

Chapitre 21**RECENT TRENDS IN COMPARATIVE CONCEPTS
AND METHODS IN FISHERIES ECOLOGY*****TENDANCES RÉCENTES DANS LES MÉTHODES
ET CONCEPTS COMPARATIFS EN ÉCOLOGIE
APPLIQUÉE AUX PECHES***

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1 - INTRODUCTION

In a field of science, such as fisheries ecology, there is always a dynamic tension between different ways of perceiving reality and of conducting scientific studies. Sometimes this tension exists within individuals, sometimes between individuals or between organized groups of workers and the institutions and agencies in which they work. Such diversity and tension appears to be beneficial in the long-term, but it is very frustrating in the short-term for the planner or administrator who would like a scientific consensus on practical matters.

Concern about such differences is of long standing. Recall the old arguments about pure versus applied science, academic vs. practical commitments, reductionistic vs. holistic approaches, mechanist vs. vitalist preconceptions, specialist vs. generalist careers, pre-eminence of abstractions over observations or vice versa, etc. A clear winner has not yet been declared with respect to any of these; these differences and others keep cropping up, in some form or other.

A number of fisheries researchers and groups have recently assessed aspects of the state of fisheries ecology. An apparent over emphasis on detailed reductionistic analysis related to simplistic abstractions has been criticized repeatedly and greater emphasis on a search for potentially useful but approximate empiric generalizations has been urged e.g., Chapman (1981), FAO (1978,1980) Kerr (1982), Pauly (1979b), Palohemio & Regier (1982) and Regier (1982)).

What seems to be at issue is the relative balance - not the ultimate utility of these complementary processes of conventional science. The question of the timeliness of useful advice looms large: approximate empiric information available within a month may be much more important, even in the long-term, than practically no information until a decade hence at which time a detailed and reliable general theory might be made available. This is why experts steeped in empiricism are usually called in to advise senior administrators instead of experts in the application of refined methods to the study of abstractions.

The emphasis in this chapter is on approximate empiric generalizations. This is not to imply that the contents are «unsophisticated». An argument can be made that the discovery of useful empiric generalizations is more demanding of perceptiveness and wit than is the reductionistic analysis of an extant concept. In fact, leading scientists sometimes progress in their careers from expert reductionist to expert empiricist, - as was the case with the late Frank Rigler of Canada.

2 - COMPARATIVE POPULATION DYNAMICS.

Hundreds of fish populations have been characterized in terms of such dynamic rates as recruitment, growth, natural mortality and fishing mortality. The motivation has usually been to determine some feature of the natural productivity of the population, such as maximum sustainable yield. It is seldom easy to estimate such rates, even if some simplifying assumptions are granted. Some features of population dynamics, such as the stock-recruitment relationship, have defied usefully precise description, except perhaps for a few well-studied populations.

2.1 - Pauly's contribution. A major advance toward mobilizing existing data on population dynamics and fostering more useful studies was achieved recently by Pauly (1979a, b). He apparently got his stimulus and direction from a careful study of Ludwig von Bertalanffy's writings on organismic systems. He focussed on parameters of growth and natural mortality, specifically the parameters L_{∞} , W_{∞} , K and t_0 of the von Bertalanffy growth formula (VBGF) and M of the usual exponential mortality function. He considered temperature of the habitat to be an important determinant of fish population dynamics and took mean annual water temperature, T , as a measure of it. He also considered aspects of the stock-recruitment relationship, but we will not deal further with that here, in the interest of brevity.

Pauly compared sets of such parameters for different populations of the same species, for different species of a genus, etc., eventually including most of the extant population data from marine species. He did not concern himself, in his early studies, with much of the large mass of data on freshwater fish populations, though he did some preliminary work with them.

Pauly found that the differences between sets of parameter values for different populations of the same species were on the whole less than the differences between parameter sets of different species within the same genus, etc. This is very reassuring, in that it implies that the variances of the estimates of the parameters are usually not so great as to render the estimates practically and conceptually useless. It is also reassuring in that such a nested hierarchy of differences could be expected from generalized study of evolutionary systematics of organisms.

