



Tropical fishes: patterns and propensities*

D. PAULY

Fisheries Center, 2204 Main Hall, University of British Columbia, Vancouver, B.C., Canada, V6T 1Z4

When key biological statistics (growth parameters, mortality rates, etc.) of a large number of fish species are plotted against other variables (notably maximum size and mean habitat temperature), clear trends or patterns tend to emerge. These patterns are usually not perceived as requiring explanation, as reflected in the rarity of pertinent hypotheses in the literature, relative to the ubiquity of the patterns. A theory is presented which has the potential to explain the propensities behind many of these observed patterns. This theory, based on the author's earlier work, is built around the notion that gill area severely constrains the respiration and hence the growth of fishes (and other water-breathing animals). The patterns generated by growth-related processes, such as mortality, reproduction or food consumption can then also be explained. In this theory, tropical fishes are not different from other fishes, once account is taken of the fact that tropical fish are, not metaphorically but literally, in hot water.

© 1998 The Fisheries Society of the British Isles

Key words: comparative studies; growth; natural mortality; metabolism; gills.

INTRODUCTION

Fish biologists, whether working in the tropics or not (Fig. 1), tend to concentrate on a species, or a group of them, but rarely, if ever, on fishes as a whole. The result, obviously, is that ichthyology consists largely of scattered accounts, each dealing with the biology of one fish or group.

The exception to this is taxonomy, whose lists often cover entire continents, but which usually does not cover the life processes of the species thus listed. CLOFFA (Daget *et al.*, 1984–1991) is an exception in that it provides at least references to papers on the various aspects of the biology of the species it covers. Fish classification (Berg, 1958; Greenwood *et al.*, 1966; Eschmeyer, 1990) also fails to cover life processes, though it reflects on phylogeny, a life-generating process if ever there was one.

This contribution is peculiar in that its raw data are dots on graphs, representing species or populations whose life processes (growth, mortality, food consumption, etc.) can be expressed by the parameter values of some standard equation. When plotted for a large number of cases, the points form the patterns of the title. On these patterns, tropical fish form sub-patterns, whose shape and position differs from those of fishes from the sub-tropical, temperate and high-latitude regions (Fig. 1), and which are used as background.

Some of these (sub)patterns are easy to see and interpret; some others require explanatory digression. Some colleagues are weary of these digressions. Some

*The seventh J. W. Jones Lecture.

E-mail: pauly@fisheries.com

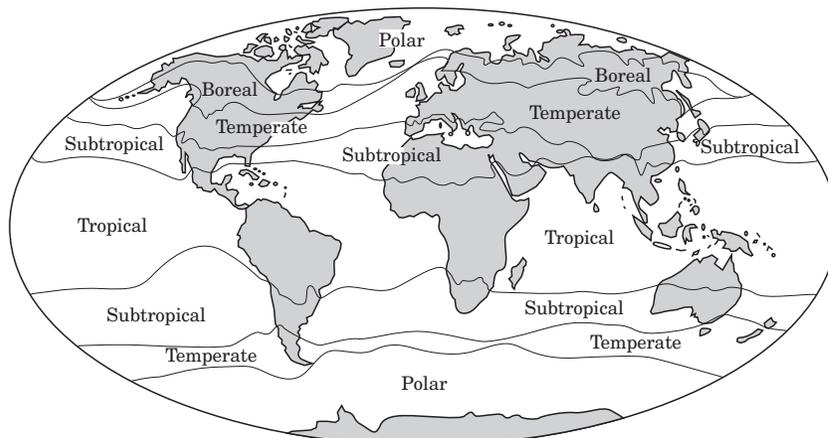


FIG. 1. Definition of the tropics, and of other climatic areas mentioned in this contribution (adapted from Anon., 1991).

other colleagues may be interested by the shape of patterns, especially those pertaining to the fish they work on, but not by the existence of the patterns themselves. Yet, their existence poses an important question: why do tropical and other fish so often arrange themselves to form clear patterns on graphs?

One answer—this is just the way it is—is clearly not acceptable. Stating that fishes are programmed genetically to form patterns will not do either, as the question of why a given pattern and why not another, still stands. Clearly, one should deal with material causes. However, in biology, identifying such causes, that is, events which are always followed by certain effects, can be tricky, and hence the propensities of the title, that is, weighted possibilities, ‘capable of producing, upon repetition, a certain statistical average’ (Popper, 1990).

To explain the propensities evident in the exhibited patterns, it will be proposed that the metabolic rate of fish, determined, among other things, by the relative size of their gills, controls growth, food consumption and related phenomena. This leads to the conclusion that tropical fishes display the very propensities one would expect from any gill-breathing organism living in warm water.

MATERIALS AND METHODS

Most of the graphs which form the core of this contribution were generated using FishBase 98, the computerized encyclopaedia of fishes (Froese & Pauly, 1998). Their (original) colour version, and related graphs, may be seen on the FishBase homepage (www.fishbase.org), where various information on this extensive database is presented, including the full text of Froese & Pauly (1998). Each of the dots in these graphs is documented in a FishBase table, via a link to the reference from which the parameter values were extracted. Thus, each of the data points behind the patterns discussed here is traceable to its source, and nothing needs to be taken at face value.

Most dots in these graphs are the result of some specific study; each dot, therefore, is extremely valuable. Thus, the single dot representing a growth curve on an auximetric plot can be estimated as incorporating work equivalent to a master’s thesis, or a short paper, requiring U.S. \$10 000–100 000 worth of inputs (Morgan & Hopkins, 1986; Pauly,

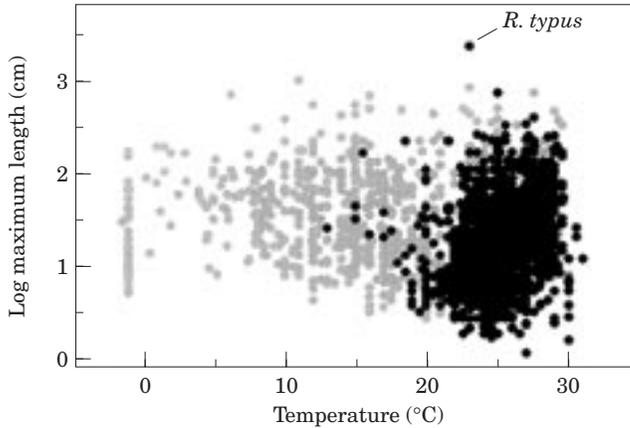


FIG. 2. Maximum length of fish species with temperature record so far included in FishBase (Froese & Pauly, 1998) v. the mean temperature of their habitat. Note that tropical fish (black dots; $n=1940$), with a range of habitat temperature of about 10°C , fill a wider range of sizes than cold-water fish (grey dots; $n=833$), despite the latter's much wider range of habitat temperatures. The largest fish is the whale shark.

