ARE INDUSTRIALIZED FISHERIES SUSTAINABLE?

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Fish stock assessment and management is currently based on the concept of sustainable surplus production. This essay argues that this concept is fallacious and that the assessment/management models which assume its existence are overly simplistic. The analysis explores some of the other issues which should be considered in any stock management regime: these include the dynamic responses of marine ecosystems to physical forcing, the real significance of the extraordinary fecundity of teleosts, the indeterminate growth pattern of fish and its consequences for the reproductive efficiency of older individuals, so that truncation of the older year classes, an apparently inevitable consequence of fishing, will hasten stock collapses. The long-term future of modern fisheries is not bright.

L'évaluation et la gestion des stocks de poisson sont actuellement fondées sur la notion de production excédentaire durable. Selon la thèse présentée ici, cette notion est fallacieuse et les modèles d'évaluation et de gestion qui la tiennent pour fondement sont trop simplistes. L'analyse envisage certains des autres facteurs qui devraient être pris en considération dans tout régime de gestion des stocks, notamment les réactions dynamiques des écosystèmes marins au forçage physique, la signification réelle de l'extraordinaire fécondité des téléostéens, le régime de croissance indéterminé des poissons et ses répercussions sur l'efficacité de la reproduction des plus vieux individus, qui font que la réduction des plus vieilles classes d'âge, conséquence apparemment inévitable de la pêche, précipitera l'effondrement des stocks. L'avenir à long terme des pêches modernes n'est pas brillant.

INTRODUCTION

It is not easy to apportion blame for the failure of fish stocks, but some of it may certainly be attributed to management advice, even if this was generated by state-of-the-art fishery science agencies: we are all too familiar with a notorious case right here on our doorstep in Atlantic Canada. There are those, myself among them, who believe that this is an inevitable result of the use of simplistic simulation models of the dynamics of populations that are quite unreal: these treat the fished stock as if it inhabited an ideal space containing neither competitors nor elusive food supplies, and they ignore the influence of environmental forcing. The result of the failures of these models, of the difficulty that politicians have in following scientific advice, and in the obduracy of fishermen in cheating on regulations, is before us all.

But the myth that commercial fishing is sustainable, in the world as it is, still lives. Every text on fishery management is based on some version of this selective conjecture, and most of them assume that it was so obviously true

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that alternatives are not discussed. Nevertheless, we are starting to come to terms with the consequences of the simple models developed 50 years ago or more, and individual and agencies are calling for more recognition of the environment in which the stocks live, when planning for their management. Yet I think that the complexity of the marine environment, and the depth of our ignorance of that environment, is not fully comprehended in the stock management strategies now being sketched out for future use.

This short essay is not intended to be a contribution towards relieving that ignorance, but is rather intended to emphasize its depth. Not long ago, Daniel Pauly (2005) suggested that an *"ability to produce a surplus that we can share, year for year, is an emergent property of marine ecosystems, contingent on their continued existence as complex entities"* but it is absolutely not clear to me what mechanisms might produce such desirable emergent properties. I suggest that they might be quite difficult to define and propose a very brief review of some candidate properties that might possibly be considered in the balance: some, I shall suggest, support the possibility that density-dependent growth of fish stocks might give what we have come to call (quite erroneously!) surplus production, while some other properties of teleosts, and of the natural history of the sea, do not at all support the concept.

