

Beyond our original horizons: the tropicalization of Beverton and Holt

DANIEL PAULY

Fisheries Centre, 2204 Main Mall, University of British Columbia, Vancouver, BC, Canada V6T 1Z4 E-mail: pauly@fisheries.com

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Abstract

The extension into tropical areas of Beverton and Holt's yield per recruit approach for stock assessment represents a straightforward case of 'normal science', the common Kuhnian counterpart to his much rarer 'paradigm shifts'. It is shown that the normal science which, in recent decades, has led to new methods for estimating growth, mortality and other statistics required for yield per recruit analyses in data-sparse environments, has not only enriched fisheries science and aquatic biology as a whole, but has also contributed to identify the limitations of the single-species research programme originally defined by Beverton and Holt. The most likely prospect for that programme, in the tropics and elsewhere, is to become a component of the 'multispecies', or rather 'ecosystem' approach that is emerging, and to which Beverton and Holt will have contributed many of the concepts, and much of the rigour.

Keywords: Beverton, gear selection, growth, Holt, mortality, multispecies modelling, Y/R analysis

Introduction

SCOPE OF THIS CONTRIBUTION

The text below – though it may have several attributes of a review – should not be evaluated by the criteria (comprehensiveness, balance, detachment, etc.) normally used for reviews: I was personally involved in the events outlined below and cannot but present a personal view.

On the other hand, the scholarly literature on the growth and development of science tends to emphasize ‘revolutions’ and ‘paradigms shifts’ (Kuhn, 1962), but gives short shrift to their counterpart – ‘normal science’ – although that is what the overwhelming majority of us do, usually all of our lives. The account below deals with the normal science that some of my colleagues and I did to extend into tropical areas, i.e. to ‘tropicalize’, the paradigm-setting classic of Beverton and Holt (1957; henceforth with ‘B&H’) – hence the second part of the title. We followed up on the implications of their contribution, refined the original panoply of methods for parameter estimation (with some emphasis to trawl fisheries), and ultimately redefined its range of applicability in both the geographic and conceptual senses. Kuhn (1962) calls this the ‘articulation’ of a paradigm. For my part in this process, Ray Beverton wrote in my copy of the classic a dedication that alluded to my contribution “in carrying the message far beyond our original horizons”. Hence the first part of the title.

THE 1957 BOOK AND ITS IMMEDIATE AFTERMATH

There are different ways B&H can be read (Pauly, 1993; Smith, 1994). My reading, at least for the purpose of this contribution, is that it presents a specific approach for yield per recruit (Y/R) analysis, superior to original efforts of Baranov (1918), as well as those of Thompson and Bell (1934) and Ricker (1958). It then shows how its parameters can be estimated and its results interpreted and generalized. In this reading, the key equation of the entire book is:

$$Y/R = F \cdot \exp(-Mr_2) W_\infty \cdot \left[\frac{1 - \exp(-Zr_3)}{Z} - \frac{3 \exp\{-Kr_1[(1 - \exp(-(Z+K)r_3])\}}{Z+K} + \frac{3 \exp(-2Kr_1)[1 - \exp(-Z+2K)r_3]}{Z+2K} - \frac{\exp[-3Kr_1(1 - \exp[-(Z+K)r_3])]}{Z+3K} \right] \quad (1)$$

where $r_1 = t_c - t_0$; $r_2 = t_c - t_r$, $r_3 = t_{\max} - t_c$, and whose parameters are defined further below (see also Fig. 1, and Pitcher, this vol.).

Equation 1 was difficult, at several levels, for many of the fisheries scientists of the time, for it implied that:

1. a single mathematical formula could capture the ‘essence’ of complex biological processes;
2. yield *per recruit* should be at the centre of attention, rather than yield itself; and more prosaically;
3. they became familiar with new parameters for expressing growth (W_∞ , K , t_0), with instantaneous rates for expressing mortalities (F , M , Z), and with other new concepts, all requiring simultaneous consideration.

Overcoming (1) was not easy: the then widespread belief that biological processes are not amenable to mathematical expression had doomed, one generation earlier, the

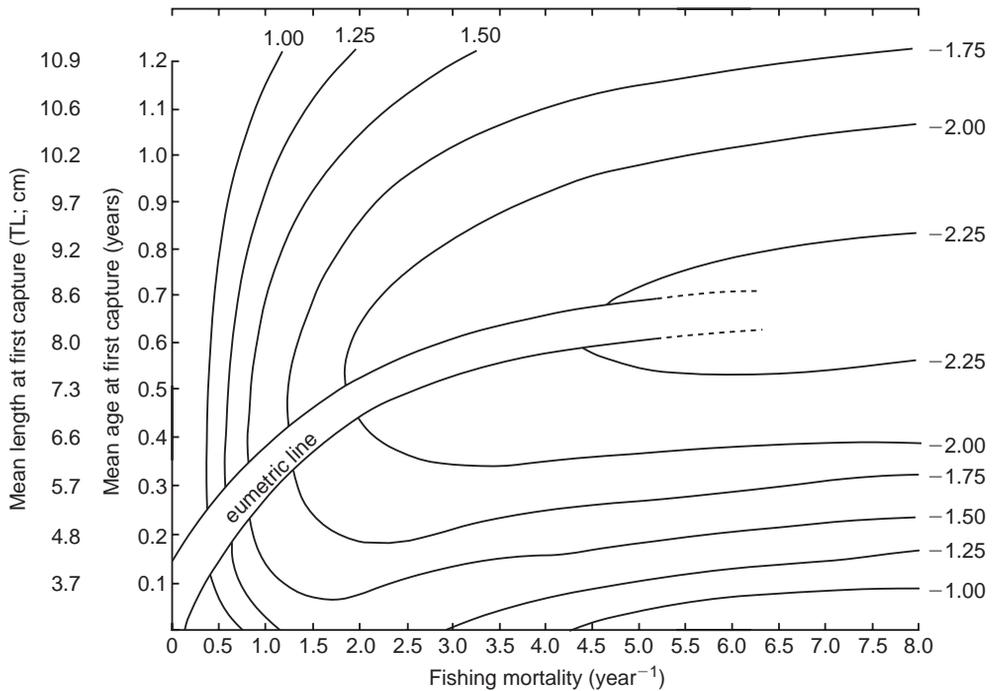


Fig. 1. Yield-isopleth diagram for slipmouth, *Leiognathus splendens*, in the Java Sea, Indonesia; based on equation (1) and the parameters $W_{\infty} = 64$ g; $K = 1$ year⁻¹; $t_0 = -0.2$ year; $M = 1.8$ year⁻¹; $t_r = 0$ and $t_{max} = \infty$ (from Pauly, 1979). Such diagrams were earlier seen as a major goal of stock assessment, as they provided a basis for selecting, along the ‘eumetric line’, an optimal combination of fishing mortality and mesh size. Hence, much work was devoted to estimating the required parameters (see text).

groundbreaking research programme implied in Baranov (1918), whose key equation was very similar in structure to Equation 1. Indeed, beliefs in the ineffability of natural processes, and their irreducibility to ‘mere’ mathematics are again *en vogue*, couched as arguments against ‘linear’, ‘deterministic’ or, even worse, ‘western’ thinking (Gross and Levitt, 1998).

Item (2) represents, I believe the crucial, and also the most misunderstood element of B&H: that a fishery can be put on a rational footing by manipulating fishing effort (i.e. fishing mortality) and mesh size (i.e. age at first capture) without ‘managers’ having to predict future recruitment. This was a most ingenious idea, redirecting as it did the energies of many fisheries scientists toward real fisheries, away from the ‘recruitment problem’, which was then, as it continues to be, an intractable problem (Pauly, 1993, 1994). The related misunderstanding started, however, right with B&H themselves who, through their flat-topped stock–recruitment curves, implied that for most practical situations, Y is proportional to Y/R ; or at least they could easily be, and often were, misunderstood that way (Holt, this vol.).

Still, the importance B&H attached to the fate of individual recruits, notwithstanding the vagaries of their numbers, must be viewed as a major breakthrough. It is this very emphasis on the existence of individual recruits, with defined growth and mortality

schedules, which made the normal science possible that is implied in item (3): estimating the parameters of (2), i.e. work with Equation 1.

These parameters consists of three sets.

