

# The tropical, the temperate and the arctic seas as media for fish production

*Erik Ursin*

The Danish Institute for Fisheries and Marine Research, Charlottenlund Castle,  
DK-2920 Charlottenlund, Denmark

## Abstract

Features of marine life at different latitudes are summarized with special reference to their effects on the dynamics of exploited populations of fish and shellfish and on the techniques to investigate these. Emphasis is given to the influence of temperature upon growth and mortality and hence upon yield assessments.

## Introduction

It has often been complained by scientists engaged in tropical fisheries (e.g. Pauly 1979) that current theory of fish population dynamics and techniques of yield assessment, as developed for high latitude seas of the Northern hemisphere, are only partly and unsatisfactorily applicable to tropical stocks. Although the need of techniques for the analysis of tropical fish stocks is rapidly being met, as witness recent volumes of series published in tropical countries, it seems relevant to highlight the main differences of conditions for marine life in high and low latitudes with particular reference to their implication upon fisheries science.

Many differences between high and low latitude seas can more or less be referred to three causes:

1. the more marked seasonal differences in high latitudes,
2. differences in metabolic rates and rates of decay caused by temperature,
3. the specialization achieved in evolutionarily old ecosystems.

Each of these may occasion disappointment when theory developed for the cold North Atlantic is applied to tropical conditions. Yet it seems to this author that wellknown methods are easily adapted once we begin to appreciate the biological reasons for the problems encountered.

## *Seasonality*

In the arctic seas with temperatures about 0°C primary production typically has a summer maximum with practically no production in winter when there is no sun and a heavy ice cover (Fig. 1). Zooplankton dependent upon phytoplankton production maintain very small stocks in the dark season and are unable to make immediate use of the plant production when the summer bloom comes.

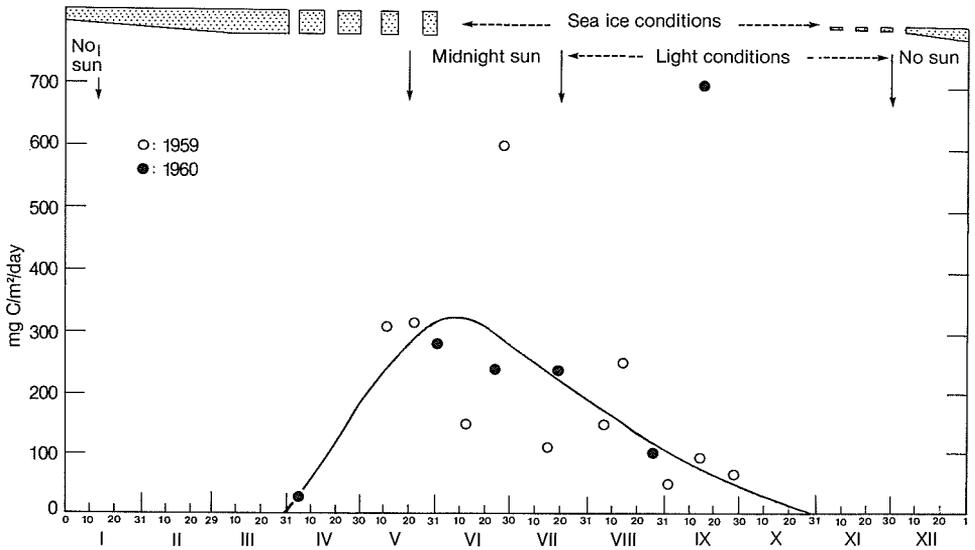


Fig. 1. Seasonal variation of primary production off an arctic coast in Northwest Greenland. From Petersen 1964, redrawn.

Zooplankton therefore appears with a time lag and cannot fully utilize the phytoplankton bloom. Dead or dying plants sink to the bottom where they become available to a rich bottom fauna which they sustain most of the year because in the arctic, life is unfolded at refrigerator temperatures and the rate of decay is accordingly low. As emphasized by Petersen & Curtis (1980) this is of paramount importance to arctic marine life: carnivorous animals are sustained by the bottom fauna most of which is burrowed in the sediment and dominated by polychaetes and bivalves. Few bottom animals in the arctic have pelagic larvae and many have brood protection (Thorson 1936). Pelagic life is too hazardous considering, that most of a summer's production turns up at the bottom anyway. Similarly, Clarke (1980) finds the antarctic shelf unsuitable to 'opportunistic' species, which take quick advantage of environmental perturbations.

Temperate seas with mean temperatures about 10°C and an annual variation from 3°C to 16°C are similar in many respects to the arctic seas. The species occurring are closely related, but the productive season is longer such that, when in arctic seas we have an annual primary production of 40 g C/m²/y we often have 100-200 g in temperate waters. Time lag problems are largely the same and may be illustrated by conditions in the North Sea. Fig. 2A shows the seasonal variation of the stocks of phytoplankton and copepods. The copepod maximum comes after the phytoplankton maximum, because it takes time to build up the stock from a low winter level. The second phytoplankton maximum is not matched by another copepod maximum because predators feeding on copepods had time to build up their stocks as shown in Fig. 2B. As in arctic seas much decaying material sinks to the bottom which is often covered by sediment rich in organic compounds and supporting a rich fauna of bottom animals. Yet, brood protection is rare and more

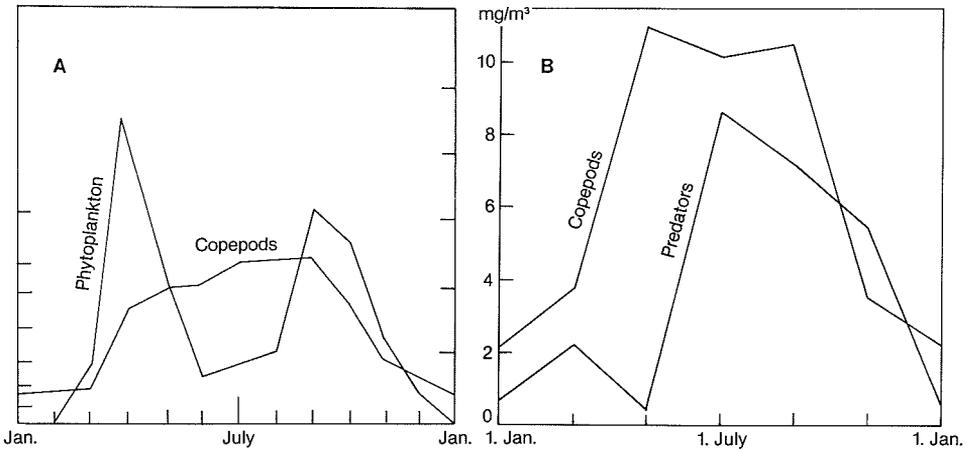


Fig. 2. Time lags in temperate climates. A, seasonal variation in abundance of phytoplankton and copepods in a sector of the North Sea. Arbitrary scales on the ordinate. From Colebrook & Robinson 1965, redrawn. B, seasonal variation in abundance of copepods and their predators in another sector of the North Sea. Data from Fransz *et al.* 1978.

species have pelagic larvae. The advantages of utilizing primary production on the spot where it is produced are higher because of the longer productive season with higher temperatures promoting a more rapid decay of dead plants.