MARINE AND TERRESTRIAL ECOSYSTEMS

Although we have come a long way since the ecosystem concept was first coined, marine scientists remain shackled in their thinking because the ecological literature is so dominated by studies of terrestrial habitats. Most of what we know (or think we know) about ecosystem function is based on observation of terrestrial or littoral habitats. Unfortunately, this knowledge has limited relevance in the oceans, principally because the dynamics of marine ecosystems respond to changes in external forcing at much shorter time scales than occurs in terrestrial habitats. Consequently, it is very difficult to understand the response of marine biota to their physical environment because we can make observations at appropriate time-scales only with great expense: marine habitats are poorly understood because few have levels of observation remotely comparable to those of, for example, the California Cooperative Oceanic Fisheries Investigations program (CALCOFI 2007), the approximately 40-year Multispecies Trawl Surveys of the major shelf areas of Atlantic Canada (Chadwick et al. 2007) now part of the Atlantic Zone Monitoring Program (AZMP) (Pepin et at. 2005) or the multispecies trawl surveys in the Gulf of Maine (conducted since 1965). Although the dynamic response of marine ecosystems to physical forcing must follow rules that we can aspire to understand, these responses are chaotic in the sense that we are quite unable to predict any future state. It is only after an event, and to the extent that we have observed and described it correctly, that our general knowledge of the biology of individual species may

be sufficient to allow us to suggest what has probably taken place — but we can rarely be sure.

In marine environments, plant growth (and herbivore biomass) responds almost instantaneously to ephemeral changes in upper ocean dynamics, as can be observed in any mesoscale image of surface chlorophyll that is matched with surface elevation to indicate motion. Remember, although these patterns are largely forced by surface wind stress this apparently simple process conceals great complexity, and the surface water mass responds quite differently in cold and warm seas; the change of the Coriolis acceleration with latitude requires that wind stress should preferentially induce mixing in cold seas, but motion in low latitudes. There are many similar complications in the forcing of marine ecosystems that are very different from what we are familiar with in terrestrial ecosystems.

At the regional scale, constant changes in water motion, stratification, convergence and divergence are induced by shifts in the strength and location of the planetary wind systems, especially in the succession of Rossby waves at high latitudes. These shifts are now codified by a series of indices of inter-regional differences in atmospheric pressure — the North Atlantic Oscillation (NAO), Pacific Decadal Oscillation (PDO), Southern Ocean Index (SOT), etc. at a quasi-decadal scale — including the novel Atmospheric Circulation Index (ACI) of Klyashtorin that has a 65-70 year period — and are reflected in the abundance of clupeids in upwelling regions. Consequently, fundamental changes of ecological state are observed to occur naturally in the sea at rates greatly exceeding those observed in terrestrial ecosystems. The ecological consequences of episodes of anomalously low atmospheric pressures and warm sea surface temperatures in the Gulf of Alaska, induced by a shift in one of the principal quasi-permanent meanders in the westerly winds indicated by the PDO are well known.

Changes of state that would seem to be equivalent to a switch from, say, tundra to boreal forest are induced in a few months in the ocean, while such a change could be completed ashore only over several centuries. Further, these are not simple shifts between two steady states, for the pelagic ecosystem is incapable of steady state, being in a perpetually dynamic imbalance; in consequence, the relative and absolute abundance of fish species is everywhere perpetually changing and thus challenging what has been called the *'classical view of sustainability'* — in which an equilibrium biomass of a stock is established as a function of fishing mortality and of the carrying capacity of the habitat.

That fish stocks vary in abundance and location is no new discovery, for already in 1865, Francis Day — then Inspector-General of Fisheries for India — noted that the oil sardines of the Malabar coast were very uncertain in their availability; accordingly, he recommended against a planned expansion of the fishery to supply the new oil and fertilizer factories then being planned. But Day was obviously a better ichthyologist than economist, for the new industry flourished and flourishes still, despite its highly variable resource base. Although on the west coast of India the response of the oil

sardine population to upwelling dynamics is unique (the upwelled water is oxygen-deficient), this is nevertheless one of the now familiar family of responses of clupeid populations of upwelling regions to changes in atmospheric forcing. Oil sardine abundance, as catch data for the 20th century suggest, follows patterns comparable to those of the other, much better known species of clupeids of upwelling regions.