- (a) *Growth parameters*: W_∞ , K , t_0 of the von Bertalanffy growth function (VBGF), of the form:

$$W_t = W_\infty \{1 - \exp[-K(t - t_0)]\}^3 \quad (2)$$

where W_t is the (mean) predicted weight at age t , W_∞ the (mean) weight the fish would reach if they were to grow indefinitely, K the rate (of dimension $1/t$) at which W_∞ is approached, and t_0 is the (predicted) 'age' at which $W = 0$. Equation 2 assumes an underlying length-weight relationship of the form:

$$W = aL^b \quad (3)$$

with $b = 3$, implying isometry.

- (b) *Mortality rates*: M , F and Z , expressing natural, fishing and total mortality, respectively, through:

$$N_2 = N_1 \cdot \exp[-F + M(t_2 - t_1)] \quad (4)$$

where N_1 is an initial number of individuals, at time t_1 , and N_2 is the predicted number of surviving individuals at time t_2 , given the mortality $Z = M + F$.

- (c) *Fishery-related parameters*: t_r , t_c and t_{\max} . The parameters t_r , t_c and t_{\max} , along with F above, link the behaviour of the fishers to the life history of an exploited population:

- t_r , the mean age at recruitment in the fishing ground, is both biological, determined by the migration patterns of the fish, and technical, i.e. determined by what part of the stock is exploited – which itself defines what a recruit is;
- t_c is in principle defined by the mesh size, with fish younger than t_c escaping through the mesh of the gear, while those that are older, and hence larger, are retained by the gear; and
- t_{\max} is the age of last effective contribution to the fishery, and is either determined by biology (as the maximum age commonly reached by the fish, i.e. their longevity), or by the behaviour of the fleet, which may e.g. operate only in shallow waters, where the young fish occur, which then reach their t_{\max} when they migrate offshore.

The immediate aftermath of the paradigmatic presentation of Equation 1 saw several suggestions to reduce this menagerie of parameters. Of these, two proposals were particularly interesting in that their implementation in the form of tables (printed by mainframe computers) made Y/R analysis potentially available in developing countries, and other areas then without access to electronic data processing.

Jones (1957) proposed to set $t_{\max} = \infty$, and to use the incomplete β -function to circumvent the requirement that $b = 3$ in Equation 2. This leads to:

$$Y/R = F/K \cdot (\exp(Zr_1 - Mr_2) \cdot W_\infty \{\beta[X, P, Q]\}) \quad (5)$$

where r_1 , r_2 are defined as above; $X = \exp(Kr_1)$; $P = Z/K$; $Q = b + 1$ (with b being the exponent in Equation 3); and β = the symbol for the incomplete beta function (Abramowitz and Stegun, 1965). Tables of the incomplete beta function, prepared by

Willimovsky and Wicklund (1963), allowed rapid computation of Y/R for various values of X, and P, and Q values ranging from 3.5 to 4.5. However, neither they, nor the calculator program directly implementing Equation 5 (in Pauly, 1984) appear to have been used much, in the tropics or elsewhere.

A more successful simplification of Equation 1 was that of Beverton and Holt (1966), which used M/K instead of M and K (see Holt, this vol.), went back to assuming isometry (i.e. $b = 3$), set $t_r = 0$, $t_{max} = \infty$, and used L_c ($= L_{50}$ in Fig. 2) as the length corresponding to t_c . Defining $c = L_c/L_\infty$ and $E = F/Z$, they then showed that relative yield per recruit (Y'/R) could be computed from:

$$Y'/R = E(1 - c)^{M/K} \cdot \frac{3(1 - c)}{1 + \frac{(1 - E)}{(M/K)}} + \frac{3(1 - c)^2}{1 + \frac{2(1 - E)}{(M/K)}} - \frac{(1 - c)^3}{1 + \frac{3(1 - E)}{(M/K)}}. \tag{6}$$

This, if need be, can be related to Equation 1 by:

$$Y/R = Y'/R \cdot W_\infty \cdot \exp[-M(t_r - t_0)]. \tag{7}$$

Because of its reduced number of parameters, computed values of Equation 6 could be presented in table form, for rows of E and columns of c ranging from 0 to 1. Each table pertained to a given value of M/K, from M/K = 0.25 to M/K = 5, spanning the

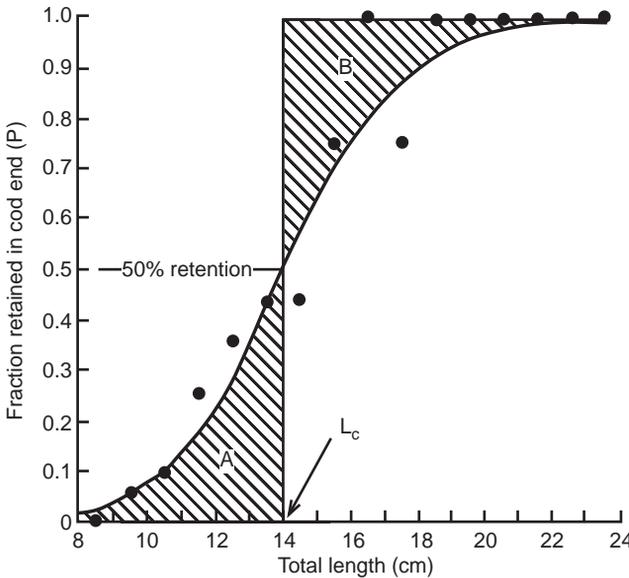


Fig. 2. Selection curve of slipmouth, *Leioognathus equulus*, caught in Mombassa harbour, Kenya, with 7.8 cm mesh nets (from Pauly, 1984). The selection range extends from 12 cm (L_{25}) to 16 cm (L_{75}); area A, representing fish caught at sizes below L_{50} ($= 14$ cm), equal area B, representing fish larger than L_{50} , but not caught. However, $A = B$ does not imply that Y/R is not affected by using L_{50} instead of the selection range; as the arrow of time is irreversible, fish caught at small sizes are not 'compensated for' (Silvestre *et al.*, 1991).

observed range of this ratio (Beverton and Holt, 1959), now called “Beverton and Holt invariant” (Charnov, 1993), although it does vary with temperature (Pauly, 1980a; Pauly and Soriano, 1986; Fig. 3).

This is the Y/R model as it stood in the 1960s, when the series of ‘Lowestoft courses’ ended that had begun in the 1950s. Gulland (1969) summarizes the concepts taught at these courses, along with the methods then available for:

- estimation of growth parameters from size-at-age data;
- re-expression of knowledge about relative age composition of caught fishes into estimates of total mortality (Z);
- estimation of M, notably from Z estimates in unfished stocks;
- re-expression of knowledge about fleet operations and of their interactions with resource species in form of estimates of fishing mortality (F), of gear selection curves, of mean length at first capture (L_c), and of mean age at recruitment (t_r) and at first capture (t_c);
- computation and interpretation of Y/R curves.

This process, which historians would call the ‘reception’ of B&H, was essentially completed by the late 1960s, at least in the countries surrounding the North Atlantic (see e.g. Hempel and Sarhage, 1961, for the example of Germany), and a few other countries where the existing scientific expertise and fisheries statistics, combined with the fact that coldwater fish could straightforwardly be aged by reading annuli on otoliths, scales or other hard parts, had allowed a direct adoption of B&H’s approach. These conditions did not exist in the tropics, and hence the need for an adaptation, or more precisely, a ‘tropicalization’ of this approach, our main topic, now properly introduced.

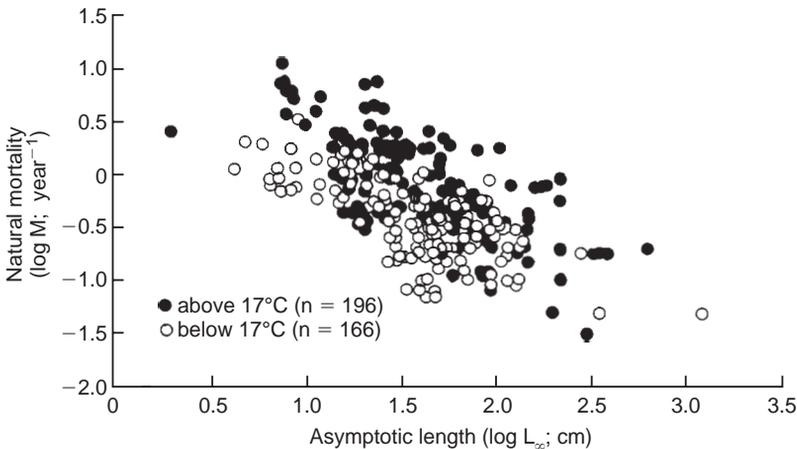


Fig. 3. Illustrating the inverse relationship between M and L_∞ in fish, and the effect of temperature on M (note that high values of M tend to originate from warmer waters and conversely for low values). Based on data in FishBase 97 (Froese and Pauly, 1997), which documents the source and estimation method of each value in this plot.