The large local and year-to-year differences in the seasonal development of plankton production make temperate shelf water the playground of opportunistic

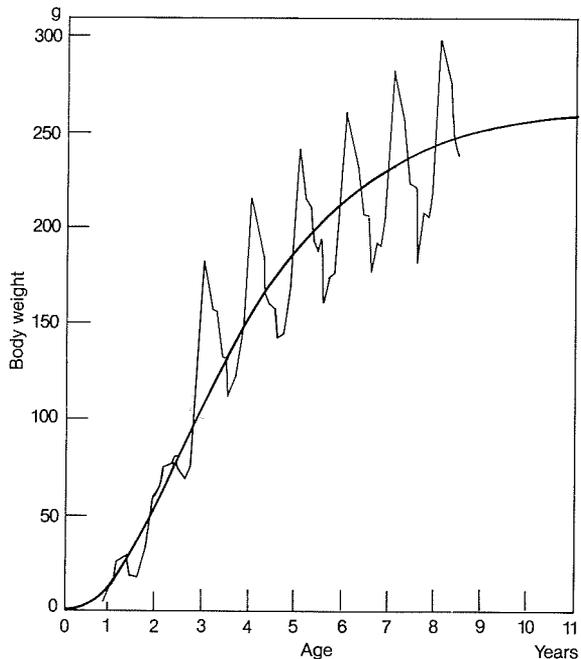


Fig. 3. Seasonal growth variation in North Sea herring (*Clupea harengus*, summer and autumn spawners). From Ursin 1979.

fish species which for instance in the North Sea rapidly replaced large stocks of longlived pelagic species when these were fished out (Ursin 1982). The seasonal variation of temperature, length of day, food concentration, etc., cause arctic and temperate fishes to grow fast in summer and to lose weight in winter. The seasonal growth variation in North Sea herring shown in Fig. 3 is a striking example of how misleading can be the usual smooth growth curves based as they are on annual observations or annual averages. Because of the backbone teleosts cannot lose length. Weight losses therefore affect the 'thickness' of the fish as expressed by the condition factor, which is the percentage occupied by the fish of a cube with body length as its side. Fig. 4 shows seasonal variation in condition factor for a small gadoid fish, the Norway pout (*Trisopterus esmarki*) living in North European waters at depths where the temperature variation is remarkably small (cf. the figure). Nevertheless the various seasonal influences cause great variation in condition with a decrease through the winter (October-April) and a rapid recovery in spring.

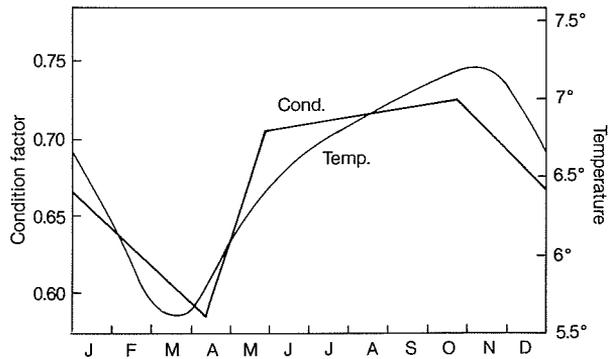


Fig. 4. Seasonal variation of the condition factor ( $=100 W/L^3$ ) in Norway pout (*Trisopterus esmarki*), a small North Atlantic gadid. Bottom temperatures in its habitats are indicated. From Ursin 1963, redrawn.

The effect of such seasonal growth variation upon hard structures (bones, scales, otoliths) attracted attention already in the last century and soon led to the development of methods of age-determination.

The age-structured hard parts in connection with the well defined and long known annual spawning seasons of most temperate fishes led to the early conception that a fish catch can be partitioned into age-groups and hence into year-classes, which can be followed through several years. This greatly promoted the evolution of theories on fish population dynamics in Northern Europe and North America and is probably the reason why the literature on fish populations (single species as well as species-interaction models) developed distinct from most other ecological literature in which age-structured models play a languishing part.

Warm temperate waters of temperatures about  $15^{\circ}\text{C}$  all the year round penetrate to low latitude coasts dominated by upwelling water, rich in nutrients, from deeper layers of the tropical oceans. Such areas of which the Peruvian coast is an example may have primary production rates of up to  $1000 \text{ g C/m}^2/\text{y}$  (Walsh 1981). Whereas the light intensity varies little during the year there are irregular, but mainly seasonal, variations in production caused by changes in the rates of upwelling. The

high primary production causes large amounts of decaying organic matter to sink to the bottom which becomes in places devoid of animal life because of an oxygen deficit created by bacterial decomposition. On the coast, however, in shallow water where wave action causes mixing of the water the standing stock of benthos in the sediment may be large.

Few fishes have adapted themselves to this unusual habitat and as demonstrated by Bakun & Parrish (1980) the fauna is extremely similar in all temperate upwelling systems. Dominating forms are sardines and anchovies, which more or less adapted themselves to feed on phytoplankton and similarly small organisms. This might be a direct effect of the high phytoplankton concentrations, but Jones (1982) points out that there is through the oceans a general tendency that high production is accompanied by large particle sizes of plants and animals. Sardines and anchovies in the rich upwelling systems fill the part of the larger omnivorous copepods in most other marine systems. In other words, man is harvesting the sea at lower trophic levels than elsewhere and accordingly, the largest fish stocks and the largest catches ever known belong in the warm temperate upwelling systems. These stocks seem extremely unstable with frequent collapses and with periods of sardine dominance alternating with periods of anchovy dominance. This, in connection with a less reliable ring formation in scales and otoliths make predictions almost impossible in these fisheries except that a collapse seems to occur the first time adversary environmental conditions are encountered after the onset of a major fishery. Fig. 5 illustrates the fate of some sardine fisheries in upwelling regions. The Chilean fishery has not (yet) collapsed.

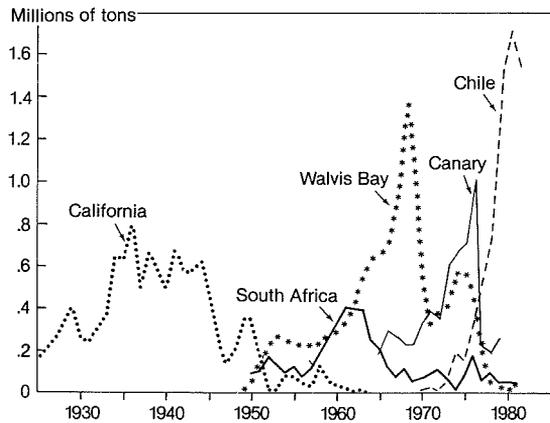


Fig. 5. Sardine landings from warm temperate upwelling systems. From Parrish *et al.* 1983, redrawn.