Although clupeid stocks have taken much of our attention, we have also come to understand that all individual fish stocks vary naturally both in abundance and location, more or less strongly depending on many factors, and even in relatively stable parts of the ocean such as the northeast Atlantic shelves. It was there that one of the earliest examples of what we now call regime shifts was observed; the classical "Russell cycle" in the western English Channel with the progressive replacement of herring by pilchard in the early 1930s, in association with reduced primary productivity and copepod abundance, and the return after 1965 to the earlier condition.

Because today we are bombarded with comment (based on another selective conjecture?) that any observed ecological change is related to the effects of the increase in atmospheric CO_2, perhaps we should remember what Campden, the 16th century English historian, wrote: "*These herrings, which in the times of our grandfathers swarmed only about Norway, now in our times... swim in great shoals around our coasts every year*". Indeed, from 1550 to 1900 there were four periods when herring were distributed preferentially towards the north, along the Bohuslan coast of Sweden, and five of more southerly distribution (Cushing 1981). There is, of course, an extensive literature to explore that discusses the natural variability of fish stocks, and the complex interactions of this with the effects of fishing mortality.

I have raised these well-known observations here only to suggest — what I cannot demonstrate — that if the marine ecosystem is characterized by more rapid and profound dynamic changes in state than terrestrial ecosystems, then perhaps individual species of fish may have evolved life history characteristics that enable them to respond more effectively than terrestrial vertebrates to rapid changes in the intensity of natural mortality. Certainly, one of the characteristics that distinguishes marine from terrestrial ecosystems is the very high link density of marine food webs compared with terrestrial: connectance - the number of links per species[2] - is very high in the oceans (Dunne et al. 2004). Individuals belonging to marine species encounter a more taxonomically-diverse range of individuals than do terrestrial species: this may offer some support to an argument that this characteristic would enhance the potential ability of populations of marine fish to absorb novel mortality more readily than do terrestrial vertebrates.

Could this be one factor that induces Pauly's emergent property? Is the relative openness of marine ecosystems associated with a greater inter-regional exchange of species than on land? If this is the case, can marine ecosystems consequently better accommodate the arrival of a novel predator than terrestrial ecosystems?

Observations do seem to point in that direction, because terrestrial vertebrates are extraordinarily sensitive to the arrival of human predation; their populations melt rapidly away when we seriously start to exploit them for food or hides. Bison fecundity was simply no match for the mortality imposed by a novel human predator, and nor could bison sustain their essential migrations after the rapid enclosure of the prairies for ranching.

Subjectively, at least, the history of fishing does suggest that ocean fish stocks are at least a little more resilient, because our efforts to eliminate them have been at least as determined as our ancestor's hunting of mammals on grasslands. Because of the extreme sensitivity of terrestrial mammals to hunting, expanding human populations could obtain sufficient food from the land only by agriculture or animal husbandry and neither of these activities may be sustainable, since the axe and the plough very easily change regional hydrologic cycles and so create aridity and desertification. Then, we should note that while the great majority of the terrestrial vertebrates that have ever been hunted seriously for food were large herbivores, the species targeted by fishing have always been — with just a few notable exceptions — predators.

So fishing has only a minimal impact on the natural productivity of the 'seascape'; oceanic primary production responds principally to variable physical forcing, and only secondarily to changes in abundance of top predators and the consequent release of herbivore populations. Most importantly, fishing does not normally modify the abundance of oceanic herbivores directly, since these are dominated by millimeter-scale zooplankton much too small to interest us as potential food. For this reason, we have comfortably supposed that trophic cascades of the kind observed in lakes or the littoral zone after the removal of top predators do not often occur in the open sea, so that the base of the trophic pyramid that supports the fish in which we are interested is relatively unmodified by fishing (Cury et al. 2001). Unfortunately, we have now learned from an understanding of the consequences of gross overfishing that occurred during the last 30 years or so in the NW Atlantic, that trophic cascades may also occur at sea (e.g. Frank et al. 2005).