TROPICAL CONDITIONS, SLIGHTLY EXAGGERATED

As described in Longhurst and Pauly (1987), the ecology of tropical oceans is extremely varied, with desert-like expanses in their central gyres, and coral reefs, the aquatic equivalent of tropical rain forests, or mangrove-lined muddy estuaries at their edges. The social and cultural conditions of the (mostly) developing countries that have tropical shores and fisheries are extremely varied as well, thus implying a great variability in the reception of B&H. As this cannot be accommodated in the space available here, we shall use 'Gondwana' as 'type' for tropical countries, well aware that slipping from the typical into the stereotypical is all too easy.

The inshore waters of Gondwana contain a multitude of fish species; until the 1970s, the only systematic account of their diversity was buried, however, in the three volumes of *The Ichthyology of Gondwana*, published in 1897, during the colonial period, and of which only one, slowly decaying set exists in the country (see also Maclean, 1994; Vakily and Pedro, 1994). The University Library's only fisheries-related journal is a 1946–1957 run of *California Fish and Game*, donated by a previous 'Learning for Freedom' campaign. Fortunately, the Food and Agriculture Organization of the United Nation (FAO) has produced Identification Sheets for most of the '*Commercial Fishes of Gondwana and Adjacent Waters*' (Fischer, 1976). These have enabled the launching of a UNDP-supported project to establish a new country-wide system of catch statistics, ultimately to quantify and identify the multispecies catch marketed at the many isolated landing places of the small-scale fisheries (Pauly, 1997a), and by the trawler fleet operating from the capital, Gondwana City. The Gondwana Fisheries Department has one single PhD, whose hard-won degree was based on a thesis on the migration of Northern salmon, and who is now the counterpart of the UNDP project leader, a Scandinavian specialised in fish nutrition. None of the fish in the country has ever been aged; indeed when confronted with the possibility of ageing tropical fish by counting daily structures in their otoliths (Pannella, 1971), a senior professor of biology at the University of Gondwana City wondered aloud "how could we ever determine the age in days of our fish, if we can't even estimate their age in years" (an authentic quote). Also, it is widely believed that length-frequency based methods for estimating growth will not work in Gondwana, because "tropical fish spawn throughout the year, and hence cohorts cannot be followed" (another authentic quote). How, under these conditions, is one to apply B&H's theory to even a single species?

Parameter estimation for tropical Y/R analyses

COMPARATIVE STUDIES OF FISH GROWTH

Beverton and Holt (1957) adopted the VBGF as a mathematical device for summarizing size-at-age data in the form of three parameter estimates (W_{∞} , K , t_0) without their assimilating the physiological theory behind that equation (Bertalanffy, 1934, 1938, 1951). This is evident when they state (on p. 32) what they believed to be one of the corollaries of that theory: "Following general physiological concepts, Bertalanffy suggests that the rate of anabolism could be assumed proportional to the resorption rate of nutritive material and therefore proportional to the magnitude of the resorbing surfaces..." However, Bertalanffy's theory, which did assume that a surface limited the growth of fish, does not at all state, nor even imply, that the limiting surface of anabolism should be the resorbing surface of their intestines. Rather, this surface is related to the

metabolic rate of fish (Bertalanffy, 1951, 1964). Assuming this surface to be the gill area (Pauly, 1981) leads to a four-parameter, 'generalized' version of the VBGF, similar in form to the equations of Richards (1959) and of Taylor (1962), occasionally used by fishery scientists. Though the generalized VBGF was then shown to be applicable to all growth-related models commonly used in fisheries science, and implemented in a series of calculator programs (Pauly, 1984), its major use may have been to help identify the conditions under which the three-parameter version can be expected to faithfully reproduce observed growth patterns, and to allow extrapolation beyond the range of observed data.

Particularly, this enabled confirmation, for a large number of species, of the rule of thumb earlier posited by Taylor (1958) and Beverton (1963), that the maximal length of fish (L_{\max}), whether observed or predicted from an extreme value approach (Formacion *et al.*, 1991), should be roughly similar to asymptotic size in the length-based form of the VBGF, viz.

$$L_t = L_{\infty} \{1 - \exp[-K(t - t_0)]\}. \quad (7)$$

This reinterpretation of L_{∞} , though seemingly trivial, means that the L_{\max} values of species in the *Ichthyology of Gondwana* can serve as guides to likely values of asymptotic length, especially in cases when the fisheries lands only small specimens, either because it operates only inshore, or because, as is increasingly the case, it is so intensive that it has made large specimens rare (Pauly *et al.*, 1998). It also means that growth studies consist essentially of optimizing K , a problem far simpler than the simultaneous estimation of L_{∞} and K (Fig. 4).

Another implication of the generalization of Bertalanffy's growth theory is that it provides, via the similarity of gill surface areas among related species (Hughes and Morgan, 1973; De Jager and Dekkers, 1975; Palzenberger and Pohla, 1992), an explanation for the surprising predictability of growth patterns in fish. Thus, on auximetric plots (from the Greek for 'grow' and 'measure'), i.e. plots of $\log(K)$ vs. $\log(\text{asymptotic size})$, clear patterns emerge, whether one deals with all fish, or any subgroup thereof (Fig. 5). Indeed, the within-species similarities are so strong that a growth performance index could be proposed (Pauly, 1980b; Pauly and Munro, 1984), of the form:

$$\Phi' = \log(K) + 2 \log(L_{\infty}) \quad (8)$$

which is now widely used to estimate K given an estimate of Φ' (from parameter sets in other areas of the same or very closely related species), and an estimate of L_{∞} derived from L_{\max} (see contributions in Venema *et al.*, 1988).

In support of this approach, the FishBase CD-ROM (Froese and Pauly, 1997) contains well over 4000 independently estimated sets of growth parameters (Fig. 5), for over 1000 species of fish important to humans, thus achieving a goal earlier sought by Banerji and Krishnan (1973). This makes it possible to quickly obtain estimates of the growth parameters required for at least preliminary Y/R analyses of the fish resources of Gondwana.

GROWTH FROM LENGTH-FREQUENCY DATA

Some colleagues will never accept to base their assessments on growth parameters derived from comparative studies, and prefer to always obtain their own growth

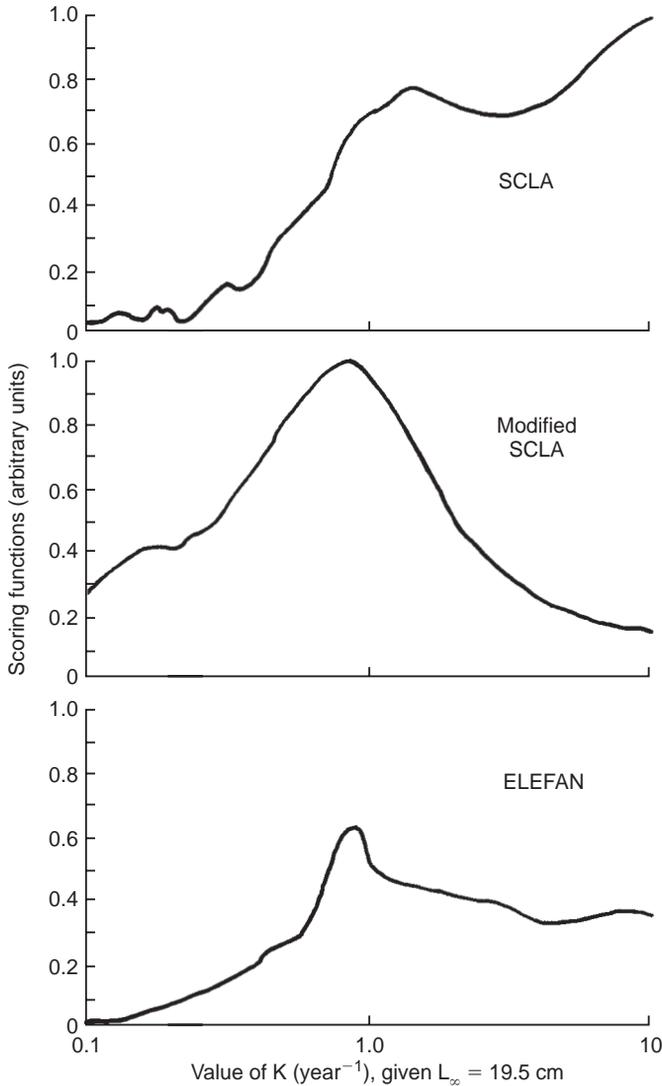


Fig. 4. Goodness of fit of different growth curves for *Upeneus moluccensis* in Ragay Gulf, Philippines, expressed by different values of K (given $L_{\infty} = 19.5$ cm) to a length-frequency data set distributed with the FiSAT software (Gayanilo *et al.*, 1996). Note that ELEFAN and SCLA, as modified by Pauly and Arreguin-Sanchez (1995) from Shepherd (1987), give similar results ($K \approx 0.9$ year⁻¹), although they optimize different functions. Note also that the shapes of the curves allow rough inferences on the precision of the K estimate (see text).