1986). Therefore, in an age of stagnating support for research, these points and the patterns they generate should be taken seriously.

OBSERVED PATTERNS

MAXIMUM SIZE

The most important attribute of organisms is their size, which determines largely the nature of their interaction with other organisms, and their demographic characteristics (e.g. large organisms tend to live longer than small ones, and their populations fluctuate less than those of small species). The maximum size reached by tropical fishes, plotted against mean environmental temperature (Fig. 2), over the background provided by all species with available data, suggests that tropical fishes, contrary to temperate and other cold water fishes, had enough evolutionary time to fill all available size-related niches, i.e. to generate the 'full house' of Gould (1996). Figure 3 suggests, however, this filling up process to be biased: tropical fish tend to be smaller than those of colder climes. At least, there are relatively more small species in the tropics than elsewhere (see later).

GROWTH

The growth of fish and other organisms defines the time they spend in different (size-related) predatory fields, and is thus the key process behind a specific life history. Though growth can take a multiplicity of forms, the major features of fish growth can usually be described by a simple asymptotic growth curve, the von Bertalanffy growth function (VBGF), whose basic shape is expressed by the parameter K (quantifying the curvature of the VBGF), and the corresponding asymptotic size (length or weight). This feature of the VBGF makes it possible to summarize and compare growth data using auximetric plots (Pauly, 1979), i.e.

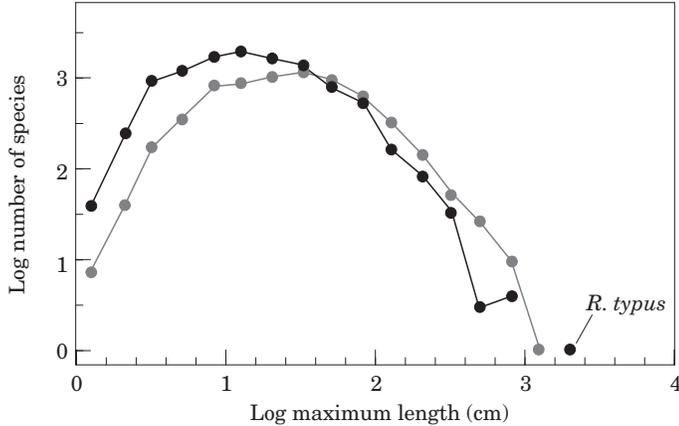


FIG. 3. Species so far included in FishBase (Froese & Pauly, 1998), by interval of log(maximum length). Note that more tropical (black dots; $n=10\,152$) than cold water fish (grey dots; $n=6\,119$) are small, whatever the definition of small. The isolated black dot on the x-axis refers to whale shark, the next (grey) dot to basking shark.

plots of $\log K$ v. \log asymptotic size, named from the Greek ‘*auxesis*’ (growth) and ‘*metron*’ (measure).

Therefore Fig. 4(a) may be seen as the key exhibits of this contribution, as it shows the pattern generated by an auximetric plot of over 4826 sets of parameter estimates of the VBGF, representing the utilization of the available growth space by over 1000 fish species so far studied. As might be seen, only a limited amount of growth space is utilized by fishes, which either tend to remain small, and have high values of K , or become large, but then have low values of K . Note also that this is not a statistical artifact, resulting from our methods for fitting size at age and other growth data: there is an order-of-magnitude range for the value of K that may be attached to an asymptotic size of say 100 cm. Indeed, that range of K values determines whether one is dealing with a fast-growing scombrid, or a slow-growing rockfish.

The other pattern evident in Fig. 4(a) is that, as expected, tropical fishes tend to be confined to the space defined by smaller asymptotic sizes, and higher values of K . An exception is the largest extant fish, the whale shark *Rhincodon typus* Smith, which may reach over 14 m, and which must be considered a tropical species. However, the large number of species with asymptotic sizes ranging from 2–4 m consists mainly of sharks and large scombroids (tuna and billfish), which range from tropical to temperate areas; for these, the subtropical label must be used.

Fig. 4(b) shows that the same pattern is obtained, whether one works with asymptotic weights or with asymptotic lengths, i.e. the observed patterns are not due to the biasing effects of comparing eel-like fish with rotund ones.

The six panels of Fig. 5 illustrate the distinct clusters that are generated in growth space when dots representing families, genera and species appear on auximetric plots. The resulting patterns can be analysed using cluster analysis, leading to dendrograms reflecting the affinities of fishes in terms of growth performance (see Pauly & Binohlan, 1996; Pauly *et al.*, 1996). Perhaps more