Finally getting to the fish themselves, if we are seeking characteristics that might suggest that they are more able to sustain fishing pressure than terrestrial mammals can sustain hunting pressure, I suggest that it might be useful to concentrate on three aspects of teleost biology that strongly differentiate them from terrestrial mammals: *(i) – their extraordinary fecundity, (ii) - their pattern of life-long growth and (iii) - the variability of their annual spawning success*. Unfortunately, only the first of these characteristics might have any potential for decreasing their sensitivity to fishing, while the third would seem to militate against their value for a modern industry which will value supply reliability in its source of raw material.

TELEOST FECUNDITY

Inevitably, when confronted with the question of the potential sustain-ability of sea fisheries, one starts by thinking about the quite extraordinary reproductive characteristics of teleosts, as people have done since the days of Lamarck, almost 200 years ago.

Teleosts reproduce by means of very many, very small eggs, and their relative fecundity increases progressively with age and weight, at rates greater than linearity. As hardly needs repeating, all other vertebrates have a characteristic fecundity that is 4-5 orders of magnitude smaller. Those who have discussed this phenomenon in the past have tended to assume that such high fecundity evolved in response to the unpredictability of the marine environment so that, after a population crash induced by changes in environmental conditions, the remnant adult stock could rapidly recover its habitual abundance. But Froese and Luna (2004) recently examined the reproductive biology of almost 50 representative teleost species and found "*no significant relationship between annual fecundity (ranging from 368 to 10 million eggs) and maximum annual reproductive rate (ranging from 0.4 to 13.5 replacement spawners per spawner at low population densities)* ".

If this is the case, we have to ask why should many teleosts, alone among vertebrates, have evolved to spend part of their life history as members of the zooplankton? It is certainly odd that general ichthyologists should have concerned themselves so little with explaining why 'typical' teleosts of the open ocean and continental shelves have evolved to produce so many small planktonic larvae rather than brooding, or giving birth to, just a few, large young. This is especially odd given that all elasmobranchs and even some teleosts, the live-bearers and nest-builders, succeed very well with a strategy which requires them to invest material and parental care in the generation of just a few, large young.

Let me examine an alternative proposition concerning the evolution of teleost reproductive habits, while admitting that the argument is somewhat teleological. The extraordinary fecundity of marine teleosts coupled with their recourse to planktonic larvae may not be primarily concerned with population regulation or distribution. Instead, it may be a solution to the general problem of the nourishment of large predators in an ecosystem that is dominated by micron-scale plants and millimeter-scale herbivores.

This possibility seems to have escaped the attention of general ich-thyologists and it was suggested to me by a remarkable — but equally remarkably ignored — contribution by Walter Nellen (1986), who thought that *"bony fish may have evolved to be nourished to some good extent by their children rather than vice versa as it is with other vertebrates "*. A very similar argument has been made by John Caddy (1983) concerning can-nibalism in pelagic cephalopods like *Illex*. He suggested that this may be a strategy to bridge gaps in the pelagic particle size spectrum so that the species as a whole is able to exploit food particles too small to be usable by larger, maturing squid.

Nellen (1986) pointed out that a rather simple food chain runs directly from phytoplankton cells, through small crustacean herbivores to small fish, starting with first- feeding larvae. Further, the same food chain may be traced through progressively larger size- classes of teleost fish, via cannibalism. If this analysis is correct, then reproduction in teleosts may not involve — as it does in all other organisms — an energy cost: on the contrary, at least some happy parents may experience an energy gain through reproduction.