parameter estimates. A wide panoply of methods are available for this, at least in principle (tagging/recapture data, examination of daily rings on otoliths, etc.). Only two of these, however, are used routinely in tropical settings: reading of annual/seasonal rings on otoliths (but see Beamish and McFarlane, 1983) and analysis of length-frequency (L/F) data (Powell, 1979; contributions in Pauly and Morgan, 1987, notably Mathews, 1987; review, Gallucci *et al.*, 1996). As L/F data have played an enormous role in the

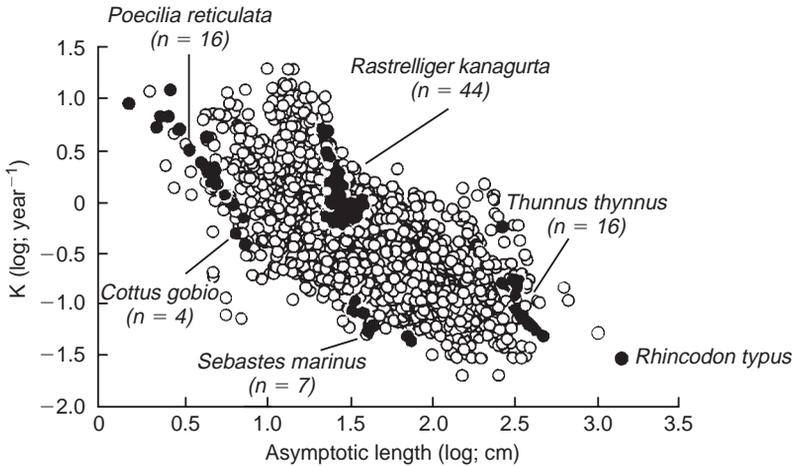


Fig. 5. Auximetric plot of all pairs (open circles) of the VBGF parameters L_{∞} and K in FishBase 97 (Froese and Pauly, 1997). Note overall shape, defining the growth space inhabited by fishes, ranging over three orders of magnitude, from $L_{\infty} = 1.5$ cm in the guppy *Poecilia reticulata* to 14 m in the whale shark *Rhincodon typus*. The growth space inhabited by the former, and four other species of fish is also defined (filled circles). The fishes with the largest gills (data in Pauly, 1981) are furthest away from the origin, as should occur if growth is limited by oxygen supply (see text).

tropicalization of B&H, it is their analysis that will be emphasized here. However, the general story having been told earlier (Pauly, 1987, 1994), and in French (Pauly, 1997b), we shall concentrate on what I think is the key problem of such analyses, with us since Petersen (1891, 1892) started this line of inquiry. This problem is that for safe inferences on growth, one should be able to trace the modes that represent individual cohorts all the way back to the size at recruitment, i.e. one must know, or be able to reliably assume, the time at which each recruitment pulse occurred (Fig. 6). Not considering this is the reason why the flamboyant D'Arcy Thompson, an early advocate of L/F analysis, misinterpreted data on Norwegian herring, thus making suspect a method previously used with great success even in the North Sea (Fulton, 1904), from which it was henceforth banned (Went, 1972).

The revival of L/F-based methods for analysis of growth thus occurred in the proverbial 'other areas' (Troadec *et al.*, 1980), through the efforts of scientists who, while "deprived of holy size-at-age data", were not "only armed with a thermometer" (Hilborn, 1992). Indeed, the key feature of this revival is that it was based on microcomputers (TRS-80, Apple II, Apricot, etc.), allowing quick comparison, given an optimization criterion, of the many alternative growth curves that can be fitted to a set of L/F data (Fig. 4).

The optimization criterion itself varied between authors: some chose rigorous least-square or maximum likelihood criteria, while others used non-parametric measures. Thus, LGTFRQ (Sparre, 1987), MULTIFAN (Fournier *et al.*, 1990), and CASA (Sullivan *et al.*, 1990) use rigorous statistical criteria for estimating growth (and related) parameters from L/F data, but are rarely used in the tropics. On the other hand, ELEFAN and SLCA of Pauly and David (1980), and Shepherd (1987), respectively, are

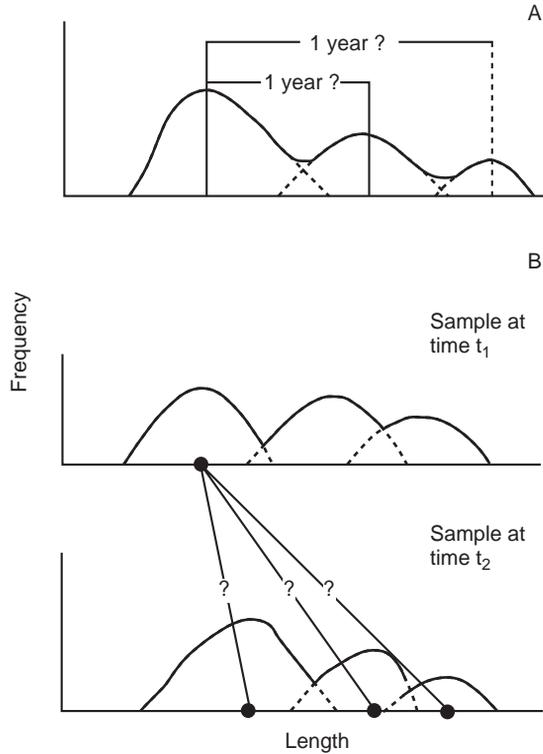


Fig. 6. Illustrating the basic problem of length-frequency analysis: the need to assign relative ages to the modes representing cohorts. (A) The Petersen method *sensu stricto*, wherein a relative age is assigned to the successive modes of a single sample. In the case, the uncertainty stems from not knowing the frequency of major recruitment pulses, which may be biannual in the tropics. (B) The situation where the time separating modes is known (because they represent samples taken at successive periods), but the links between the modes, representing growth, are not known. The solution to this quandary is to fit a large number of growth curves to the entire set of modes, and to compare their parameters in terms of how well they explain the position of all modes in the data set. In this case, the answer to (A) will have to be compatible with the answer to (B) and vice versa. A number of computer models now exist which utilize this logic for curve fitting (see text).

widely used, in spite of their being only ‘weakly parametric.’ (The phrase is from Shepherd, 1987, and refers to the fact that SLCA, like ELEFAN, can output response surfaces whose shapes can be interpreted as if they were those of a parametric model; Fig. 4.)

The reason for this, besides the fact that they are more transparent, and thus easier to understand, is that these packages have been maintained and updated, and made widely available at very low cost or free of charge (Pauly *et al.*, 1995). This particularly applies to the FiSAT software package distributed by FAO, and used for its Danish-funded series of tropical fish stock assessment courses, and which incorporates ELEFAN and SCLA as routines of a comprehensive package for L/F analysis (Gayanilo *et al.*, 1996; Gayanilo and Pauly, 1998).

SEASONAL GROWTH OF TROPICAL FISHES

One paradoxical result of the tropicalization of B&H was the need to deal explicitly with seasonal growth oscillations in the growth of fish, although these oscillations have low amplitudes in areas of low latitude (Fig. 7). The reason for this is that seasonal growth oscillations in large, high-latitude fishes are usually small relative to overall sizes, thus allowing interpolation of growth between annuli. On the other hand, analysis of L/F data is usually based on samples collected at monthly or similarly short intervals, and the growth oscillations tend to be large relative to the smaller body sizes of the investigated fishes or invertebrates. Thus if seasonal oscillations occur, they will affect the fit of a growth curve to the L/F data, whatever the criterion chosen to express the fit (Fig. 7).

The growth curve initially incorporated in ELEFAN, and later in MULTIFAN and LGTFRQ, was adapted from Pitcher and MacDonald (1973) by Pauly and Gaschütz (1979). It combined a sine curve with the VBGF, and had the important feature that one of its parameters (C) was proportional to the amplitude of the seasonal growth oscillations, thus allowing comparisons of the seasonal oscillations in various stocks of fishes and invertebrates. The powerful generalization which emerged from these (Fig. 8) provides a further link between growth phenomena and the underlying physiology of gill-breathing organisms.