For purposes of a grand generalization, necessarily of somewhat low precision for any particular population, Pauly found that

$$\log M = 0.1228 - 0.1912 \log L_{\infty} + 0.7485 \log K + 0.2391 \log T.$$

In this equation, the parameters L_{∞} , K and T can usually be estimated reliably far more easily for a population than can M . If one has available estimates of the first three, then one may use the equation to get a first approximation to M . For purposes of assessing the relative intensity of the fishery (see Pauly, 1979b) such an estimate of M is clearly better than no estimate.

How well Pauly's statistical, comparative generalizations apply to freshwater populations in Africa or elsewhere is not yet clear. The success with marine populations is such as to encourage parallel work with freshwater populations. Somewhat similar work has been done with some freshwater populations (Abrosov, 1969; Colby & Nepszy, 1981) and these also provide a basis for confidence that more work along these lines would likely soon contribute much to the operational usefulness of the population dynamics approach to fisheries.

2.2 - Marten's contribution. Marten (1979) performed a comparative analysis of interactive dynamics of populations of different species with Lake Victoria data. For the years 1972 and 1973 data were available for 50 recording stations distributed over the 2 000-mile shoreline of the lake. The basic ecology of the whole shoreline was quite similar, and the nearshore fish did not migrate far and neither did the artisanal fisherman, hence the 50 recording stations could be treated as ecological replicates. Types of fishing gear used, fishing intensity by different gear, as well as the compositions and quantities of catch did differ between stations. Given these conditions Marten chose to search for empiric relationships between the qualitative and quantitative characteristics of catches landed or yield on the one hand, and the qualitative and quantitative characteristics of the fishing methods used.

With multiple regression techniques he found the following relationship, among others :

$$Y = 48 X_{SM} + 50 X_L + 10 X_E + 110 X_H$$

where Y is the yield, X_{SM} is the contribution of small gillnets, X_L of large gillnets, X_E of extra large gillnets, and X_H of hooks.

Marten then interpreted his generalizations to mean that fishery returns could be optimized by severely overfishing the predatory fish with hooks to the advantage of herbivorous fish taken by gillnets. This interpretation follows from the observation that the coefficient of X_H in the equation, i.e., 110 was large and positive; thus a measure of X_H sufficiently large to cause severe overfishing of the predators nevertheless contributed positively to the overall summed catch.

3 - COMPARATIVE STUDY OF FISHERIES OF WHOLE SYSTEMS

Ever since the beginnings of the science of limnology early in the 20th century it has been apparent that bodies of water can be classified into different types, usually rather easily. Reference here is not to the primary classifications of waters into lakes, reservoirs, streams, ponds, etc., which have been distinguished since the distant past. Rather it is to secondary levels of classification within each of those primary types. In a particular region such as Europe it has long been known that certain species of fish thrive in certain specific kinds of waters, and management has long put such information to good use (see e.g., Müller, 1966). Such qualitative understanding also exists in various African, Asian or American regions, but has in general not yet been used as effectively as in Europe.

In more recent decades there has been a series of attempts to discover quantitative relationships between fisheries variables of practical interest and some readily measured limnological or ecological variables. Initially this attempt was made for bodies of water which seemed very similar limnologically - such as the streams of Europe (Huet, 1964) and the oligotrophic lakes of Central Canada (Rawson, 1952). (Note the analogy with Marten's empiric approach to fisheries in limnologically similar parts of Lake Victoria, sketched above.) In effect this led to a tertiary level of classification, but at this third level, quantitative continuous scales were employed rather than qualitative discontinuous classes (see below). With a measure of success at this tertiary level, it was found that some of the continuous variables used were also helpful in explaining some of the difference between oligotrophic and eutrophic lakes of central Canada (Ryder, 1982) or between natural lakes in all parts of the world (Schlesinger & Regier, 1982).

A somewhat similar progression toward characterization of qualitative criteria as quantitative variables has also occurred with reservoirs in the southeastern USA (Jenkins, 1982). Rapid progress is also being made with large rivers (Welcomme, 1979a, b), lagoons (Kapetsky, 1981), intertidal wetlands (Turner, 1977), ponds (Liang *et al.*, 1981), small marine systems (Marten & Polovina, 1982), etc. These classes, except the last, will now be examined with respect to simple quantitative empiric relationships.