This apparently ridiculous suggestion may be evaluated by comparing the energetics of dogfish (*Squalus canis*) and cod (*Gadus morhua*). Large individuals of each species are about one metre in length, but the annual reproductive output of their females is strikingly different: the viviparous dogfish produces 10-15 young in the range 20-25 cm in length while the oviparous cod releases 5-10 million ova, each <2 mm in diameter, batch-spawned over a relatively short season of less than 2 months. If even a tiny fraction of these survive their first year and reach the same life stage as the newborn dogfish, the initial energy expenditure of the female cod has been enormously more effective in terms of potential population increase than that of the female dogfish. Moreover, the tiny cod larvae nourished themselves rather than depending, as did the young dogfish, on a significant maternal contribution to the ovum from which each individual has devel-oped. Subsequently, many small cod contribute nourishment to the adult cod by cannibalism, thus returning to their parent cohorts at least a part of their original maternal energy contribution: individuals that are consumed in this way are <3 years old, after which they appear to become exempt. Cannibalism in cod increases progressively with age, becoming especially characteristic of individuals >100 cm in length.

The instantaneous level of cannibalism by cod depends principally on the relative abundance of small cod in the regional population (Bogstad et al. 1994). When the incoming year-class is unusually strong, many 1-2 year olds will be consumed, as occurred on Flemish Cap in 1991 when a very large class of 1-year old recruits induced a rapid increase in cannibalism by older fish: obviously, events such as this may contribute to a natural, density- dependent mechanism for population regulation, as in the case of the cyclical alternation in relative abundance of adults and young fish that has been observed in the Arcto-Norwegian cod stock.

The same process occurs in the eastern Baltic, where stomach content analysis of more than 60,000 cod over a period of 17 years showed that 25-38% of each incoming 0-group was consumed by adult cod, together with 11-17% of the subsequent 1-group (Link & Garrison 2002); thus, 24% of the post-larval fish of the initial cohort is consumed before it reaches the age of 2 years. Although cannibalism rarely exceeds 20% of the dietary intake of even the largest cod in various North Atlantic regions, in other gadoids (e.g. *Theragra chalcigramma* and *Merluccius* spp.) the overall contribution may be much greater (Neuenfeld & Köster 2000). *Micromesistius poutas-sou* and *Scomber scombrus* may also be strongly cannibalistic, with as

many as 80% by number of prey items comprising smaller individuals of the same species.

Several authors comment that cannibalism is widespread among teleosts. Reviewing this topic, Smith and Reay (1991) found evidence for cannibalism in 31 families of teleosts and suggested that *"it is considered to be more widespread than this. Finding examples of cannibalism is not difficult, and it may be more interesting to look for taxa in which the behaviour does not take place"*. Unfortunately, it is difficult to ascertain to what extent the characteristic extent of cannibalism differs in different marine habitats, at different depths or in different latitudes.

If, as Smith and Reay (1991) conclude *"the main proximate advantage conferred by cannibalism is assumed to be nutritional"*, then it would be reasonable to suppose that the utility of cannibalism would be greater in low-diversity ecosystems of cold seas. In tropical seas, a wide range of fish species occupies the entire size spectrum from centimetre to metre scale, enabling an efficient transfer of energy from very small to very large species by predation. In cold seas, gaps occur in this size spectrum and these may effectively be filled only by young individuals of the dominant large species.

The very few accounts of cannibalism in tropical environments that I have found conform to this pattern: for instance, although adult *Cynoscion* off Mexico do consume small individuals of their own species, these comprise less than 5% by weight of the adult diet. In tropical tuna, the rate of cannibalsm is not much higher. Finally, it is worth noting that nest- builders may also be filial cannibals, consuming their growing families in the event that other food is scarce: for these fish, reproductive loss is balanced by energy gain.

There is, therefore, plenty of support for Walter Nellen's suggestion that a transfer of energy occurs along a food chain from small to large individuals of many teleost species. For these, we might very well conclude that the function of large incoming year-classes is not to enable rapid population growth, but rather to contribute to the nourishment of the entire adult population by transforming food particles that are too small to be useful to adults (even smaller fish, euphausiids, hyperiids, etc) into items of food (themselves) large enough to be consumed profitably. Elsewhere (Longhurst 1999), I have suggested that perhaps the main function of young gadoids in high latitudes was to nourish their elders and their betters!