In the meantime, the equation of Pauly and Gaschütz (1979) has been shown to produce biased estimates of t_0 when fitted to length-at-age data, and it was thus replaced, in FISAT, by variants proposed by Appeldoorn (1987) and Somers (1988). The latter version has the form

$$L_t = L_\infty \{1 - \exp[-K(t - t_0) + S_{ts} - S_{t0}]\} \quad (9)$$

where $S_{ts} = (CK/2\pi) \cdot \sin[2\pi(t - t_s)]$, $S_{t0} = (CK/2\pi) \cdot \sin[2\pi(t - t_0)]$, and the other parameters are as defined above.

ESTIMATION OF TOTAL MORTALITY

Two basic techniques for estimating total mortality were available to the participants of the above-mentioned Lowestoft courses: mean lengths and catch curves (some other techniques, summarized in Ricker, 1958, were also available, but are of only historical interest – Smith, 1994). The estimation of Z from mean length is based on a simple equation derived by Beverton and Holt (1956), of the form:

$$Z = K \cdot (L_\infty - \bar{L}) / (\bar{L} - L') \quad (10)$$

where Z , K and L_∞ are as defined above, and \bar{L} is the mean length of the fish, measured from the cutoff length L' , i.e. the length at which the fish are assumed to be fully recruited and selected. Thus all one need here to estimate Z are growth parameters, and an L/F sample representative of an equilibrium population (\bar{L} and L' are estimated from the sample itself, see below). This equation has not been used much in temperate areas, probably because of the availability of catch-at-age data from which catch curves could be constructed.

Ricker (1975) declared that this [and related] “formulae have been little used, and it seems unnecessary to repeat the synopsis given by Ricker (1958)”. Yet several applications to tropical stocks existed in the early 1970s, notably by LeGuen (1971) and by J.L. Munro and associates who, from 1969 to 1973, applied this model to a multitude of coral reef fishes (Munro, 1983).

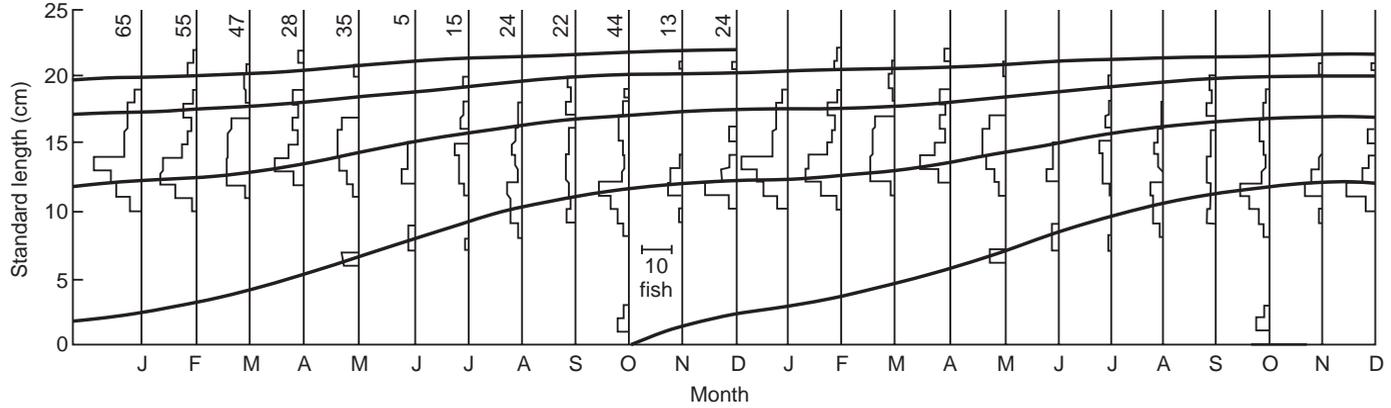


Fig. 7. Seasonal growth of checkered puffer, *Sphoeroides testudineus*, based on L/F data sampled by Targett (1979) in Biscayne Bay, Florida (from Pauly and Ingles, 1981). The growth curve, fitted with ELEFAN, has the parameters $SL_{\infty} = 25$ cm ($TL_{\infty} = 30$), $K = 0.51$ year⁻¹, and $C = 0.7$, a value corresponding to those reported from other subtropical areas (Fig. 8).

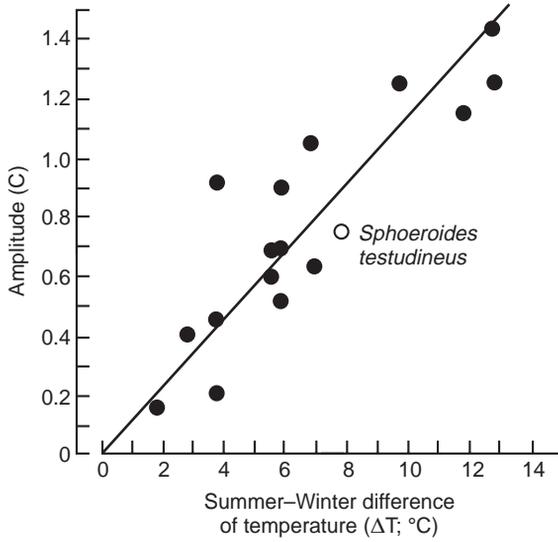


Fig. 8. Relationship between the amplitude of seasonal growth oscillations in various fishes (including *S. testudineus*, from Fig. 7) and invertebrates, expressed by the parameter C of a seasonalized version of the VBGF (Equation 9), and the difference between the mean monthly summer and winter temperatures of their habitat (from Pauly, 1990, with updates from FishBase 97 – Froese and Pauly, 1997). The range of temperature corresponding to C = 1, within which winter growth is reduced but not halted, is about 10 °C, and may define the range within which the enzymes of aquatic poikilotherms can function, if at reduced rates. Values of C > 1 describe periods of growth stagnation, discussed in Pauly *et al.*, 1992).

Ehrhardt and Ault (1992) pointed out that the assumption $t_{max} = \infty$, required in the derivation of Equation 10, is not realistic. Indeed, t_{max} changes with mortality (Hoenig, 1983). Therefore, they proposed as an alternative:

$$[(L_{\infty} - L_{max})/(\bar{L} - L')]^{Z/K} = A_{(L')}/A_{(L_{max})} \tag{11}$$

where $A_{(L')} = Z(L' - \bar{L}) + K(L_{\infty} - \bar{L})$, $A_{(L_{max})} = Z(L_{max} - \bar{L}) + K(L_{\infty} - \bar{L})$, and whose other parameters are defined as above. As this does not have a direct solution, an iterative solution is provided in FiSAT, which includes this model along with Equation 10.

There are other variants of Equation 10; probably the most interesting is that of Wetherall (1986), of the form:

$$\bar{L}_i = a + bL'_i \tag{12}$$

where \bar{L}_i and L'_i represent successive values of the mean and cutoff lengths and which has as solution $Z/K = b/(1 - b)$, and $L_{\infty} = a/(1 - b)$. Thus, L_{∞} is a growth parameter that can be estimated in the absence of growth data, as suggested above, and shown in Fig. 9.

Once L_{∞} has been estimated, it is straightforward to estimate K from growth increment data, as obtained from a tagging/recapture study (e.g. Randall, 1962), or by following the progression of a few clear peaks in a L/F data set otherwise difficult to analyse. Given K, one can then calculate Z from Z/K (see contributions in Venema *et*

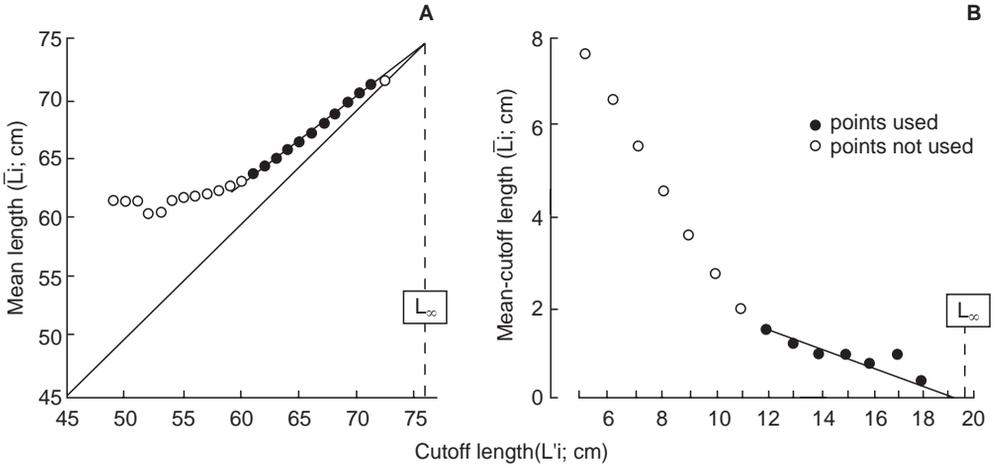


Fig. 9. Estimation of L_{∞} and Z/K using: (A) original Wetherall plot, applied to L/F data on *Sarda chiliensis* off Peru ($FL_{\infty} = 76$ cm, $Z/K = 4.34$; from Pauly *et al.*, 1987); and (B), modified version of the Wetherall plot, applied to L/F data on *Upeneus moluccensis* from Ragay Gulf, Philippines ($TL_{\infty} = 19.5$ cm; $Z/K = 3.81$; see Fig. 4 for L/F data source).

al., 1988, or Posada and Appeldoorn, 1996). Indeed, the key remaining issue is the representativeness of one's data, a problem independent of latitude.