By contrast, the tropical shelves proper, with temperatures about 27°C all the year round, usually show little seasonal variation in primary production, and we do not experience the time lags characteristic of higher latitudes. The great difference is between the open sea with low production rates of 40 g C/m<sup>2</sup>/y as in the arctic, and the coastal waters often with production levels of 200-400 g as known from the Indian Ocean coast of Thailand (Petersen & Curtis 1980). In the open sea

much production is lost by sinking below the euphotic zone. It is either sedimented or turns up again in areas of upwelling.

The high production rates in tropical coastal waters have effects markedly different from temperate coasts with a similar production. The tropical pelagic environment is a stable one supporting a steady production of zooplankton. Fish, though, generally maintain a seasonal spawning pattern often connected with the monsoons. With two spawning seasons tending to overlap, the concept of a year-class as a recognizable unit becomes less useful. Also, in the stable tropical environment the annual, or seasonal, rings of scales and otoliths are usually absent. The much investigated threadfin breams (*Nemipterus*) can be aged from otoliths or scales from Japan to Hongkong, but not south of Hongkong, judging from the absence from the literature of age-ring readings from truly tropical areas.

Sometimes, however, daily rings are laid down in otoliths of temperate as well as tropical fishes (Pannella 1974), in the statoliths of squid (Kristensen 1980) and in the shells of bivalves (Petersen 1958). Usually, only the growth of the juveniles can be traced this way, but even that is useful because a curve of growth in length is largely determined by the steepness of its left hand limb and the asymptote. The latter can often be guessed from the sizes of the larger fish in the catch.

With the absence of time-lags between biomass maxima of the various trophic levels the utilization of pelagic production becomes more efficient. As emphasized by Petersen & Curtis (1980) such production as might fall out (faeces, if nothing else) decay rapidly at the high temperatures prevailing from surface to bottom in shallow water. Consequently, there is little for benthos to feed on and indeed, benthos proper as we know it from high latitudes is often virtually absent. The bottom fauna consists mostly of animals seeking rest and shelter at the bottom, but feeding pelagically or on other shelter-seeking animals. Large crabs with legs

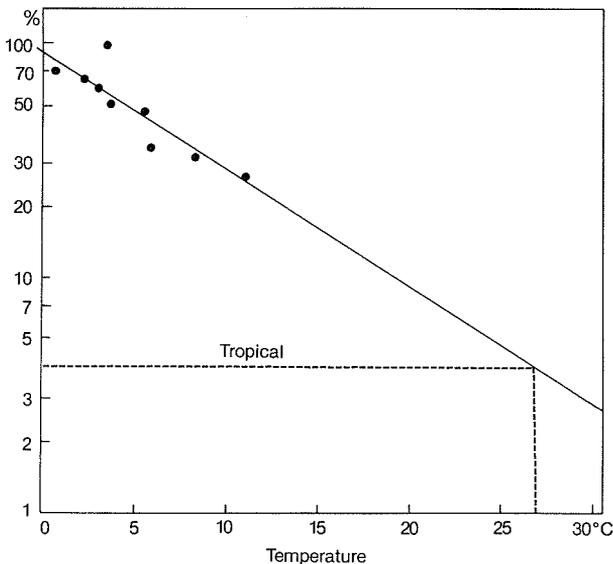


Fig. 6. Percentage of fish feeding on bottom animals proper in commercial landings, as a function of temperature. From Jones & Martin 1981, redrawn.

adapted for swimming form a conspicuous element in this fauna. At higher latitudes large crabs usually are of the walking type. Demersal fisheries in the tropics have to be based to a large extent upon species feeding more or less pelagically and certainly not picking their food out of the sediment as many important demersal fish do in temperate and arctic waters.

Jones & Martin (1981) calculated the percentages of demersal (bottom feeding) fish in commercial catches from the North Atlantic (Fig. 6), finding an exponential decrease over the temperature interval from 0 to 11°C. Extrapolation predicts a decrease from 100 % at 0°C to 4 % at 27°C, which may be realistic when fishes not feeding on benthos proper are excluded from demersal catches in the tropics as they were in higher latitudes.

Coral reefs and coralline shelves are a special case, based as they are on sessile organisms building themselves up to heights where they can feed on pelagic fauna. An important feature is the intensive symbiosis of animals of coral reefs with unicellular algae by which a shortcut in the foodweb is established. At the high tropical temperatures with rapid decay and high metabolic rates the symbiotic algae deliver their production (and perhaps the extracellular production in particular) directly to the consumer. This is hardly feasible at high latitudes because the plants would be no use most of the year when light intensity is low.

Fig. 7 summarizes pelagic and benthic production in an arctic, a temperate and a tropical shelf area. In this diagram the expression 'demersal catches' cover truly benthos-feeding animals only.

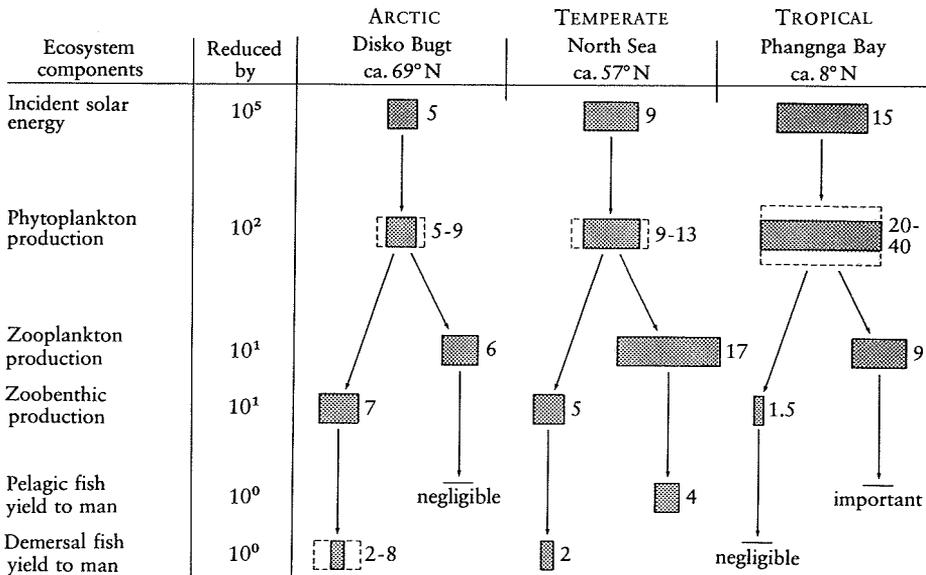


Fig. 7. Incident solar energy, phytoplankton production, secondary planktonic and benthic production and fishery yield in arctic, temperate and tropical shelf areas. All values expressed as kcal/m<sup>2</sup>/year. In fishery statistics 'demersal' means caught near the bottom, in biology it means feeding on bottom animals. The word is used in the latter sense here. From Petersen & Curtis 1980.