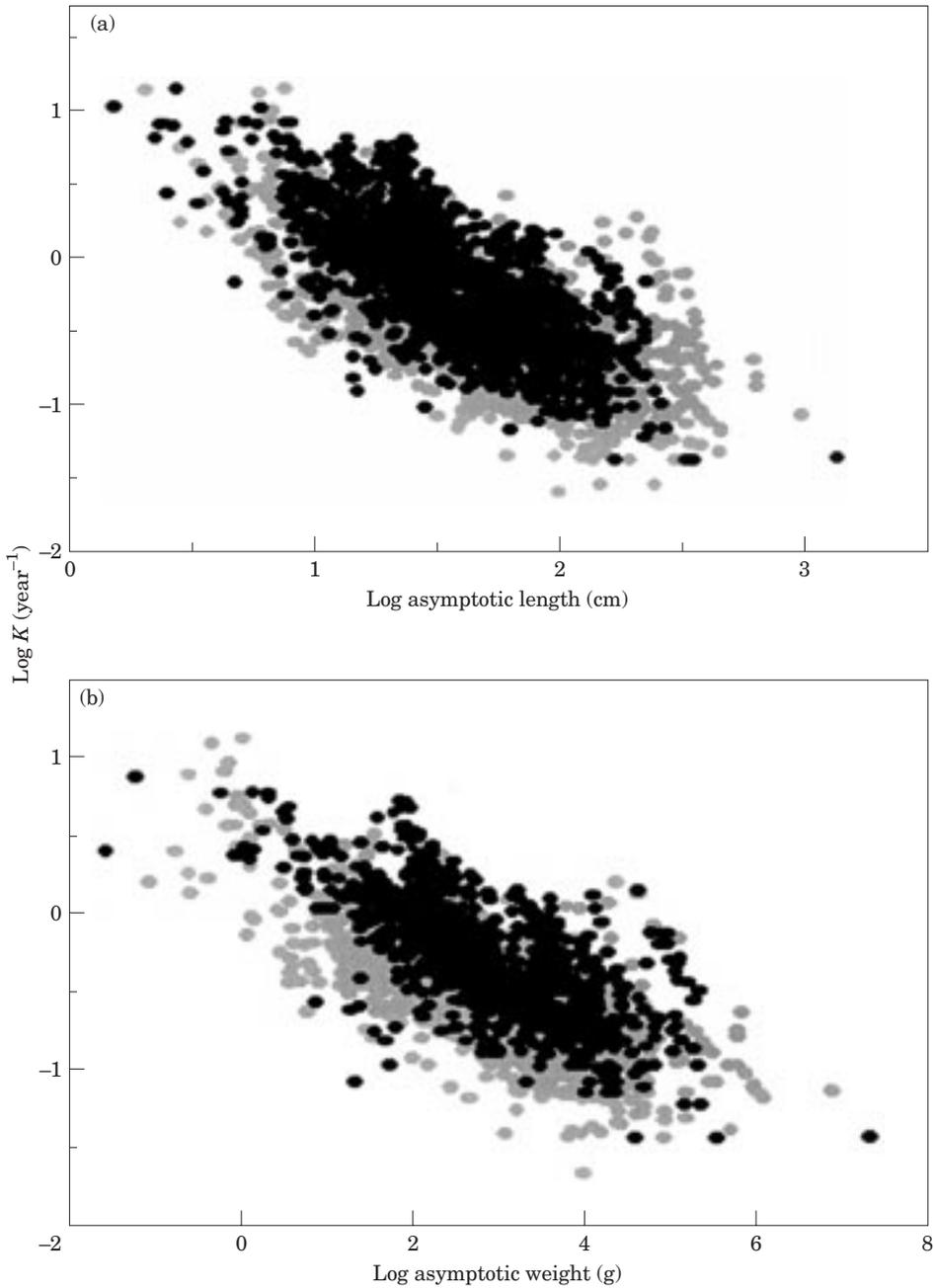


FIG. 4. Plot of the parameter K of the von Bertalanffy growth function v , the corresponding estimate of asymptotic size in different populations (n) of over 1000 species. (a) K v . asymptotic length ($n=4826$). (b) K v . asymptotic weight ($n=2948$). Note propensity of tropical fishes (black dots, n for length=1851; n for weight=1077) to have the higher value of K corresponding to a given asymptotic size (data from Binohlan & Pauly, 1998).

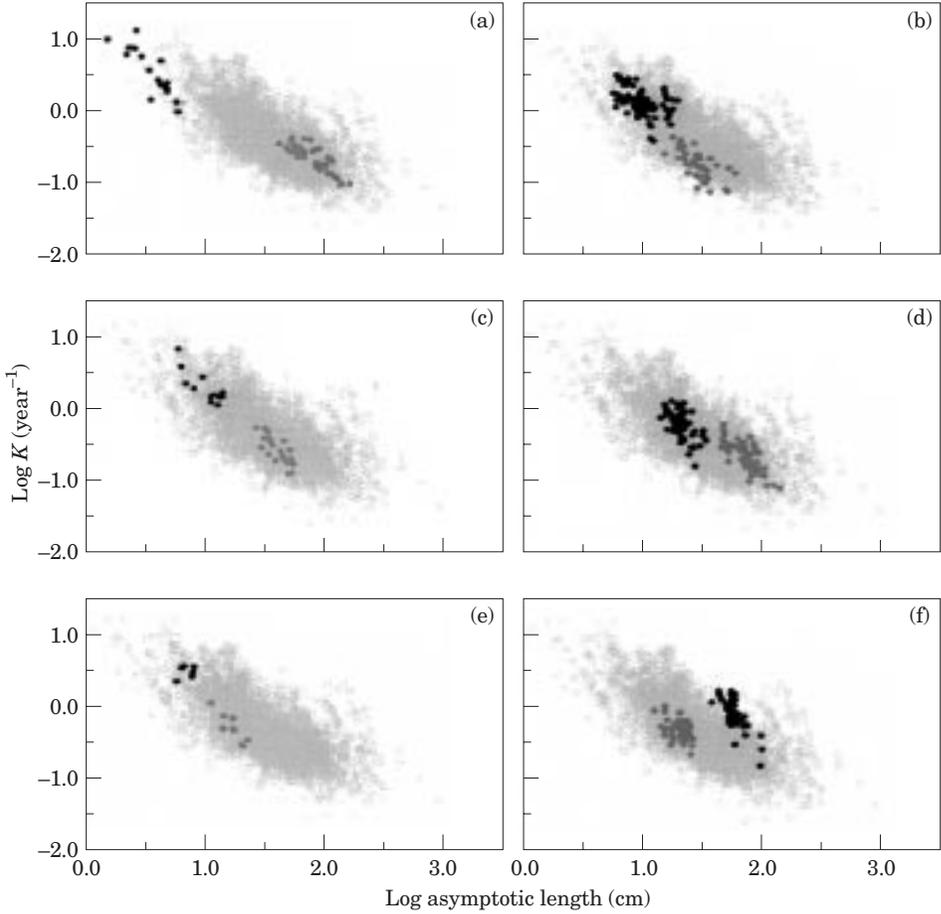


FIG. 5. Auximetric plots for some predominantly tropical fish families, genera and species, with (unrelated) cold water taxa provided for contrast; left: freshwater, right marine taxa. (a) Poeciliidae (black) v. Esocidae (grey); (b) Leiognathidae (black) v. Sebastidae (grey); (c) *Limnothrissa* spp. (black) v. *Thymallus* spp. (grey); (d) *Nemipterus* spp. (black) v. *Gadus* spp. (grey); (e) *Stolothrissa tanganicae* (black) v. *Lepomis macrochirus* (grey); (f) *Katuswonus pelamis* (black) v. *Clupea harengus* (grey). Data from Binohlan & Pauly (1998).

importantly, they lead to the question why a certain cluster is located where it is, rather than somewhere else: a theme to which this paper returns.

NATURAL MORTALITY

The natural mortality (M) of fish is difficult to estimate, requiring either that we estimate total mortality (Z) in an unexploited stock or, since $Z = M + F$, where F is fishing mortality. It is astonishing that estimates of M in fish should relate to their growth parameters in the first place, given that M values do not actually describe the fate of individuals. Natural mortality differs in this from growth parameters, which describe a process observable at the level of single specimens. Yet, M values correlate strongly with growth parameters. This is illustrated here by Fig. 6(a), i.e. a plot of M values v. asymptotic size, and by Fig. 6(b), a plot of M v. the parameter K of the VBGF.