A catch curve is a plot of $\ln(\text{catch at age})$ against age, whose slope, with sign changed, is an estimate of Z . This assumes that recruitment has varied little, and only randomly during the period covered by the cohorts included in the analysis (Ricker, 1975).

Given the vast amount of historic L/F data usually available for study in tropical developing countries (often the result of projects such as the one in Gondwana, mentioned above), it is tempting to construct catch curves using length instead of age, even in fishes that have been aged. And indeed, it can be done, once account is taken of two biasing factors, one obvious, the other less so.

The obvious factor is that, the growth in length of fish being highly non-linear, fish from a number of cohorts tend to 'pile', or 'stack up' (van Sickle, 1977) in the larger length classes, representing old fishes. Adjusting for this is straightforward, and one way of doing it consists of dividing the numbers in each length class by the time (Δt) needed by the fish to grow through that length class, estimated from:

$$\Delta t_i = (-1/K) \cdot \ln[(L - L_{i2}) / (L - L_{i1})] \tag{13}$$

where, given the VBGF, L_{i1} and L_{i2} are the lower and upper limits, respectively, of length class i , and all other parameters are defined as previously (Pauly, 1984).

Thus, a length-converted catch curve can be constructed with, and Z estimated from, the slope of the descending, right arm of a series of points defined by:

$$\ln(N_i / \Delta t_i) = a + b \cdot t_i' \tag{14}$$

where t_i' is the age corresponding to the midpoint of length class i , itself estimated by inverting the VBGF (Fig. 10).

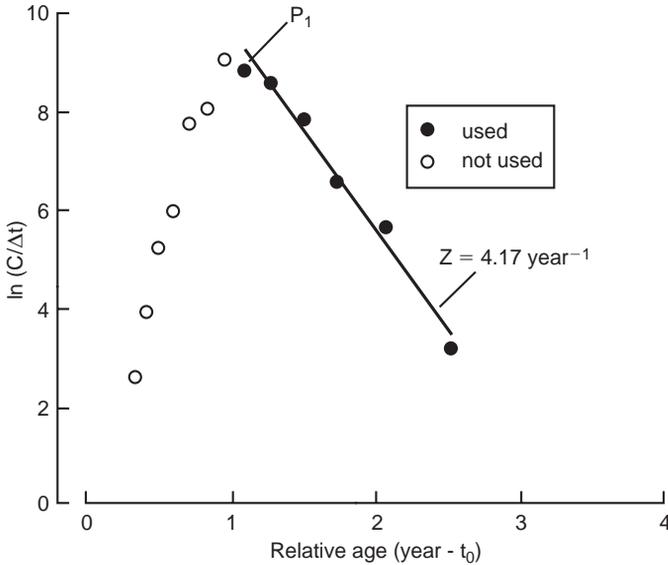


Fig. 10. Example of a length-converted catch curve for *Upeneus moluccensis* from Ragay Gulf, Philippines ($L_{\infty} = 19.5$ cm and $K = 0.9$ year $^{-1}$). The first point to be included in the estimation of Z (P_1) represents the length class of which L' (in Equation 10) is the lower limit.

Detailed analysis of the derivation of Equation 14, and comparisons with alternative formulations (Pauly, 1984), as well as simulations (Hampton and Majkowsky, 1987; Sparre, 1990; Isaac, 1990) suggest that this model is free of bias, given: (a) representative L/F samples upon which to base the analysis; (b) little growth variability between individuals; and (c) either a long life span, or no seasonal growth oscillations.

Item (c), discovered by Sparre (1990), was remedied through the development of a new form of length-structured catch curve which explicitly accounts for seasonal growth (Pauly, 1990; Fig. 11).

Estimates of Z obtained by any of the above methods can be used for further analyses, e.g. for plots of Z against effort (f), with an estimate of M being obtained from the intercept with the ordinate, a classical method first applied, in the tropics, to the now extinct population of '*Tilapia esculenta*' in Lake Victoria (Garrod, 1963). (This work was, indeed, so early in applying B&H's approach to a tropical fishery that it had no conceptual or methodological follow up, a situation reminiscent of what happened earlier to the brilliant work of F.I. Baranov; see above.)

ESTIMATION OF NATURAL MORTALITY

The instantaneous rates implied in Equation 4 required quite a while to be assimilated by fisheries scientists, who had long used per cent mortalities, seemingly more intuitive, but ultimately misleading (how many times higher is a annual mortality of 99.95% than one of 99.99%?). (Interestingly, aquaculturists still have not made their transition to instantaneous rates: Hopkins, 1992.)

To fully assimilate these new rates, fisheries scientists needed to get a 'feel' for the values they were likely to encounter, and this was provided by Beverton and Holt

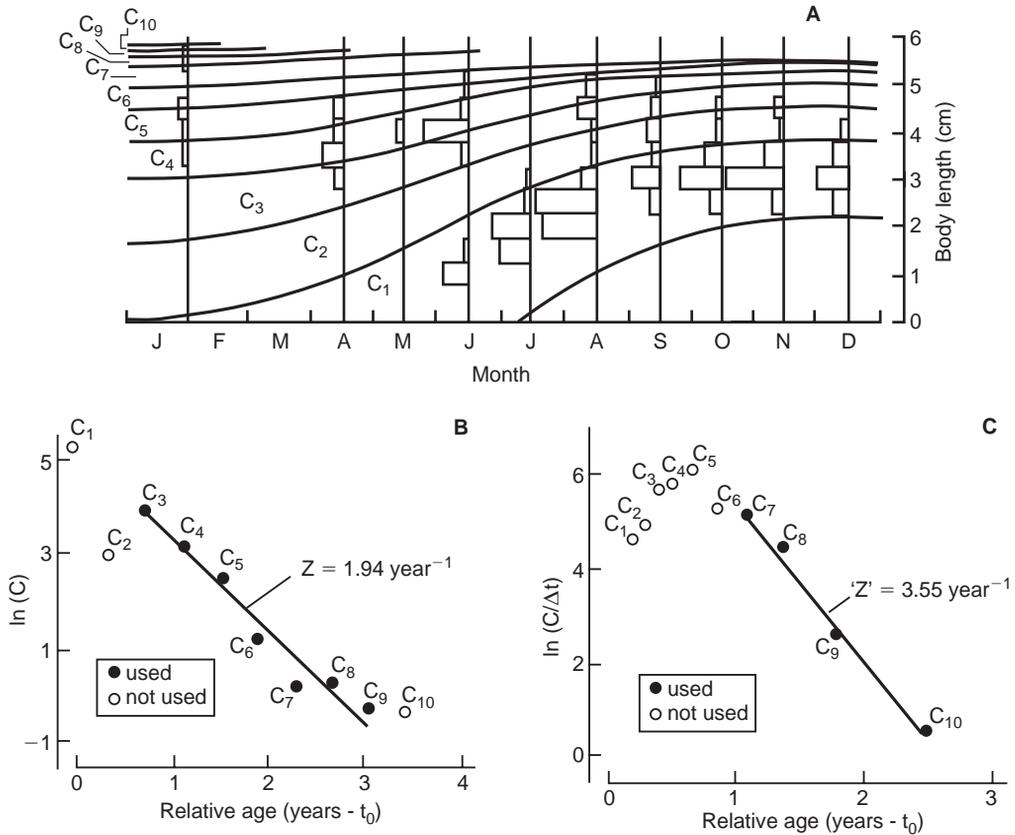


Fig. 11. Schematic representation of method for construction of length-converted catch curves accounting for seasonality. (A) The first step uses the parameters of a seasonally oscillating growth curve to identify a number of (pseudo) cohorts, i.e. fish between two successive growth curves; the next step is adding fish belonging to different samples, but to the same (pseudo) cohort to obtain successive catches (C_j). (B) Construction of catch curve as a plot of $\ln(C_i)$ vs. relative ages, and estimation of Z from straight descending arm. (C) Standard length-converted catch curve, also based on data in (A), but not accounting for seasonal growth. Note overestimation of Z (from Pauly, 1990).