### Metabolism

Ege & Krogh (1914) found that the metabolism of a goldfish increased about 40 times when the temperature was increased from 0°C to 30°C (i.e.,  $Q_{10} = 3.4$ ). Thorson (1936) and others discovered that when experiments with the same or similar species were made at different latitudes and at the temperatures at which the animals actually lived, the rate of increase was smaller or none. Scholander *et al.* (1953) made extensive experiments with tropical animals at tropical temperatures and arctic animals at arctic temperatures and found the increase over the range from 0 to 30°C to be about 4-5 times, corresponding to a  $Q_{10}$  of 1.6 only. This held for fish and crustaceans alike. Fig. 8 shows the results for fishes.

Recently, A. Clarke and others (see Clarke 1980) cast doubt upon the results of

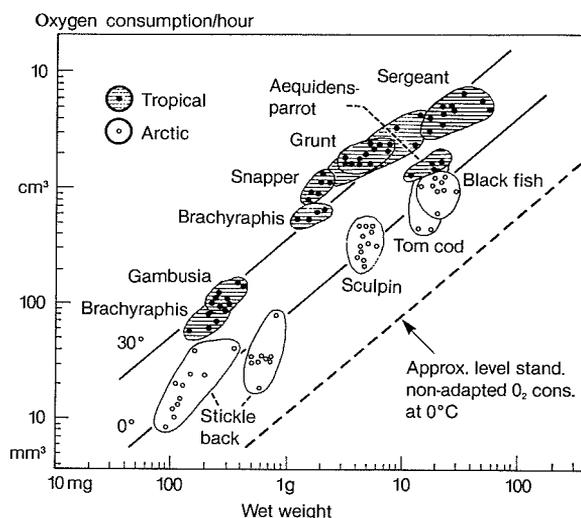


Fig. 8. Respiration rates of tropical fishes at 30°C and of arctic fishes at 0°C as a function of body size. From Scholander *et al.* 1953, redrawn.

Scholander *et al.* and of other authors supporting them. They argue that the early respiration experiments on arctic and antarctic animals were conducted on excited specimens with increased metabolic rates. Also, they present material showing extremely low respiratory rates for antarctic animals, but the difficulties in obtaining comparable respiration data persist.

Growth parameters, however, can be analysed instead of oxygen consumption which removes the problem and makes it possible to estimate the metabolic level of species for which oxygen consumption has not been measured. According to one interpretation (Ursin 1979) of the traditional growth equation

$$dw/dt = Hw^{2/3} - kw,$$

the second right hand term represents the routine metabolism, or the rate of weight loss of a fasting animal which is approximately proportional to oxygen consumption. Strictly, we should write  $kw^n$  where  $n \approx 0.8$ . Using the simpler  $kw$  requires that only animals of approximately the same size are compared directly.

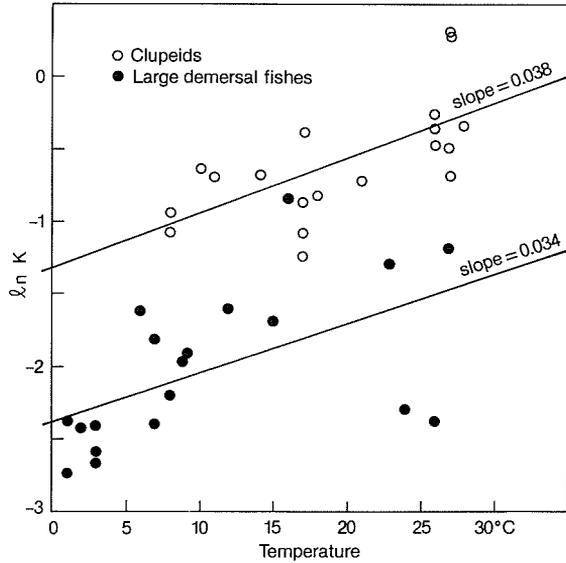


Fig. 9. The growth parameter  $K$  as a logarithmic function of surface mean temperature. Data from Pauly 1978a.

Pauly (1978a) listed  $L_\infty$  and  $K$  ( $K = k/3$ ) for a large number of fish species and Dietrich (1957) supplied a world map of surface temperatures. Fig. 9 shows  $\ln K$  as a function of temperature for large demersal fishes ( $L_\infty > 100$  cm) and for clupeids including only such species for which at least two estimates of  $K$  could be averaged. With  $T$  the temperature in degrees Celcius we find:  
Large demersal fishes,

$$K = 0.093 \exp(0.034T); \quad Q_{10} = \exp(0.34) = 1.4;$$

Clupeids,

$$K = 0.27 \exp(0.038T); \quad Q_{10} = \exp(0.38) = 1.5.$$

Considering the scatter of the points these values of  $Q_{10}$  are in good agreement with the value of 1.6 found by Scholander *et al.* Similarly, comparing small demersal fishes in cold water (many families, about 8°C) with such in warm water (Leiognathidae, Gerridae, about 26°C) gives mean  $K$  values of 0.70 and 2.0 respectively, corresponding to a temperature coefficient of 0.060 and  $Q_{10} = 1.8$ . Mean  $L_\infty$  was 14 cm in both cases. Averaging the three observations gives  $Q_{10} = 1.6$  as found by Scholander *et al.*

Small coral reef fishes were omitted from the analysis because they seem to have particularly low metabolic rates. Nine observations (seven species) of  $L_\infty$  and  $K$  (Pauly 1978a, Munro 1976, Pauly & Ingles 1981) have mean values of  $L_\infty = 16$  cm,  $K = 0.51$ , which is about the same as for the small cold water demersals above. It seems that whereas tropical fishes generally have a routine metabolism two or three times higher than fishes of cold temperate waters, small coral reef fishes managed to keep theirs at the same low level as in fishes of temperate waters. This may have been achieved by seldom swimming over long distances (territorial

habits) and by seeking shelter rather than fleeing when disturbed. Some fishes living in other habitats may have adapted themselves similarly, too. For instance, Pauly's (1978a) collected data on threadfin breams (*Nemipterus*) show remarkably small  $K$  values.

In contrast to this adaption we have in antarctic shallow water some fish species (see Clarke 1980) which have such extremely low respiratory rates that they are easily picked up by hand, unable to escape once deprived of their shelter. These seem to be the rare exceptions when the first experimental results quoted above, that respiration changes drastically with temperature, are confirmed.