It is important to emphasize that quantification usually involves conceptual simplification. It should not be viewed as displacing good qualitative understanding, but rather as complementing it. In the long run, both qualitative and quantitative types of information are likely to be equally useful. An effective management system can be devised that relies primarily on qualitative characterizations, another that relies primarily on quantitative characterizations. They will differ in important ways, but neither will necessarily be better than the other. In practice both are likely to be used, each to complement the other.

3.1 - Natural lakes. Just over thirty years ago, Rawson (1952) related total fish catches from a series of somewhat similar Canadian lakes to one of their limnological variables - mean depth. These lakes were fished at comparable levels of fishing intensity, in effect at moderate intensity so as to provide continuing harvests of the more preferred fish species. Rawson's work began a tradition that has led to the publication of over 100 papers, many of which were recently reviewed by Ryder (1982). Ryder is rightly recognized as responsible for continuing the work of Rawson who died at a relatively young age in 1959.

During the 1970s the Rawson-Ryder approach was applied to African lakes (and also to reservoirs, see below) by Henderson *et al.* (1973), Henderson & Welcomme (1974), Toews & Grifith (1979) and others. Of the various quantitative relationships discovered for African waters, that by Henderson & Welcomme (1974) is especially interesting in that it interrelated not only fish catches and limnological variables but also incorporated a fishing effort variable.

It was discovered, over a decade ago, that the relationships between fish catches and limnological variables were roughly similar in shape for several different lake regions of the world but were offset from each other. The catches for tropical systems were much higher than those for systems of mid to high northern latitudes at similar levels of the limnological variables in use (Henderson *et al.*, 1973). From much work in ecology on temperature effects it was hypothesized that at least part of these low latitude to high latitude differences were due to a climatic temperature effect. Schlesinger & Regier (1982) examined this hypothesis using multiple regression techniques and found a significant positive relationship between fish catches and average annual air temperature.

One of their relationships is as follows :

$$\log Y = 0.0236 + 0.280 \log \text{MEI} + 0.050 T$$

where Y is an estimate of the maximum sustained yield, per unit area of the lake, of all preferred species combined; MEI is the Morpho-edaphic Index of Ryder (1982), which equals total dissolved solids divided by mean depth; T is average annual air temperature in degrees C; and logarithms are to the base 10.

The meaning of the above relationship may be clarified with an example. Suppose the difference in annual average air temperature of a lake on an Arctic Island and a lake in tropical Africa is 40 Celsius degrees, but that the MEI measures of the two lakes are equal. The relationship implies that the difference in total catches would be 2.0 logarithm units i.e., $0.050 \times 40 = 2.0$.

This interval on a logarithmic scale translates to a factor of 100 on the usual arithmetic scale. Thus this tropical lake should produce 100 times as much as the Arctic lake, at equivalent levels of other limnological variables and of fishing intensity.

Fish catches of different lakes all fished at comparable intensities have been related to quite a variety of variables besides those mentioned above. No comprehensive review is now available for all of this work but the paper by Ryder (1982) provides a most useful entry into the subject.

It bears emphasis that the regression relationships described above provide only very approximate fits to the data from individual lakes. The scatter of points about the line of best fit is still quite broad, especially when one notes that several variables (e.g., yield, mean depth and total dissolved solids) have been transformed to logarithms. Though they have great value to scientists, administrators would probably find information contained in such relationships useful mostly for purposes of a first objective approximation of yield to be expected from a particular lake. The prediction would be far too crude to be used to set precise goals for the fishery of a particular lake.

If the significance of the temperature variable in lakes is supported by future work, as seems likely, then it is reasonable to expect that a similar variable might be incorporated into some of the regression relationships with reservoirs in order to extend the findings from Jenkins' set of reservoirs of southeastern USA into both lower latitudes as in Africa and higher latitudes as in northern Canada. In the absence of direct estimates, a temperature term for lakes found by Schlesinger & Regier (1982), i.e., $0.050 T$ where T is average annual air temperature, might be incorporated into the appropriate relationship from Jenkins' work, as a first approximation. This has not yet been attempted.