(1959), which also showed how to estimate M in little-studied stocks. As the basis for this other classic paper, B&H had assembled estimates of M covering a wide range of fish species, and calculated the corresponding pairs of growth parameters (L_∞ and K) – a feat in itself, given the tediousness of such calculations at that time (see Holt, this vol.). They then went on to show that in various groups of fish, M and K were strongly related, so much indeed that M can be predicted from K (Fig. 12; Ralston, 1987).

I extended on this work and demonstrated, based on a larger data set, including many estimates from the tropics, that besides K , asymptotic size (L_∞ or W_∞) and mean environmental temperature correlated with M , and hence could be used for estimating natural mortality (Fig. 3; Pauly, 1980a).

The empirical equations resulting from them have been widely used in the tropics and elsewhere, to parametrize Y/R or related analyses. Presumably, this paper did for

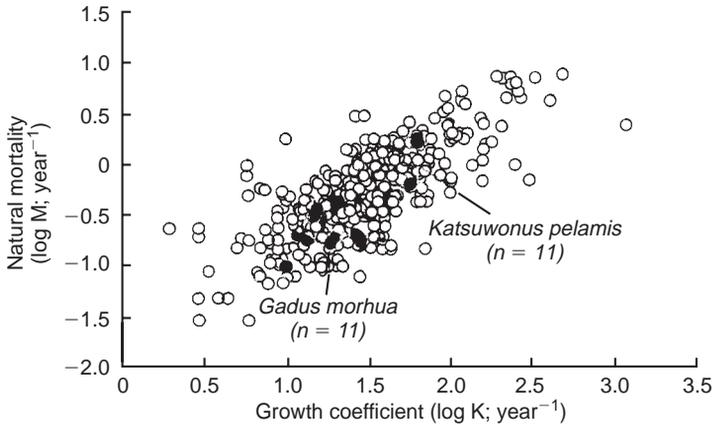


Fig. 12. Plot of log M vs. log K in all fish populations for which both estimates are available (open circles). The (full) dots for *Gadus morhua* show that in this species, M is not always 0.2 year^{-1} , while the dots for *Katsuwonus pelamis* show where a tropical tuna fits on such a plot (from FishBase 97 – Froese and Pauly, 1997, building on a similar plot in Beverton and Holt, 1959).

colleagues working on tropical fishes with B&H's paper of 1959 had done a generation earlier for colleagues working on North Atlantic fishes: it had given them a 'feel' for the range of M values they could expect. Further, with estimates of M available for any fish whose growth parameters were known, it became possible to quickly obtain, by subtraction from Z, at least preliminary estimates of fishing mortality (F), and thence of catchability (q), given effort (f), and the definition $F = q \cdot f$, important in B&H's approach. For example, an exercise of this sort, involving six demersal species, allowed the estimation of catchability in Gulf of Thailand trawlers, and of the average escapement from the path of their gear (Pauly, 1980b).

This work, it must be mentioned here, did not consider the uncertainties inherent in such analyses, i.e. the propagation of errors that occurs when approximate growth parameters are used to infer an uncertain M value that is then subtracted from a biased estimate of Z, etc. In retrospect, it is obvious that too much attention went into estimation of point estimates, while the variance was neglected (see Holt, this vol., and Hilborn, this vol.).

Moreover, several of the assumptions used in this approach turned out not to apply. This is particularly true for q, which has since been shown to be a very complex parameter (Arreguin-Sanchez, 1996), its value changing with, among other things, the biomass of the fish that are being exploited (McCall, 1976; Csirke, 1989). Some spectacular fisheries collapses may be in part attributable to the implications of this feature of q (Walters and Maguire, 1996), which is seen as an 'anomaly', when viewed from the perspective of B&H's theory. Another anomaly is that natural mortality is not constant: it declines in the course of the ontogeny of fishes (Caddy, 1991, 1996). This effect, which has a strong impact on the results of Y/R analyses is, however, relatively easy to accommodate within the context of B&H's theory (Moreau *et al.*, 1984; Pauly, 1997b). On the other hand, natural mortality also varies with predator abundances (Munro, 1982), and this is the Achilles' heel of the theory, and the subtheme with which we shall deal last, following a brief discussion of gear selection.

PROBLEMS OF GEAR SELECTION

That the concepts related to gear selection would require as much tropicalizing as did growth and mortality came as a surprise, because at first it seemed as though all that was involved here was to linearly scale things down, from the large fish and relatively large meshes in temperate waters to the much smaller fishes occurring, and the often absurdly small meshes used, for example, in South East Asia.

However, most trawl-caught fish in South East Asia are small relative to their selection range, i.e. the range between the length at which 25% of the fish in the path of the trawl are retained by the gear (L_{25}) and the length at which 75% are retained (L_{75}). This implies that the ‘knife edge’ selection of B&H, occurring in one step (at L_{50}), assumes symmetry where none exists, because the arrow of time, and the deaths that go along with it, cannot be reversed (Fig. 2).

The implications of this seemingly minor feature of an unglamorous parameter of Equation 1 are profound – at least if one is to believe the results of Y/R analyses. Thus, using a version of Equation 6 which allows consideration of realistic selection ranges (Table 1; Pauly and Soriano, 1986) leads in small fish to curves whose maxima occur at a much lower fishing mortality than when knife-edge selection is assumed (Silvestre *et al.*, 1991). Also the misleading, high Y/R values predicted by Beverton and Holt’s yield tables for infinitely high level of fishing mortality (when $E = 1$, $F = \infty$; see Holt, this vol.) are replaced by zero values (Fig. 13).

In retrospect, it can be inferred from this that management advice for small tropical fish and shrimps based on the knife-edge assumption (e.g. as implied in Fig. 1) must have been systematically biased toward overoptimistic predictions of optimum fishing mortality, even within the single-species Y/R paradigm, and even when $F_{0.1}$ (Gulland and Boerema, 1973) was used as the reference point. This is also true when one considers utility-per-recruit (Die *et al.*, 1988) instead of Y/R.

A related conclusion is that B&H’s Y/R model cannot be used to justify, at least in the tropical settings for which it was proposed, the approximation $F_{max} \approx M$, which led to the famous ‘Gulland equation’, i.e.:

$$\text{Potential yield} = 0.5 \cdot M \cdot \text{Unexploited biomass} \tag{15}$$

(Gulland, 1971), already shown, if on different grounds, to overestimate potential yields (Beddington and Cooke, 1983).

These considerations take us again towards the limits of what normal science can do, into what Kuhn (1962) calls ‘anomalies’, i.e. findings not predicted by, or even undermining the paradigm that is being articulated. Anomalies increase when one tries

Table 1. Probabilities of capture for simulating the effects of increasing the selection range on relative yield per recruit ($L_{\infty} = 10$, $M/K = 2$)

	Length							
	1.0–1.9	2.0–2.9	3.0–3.9	4.0–4.9	5.0–5.9	6.0–6.9	7.0–7.9	8.0–8.9
Case 1	0	0	0	0	1	1	1	1
Case 2	0	0	0.1	0.3	0.7	0.9	1	1
Case 3	0	0.1	0.2	0.4	0.6	0.8	0.9	1

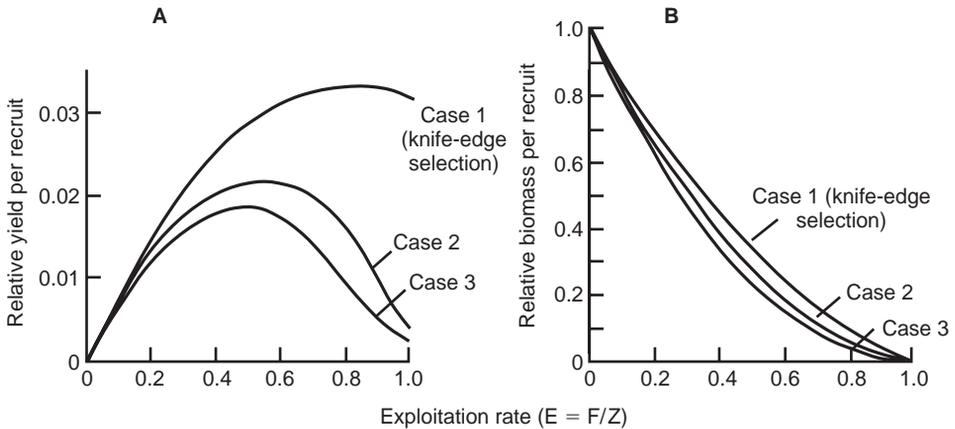


Fig. 13. Effect of an increasingly wide selection range on relative yield per recruit (A), and relative biomasses per recruit (B), as assessed through the data on Table 1, applied to Equation 7, and a modification thereof (in Pauly and Soriano, 1986). Note that the knife-edge assumption leads to overestimates of yields and of optimum fishing mortality [$F = M \cdot E(1 - E)$].

to implement the ultimate step in tropicalizing B&H's Y/R approach, i.e. when dealing with multispecies situations, our next and last topic.