Natural mortality (i.e., all mortality not caused by the fishery) is closely related to the metabolic level and hence to  $K$  which in many species tends to be smaller in longlived populations (Taylor 1960). Natural mortality is partly caused by extrinsic agents of which predation is one, but as Pauly (1978a) points out, the generally higher metabolic activity in the tropics may be expected to speed up predation, too. Using models of exponential extinction we therefore generally find higher values of the coefficient  $M$  of natural mortality in the tropics. Using all available sets of estimates of  $L_\infty$ ,  $K$ ,  $M$  and temperature Pauly (1978b) derived the linear relationship

$$\ln M = 0.2828 - 0.1912 \ln L_\infty + 0.7485 \ln K + 0.2391 \ln T,$$

which, with the data referred to above, leads to the estimates of  $M$  given in Table 1. The influence of temperature upon  $M$  turns out to be almost the same as of  $K$  or perhaps slightly higher, as witness the  $M/K$  ratios. It should be noted, however, that Pauly includes in the variance the real differences between species and between families. Estimates of  $M$  from his formula are therefore less realistic for individual species or single families than for a medley of species. For instance, the mortalities of clupeids are probably overestimated in Table 1. Another dubious point in Pauly's approach is that  $K$  is assumed independent of temperature.

Table 1. Estimates (Pauly's formula) of the coefficient  $M$  of natural mortality for the groups of fishes referred to in the text.

	$L_\infty$ cm	$K$ $y^{-1}$	$T$ $^\circ\text{C}$	$M$ $y^{-1}$	Ratios of values		
					of $K$	of $M$	$M/K$
Small demersal fishes, temperate waters tropical waters	14	0.70	8	1.00	2.9	2.9	1.4
	14	2.0	26	2.9			1.4
Large demersal fishes, temperate waters tropical waters	136	0.12	8	0.17	1.7	2.0	1.4
	136	0.20	26	0.34			1.7
Clupeids, temperate waters tropical waters	26	0.36	8	0.54	2.0	2.2	1.5
	26	0.72	26	1.2			1.7
Small coral reef fishes	16	0.51	26	1.0			2.0

The short life and fast growth in the tropics has repercussions on studies of population dynamics. Even when ageing by direct reading of otoliths etc. is not possible it may be feasible to follow specimens of the same age (a cohort) in a time series of samples. For instance, the shrimp *Penaeus semisulcatus* spawns once a year and has a total mortality of 50% per month (Jones & van Zalinge 1981), so that they are practically gone after a year. There are never more than two cohorts in the fishery at the same time and they are distinct from each other. It is therefore simple to estimate their growth and mortality whereas a similarly sized shrimp in arctic waters lives to be many years old and is difficult to age (Rasmussen 1953). It is also possible to follow a cohort even when two or three cohorts occur together and overlap in the size-frequency distributions. The method has been practised in high latitude areas since the turn of the century, when other means of ageing failed and there was reason to believe the species in question shortlived. The method is more relevant for the tropics with their abundance of shortlived species and indeed, increasingly sophisticated methods (graphical or computational) of splitting composite distributions are coming into use in tropical fisheries science. An example is the 'ELEFAN' method (Pauly 1982) which includes an iterative procedure for estimation of growth parameters.

In case of fish the short life makes the reading of daily rings in otoliths more important in the tropics, because the fairly short time such rings can be followed (perhaps 100-300 days) is a substantial part of the lifetime. Similar information on a shortlived fish in high latitude waters is less useful because of seasonal growth variations. Instead, one would want to know a full year's growth, which is often estimable from the annual ring pattern in such fishes.

Data on shortlived species are not directly applicable to such important tools as cohort analysis and virtual population analysis in which numbers caught of each age-group in a range of years are arranged in an array whose entries are analyzed diagonally, following each cohort. The techniques can be modified, though, for use in the tropics as shown by Jones & van Zalinge (1981) for the shrimp stock referred to above.

It was found above that unless available age-determinations are erroneous enough to be directly misleading, metabolic rates are doubled or tripled in the tropics just as generation times are reduced to half or one third. It is more dubious whether growth rates and rates of food consumption are also doubled or tripled. This is difficult to investigate, because what is needed is a frequency-distribution function for asymptotic lengths in each place. Consider again the growth equation, but this time the growth in length:

$$\begin{aligned} dl/dt &= E - Kl; \\ dl/dt = 0 &\text{ implies } l = L_{\infty} = E/K. \end{aligned}$$

When  $K$  is doubled the positive (food consumption) term  $E$ , and hence the growth rates, must be doubled too, in order to maintain the same value of  $L_{\infty}$ . Therefore, if  $K$  is doubled in the tropics and animals are 'the same size' as in temperate waters, food consumption and growth rates are also doubled. It is not yet possible to refer an  $L_{\infty}$  value to each abundant species in a tropical trawl catch, but there is a

notable abundance of small species in tropical seas. It may be suspected, therefore, that  $L_{\infty}$  is generally lower in the tropics and that  $E$  does not increase as much as  $K$  so that growth rates and rates of food consumption increase less than respiration and natural mortality.

### *Specialization*

Geologically, the Pacific is supposed to be the oldest sea in the world, with the highest number of species and the highest degree of specialization represented in the fauna. In contrast, the cold temperate and arctic North Atlantic, where so many fish population studies have been made and so many methods developed, is an extremely young region. Much of it was permanently ice-clad in diluvial times (20 000 years ago) and the North Sea was dry land. There has been little time for evolutionary adaptation, and most species may be called ubiquists as compared to the varied and highly specialized fauna of the tropical Pacific and the Indian Ocean. Characteristic of high latitudes is the preponderance of flatfish in the demersal fauna. Many of these are adapted to picking out molluscs and worms from the sediment and therefore feed on the true bottom fauna so poorly represented in tropical shelf areas.

The poverty in species characterizing high latitudes is observed also in the upwelling regions of the continental coasts, an environment of much physical perturbation. Everywhere in such regions a similar, small set of fish species dominate (Bakun & Parrish 1980). A condition that a fish becomes part of this fauna seems to be that it can stand the perturbations peculiar to coastal upwelling ecosystems and finds ways and means to prevent a loss of juveniles by offshore transport.

The ability of an ecosystem to withstand the effects of a major fishery seems related to its specialization: the more specialized, the more vulnerable. The North Sea is an example of a particularly robust system. In spite of a massive reduction of the stocks of herring and mackerel as an effect of introducing new technology the total fish biomass remained almost the same (Fig. 10) or, according to a different set of estimates (Helgason & Gislason, in press), was only moderately reduced.