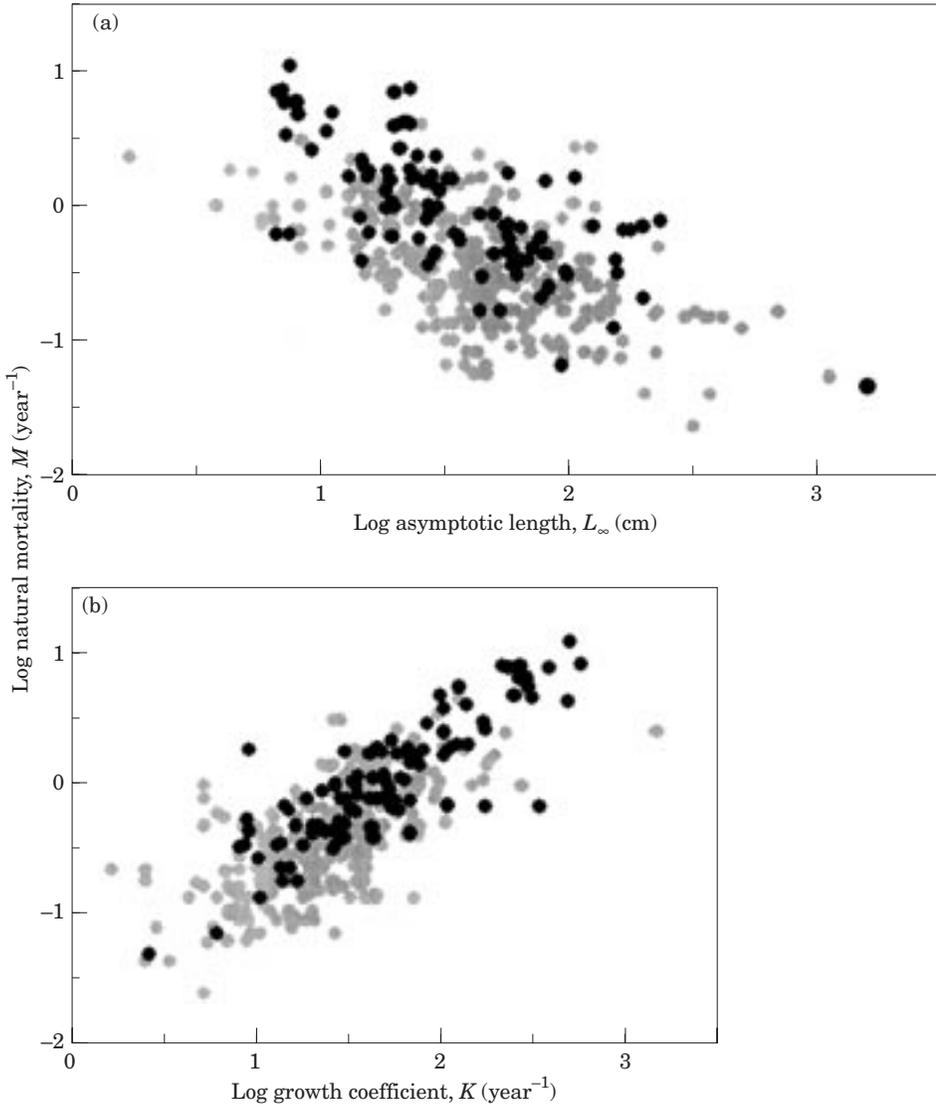


FIG. 6. Relations between natural mortality (M) and growth parameters ($n=358$). (a) Plot of M v. asymptotic length. (b) Plot of M v. the parameter K of the VBGF. Note propensity of M to be higher in tropical (black dots, $n=105$) than in other species, given values of asymptotic length (a) or K (b).

On these plots, tropical fishes are right where one would expect them, given the analysis of Pauly (1980), in which, on the basis of 175 data triplets covering a wide range of taxa, sizes and habitats, M was shown to depend on K , on asymptotic size and on mean environmental temperature. Thus, tropical fishes tend to have, for any asymptotic size, higher values of M than other fishes [Fig. 6(a)]. This is similar for K , i.e. tropical fishes tend to have, for any value of K , higher values of M than temperate fishes [Fig. 6(b)].

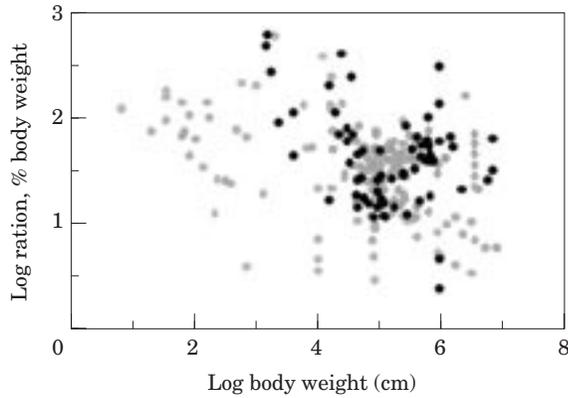


FIG. 7. Relationship between the relative food consumption (daily ration per unit body weight) *v.* body weight of fish ($n=249$) in FishBase 98. Tropical fish (black dots, $n=72$) tend to consume more than other fish, as may be expected, given the high temperatures of their habitats. This well-documented effect is there partly masked by the variance due to different food types.

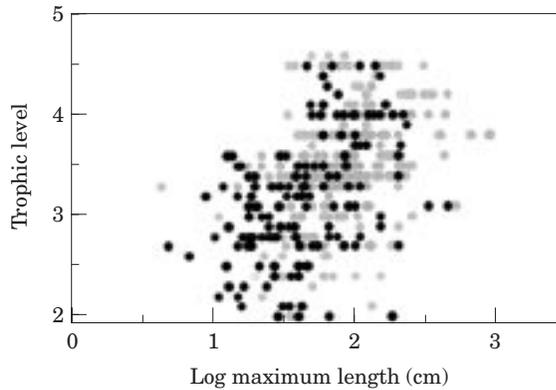


FIG. 8. Relationship between the trophic level and the maximum length reached by 454 fish species in FishBase 98. The graph confirms earlier assumptions about the sign of the trend; that tropical fishes (black dots, $n=152$) may have higher trophic levels than other fishes of the same size is a new finding.

Note that these effects are not due to the M values all having been estimated via the same rule of thumb (e.g. $M=0.2$): the values of M included in FishBase are all independent, and were all estimated from local data (Pauly & Binohlan, 1998). The plots in Fig. 6 thus confirm that M varies with size and temperature in addition to varying with K , and that hence, the ratio M/K is not the invariant as stated by Charnov (1993).

FOOD CONSUMPTION

Figures 7 and 8 deal with the food consumption fuelling the growth documented in Figs 4 and 5, and the natural mortality of some of the smaller fishes in Fig. 6. The data in Fig. 7, though scattered due to different food types, generate a pattern reflecting known trends: relative ration declines with body

weight, and warm water, i.e. tropical fishes tend to consume more than their colder-water counterparts, other things being equal. Thus, this pattern illustrates the empirical relationship of [Palomares & Pauly \(1989\)](#), allowing prediction of food consumption as a function of body weight, food type and temperature.