Beyond single-species analyses

MULTISPECIES EXTENSIONS OF THE Y/R APPROACHES

While Beverton and Holt's Y/R approach is based on single-species concepts, it can be straightforwardly extended to cover an assemblage of species exploited by the same gear, if a few hard-to-swallow assumptions are made as to the constancy of recruitment and natural mortality.

Thus, provided one is willing to assume that relative recruitment among species remains constant over a wide range of fishing mortality, multispecies Y/R assessments can be performed by simply stacking single-species assessments on top of each other, using either yield/recruit or utility/recruit (see above) as common currency (Beverton and Holt, 1957, pp. 421–431).

This work is rather tedious, and few applications exist. Munro (1983; see above) presented the first application to the tropics. Another application, to demersal fishes in the Samar Sea, Philippines (Silvestre and Soriano, 1988; Fig. 14) is included among the contributions in Venema *et al.* (1988), which documents many of the applications of Beverton and Holt's theory that resulted from the above-mentioned FAO courses in tropical fish population dynamics.

Jointly, these studies illustrate a strong propensity of tropical demersal fisheries toward growth overfishing. Single-species Y/R studies show this for major commercial species, while the multispecies analyses confirmed B&H's observation (p. 425) that the fear of losing certain species (e.g. penaeid shrimps in most demersal fisheries of the tropics) precludes trawl operators from using the larger mesh that would benefit the fishery as a whole.

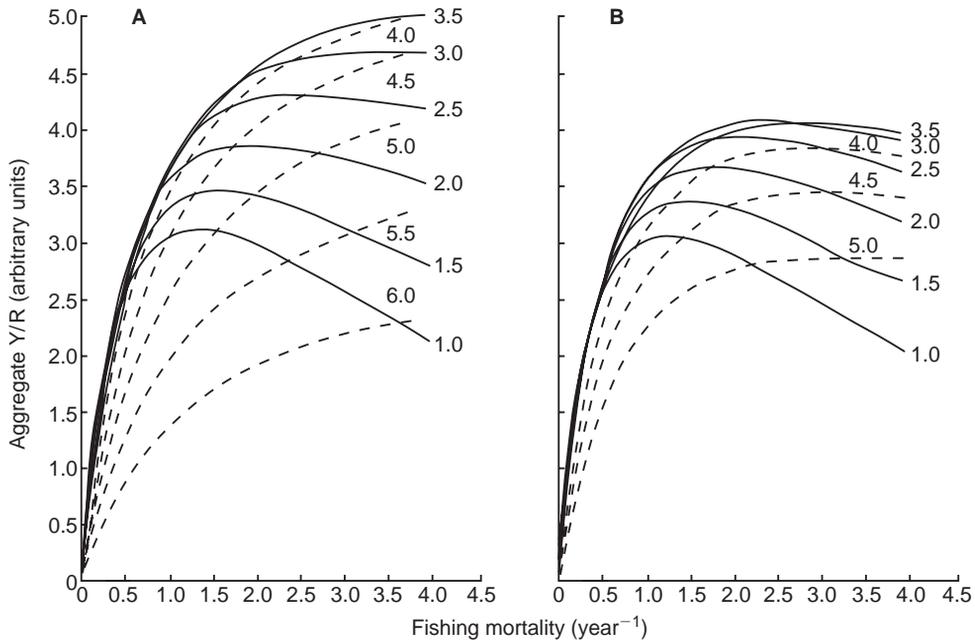


Fig. 14. Aggregate Y/R for 12 species of trawl-caught fishes of the Samar Sea, Philippines, illustrating differences between computations assuming knife-edge selection (A) and computations using realistic selection ogive (B). Mesh sizes range from 1.0 cm to the size that maximizes Y/R at high levels of fishing mortality ($F \approx 4 \text{ year}^{-1}$); broken curves refer to mesh sizes beyond that optimum (from Silvestre and Soriano, 1988).

The FiSAT software which emanated from the FAO courses includes a routine for performing multispecies Y/R, though based on an extension of the approach of Thompson and Bell (1934). This made it straightforward to consider utility/recruit and realistic selection ogives for up to 20 species exploited by four fleets (Gayanilo *et al.*, 1996).

The obvious limitation of this approach is that it assumes constant M values and fixed relative recruitment rates, assumptions that are unrealistic when an assemblage of species are exploited that feed on each other (Larkin and Gazey, 1982; Christensen, 1996; Walters *et al.*, 1997). These limitations also apply, evidently, to instances when Equation 15 is applied to a complex of species, as is still commonly done.

ECOSYSTEM APPROACHES DERIVED FROM BEVERTON & HOLT'S WORK

More dynamic approaches explicitly based on B&H involve the extremely complex North Sea model of Andersen and Ursin (1977) and its derivative, the multispecies virtual population analysis (MSVPA) model of the International Council for the Exploration of the Sea's Multispecies Working Group (ICES, 1989).

Following Pope and Yang Jiming (1987), Christensen (1995) developed and illustrated through an application to Lake Tanganyika a generic version of MSVPA for use in the tropics. However, it is too early to see if this will catch on.

On the other hand, mass-balance trophic models of aquatic ecosystems have shown their utility in the tropics (see contributions in Christensen and Pauly, 1993), as a tool for summarizing available knowledge on biomasses and trophic flows in exploited systems.

One of the uses of such models for fisheries management in an ecosystem context is that they allow partitioning of M among different predators. Results so far confirm the impression gained from MSVPA that the younger stages of commercial fishes experience much higher natural mortality rates than used in earlier, single species assessment (also a result of Andersen and Ursin, 1977).

Even more importantly, such mass-balance models can serve to parametrize dynamic simulation models of ecosystems, and thus make accessible to a wide range of practitioners, in the tropics and elsewhere, a tool that was earlier largely inaccessible (Andersen and Ursin, 1977; Larkin and Gazey, 1982).

In particular, it has become possible, using the Ecopath software, to quickly construct a mass-balance model of a representative state of any aquatic ecosystem (Christensen and Pauly, 1992), then, based on the resulting file, to run a dynamic simulation model of that same system, using the Ecosim software of Walters *et al.* (1997). Several tropical applications of this approach exist, and more are forthcoming. Those so far performed suggest that single-species analyses, by their very focus, mislead researchers and managers into neglecting the gear and trophic interactions which determine long-term yields and ecosystem health (Pauly *et al.*, 1998).

And here the cycle closes. As it happens, Ecosim incorporates key concepts from B&H: the representation of mortality, graduation flows between age groups, the food consumption and conversion, and the growth models are all adapted or ultimately derived from their classic (Walters *et al.*, 1997), which thus lives on even as we move beyond its original horizons.

Acknowledgements

This contribution summarizes much of what I did in the last two decades, and hence I could not but fail if I tried to list all the colleagues and friends from whom I have drawn inspiration. I would be remiss, however, if I failed to thank Professor G. Hempel, for all that he did for me while I was in Kiel; J.A. Gulland for his critical examination of my earlier work; S. Venema for the opportunity to test the resulting ideas at successive FAO courses; S.J. Holt for his encouragement; J. Hoenig for reading boring drafts; V. Christensen, R. Froese, A. Jarre-Teichmann, I. Tsukayama, J. Mendo, T.J. Pitcher and Carl Walters for their collaboration, and my (other) colleagues at ICLARM and UBC for their patience. Finally, I wish to express my respect for the inspiring professionalism of Ray Beverton, and my regret for having lost a friend.

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