

Viewpoint

Murphy's law revisited: longevity as a factor in recruitment to fish populations

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Received 22 May 2001; received in revised form 1 June 2001; accepted 15 June 2001

Abstract

Most fisheries selectively remove larger, older individuals from the pristine stock, thus, truncating its natural pyramid of age classes and reducing its natural and characteristic longevity. Theoretically, this may lead to a reduction in its fitness despite compensatory growth of survivors; this largely forgotten suggestion of Garth Murphy is supported by new evidence relating recruitment variability to natural longevity. For at least those stocks with highly episodic recruitment, the consequences of age-class truncation may be catastrophic, but this possibility is ignored by conventional fish stock management techniques. © 2002 Published by Elsevier Science B.V.

Keywords: Recruitment; Life history traits; Iteroparity; Longevity

At a meeting on the effects of fishing on marine ecosystems in Montpellier a couple of years ago, we were told by a representative of the World Wildlife Fund (WWF) that a good practical definition of an endangered species was one whose population was currently below 50% of the pristine size. This was greeted with some hilarity by the group, most of whom probably subscribed to the classical mantra of fishing theory that the pristine biomass of a stock should be fished down by about a half so as to induce compensatory growth of the survivors. But, for some important species, it seems to me that the WWF may have a point—an idea I want to explore here.

During the same period in which fishing theory evolved, a central theme of theoretical ecology was how life history strategies, maximising fitness of each species to its natural habitat could be generalised (MacArthur and Wilson, 1967). Studies of terrestrial

plants, insects and birds suggested that populations which must repeatedly re-colonise their habitat should mature early, have high fecundity and a short life span ('*r*'-selection) and populations having density-dependent mortality or constant population density should mature late, live long and have few offspring ('*K*'-selection) (Stearns, 1977). These findings have been taken into fish management theory in a very simple manner; it is suggested that fisheries based "on *r*-selected species are liable to be of boom and bust nature", while those based "on *K*-selected species will be characterised by relatively stable population sizes and catch levels" (Adams, 1980). Unfortunately, however, there is no agreement about which groups of fish ought, theoretically, to be most at risk from fishing; exactly the opposite case was made recently—that *K*-selected species "are more likely to be vulnerable to intensive exploitation, despite naturally more stable populations buffered against occasional recruitment failure by numerous year classes" (Jennings et al., 2001).

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But, in any event, the classic *r*-selection, *K*-selection hypothesis ignores fluctuations in mortality and fecundity schedules (Rochet, 2000) and was intended to refer only to species having fluctuating or stable adult mortality as was pointed out long ago (Stearns, 1976). For this reason, the model is not really appropriate for marine teleosts, most of which have planktonic larvae for which Murphy's law might be restated thus: "If something can go terminally wrong, it will, to a probability of at least 99.99%". Planktonic eggs and larvae typically suffer a mortality rate of 25–75% per day (Bailey and Houde, 1989) and it is only after some weeks that the mortality schedule of teleosts comes to resemble that of insects and birds, the organisms classically used in *r*-selection, *K*-selection simulations. Indeed, when fluctuating juvenile mortality is introduced to such a simulation, a population having the characteristic longevity of a *K*-selected stock then has competitive advantage over an *r*-selected stock. This was the contradictory and unexpected finding of another Murphy who supported his simulation by observing that among five species of herrings, sardines and anchovies, those with the most variable recruitment had the greatest longevity (Murphy, 1967).

Though largely ignored by fisheries scientists even in studies to which it would be directly applicable, this result came to exemplify the 'bet-hedging' reproductive strategy of general ecologists to express the concept that iteroparity within years would maximise the probability of recruitment success (McQuinn, 1997). This, of course, was not what Garth Murphy had in mind, but the concept was subsequently generalised to suggest that in a fluctuating environment with high juvenile mortality, the following combination of traits is desirable—late maturity, iteroparity, smaller reproductive effort, longer life, fewer young per brood and more broods (Schaffer, 1974). Translated into terms relevant to, say, the cod of the Grand Banks, this model appears to be a match for what we know of the life history strategy of its natural, unfished population.