[Figure 8](#), on the other hand, presents evidence never shown before, though illustrating a relationship assumed by a number of authors ([Sheldon & Kerr, 1972](#); [Paloheimo, 1988](#); [Thiebaut & Dickie, 1993](#); [Pauly *et al.*, 1998](#)): that trophic level increases with fish size. [The L_T values used for this plot were based either on diet composition of the specimens of the species in question (with L_T then estimated as 1 + weighted mean L_T of the diet items; [Pauly & Christensen, 1998](#)), or as part of the output of mass-balance food web models ([Christensen & Pauly, 1992, 1993](#)), with cross-validation using $^{15}\text{N}/^{14}\text{N}$ ratios ([Kline & Pauly, 1998](#)).]

[Figure 8](#) suggests that the trophic levels of tropical fish species may be higher than those of colder water fishes, given the same maximum size—an unanticipated, but not surprising discovery, given the large number of species in tropical systems, and hence the high connectance—at least potentially—of food webs describing their trophic interactions (see contributions in [Christensen & Pauly, 1993](#)).

METABOLISM AND GILL SURFACE AREA

The metabolism of fish is what turns their food into useful energy. This process is illustrated here with a single figure, illustrating that indeed, warm-water fishes consume more oxygen than cold-water fishes ([Fig. 9](#)). Note that the issue here is not that the metabolic rate of an individual fish increases when its experimental temperature is increased—a well-studied phenomenon—rather, it is that warm-water fishes (subtropical and tropical species) have elevated metabolic rates, compared to fishes of temperate and cold waters (deep and polar seas).

Considering metabolism, i.e. oxygen consumption, brings us somewhat closer to the mechanism proposed here to explain the propensities evident in the previous graphs. First, however, one needs to recall that in order to be useful metabolically, oxygen must occur within the body of a fish, i.e. it must have passed across its gills. Gills, being a surface area, cannot grow, for insurmountable geometric reasons, as fast as the volume they are meant to supply with oxygen. Indeed, in most fish, gill surface area, and hence metabolic rate, increases in proportion to a power of weight equal to 0.7–0.8. Lower values (down to 0.5) are typical of fish that remain small; higher values (up to 0.9) occur in tuna and presumably in other large, metabolically active fishes such as pelagic sharks ([Pauly, 1981, 1997](#)).

One major implication of this is illustrated in [Fig. 10](#), which also explains why tropical fish, which have elevated metabolic rates ([Fig. 9](#)), would tend to remain smaller than cold-water fishes, other things being equal. [Figure 10](#) may be seen as expressing the core of the theory of growth whose details are provided in [Pauly \(1981, 1984\)](#), [Longhurst & Pauly \(1987\)](#), and restated in [Pauly \(1997, 1998\)](#). Until recently, that theory had been ignored, or rejected in passing, i.e. without any tests of its corollaries (see e.g. [Weatherley & Gill, 1987](#)).

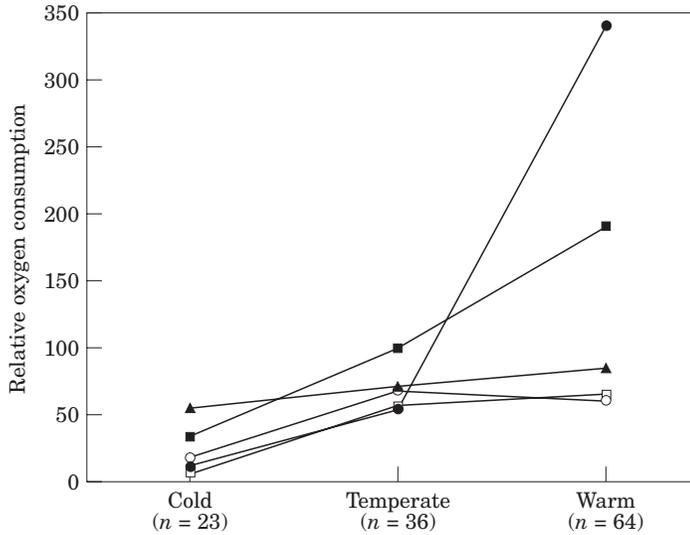


FIG. 9. Mean metabolic rate of fish, by habitat temperature. Based on 3693 individual measurements documented in Torres & Froese (1998); number of species are given for each of the temperature regimes: cold (mean = $7.6 \pm 5.0^\circ\text{C}$) includes species from deep-water, and polar habitats; temperate refers to species from that zone in Fig. 1 (mean = $15.6 \pm 4.8^\circ\text{C}$); warm includes species from subtropical and tropical waters (mean = $22.1 \pm 5.3^\circ\text{C}$). The high metabolic rates of warm-water fishes reduces the size at which oxygen supplies become limiting to their growth (see text). Weight classes (g): ●, 0-0.9; ○, 1-9.9; □, 10-20; ▲, 100-200; ■, 1000-2000.

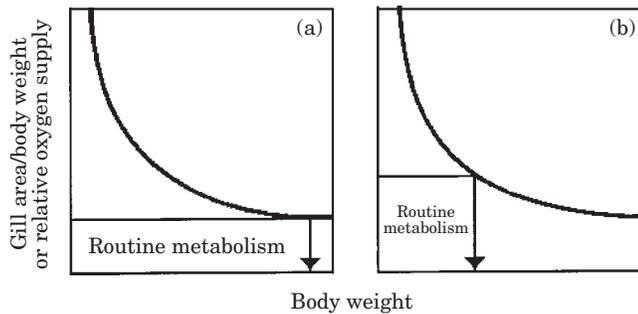


FIG. 10. Schematic illustration of the effect of gills that increase in proportion to a power of weight < 1 , given geometrical constraints. (a) as a fish grows, its gill area per unit weight declines, which reduces the oxygen supply to its body. Hence a size can be defined at which oxygen supply is just sufficient to cover routine metabolism (see downward-pointing arrow). This defines the maximum (and the asymptotic) size of fish. (b) the elevated metabolic rates occurring in warmer habitats (and/or other stressors, such as e.g. sparse food, or competitive interactions) cause the limiting effect in A to occur at a smaller size (from Pauly, 1984; see Longhurst & Pauly, 1987 for modifications of this basic scheme).

DIGRESSION: THE EFFECT OF SWIMMING CAPACITY

Recently, Blier *et al.* (1997) suggested that the correlation in Pauly (1981) between an index of the gill area of fishes, and an index of their growth performance, besides being weak, was due to the fact that gill area correlates with swimming capacity, which itself correlates with growth. In other words,

they suggest that fish with large gills use them for fast swimming and not necessarily for rapid growth. Indeed, when they removed what they assumed were poor swimmers from a bivariate data set extracted from Pauly (1981), the correlation between gill area and growth performance no longer held.