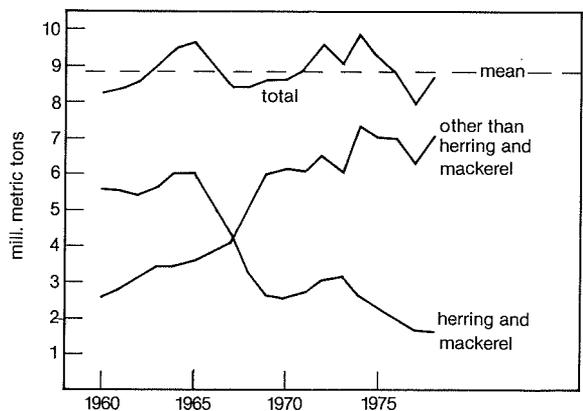


Fig. 10. Fish biomass in the North Sea under influence of an extensive fishery for herring (*Clupea harengus*) and mackerel (*Scomber scombrus*). From Ursin 1982, redrawn.

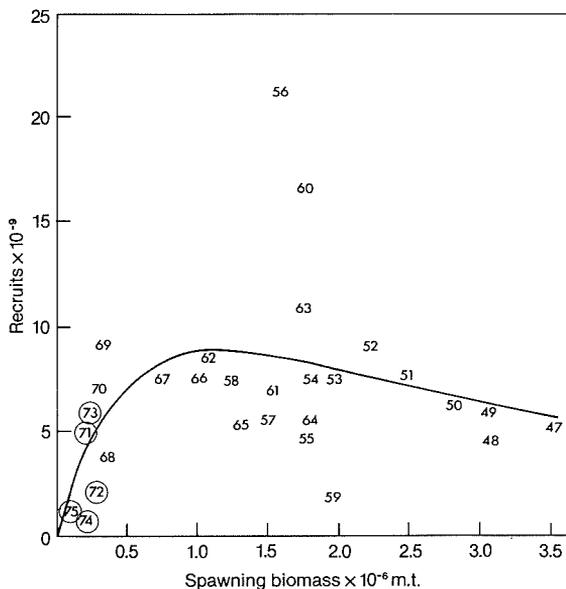


Fig. 11. Recruitment to the North Sea stock of herring. Numbers are the two last digits of the year of spawning. Circles indicate the last 5 years of the investigation. Courtesy of Dr. J.R. Beddington.

One species only, the Atlantic herring (*Clupea harengus*) collapsed under fishery pressure. This is a longlived species which for centuries had a permanently high biomass. Apparently, it is not evolutionarily tuned to withstand severe reduction, as witnessed an observed recruitment failure in the years of low spawning stock (Fig. 11). Exercises with an ecosystem model described by Andersen & Ursin (1977) indicated, that with the same slope at the origin as in Fig. 11 only species with a permanently high biomass could survive. Particularly, some small, short-lived, 'opportunistic' species, which rapidly replaced the herring, became unable to do so as quickly as observed. Increasing the slope at the origin by factors 2-4 changed the situation: the actual biomass variations of these species could be simulated.

In contrast to this we find that in the Gulf of Thailand and in the Andaman Sea (Pauly 1979) many species and particularly, many small, shortlived ones went almost extinct a few years after the initiation of an efficient trawl fishery (Table 2). The reason why trawling had such almost catastrophic effects on large species groups may be that most tropical shelf fishes are tuned through evolution to live in a stable habitat and seldom need recovery after perturbations of the environment. In the tropics, therefore, even shortlived species can afford to lose the ability to recover quickly. In the unsteady environment of higher latitudes this ability is lost only in longlived species like the herring which can rely on a large spawning biomass still after several years of recruitment failures. This may be why interference by man has markedly different effects in the two regions, but there are other possible causes (Pauly 1979, Larkin 1982). For instance, many small species in the Gulf of Thailand might require some bottom structure which was destroyed in the process of trawling.

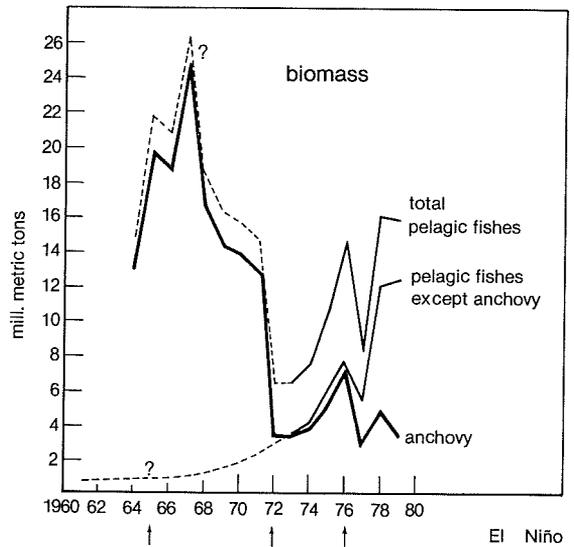


Fig. 12. The collapse of Peruvian anchovy (*Engraulis ringens*) and the supposed replacement by other pelagic fishes. From Arntz & Robles 1980, redrawn.

In the coastal upwelling systems characterized by much perturbation and little specialization replacement of one fish species by another is an often observed phenomenon. Periods of sardine dominance change with periods of anchovy dominance. In Peru, following the at least partly fishery induced collapse of the anchovy there was experienced an increased sedimentation of organic matter (Walsh 1981), but also a biomass increase of several pelagic fish species, including sardine and mackerel (Fig. 12). Although taking place at tropical latitudes this development recalls what happened in the North Sea more than what happened in the Gulf of Thailand, where replacement was less conspicuous (Table 2).

Table 2. Changes in stock sizes of commercial species in the Gulf of Thailand, from Pauly (1979). Two significant digits retained.

Ecological group	Units of 1000 metric tonnes		
	Virgin stock	Exploited stock	$\frac{\text{Exploited}}{\text{Virgin}}$
1. Large benthos feeders	150	1.3	0.0087
2. Small demersal prey	830	21	0.025
3. Intermediate predators	620	74	0.12
4. Large predators	21	5.3	0.25
5. Pelagic fishes	13	5.7	0.44
6. Flatfish	3.5	7.6	2.2
7. Squid and crustaceans	30	90	3.0
Depleted stocks (1-5)	1600	110	0.066
Replacing stocks (6-7)	33	97	2.9

The large number of species in the tropics has hampered the introduction of methods developed in high latitude areas. One way out is to lump for instance all trawl catches and treat them as one species as in Fig. 14, for the Gulf of Thailand. Changes in species composition of the catch go unnoticed with this approach. This is avoided by lumping species according to growth, mortality and food, and treat each group as one species. This was attempted by Larkin & Gazey (1982) in a species-interaction model for the Gulf of Thailand and easily brings the number of 'species' down to the level of high latitude seas. Munro (1975) in his remarkable essays on Caribbean coral-reef fisheries chose a different approach, doing a yield-per-recruit assessment for each reasonably abundant species, weighting each species by its market value and adding up the yields predicted for each mesh size. Until recently, the work involved might have been considered prohibitive, but estimates of stock size and of growth and mortality parameters abound in tropical literature these days.