So, it is difficult to sustain so easily as we might have done in the old days an assumption that their great fecundity - especially compared with terrestrial mammals and birds - might in some way enable us to take what is wrongly called an annual harvest from their stocks: we can no longer so simply assume that there's plenty more where the ones we took came from.

EFFICIENT OLD FEMALES – A CONSEQUENCE OF THE
INDETERMINATE GROWTH OF TELEOSTS

Another aspect of teleost biology that comes to mind in the context of the sustainability of fisheries is their indeterminate growth pattern — from which flows several important consequences for their resilience to fishing pressure: unfortunately, these are negative, in the sense that the apparently inevitable truncation of the older year-classes by any fishery must reduce the ecological efficiency of the stock in relation to the exigencies of its natural habitat. It is easy to forget that the ability to grow throughout life is nothing very special in the living world — it is, in fact, a trait that fish share with the great majority of multicellular organisms from oak trees to jellyfish, and it is associated with a pattern of senescence that is totally foreign to you and me.

Our own pattern of determinate growth — which we share only with other terrestrial mammals, with birds and with some higher insects — means that we do not easily appreciate the consequences of life-long growth. I suggest, however, that we need to think about it very carefully, because it holds both promise and dangers for industrial fisheries. Teleosts, although a highly diverse group, are characterized by indeterminate growth, although the balance between investment in growth and reproduction varies strongly between groups. Among teleosts there is a fast-slow continuum from short-lived and early maturing species (e.g. *Clupea*) to long-lived fish that mature relatively late and spawn larger eggs (e.g. *Sebastes*) (Rochet et al. 2000).

In thinking about the ecological consequences of the teleost growth pattern, what comes first to mind is the ability that it gives to teleosts to respond to an enhanced availability of food by an increase in the rate of growth throughout the life of each individual and not only, as in mammals, during the relatively short period when growth is actually occurring. This response is a factor in the apparently greater sustainability of marine fisheries than of hunting on land. Not so long ago, it was thought to be desirable that a fishery should selectively remove the older, slower-growing individuals to increase the overall productivity of the stock. Unfortunately for this well-worn thesis, it is now understood that the presence of older individuals may be critical to the well-being of a population of teleosts. This is a consequence of the potential immortality of organisms that grow throughout their entire life, and therefore experience negligible senescence, as was suggested by Bidder (1932). Most fish follow this typical pattern, discussed again recently in more realistic terms than those of Bidder by Vaupel et al. (2004) who suggested, in an essay on negative senescence, that *"Youth comes with age"*!

This astonishing statement is based on the fact that indeterminate growth requires that all somatic cells should be capable of active proliferation throughout life, unlike the cells of organisms like you and me. Our own somatic cells have an average age that is close to our chronological age less, say, 20 years: in my own case, my somatic cells have been progres-

sively accumulating errors and inducing senescence for about 60 years now. But organisms with indeterminate growth have a quite different pattern of cell ageing: the somatic cells of a centenarian *Sebastes* are collectively far younger than those of a centenarian man, and they also contain high levels of telomerase, an enzyme required to prevent cell ageing during progressive replication (Klapper et al. 1998). For at least part of their adult lives, the average age of somatic cells in long-lived fish may even become progressively younger as the whole organism ages!

It is only in the terminal phase of their lives that large cod or large rockfish exhibit any sign of senescence, as is also true of tiny tropical freshwater fish that live for no more than 90 days. Others, like Pacific salmon, endure terminal and catastrophic mortality that is not preceded by any period of senescence. The key observation is that delayed senescence in teleosts is associated with the fact that these fish become progressively more "*efficient*" as they age: their natural mortality progressively decreases, their fecundity increases approximately with the cube of their length and, finally, ova and larvae from older females have better survival rates than those from younger fish. Consequently, just a few large, old females have the same reproductive potential as many tens of younger fish and the longer spawning season of old fish increases the probability of a match occurring between larval food requirements and the availability of suitable food items.