There are 17 species in FishBase 98 for which independent estimates of (sustained) swimming speed (an index of swimming capacity), of gill area (in cm^2), and of growth parameters are available. From these, one can compute a gill area index (I_{GA}), defined by

$$I_{\text{GA}} = \text{gill area}/(\text{body weight})^d \quad (1)$$

with d set at an average value of 0.8 for all species (Pauly, 1981), and individual values of I_{GA} averaged within species to obtain species-specific estimates.

Also, a growth performance index (φ) can be defined by

$$\varphi = \log K + 2/3 \log W_{\infty} \quad (2)$$

where K is the curvature parameter of the VBGF (year^{-1}) and W_{∞} , the asymptotic weight (Pauly, 1979; Pauly *et al.*, 1996). Species-specific estimates were derived by averaging in cases where several data sets were available for a given species.

Finally, a swimming capacity index (I_{S}) was derived from VL^{-1} , where V is the sustained swimming speed of a fish, in cm s^{-1} , and L is its body length, in cm. Again, means were taken when several records were available for a given species.

The data in Table I allow following up on the point made by Blier *et al.* (1997). These lead to -0.599 , 0.590 , and -0.558 for the correlations between growth performance index and swimming index, growth performance index and gill area index, and swimming capacity index and gill area index, respectively. However, these values are pointless if gill area, swimming and growth interact with each other. A multiple regression should be more useful, and indeed we obtained, using the data in Table I:

$$\varphi = 1.94 + 0.011 (I_{\text{GA}}) - 0.049 (I_{\text{S}}) \quad (3)$$

for which $r = 0.674$ ($r^2 = 0.454$), and which, with 15 d.f., is significant ($P < 0.02$; Fig. 11).

This finding is rather easy to interpret: given a specific gill area, fish can either grow or swim a lot, but not both. Hence, considering swimming capacity does not invalidate the contention that gill area is limiting for growth. Rather, the relationship between gill area and growth performance becomes tighter once swimming speed is considered (*cf.* the above-cited correlation of 0.590 with that of 0.674 in Fig. 11).

And indeed, P. U. Blier (pers. comm.), who examined potentially limiting factors for growth one at a time, under laboratory conditions where food was provided *ad libitum*, suggests that 'under natural conditions, particularly when fish have to move at the same time as they feed or digest, it remains very

TABLE I. Data for establishing interrelationships between gill surface area, swimming capacity and growth performance in fish (extracted and/or computed from entries in FishBase 98; Froese & Pauly, 1998)

No.	Species*	Gill index†	Swim index‡	Growth index§
1	<i>Katsuwonus pelamis</i>	76.9	4.24	2.32
2	<i>Thunnus thynnus</i>	64.4	0.53	2.81
3	<i>Thunnus albacares</i>	59.0	1.77	2.90
4	<i>Brevoortia tyrannus</i>	46.1	2.04	1.32
5	<i>Sarda sarda</i>	27.7	13.6	2.20
6	<i>Pomatomus saltator</i>	26.1	8.32	1.80
7	<i>Esox lucius</i>	23.7	10.5	1.73
8	<i>Coryphaena hippurus</i>	23.6	1.25	2.98
9	<i>Scomber scombrus</i>	19.9	11.5	1.41
10	<i>Merlangius merlangus</i>	19.0	7.65	1.43
11	<i>Pollachius virens</i>	17.4	9.19	1.95
12	<i>Perca fluviatilis</i>	15.5	20.0	1.06
13	<i>Morone saxatilis</i>	15.0	8.55	1.97
14	<i>Clupea harengus</i>	12.9	9.63	1.02
15	<i>Salmo trutta</i>	12.0	7.94	1.54
16	<i>Zeus faber</i>	5.54	8.42	1.86
17	<i>Carassius auratus</i>	3.32	6.62	1.18

*Only 17 species included records for all three measures.

†The gill area index (I_{GA} : for gill in cm^2 , and body weight in g) is defined by $\text{gill area} = I_{GA} (\text{weight})^d$, d was set at 0.8 for all species (see Fig. 10), and estimates of I_{GA} were averaged when several gill area records were available for a given species.

‡The swimming capacity index is based on $V L^{-1}$ where V is the sustained swimming speed in cm s^{-1} and L the body length in cm. Means were taken when several records were available.

§The growth performance index is defined as $\phi = \log K + 2/3 \log W_{\infty}$ where K is the curvature parameter of the VBGF (year^{-1}) and W_{∞} the asymptotic weight (g).

probable that aerobic scope, i.e., the oxygen supply through the gills, acts as a limiting factor . . .' (my translation from French).

CLOSING THE LOOP: PATTERNS OF GROWTH AND GILL AREA

Having dealt with swimming capacity as a potentially disrupting factor, one can return now to what was referred above as the key exhibits of this contribution, the auximetric plots in Fig. 4.

There are 52 species in FishBase 98 for which both estimates of gill area and growth parameters are available. From these 52 sets of estimates of mean gill area index, as defined above, mean asymptotic weight (for all cases with more than one set of growth parameters) and mean K [estimated via mean values of ϕ , see equation (2) above] were derived. They led to the multiple regression

$$\log K = -0.273 - 0.415 \log W_{\infty} + 0.268 \log (I_{GA} W_{\infty}^{0.8}) \quad (4)$$

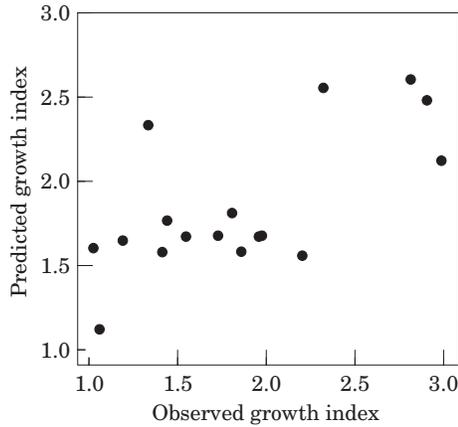


FIG. 11. Plot of the predicted *v.* the observed growth performance of 17 species of fish [data from Table I and equation (1)]. $r^2=0.674$.

