid will prove to have the same kind of life cycle as we have noted above for *Sepia officinalis* off Senegal.

Food Consumption of Squids

Because there are now several known instances of tropical squid outbursts following reduction of fish biomass by commercial fishing, the trophic relations between these two ecologically similar, but morphologically very different, groups are important to understand. We have already noted (Chapter 4) that cephalopods are capable of capturing unusually large prey, frequently including smaller individuals of the same species. Squids in tropical ecosystems act, as elsewhere, both as predators and prey (Fig. 10.14) and we shall discuss these two roles, using *Loligo duvauceli* and *Sepioteuthis lessoniana* as representative species, to illustrate the consequences of cephalopods as components of pelagic ecosystems.

The food intake of *L. duvauceli*, which like other squids is reported to feed on crustaceans, fishes, and squids, has not been estimated directly. However, we can apply the recently developed method of Pauly (1986b) and Chapter 9, based on food conversion data for *L. opalescens* (Fig. 10.15), which is a species very similar in size and morphology to *L. duvauceli*. The results (Table 10.5), which have been corrected for the different temperatures of the habitats of these two species, suggests that a population of *L. duvauceli* will eat approximately 9.4% of its own weight per day or 34 times its own weight per year. This is well within the range of food consumption estimated for other squid populations (Table 10.6),

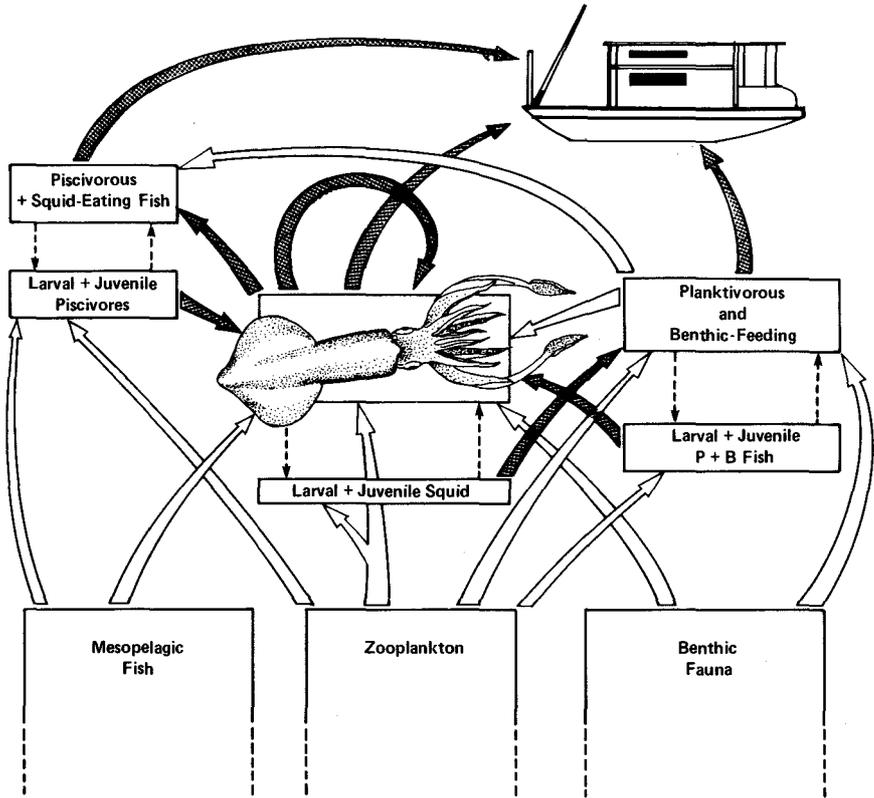


Fig. 10.14. Hypothesized trophic relations of squid with their biotic environment after intensive fishing for finfish and prior to a major squid fishery. Open arrows indicate flow of biomass, solid arrows are flows thought to be of key importance in determining abundance of squid and larger fish. Box size approximately corresponds to relative standing stocks of components. (Modified from Caddy, 1983.)

which covers an unrealistically wide range of 0.7–21.3% of body weight per day, or 4.4–78 times body weight per year. More interesting is the fact that our estimates for *L. duvauceli* approach those for *Katsuwonus pelamis*, a very active pelagic fish.