3.2 - Man-made reservoirs. The Rawson-Ryder approach to lakes relied on the gradual accumulation of information from many independent workers. It produced, eventually, an approximate global relationship. The main work done to date on reservoirs took a somewhat different course. Jenkins (1982) began a longterm study of US reservoirs in 1963, with the comparative work of D.S. Rawson, H.S. Swingle and other limnological empiricists clearly in mind. His programme was funded continuously for nearly two decades to permit accumulation of much carefully selected information on some 294 reservoirs.

From the rich base in data Jenkins and his colleagues produced a large number of regression formulae of potential use to planners and administrators of fisheries in US reservoirs (see Jenkins (1982) for a selection of the more general relationships).

Jenkins (personal communication) has applied his estimates to some data on reservoirs in

India but that work has apparently not been published. Application to data on African reservoirs has not been attempted, apparently.

Some useful relationship of fish yield in Nigerian reservoirs have been derived for effective management of the fish stock (Ita, 1986). One of such relationships is the fish catch per boat (kg) in artisanal canoe fish landings and the biological/experimental fish catch (kg) per 1,000 m² of graded multifleet gill-nets described in Ita (1978). The relationship is expressed in the regression equation :

$$Y = 2.8 + 1.3x \quad (r = 0.7219)$$

The comparison is limited only to artisanal fisheries with relatively low efficiency gears such as gill-nets, hooks, traps and cast nets. It is useful in extrapolating yields indices of commercial fish landings in different zones of a reservoir where survey cost is a major constraint in organized statistical surveys of artisanal fish landings. It would be possible to estimate total fish landings in small reservoirs if the total boat count is known.

Another useful relationship is that of standing crop of fish (kg) per hectare along the inshore areas of Nigerian reservoirs and fish yield (kg) per 1,000 m² of graded experimental multifleet gill-nets. The relationship is expressed in the regression equation :

$$Y = 13.2 + 17.7x \quad (r = 0.8118)$$

This relationship is useful in estimating, with limited degree of accuracy, the expected standing crop of fish domestic water supply reservoirs not usually sampled with fish toxicants. Fish standing crop per hectare is also highly correlated with fish density per hectare (Ita, 1986) with the equation :

$$\text{Log } Y = 1.995 + 0.787 \text{ Log } x \quad (r = 0.868)$$

It is possible to estimate the expected fish density in the inshore habitats of any reservoir in Nigeria sampled with the same surface area of graded gill-net fleet used in the study. These estimates could help in narrowing down the gap between potential yield estimates based on Ryder's (1982) Morpho-edaphic Index (MEI) and the actual standing crop of fish in the studied reservoir. This would permit the right management and development decision to be taken at any point in time.

One of the relationships for hydropower storage reservoirs of the southeastern USA is as follow :

$$\log Y = 1.752 + 0.896 \log \text{MEI} - 0.223 (\log \text{MEI})^2$$

where Y is total catch per unit area and MEI is Ryder's index as defined in the previous section. It may be noted that the relationship is curvilinear, bending downwards at higher levels of MEI. There are also indications that the relationship in lakes is curvilinear (see Henderson *et al.*, 1973), but the curvilinearity was not found to be significant by Schlesinger & Regier (1982) when they incorporated a climatic temperature variable into the regression relationship.

3.3 - Rivers. An approach conceptually similar to those of D.S. Rawson, R.A. Ryder and colleagues for lakes and to those of R.M. Jenkins and colleagues for reservoirs was followed by L. Léger, M. Huet and P. Lasseben for flowing waters. In the rather simplified version of Huet (1964)), the following comparative relationship was used for European streams :

$$K = BLk$$

where K is the annual productivity of the water in terms of mass per unit length of the stream, L is the average width of the stream, B is the «biogenic capacity» and k is a coefficient of productivity. B is a function of the amount of fish food available, for which the amount of aquatic vegetation may be a useful surrogate. In turn, k is a product of four other coefficients, k₁ to k₄. Here k₁ is a temperature coefficient, k₂ is a measure of alkalinity or acidity, k₃ is a measure of the growth efficiency of the fish, and k₄ is a measure of the turnover rate of the fish populations.