We can now be reasonably confident of the generality of the mechanisms involved in these processes: in *Sebastes*, on the west coast, the metabolic endowment (in terms of the size of their oil droplets) received by individual larvae from old females is much greater than the endowment offered by young females to their larvae. Consequently, the survival rate of larvae from old females is significantly higher: a doubling of maternal age translates, approximately into a doubling of time to larval starvation, and to a tripling of larval growth rate. These studies by the late Steve Berkeley and his team (Berkeley et al. 2004) have rightly become classics of the fisheries literature, giving us a good understanding of the mechanisms controlling the survival of teleost larvae. This mechanism, or something very like it, appears to be representative of a wide variety of teleost families, in which older females have higher fecundity, spawn more frequently, and start earlier in the season, spawn larger and more buoyant eggs which have higher fertilization and hatching rates, and which produce larvae that swim faster.

This pattern has now been observed in a wide range of commercial teleosts, very largely in the North Atlantic: cod, haddock, winter flounder, turbot, striped bass, herring and capelin (Trippel et al. 1997). Evidence is accumulating from other species to confirm the generality of the model: for instance, for South Atlantic hake, and species of rockfish other than *S. melanops*.

Clearly the reproductive success of many teleosts is very sensitive to the apparently inevitable truncation of the age structure when they are targeted by a commercial fishery, and this cannot be ignored in evaluating the sustainability of industrial fisheries. In the early years of fishery science in

the North Sea, the age composition of each stock was carefully monitored, although mostly in order to compute stock size from egg and larval surveys (Holt 2008). Apparently, less concern was given later in the 20th century to the truncation of the age structure of a stock by fishing, and that shall be the next problem to be addressed.

TRUNCATION OF THE NATURAL REPRODUCTIVE PERIOD OF EACH YEAR-CLASS

Apart from the reproductive role of older females, the natural longevity of a stock is one of the wider set of characteristics that have evolved to enable it to survive in the variable environment of a particular region of the ocean. This axiom is consistent with the observation that different age structures are characteristic of different parts of each species habitat, and that this structure changes under changing external stresses, such as when a species is invading new habitat.

We observe that age structure of each population takes only a limited range, and will return to the undisturbed state when unusual environmental stress is removed. Lotka discussed this limitation in 1925: *"Now, age distribution is indeed variable, but only within restricted limits. Certain age distributions will practically never occur... There is, in fact, a certain stable age distribution about which the actual age distribution varies, and towards which it returns if through any agency disturbed therefrom"* . Truncation of the age structure is a very strong violation of ecosystem balance, yet the extent to which some populations have been truncated by fishing, even right under the noses of apparently competent fish stock managers, is quite remarkable. Perhaps the most blatant example in the fisheries literature is the 30-year regression of older fish in the 2J3KL cod stock of the Canadian Atlantic area. Both the maximum age of females in the population, and also the age at which they achieved maturity were reduced by 50% between 1962 and 1992 partly due to changing environmental conditions but also to the offshore trawl fisheries: high-lining and discarding were rife during this period.

Generally, after several decades of intensive trawling, none of the larger species in a fishery retains an age distribution that is appropriate to the exigencies of the natural environment (Stearns 1976). In cold seas, a population age structure will be evolved in this way that would be more appropriate for a fish in warm seas — but with one important difference: as in the 2J3KL cod, only a few of their older year-classes will be mature. In ecosystems that have been modified in this way, few individual species may retain enough reproductive competence for continued survival and the ecosystem itself may become seriously unbalanced.

The relationship between the natural length of life of a species and the variability of its annual recruitment was well known to the early fishery scientists. Those who worked on the problems of the herring fisheries

were more concerned with the elusive spawner/recruitment relationship while those studying demersal fish were more interested in the survival of spawners in the adult population (Holt 2008). It was Garth Murphy (1967) who first published observations to demonstrate that among groups of related species, those with the most variable recruitment had the greatest longevity; he explicitly suggested that such species needed to maintain a reproductive population over a longer period than congeners living in more stable environments.