In absolute terms, our estimates imply that the cephalopod biomass of the Gulf of Thailand (if one accepts that it behaves similarly to *D. duvauceli*, its major component species) consumed about 700,000 tons of prey in the early 1960s, and 500,000 tons in the early 1980s when the biomass of squid was about 20,000 and 10,000 tons, respectively (Pauly, 1985b). The lack of direct proportionality is due to the fact that a strongly

TABLE 10.5. Food Consumption as Percentage of Body Weight of Squids and Skipjack, *Katsuwonus pelamis*

Species	Area	Temp (°C)	Daily food intake (%)	Comment	Reference
<i>Illex illecebrosus</i>	N.W. Atlantic	10°C	0.7 & 21.3	Spring (2 years)	Maurer and Bowman, 1985
		9°C	3.7 & 7.2	Summer (2 years)	Maurer and Bowman, 1985
		10°C	1.2 & 3.3	Fall (2 years)	Maurer and Bowman, 1985
<i>Loligo pealei</i>	N.W. Atlantic	10°C	8.3 & 20.9	Spring (2 years)	Maurer and Bowman, 1985
		13°C	3.6 & 9.9	Summer (2 years)	Maurer and Bowman, 1985
		14°C	1.4 & 18.6	Fall (2 years)	Maurer and Bowman, 1985
<i>Loligo duvauceli</i>	Gulf of Thailand	27°C	9.4	Annual mean	Table 10.5
<i>Sepioteuthis lessoniana</i>	Southern India	27°C	5.3	Annual mean	Table 10.5
<i>Katsuwonus pelamis</i>	East Tropical Pacific	26°C	5.9	Maintenance	Kitchell <i>et al.</i> , 1978
		26°C	7.9–19.0	Fast growth fish	Kitchell <i>et al.</i> , 1978
		26°C	30	Maximum intake	Kitchell <i>et al.</i> , 1978

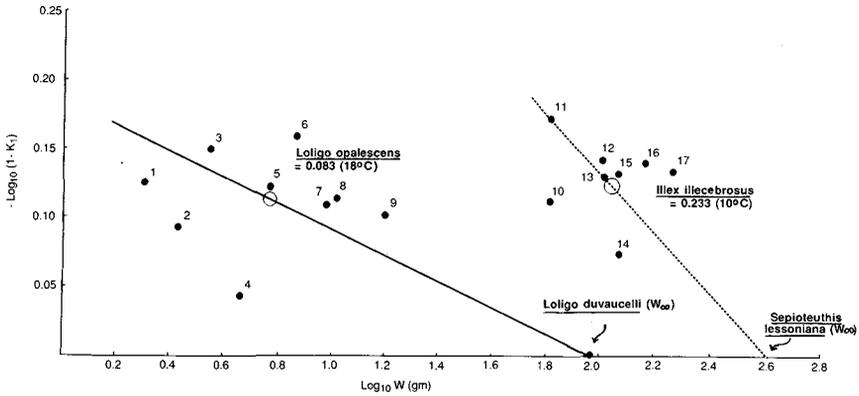


Fig. 10.15. Relationship between food conversion efficiency (K_1) and weight (W) in two species of squids, as used to estimate food conversion of squids of similar size (*L. duvauceli* and *Sepioteuthis lessoniana*, respectively). (Data from Hanlon *et al.*, 1983; O'Dor *et al.*, 1980.)

TABLE 10.6. Dimensions and Population Parameters of Tropical Squids

Dimension or parameter	<i>Loligo duvauceli</i>	<i>Sepioteuthis lessoniana</i> (= <i>arctipinnis</i>)
ML max (cm) ^a	29.00	33.00
W max (g) ^a	150.00	1200.00 ^b
ML inf (cm)	29.00 ^a	27.00 ^d
W inf (g)	150.00 ^c	650.00 ^d
$K(y^{-1})$	1.00 ^c	0.73 ^d
t (y)	0 (set value)	0 (set value)
$M(y^{-1})$	1.50 ^e	1.10 ^e
β	0.083 ^f	0.23 ^g
Q/B (exptl. temps.) ^h	4.25% (18°C)	1.22 (10°C)
Q/B (adjusted for higher metabolism) ⁱ	9.4% (27°C)	5.3% (27°C)

^a Mantle length based on data of Roper *et al.* (1984).

^b Based on length/weight relationship given by Rao (1954).

^c From Pauly (1985b).

^d See Fig. 10.12.

^e Assumes $M/K = 1.5$ (see text, Chapter 10).

^f Assumes data from Fig. 10.16 for *L. opalescens* are relevant.

^g Assumes data from Fig. 10.16 for *I. illecebrosus* are relevant.

^h Daily food consumption, % body weight, specific for temperature (see text).

ⁱ Temperature adjustment based on Winberg (1971, Table 3.3).

exploited stock, consisting of small individuals, has higher consumption per unit biomass than an exploited stock.

Sepioteuthis lessoniana in Southern India is often found associated with schools of juvenile fish (*Sardinella* spp., *Leiognathus* spp., etc) and the available evidence suggests that these fish constitute its main food. As in the case of *L. duvauceli*, food consumption has not been estimated directly. However, information is available on the gross food conversion efficiency for *Illex illecebrosus*, which reaches a similar weight to *S. lessoniana* off southern India (Fig. 10.15), and together with directly estimated growth parameters we can obtain a first approximation of the temperature-adjusted food consumption of *S. lessoniana*.