Holcik (in Welcomme, 1979b) has sketched the nature of some improvements made by Lasseben (1977) on the contribution by Huet (1964). Apparently these methods have not been tried for streams outside of Europe.

Welcomme (1979a, b) has led the way in the comparative empirical study of fisheries of large rivers, especially those with floodplains. His approach was similar to those of Rawson, Ryder, Jenkins and Huet sketched above. He found that total catches were strongly and directly related

to the areas of the drainage basin of the rivers involved, their lengths, and also to the relative size of floodplain development. Considering now only the length variable, he found for African rivers that

$$Y = 0.0033 L^{1.95}$$

or approximately $Y = L^2/300$

where Y is total catch and L is the main channel length (Welcomme, 1979a).

With respect to flooded area, Welcomme estimated that

$$Y = 3.83 A$$

where Y is total catch and A is the maximum flooded area.

Welcomme's data set related mostly to large rivers with flood plains in low latitudes. Presumably a climatic temperature variable would improve the fit for rivers that differed much in latitudinal location.

Some Americans have recently begun a concerted ecological study under the title of the River Continuum (Vannote *et al.*, 1980; see also Platts, 1979). Perhaps these will help to clarify a series of well-known generalizations, such as those sketched above, and make them more precise for purposes of practical application as well as of scientific understanding.

3.4 - Ponds. The comparative literature on ponds and small, enriched lakes is quite large. Here we select for reference one tradition that parallels those of the systems of the preceding sections.

Liang *et al.* (1981) built on earlier work by Melack (1976) and Oglesby (1977) with lakes and adapted it to Chinese ponds and lakes. They found that

$$\log Y = 2.44 + 0.047 P$$

where Y is total fish catches and P is a measure of gross photosynthesis.

These authors also proposed the interesting hypothesis that fish catches are a sigmoid ascending function of gross photosynthesis - an hypothesis that would bring together a series of apparently different functions found by different workers, but located in different ranges of these two variables.

3.5 - Intertidal areas, lagoons and swamps. Comparative empiric work on these types of systems has just got underway in recent years.

With respect to intertidal areas, Turner (1977) related commercial catches of penaeid shrimps to area of intertidal vegetation and to latitude and found that

$$Y/A = 158.7e^{-0.070X}$$

where Y is total catch, A is area of intertidal vegetation and X is degrees of latitude between 0° and 35°.

Schlesinger & Regier (1982) used Turner's data to recalculate a relationship using average annual air temperature instead of latitude. They found that the temperature coefficient for the shrimp-intertidal systems was quite similar to that of their fish-lake systems, i.e., 0.071 vs 0.050 respectively. Perhaps this degree of agreement was fortuitous, but at least it encourages the hope that some temperature relationship might be found that would be quite general over all the different primary types of aquatic systems mentioned above.

Kapetsky (1983) has made the first serious attempt to assemble and examine data from lagoons. His early findings include the following :

(a) Finfish yield in coastal lagoons can be related to lagoon size by :

$$Y = 112.39 A^{-0.29}$$

where Y is annual yield in kg ha⁻¹yr⁻¹ and A is lagoon surface area in km²; however despite the large sample (93 lagoon fisheries), the relationship is weak (R² = 0.27).

(b) There was no apparent relationship between lagoon finfish yield and latitude for a sample of 104 coastal lagoon fisheries ranging in latitude from 5° to 54°

(c) Kapetsky (in press) compared fishery yields from a number of diverse aquatic systems - tropical reservoirs, temperate reservoirs, natural lakes (cold temperate to tropical), river floodplains (tropical to temperate), continental shelves (tropical, sub-tropical and temperate), and coral

reefs - to coastal lagoon fishery yields (finfishes + shrimps + crabs, but not including molluscs). Coastal lagoon fishery yields ($n = 108$) ranged higher and had a higher mean than fishery yields from any of the other systems.

Although coastal lagoons are inherently productive as natural systems, it appeared that, in this sample, lagoon yields greater than $400 \text{ kg ha}^{-1}\text{yr}^{-1}$ could be attributed almost entirely to man-made eutrophication. There also was evidence that such man-caused nutrient enrichment contributes to fishery yields to a greater or lesser extent in many other coastal lagoons.