#### *Stock and yield assessments in high and low latitude seas*

The differences in  $K$  and  $M$  between temperate and tropical fish species have implications on stock and yield assessments. These are illustrated in Fig. 13 for two arbitrary species with parameter values likely to be found in temperate and tropical waters respectively, although the two species do not differ more than they could be found together in either a temperate or a tropical area. The only difference between them is that  $M$  and  $K$  are twice as high in the tropical species. The exercise assumes constant recruitment. The Beverton and Holt yield per recruit model was applied in Ricker's (1975) formulation. Yield and biomass are plotted against effort in terms of the coefficient  $F$  of fishing mortality.

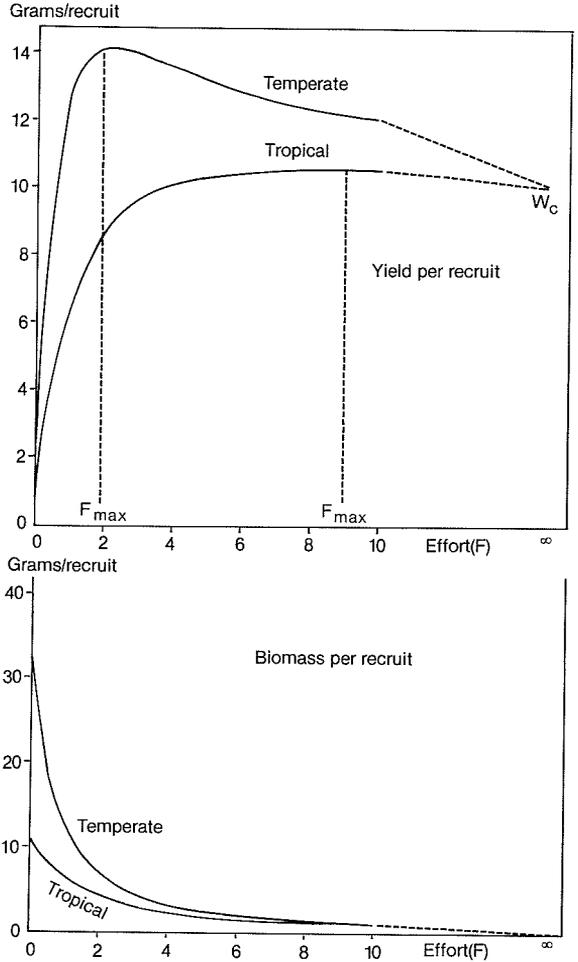
The curves of Fig. 13 emphasize two important differences of tropical and temperate fish stocks:

1. The maximum of the yield curve (if any) is reached at higher effort levels in the tropics. The kind of overfishing experienced at effort levels higher than the one ( $F_{\max}$ ) giving maximum yield is not likely to be observed in a multispecies tropical fishery.
2. Temperate seas are characterized by relatively high virgin biomasses because of the lower natural mortalities, which permit more age-groups to contribute to the biomass. The difference levels off with increasing effort as  $F$  achieves more influence than  $M$ . A fishery, profitable in its early stage when the stock is almost virgin, is more likely to prove unprofitable already at low effort levels in temperate seas. In our example the catch per unit effort is reduced to half its original value at  $F = 1.2$  in the tropical species, but at  $F = 0.6$  in the temperate one. In fully exploited tropical fisheries we shall therefore expect higher  $F$  values than experienced in temperate waters.

Note that these conclusions are based on the yield per recruit model, which is realistic at all effort levels only when the weight ( $W_c$ ) of a fish at entry to the fishery is so much higher than the size at first maturity that reproduction is not hampered by removal of prospective spawners. This is seldom the case and a

Fig. 13. Yield and biomass of two species differing by a factor 2 in the values of  $M$  and  $K$  as do fishes of temperate and tropical seas. Beverton & Holt yield-per-recruit model. Biomass is proportional to catch per unit effort.

Asymptotic weight:  $W_{\infty} = 100$  g  
 Weight at recruitment:  $W_r = 10$  g  
 Weight at entry to fishery:  $W_c = 10$  g  
 Origin of growth curve:  $t_0 = 0$   
 $M/K = 1.5$ ; Temperate:  $M = 1.2$ ;  
 Tropical:  $M = 2.4$ .



collapse of the fishery due to the so-called recruitment overfishing is likely to occur at some effort level, which is difficult to predict.

Now, consider the situation in the Gulf of Thailand (Table 2) in the light of observations made in this paragraph. The mere fact that exploited biomass is much smaller than virgin biomass is no indication of overfishing, let alone collapse of a fishery, as can be seen from the biomass curves of Fig. 13. Neither is a change in relative abundance in itself an indication of overfishing of species becoming relatively less abundant because the biomass reduction caused by fishing varies from one species to another and is more drastic for longlived species.

Based on these general observations we expect a yield curve similar to that for the tropical species in Fig. 13, with a maximum for a high value of  $F$  or without any maximum. This is also what was found as shown in Fig. 14.

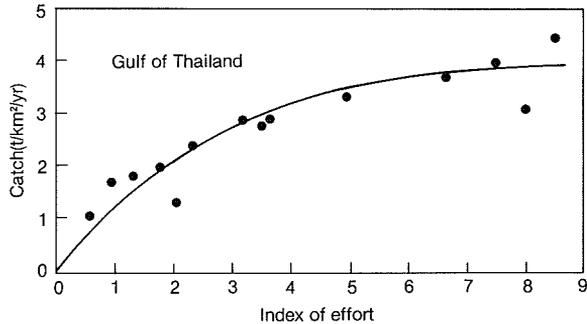


Fig. 14. Annual catch in the demersal fisheries of the Gulf of Thailand as a function of fishing effort. From Marten & Polovina 1982, redrawn.

There are, however, a few features of Table 2 which are not consistent with the yield per recruit model. The 'small demersal prey' species, which suffered a drastic biomass reduction, are mainly shortlived species of which a moderate biomass reduction was expected. These stocks actually seem to have collapsed for one reason or another, as discussed in a previous paragraph. Such collapses should cause a descending right hand limb of the yield curve in Fig. 14, but this was prevented by a biomass increase of flatfish, squid and crustaceans whose contribution to the catch increased from 2% to almost 50%.

Under an increasing fishing pressure this can have been achieved only by increasing the number of recruits. This again may have been caused by the fishery through removal of competitors or predators or it may have had other, so far unknown causes.