Our estimate (Table 10.5) is 5.3% body weight per day, so that a *S. lessoniana* population would consume 19 times its own weight per year. This is slightly less than estimated for *L. duvauceli*, which seems appropriate given that *S. lessoniana* is the larger organism. Our two estimates of food consumption by tropical squid suggest that these animals have the potential for a major impact on their ecosystems. We have presently no measure of the relevance of cannibalism in their role in the ecosystem, but it seems likely, as Caddy (1983) has suggested, that this may be a strategy to enable cephalopods to bridge gaps in the pelagic particle size spectrum and for the species as a whole to exploit indirectly, in an energy-efficient manner, food that is too small to be useful to the larger, maturing individuals. Nellen (1986) makes the same suggestion for fish, explaining the very high fecundity of fish principally as a mechanism for enabling large individuals to exploit small planktonic food at second hand. Alternatively, observations on squid in large tanks suggest that cannibalism is a mechanism by which a school survives a short period of food dearth; large individuals of *Illex* kill and share in the consumption of smaller individuals after only about 3 days food deprivation.

Predator-Prey Interactions between Squids and Fishes

Squids are exploited currently with demersal fishes and penaeid shrimps in a number of tropical fisheries throughout the world. These mixed fisheries are relatively well documented in Southeast Asia (Ritrasaga, 1976; Hernando and Flores, 1981), and some data are available (Pauly, 1979, 1985b; Larkin and Gazey, 1982; Chikuni, 1983) from the Gulf of Thailand which allow analysis of the cause of the squid outburst we have discussed already in Chapter 6.

Larkin and Gazey (1982) showed that a simple assumption of reduced trophic competition with pelagic fishes could not explain the increase of squids that took place in the 1970s when, moreover, demersal fish de-

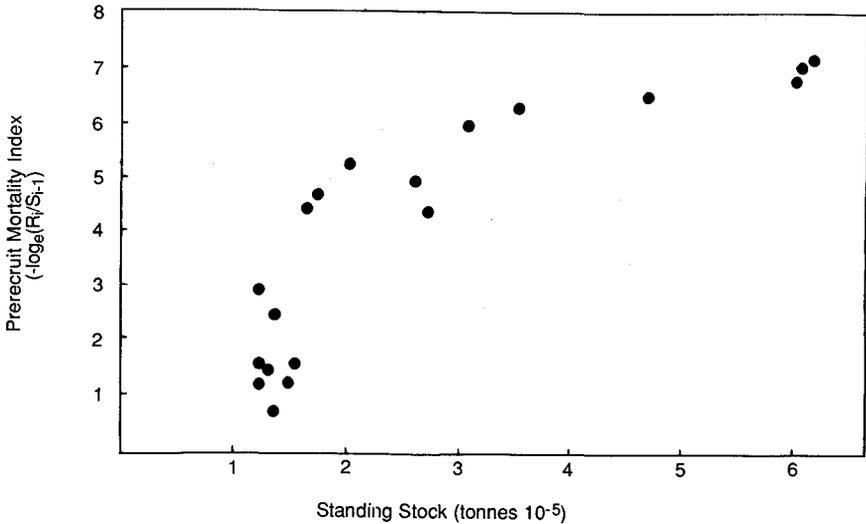


Fig. 10.16. Relationship between estimated prerecruit mortality of cephalopods in the Gulf of Thailand and total fish biomass in the inshore waters of the Gulf, 1961–1980 (Pauly, 1985b).

clined much more than the pelagic fish (Pauly, 1979). A more probable explanation, originally due to Jones (1982), is that the increase in squid was a direct consequence of a reduction of predation on their young.

Evidence along this line has been presented by Pauly (1985a) from which Fig. 10.16 is taken. This shows squid prerecruit mortality (e.g., of eggs and larvae) as a negative function of fish biomass and that there was a marked decline (of about one order of magnitude) in the daily prerecruit mortality as total fish biomass in the Gulf of Thailand declined. This confirms that the Gulf of Thailand squid outburst was due to a release of predator control on squid eggs and/or prerecruits.

This finding is in line with anecdotal evidence on the behavior of squid stocks (Gulland, 1982) and cephalopods in general (Caddy, 1983). It is also similar to what seems to happen with penaeid shrimp stocks, as we have discussed above. It is possible that a similar explanation lies behind the cephalopod outburst off Mauretania (Caddy, 1983) in which the decline in continental shelf sparid stocks after a decade of commercial fishing released first an outburst of *Sepia officinalis* and subsequently of *Octopus vulgaris*.

In this chapter we have shown that the population dynamics of tropical animals as diverse as sea urchins, shrimps, and squid can, at least in part,

be investigated by means of models developed for the management of fish by an understanding of their population biology. This confirms an earlier suggestion (Pauly, 1985b) that nothing can be gained by emphasizing the differences between squids and other pelagic animals and by inferring that methods that have been developed to study fishes will not work when they are applied to other aquatic animals. Rather, fish models of known properties should be applied systematically to these animals and the deviations from such models studied in detail, because it is these deviations that will indicate how these animals are different from fishes.

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