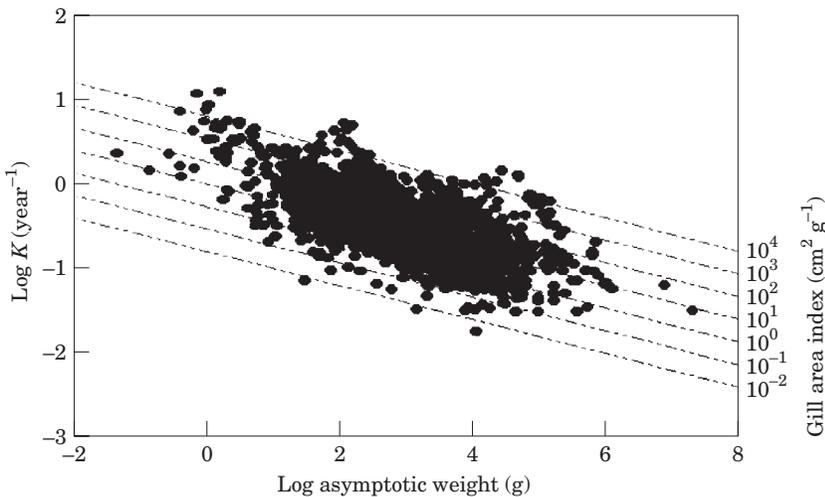


FIG. 12. Plot of the parameter K of the VBGF *v.* the corresponding estimate of asymptotic weight (W_∞) in 2948 species of fish, with superimposed isolines [from equation (3)] predicting K , given W_∞ and gill area index (I_{GA} ; in $\text{cm}^2 \text{g}^{-1}$) values. This plot suggests that fish of a given size can exhibit rapid growth (=high K values) only if they have large gills.

for which $r=0.640$ ($r^2=0.410$), and for whose regression coefficients are both significantly different from zero ($P<0.001$).

Solving this equation for different values of I_{GA} , and superimposing the resulting isolines onto the auximetric plot in Fig. 4(b) leads to Fig. 12.

As might be seen, this graph explains the pattern formed by the growth parameters in Fig. 12 in terms of the gill area of the species in question, with large-gilled species exhibiting high values of K (i.e. rapid growth) for a given asymptotic size.

DISCUSSION

Now one can return to the graphs presented so far, and discuss the propensities illustrated by the different patterns.

Given the climate definitions in Fig. 1, tropical fishes are exposed, throughout their lives, to temperatures $>20^{\circ}\text{C}$. This implies, given that metabolic rates increase with temperature (Fig. 9), and that growth is limited by respiratory metabolism (Fig. 10), that tropical fishes should generally remain small. And indeed, in spite of a wider variety of size-specific niches having been colonized in the tropics than elsewhere (Fig. 2), the fish there tend to be smaller than their cold-water counterparts (Fig. 3).

The scheme in Fig. 10 also implies that K , in tropical fishes, should tend to be higher than for their cold-water counterparts, while their asymptotic sizes should tend to be smaller. This is indeed the case [Fig. 4(a) and (b)]. The specific location of a given taxon in growth space (see examples in Fig. 5) is then a matter of their gill area [equation (3)], and of their level of (swimming) activity [equation (1)].

Swimming activity, and growth (and size) jointly define the niche of a species (e.g. small or large, and pelagic; small or large, and benthic). Body size and habitat thus defined provide different type of refuges from predators (large size is an anatomical refuge; benthic structures provide physical refuges). In either case, the effect of the refuge must be sufficient to allow the natural mortality caused by prevailing predation levels to remain low, such that a sufficient number of recruits grow into adults, and reproduce. Species which, over evolutionary time, do not manage to keep their natural mortality down to that level go extinct. Species which succeed initially in keeping their natural mortality below that critical level will increase in abundance, and thus attract new predators. Hence natural mortality will tend to be coupled with growth, given that adult size will tend also to correlate with fecundity. Therefore, there is a tight fit between growth parameters and M in Fig. 6.

As food consumption increases with temperature, prevailing predation rates also generate the relation between temperature and M or put differently, the natural mortality of fish is higher in the tropics because their predators (mainly fish; see Christensen, 1996) must consume more prey per unit time than their cold water counterparts (see also Fig. 8).

The question may now be asked why fish, if their gill surface area is limiting, simply do not grow bigger gills, i.e. evolve around this constraint. Some answers to this are as follows. Fishes have indeed evolved larger gills since their sluggish ancestors first appeared in the fossil record (Pauly, 1981). Large-gilled fish such as tuna took a long time to evolve, and their open ocean niche was empty until the required gills and associated adaptations evolved. Fishes have the gills they need to reach maturity, in their optimal habitat, within a time span short enough for the surviving adults to generate sufficient number of recruits. When adult fish get older and larger, and/or move outside their optimum habitat, respiratory stress can quickly become constraining (Sharp, 1978). Geometric constraints prevent surfaces from growing as fast as volumes. When the body that is supplied by a given set of gills grows, gill area per unit weight declines (see Fig. 10), until a level is reached where routine metabolism is just met—at which point growth must cease.

A comprehensive theory can be articulated about Fig. 10 (Pauly, 1981, 1997) and a number of corollaries have been tested, notably concerning fish reproduction (Pauly, 1984), their swimming speed (see Table I, and above text) and distribution in depth and space (Longhurst & Pauly, 1987), the growth of gill-breathing invertebrates such as squids and other cephalopods (Pauly, 1998), the growth of fishes under aquaculture conditions (van Dam & Pauly, 1995), and even the (calm) behaviour of Nile tilapia *Oreochromis niloticus* L., bred selectively for fast growth, compared with that of slower-growing, wild controls (Bozynski, 1998).

As illustrated here, this theory can be used to explain the propensities behind the patterns in the above plots. Given the data it contains, FishBase 98 can generate many more plots than shown above, documenting different aspects of this theory. I invite readers to evaluate its explanatory power when applied to the fish they know best.

This contribution would not have been possible, had not two friends come to the rescue: R. Froese, for implementing in FishBase a rather sophisticated scheme for automatic identification of the climatic zone to which different fish species may be assigned (this choice is now a field of FishBase 98), and for useful comments on the draft; and D. Palomares, for performing the rather complex FishBase searches behind, e.g. Fig. 12 and Table I, and for regenerating the graphs, kindly finalized by A. Atanacio.