This provides an explanation for the difficulty in relating lagoon fishery productivity to factors such as annual temperature or latitude (a and b above).

(d) Yield as a function of fishing effort is described by :

$$Y = 54.3 + 10.3E \quad (R^2 = 0.81)$$

for 42 coastal lagoon fisheries among which yield (Y) ranged up to more than $900 \text{ kg ha}^{-1}\text{yr}^{-1}$ and effort (E) to nearly $100 \text{ fishermen km}^{-2}$.

This does not imply that increasing effort brings out increasing yield per unit area indefinitely, as the model suggests. Rather, the model describes a yield-effort path over a broad range of lagoon productivities. Those lagoons with high biological productivity values can support intensive fishing effort while still maintaining high per unit area yields. However, as fishing effort increases (as fisherman km^{-2}) CPUE (as catch fisherman $^{-1}\text{yr}^{-1}$) decreases rather rapidly :

$$Y = 1.61(1 - E) + 5.61 \quad (R^2 = 0.39)$$

but even at very high effort levels, CPUE of 1 to 2 t fisherman $^{-1}\text{yr}^{-1}$ can be maintained, if the lagoons are highly productive.

Comparative empiric work with swamps comparable to that sketched with other systems above is yet to be initiated. Perhaps there is not yet sufficient information on hand to render such an effort timely. On the other hand, if useful and reliable information were assembled for all the other types of a region, say of the low latitude areas of Africa, then it might be possible to « interpolate » useful information on swamps from these other relationships. This kind of challenge may now be timely.

4 - DISCUSSION.

The contents of the preceding sections implicitly focus on fisheries of aquatic systems that are not degraded by other human uses such as toxic pollution, intense eutrophication, excessive sedimentation, stream channelization, etc. Each of these stresses, in turn, have been characterized qualitatively and quantitatively by comparative empiric methods.

The comparative work on eutrophication by Vollenweider (1980, 1981) and colleagues is well known. There are strong interrelationships between the eutrophication and fishery stresses (Ryder, 1981) but these have only been explored rather superficially as yet. Much remains to be done with interactions of fisheries and other stresses (Francis *et al.*, 1980). Progress will likely come rapidly in the temperate parts of the world. If we then understand how to take latitudinal effects into account, it may be possible to extrapolate this information into African situations, at least to serve as first approximations.

In conclusion, the contents of this chapter demonstrate some promising developments with empirical generalizations with various kinds of aquatic systems in various parts of the world. Much more of this can be developed further and made relevant to African fisheries. Cooperative, collegial activities are now needed to move this process along - the kinds of activities that have been fostered by the Committee on Inland Fisheries of Africa (CIFA).

RESUME

Ce chapitre porte essentiellement sur les pêcheries dans les systèmes aquatiques non dégradés par les autres activités humaines, telles que la pollution toxique, l'eutrophisation intense, la sédimentation excessive, la canalisation des cours d'eaux. Chacune de ces agressions a cependant bien été caractérisée par des approches comparatives, qualitatives ou quantitatives.

Les études comparatives sur l'eutrophisation entreprises par de nombreux auteurs sont bien connues. Il existe des relations étroites entre l'eutrophisation et les pressions exercées par la pêche mais elles n'ont encore été exploitées que superficiellement. Il reste encore beaucoup à faire en ce qui concerne les interactions entre la pêche et les autres types d'agression.

Les progrès seront vraisemblablement rapides dans les régions hyperdéveloppées du monde. Si les effets de la latitude peuvent alors être pris en compte, il pourrait être possible d'extrapoler cette information aux situations prévalant en Afrique, au moins au titre de premières approximations.

Le contenu de ce chapitre illustre quelques développements prometteurs obtenus à partir de généralisations empiriques concernant divers écosystèmes aquatiques dans différentes parties du monde. D'importants développements ultérieurs sont encore possibles et peuvent être adaptés aux pêcheries africaines.

Des activités coordonnées sont maintenant nécessaires pour aller de l'avant, du type de celles encouragées par le Comité des pêches continentales pour l'Afrique.

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