So a reappraisal of Murphy's observations and deduction is desirable and has been performed for 251 stocks of marine teleost fish using data in the Myers recruitment series to which access can be had through the FishBase archives of the International Centre for Living Aquatic Resources Management (ICLARM), Manila. ICLARM maintains a continually updated version of the original archive, integrated

with other useful parameters including longevity. It must be emphasised that statistical variability (cvR), the measure used by Murphy and in what follows, is not the ideal indicator; what is really required is a relative measure of gaps between years of good recruitment episodes. And to assign appropriate significance to the variance found to be characteristic of each stock would then require a detailed understanding of their natural, unfished ecology.

However, the simple longevity and cvR data unequivocally confirm Murphy's observations, though more strongly for some groups than for others, as we might expect. Clupeid stocks having more variable recruitment clearly both live longer and mature later (Fig. 1) though different genera cluster differently, exactly as we should expect from the concept of "design constraint barriers" of Stearns (1977).

Clupea recruitment is most variable where subtropical western boundary currents encounter cold sub-polar gyral water and here, unsurprisingly, cvR for *Clupea* is maximal, taking a value of 197% off Newfoundland and 183% off Hokkaido. But the Baltic is protected from basin-scale oceanographic forcing and two stocks of Baltic herring have a cvR of only 34%. Relative longevity in *Clupea* follows a similar pattern and is not, as has been suggested for herring around Britain, simply a function of latitude and hence of water temperature (Fig. 2).

For demersal fish of the continental shelves, dominated by Gadiformes at higher latitudes and a variety of Perciformes in tropical seas, longevity is a weaker function of recruitment variability than among clupeids even when the data are reasonably stratified. This is to be expected since available values for longevity are much modified by fishing effects, and rather poorly represent the pristine age-structure; this observation is probably pertinent for all trawl-caught fish compared with those taken in gill-nets and seines, because these gears do not preferentially take larger individuals to the same extent as does a trawl. The relationship among demersal fish is most strongly expressed when, as for clupeids, an ensemble of closely related genera is analysed (Fig. 3).

Longevity of pleuronectiform flatfish is a very weak negative function of recruitment variability, and these fish form a useful exception to the remainder: for 32 stocks of flatfish, the mean value for cvR is only 49.1% and some very low values indeed are recorded, as for

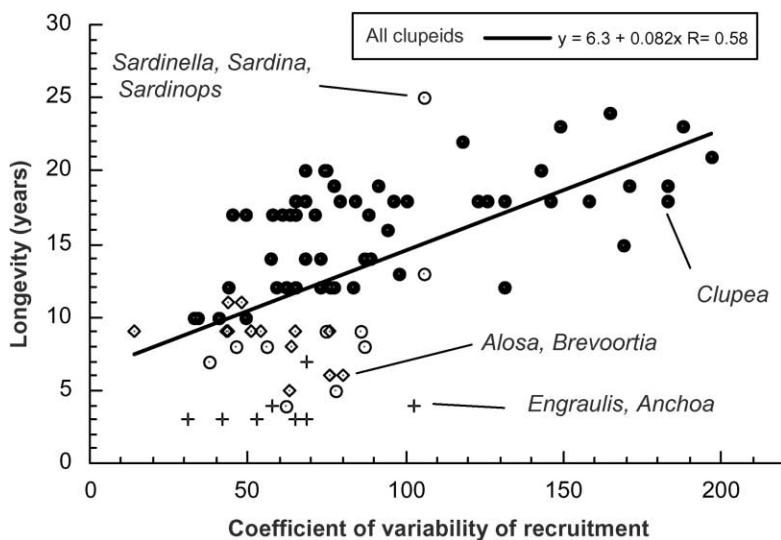


Fig. 1. Recruitment variability as a function of longevity among individual stocks of different genera of clupeids.