## References

- Andersen, K.P. & E. Ursin, 1977: A multispecies extension to the Beverton and Holt theory of fishing with accounts of phosphorus circulation and primary production. – Meddr Danm. Fisk.- og Havunders., N.S. 7: 319-435.
- Arntz, W.E. & A.P. Robles, 1980: Estudio del potencial pesquero de interés para el complejo pesquero 'La Puntilla' (Pisco, Perú). – Programa Cooperativo Peruano-Alemán de Inv. Pesquera. Callao (mimeo).
- Bakun, A. & R.H. Parrish, 1980: Environmental inputs to fishery population models for Eastern boundary current regions. – Intergovernmental Oceanographic Commission, UNESCO, Paris, Workshop Rep. 28: 67-104.
- Clarke, A., 1980: A reappraisal of the concept of metabolic cold adaption in polar marine invertebrates. – Biol. J. Linn. Soc. 14: 77-92.
- Colebrook, J.M. & G.A. Robinson, 1965: Seasonal Cycles of phytoplankton and copepods in the North-Eastern Atlantic and the North Sea. – Bull. Mar. Ecol. 6: 123-139.
- Dietrich, G., 1957: Allgemeine Meereskunde. – Berlin.
- Ege, R. & A. Krogh, 1914: On the relation between the temperature and the respiratory exchange in fishes. – Internat. Revue Ges. Hydrobiol. Hydrogr. 7: 48-55.
- Fransz, H.G., M. Ottema & P.A. Seip, 1978: Abundance and growth of fish larvae during the summer decline of copepod populations in Dutch coastal waters of the North Sea and possible interactions with jellyfish and ctenophores. – ICES C.M. 1978/L: 19 (mimeo).
- Helgason, Th. & H. Gislason, in press. Multispecies assessment of fish stocks with special application to the North Sea. – Dana 5.
- Jones, R. & J.H.A. Martin, 1981: The relationship between demersal fish landings and bottom temperature. – ICES, C.M. 1981/G: 44 (mimeo).

- Jones, R. & N.P. van Zalinge, 1981: Estimates of mortality rate and population size for shrimp in Kuwait waters. – Kuwait Bull. Mar. Sc. 2: 273-288.
- Kristensen, T.K., 1980: Periodical growth rings in cephalopod statoliths. – Dana 1: 39-51.
- Larkin, P.A., 1982: Directions for future research in tropical multispecies fisheries. – In D. Pauly & G.I. Murphy (eds): Theory and Management of Tropical Fisheries, pp. 309-328. ICLARM Conference Proceedings 9. Manila.
- Larkin, P.A. & W. Gazey, 1982: Applications of ecological simulation models to management of tropical multispecies fisheries. – In D. Pauly & G.I. Murphy (eds): Theory and Management of Tropical Fisheries, pp. 123-140. ICLARM Conference Proceedings 9, Manila.
- Marten, G.E. & J.J. Polovina, 1982: A comparative study of fish yields from various tropical ecosystems. – In D. Pauly & G.I. Murphy (eds): Theory and Management of Tropical Fisheries, pp. 255-285. ICLARM Conference Proceedings 9, Manila.
- Munro, J.L., 1975: The biology, ecology, exploitation and management of Caribbean reef fishes. VI. Assessment of the potential productivity of Jamaican fisheries. – Res. Rep. Zool. Dept., Univ. West Indies 3(6): 1-56. Kingston.
- Munro, J.L., 1976: Aspects of the biology and ecology of Caribbean reef fishes: *Mullidae* (goat-fishes). – J. Fish. Biol. 9: 79-97.
- Pannella, G., 1974: Otolith growth patterns: an aid in age determination in temperate and tropical fishes. – In T.B. Bagenal (ed.): The Ageing of Fish, pp. 28-39.
- Parrish, R.H., A. Bakun, D.M. Husby & C.S. Nelson, 1983: Comparative climatology of selected environmental processes in relation to eastern boundary current pelagic fish reproduction. – FAO Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Stocks. San José, Costa Rica, 18-29 April 1983. (Mimeo.)
- Pauly, D., 1978a: A preliminary compilation of fish length growth parameters. – Ber. Inst. Meeresk. Kiel 55: 1-200.
- Pauly, D., 1978b: A discussion of the potential use in population dynamics of the interrelationships between natural mortality, growth parameters and mean environmental temperature in 122 fish stocks. – ICES C.M. 1978/G: 21 (mimeo).
- Pauly, D., 1979: Theory and management of tropical multispecies stocks. – ICLARM Studies and Reviews 1: 1-35. Manila.
- Pauly, D., 1982: Studying single-species dynamics in a tropical multispecies context. – In D. Pauly & G.I. Murphy (eds): Theory and Management of Tropical Fisheries, pp. 33-70. ICLARM Conference Proceedings 9. Manila.
- Pauly, D. & J. Ingles, 1981: Aspects of the growth and natural mortality of exploited coral reef fishes. – Fourth Intern. Coral Reef Symp. Manila 1981. 24 pp. (mimeo).
- Petersen, G.H., 1958: Notes on the growth and biology of the different *Cardium* species in Danish brackish water areas. – Meddr Danm. Fisk.- og Havunders. N.S. 2(22): 1-31.
- Petersen, G.H., 1964: The hydrography, primary production, bathymetry and 'tagsaq' of Disko Bugt, West Greenland. – Medd. Grønland 159(1): 1-45.
- Petersen, G.H. & M.A. Curtis, 1980: Differences in energy flow through major components of sub-arctic, temperate and tropical marine shelf ecosystems. – Dana 1: 53-64.
- Rasmussen, B., 1953: On the geographical variation in growth and sexual development of the deep sea prawn (*Pandalus borealis* Kr.). – Rep. Norw. Fish. Mar. Inv. 10(3): 1-160.
- Ricker, W.E., 1975: Computation and Interpretation of Biological Statistics of Fish Populations. – Bull. Fish. Res. Bd. Canada 191: 1-382.
- Scholander, P.F., W. Flagg, V. Walters & L. Irving, 1953: Climatic adaption in arctic and tropical poikilotherms. – Phys. Zool. 26: 67-92.
- Taylor, C.C., 1960: Temperature, growth and mortality. – The Pacific cockle. – Cons. Perm. Int. Expl. Mer., Journ. Cons. 26: 117-124.
- Thorson, G., 1936: The larval development, growth and metabolism of arctic marine bottom invertebrates. – Medd. om Grønland 100(6): 1-155.
- Ursin, E., 1963: On the seasonal variation of growth rate and growth parameters in Norway pout (*Gadus esmarki*) in the Skagerak. – Meddr Danm. Fisk.- og Havunders., N.S. 4: 17-29.
- Ursin, E., 1979: Principles of growth in fishes. – Symp. zool. Soc. Lond. 44: 63-87.
- Ursin, E., 1982: Stability and variability in the marine ecosystem. – Dana 2: 51-67.
- Walsh, J.J., 1981: A carbon budget for overfishing off Peru. – Nature 290: 300-304.