Using the late Ransom Myers' data-base of recruitment in 250-odd stocks, it is easy to demonstrate that longevity responds principally to recruitment variability rather than to latitude and that the Murphy relationship described above holds among about 75 clupeid stocks, rather than his original 5 - and also in other groups as diverse as gadoids (68 stocks) and scombroids and tuna (18 stocks): only flatfish appear to be exceptional, for reasons easily understood from the manner in which they settle into their characteristic habitat after larval life (Longhurst 2002).

In a population with a pristine age distribution, each cohort maintains a hypothetical fecundity level that remains almost unchanged from first maturity through to the very last years of life — over, that is, a period of 15-20 years — even as their numbers are progressively reduced by natural mortality. There is thus a simple relationship between the extent to which longevity is reduced by fishing and the period over which a dominant year-class is able to continue to produce ova at an almost constant rate (Longhurst 1999).

Here, then, is a second reason to suppose that the progressive loss of older fish in the population is likely to reduce the success of a fished stock. If industrial fishing so modifies stocks that the surviving females are able to produce only less-than-normally successful larvae, and only over a shorter-than-normal period of years, then it is very difficult to be optimistic about the sustainability of the enterprise.

CONCLUSIONS

I have no illusions that this short essay has actually shed any light on the truth or otherwise of the axiom that their surplus production is offered to us by the marine ecosystems. But I hope that I may at least have reminded my readers of the depth of our ignorance about the functioning of marine ecosystems, and how little we know about the life history parameters of marine fish. The extent of our inability to predict future states - or even to specify instantaneous states - of fishery ecosystems appears to be very largely ignored by those who are presently planning for the future of fish stock management. It seems to be assumed that if information or understanding is needed, it will be available; the paucity of descriptive data, and the depth of our ignorance of biological processes, is little discussed.

Exactly who started the stampede towards ecosystem-based fishery management doesn't matter, but his or her success has been astonishing. Nor does it matter that many people have emphasised that the term

doesn't really mean what it seems to mean, and that all that is implied is the recognition that both physical and biological environmental variability have consequences for stock status. One still reads bizarre statements - such as this gem that I found in a University of Miami forum of 2004: *"Ecosystem-based fishery management (EBFM) is a new direction for fishery management, essentially reversing the order of management priorities to start with the ecosystem rather than the target species"*.

It is astonishing to what extent organizations like FAO, NOAA and DFO have developed and embraced unproven approaches like EBFM and to what extent EBFM is formalized in policy statements, and even in international agreements. The assumptions about what may be possible are breath-taking. It is for that reason that I suggest that simple "selective conjectures" such as the assumption of surplus production from fish stocks, should be examined very carefully at the present time.

Perhaps fisheries scientists should be spending as much time thinking about their fundamental assumptions as they currently do in thinking about how their management procedures could be fixed. I offer for their further consideration, without any comment on my part, the ecological concept of population regulation, which is - and always has been - a necessary axiom of fishery science. Yet density-dependent population regulation, according to ecologist Barryman in 2002, had been described in the previous 15 years or so as a *"bankrupt paradigm", "a monumental obstacle to progress", "a mind-set, a dogma, a faith"*, without "*emerging consensus*" and lacking "*widespread evidence*" for its existence. He concludes that population regulation is really nothing more than a descriptive term for one of the emergent properties of population dynamics, that may or may not be exhibited by some natural populations, but not by others, and according to varying circumstances...

No wonder, then, that Sidney Holt (who, after all, helped to write the book on fishery science) suggested in 2006 that he had spent most of his life "*opposing the hubris of managing the ocean and its contents: a losing battle, I'm afraid*...".

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