References

- Anonymous (1991). *Bartholomew Illustrated World Atlas*. Edinburgh: HarperCollins.
- Berg, L. S. (1958). *System der rezenten und fossilen Fischartigen und Fischen*. Berlin: VEB Verlag der Wissenschaften.
- Binohlan, C. & Pauly, D. (1998). The POPGROWTH Table. In *FishBase 98: Concepts Design Data Sources* (Froese, R. & Pauly, D., eds) Manila: ICLARM.
- Blier, P. U., Pelletier, D. & Dutil, J. D. (1997). Does aerobic capacity set a limit on fish growth rate? *Reviews in Fisheries Science* **5**, 323–340.
- Bozynski, C. (1998). *Interactions between growth, sex, reproduction, and activity levels in control and fast-growing strains of Nile tilapia (Oreochromis niloticus)*. M.Sc. thesis, Zoology Department, The University of British Columbia, Vancouver.
- Charnov, E. (1993). *Life-History Invariants: Some Explorations of Symmetry in Evolutionary Ecology*. Oxford: Oxford University Press.
- Christensen, V. (1996). Managing fisheries involving top predator and prey species components. *Reviews in Fish Biology and Fisheries* **6**, 417–442.
- Christensen, V. & Pauly, D. (1992). The ECOPATH II—a software for balancing steady-state ecosystem models and calculating network characteristics. *Ecological Modelling* **61**, 169–185.
- Christensen, V. & Pauly, D. (Eds) (1993). *Trophic Models of Aquatic Ecosystems*. ICLARM Conference Proceedings **26**.
- Daget, J., Gosse, J. P., Teugels, G. G. & Thys van den Audenaerde, D. F. E. (Eds) (1984–1991). *Checklist of the Freshwater Fishes of Africa (CLOFFA)*. Institut Royal des Sciences Naturelles de Belgique, Bruxelles, Musée Royal de l'Afrique Centrale, Tervuren, and Institut Français de Recherche Scientifique pour le Développement en Coopération (ORSTOM), Paris. Vol. 1–4.
- Eschmeyer, W. N. (1990). *Catalog of the Genera of Recent Fishes*. San Francisco: California Academy of Sciences.
- Froese, R. & Pauly, D. (Eds) (1998). *FishBase 98: Concepts, Design and Data Sources*. Manila: ICLARM.
- Gould, S. J. (1996). *Full House: the Spread of Excellence from Plato to Darwin*. New York: Harmony Book.

- Greenwood, P. H., Rosen, D. E., Weizman, S. H. & Myers, G. S. (1966). Phyletic studies of teleostean fishes with a provisional classification of living forms. *Bulletin of the American Museum of Natural History* **131**, 339–455.
- Kline, T. & Pauly, D. (1998). Cross-validation of trophic level estimates from a mass-balance model of Prince William Sound using $^{15}\text{N}/^{14}\text{N}$ data. In *Fish Stock Assessment models*. Alaska Sea Grant College Program. AK-SG-98-01.
- Longhurst, A. & Pauly, D. (1987). *Ecology of Tropical Oceans*. San Diego: Academic Press.
- Morgan, G. R. & Hopkins, K. D. (1986). Productivity of fisheries laboratories in lesser developed countries. *Naga* **9**(2), 3–4.
- Paloheimo, J. E. (1988). Estimation of marine production from size spectrum. *Ecological Modelling* **42**, 33–44.
- Palomares, M. L. & Pauly, D. (1989). A multiple regression model for predicting the food consumption of marine fish population. *Australian Journal of Marine and Freshwater Research* **40**, 259–284.
- Pauly, D. (1979). Gill size and temperature as governing factors in fish growth: a generalization of von Bertalanffy's growth formula. *Berichte des Institut für Meereskunde an der Universität Kiel* **63**.
- Pauly, D. (1980). On the interrelationships between natural mortality, growth parameters and mean environmental temperature in 175 fish stocks. *Journal du Conseil international pour l'Exploration de la Mer* **39**, 175–192.
- Pauly, D. (1981). The relationships between gill surface area and growth performance in fish: a generalization of von Bertalanffy's theory of growth. *Meeresforschung* **28**, 251–282.
- Pauly, D. (1984). A mechanism for the juvenile-to-adult transition in fishes. *Journal du Conseil international pour l'Exploration de la Mer* **41**, 280–284.
- Pauly, D. (1986). On identifying fish species rather than assessing fish stocks: a review of two books on the taxonomy of the neritic fishes of the Western Indian Ocean. *Naga* **9** (3), 21.
- Pauly, D. (1997). Geometrical constraints on body size. *Trends in Ecology and Evolution* **12**, 442–443.
- Pauly, D. (1998). Why squids, though not fish, should be studied as if they were. *South African Journal of Marine Sciences*, in press.
- Pauly, D. & Binohlan, C. (1996). FishBase and AUXIMS tools for comparing life-history patterns, growth and natural mortality of fish: applications to snapper and groupers. In *Biology, Fisheries and Culture of Tropical Groupers and Snappers* (Arreguín-Sánchez, F., Munro, J. L., Balgos, M. C. & Pauly, D., eds), pp. 218–243. Manila: ICLARM Conference Proceedings **48**.
- Pauly, D. & Binohlan, C. (1998). Natural mortality. In *FishBase 98: Concepts, Design and Data Sources* (Froese, R. & Pauly, D., eds) Manila: ICLARM.
- Pauly, D. & Christensen, V. (1998). Trophic levels of fishes. In *FishBase 98: Concepts, Design and Data Sources* (Froese, R. & Pauly, D., eds). Manila: ICLARM.
- Pauly, D., Moreau, J. & Gayanilo, F. C., Jr (1996). A new method for comparing the growth performance of fishes, applied to wild and farmed tilapias. In *Proceedings of the Third International Conference on Tilapia in Aquaculture, 11–16 November 1991, Abidjan, Côte d'Ivoire* (Pullin, R. S. V., Lazard, J., Legendre, M., Amon Kothias, J. B. & Pauly, D., eds), pp. 433–441. Manila: ICLARM Conference Proceedings **41**.
- Pauly, D., Christensen, V., Dalsgaard, J., Froese, R. & Torres, F. C., Jr (1998). Fishing down marine food webs. *Science* **279**, 860–863.
- Popper, K. R. (1990). *A World of Propensities*. Bristol: Thoemmes.
- Sharp, G. (1978). Behavioural and physiological properties of tuna and their effects on vulnerability of fishing gear. In *The Physiological Ecology of Tunas* (Sharp, G. & Dizon, A. E., eds), pp. 397–449. New York: Academic Press.
- Sheldon, R. W. & Kerr, S. R. (1972). The population density of monsters in Loch Ness. *Limnology & Oceanography* **17**, 796–798.

- Thiebaut, M. L. & Dickie, L. M. (1993). Structure of the body-size spectrum of the biomass in aquatic ecosystems: a consequence of allometry in predator-prey interactions. *Canadian Journal of Fisheries & Aquatic Sciences* **50**, 1308–1317.
- Torres, A. & Froese, R. (1998). The Oxygen Table. In *FishBase 98: Concepts, Design and Data Sources* (Froese, R. & Pauly, D., eds), Manila: ICLARM.
- van Dam, A. A. & Pauly, D. (1995). Simulation of the effects of oxygen on food consumption and growth of Nile tilapia, *Oreochromis niloticus* (L.). *Aquaculture Research* **26**, 427–440.
- Weatherley, A. H. & Gill, H. S. (1987). *The Biology of Fish Growth*. London: Academic Press.