Solea in the Bay of Biscay (cvR = 15.8%). It is, perhaps, not coincidental that flatfish have a unique pattern of larval metamorphosis; this is categorised as abrupt, systemic and “apparent even to casual observation” (Chambers and Leggett, 1992). It has also been suggested that the limited areal extent of suitable sediments for larval settlement acts as a density-dependent,

two-dimensional spatial filter to regulate year-class strength.

Fish of deep banks and sea-mounts are extremely long-lived (see below) and perhaps have more intermittent recruitment than any other group of fish. The most extreme case known to me is the *Hoplostethus atlanticus* fishery south of Tasmania where almost all

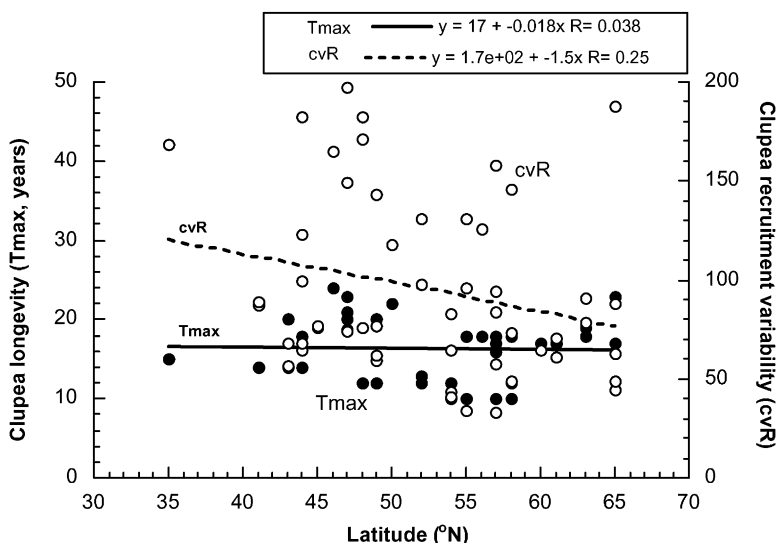


Fig. 2. Neither longevity nor recruitment variability is a simple function of latitude in functional groups of clupeids, here illustrated by stocks of *Clupea harengus* and *Clupea pallasii*.

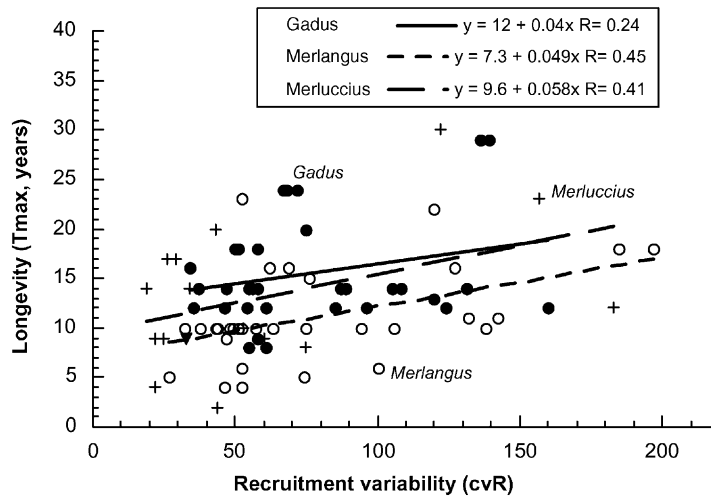


Fig. 3. Recruitment variability as a function of longevity among three groups of gadoid stocks: (i) *Gadus* and *Boreogadus*; (ii) *Merlangus* and *Pollachius*; (iii) *Merluccius* and *Micromesistius*.

fish are from a single, middle-aged year-class; similarly, the age-structure of the eastern Australian stock of the same species suggests at least a 20-year hiatus in recruitment (Koslow, pers. comm.). Ten species of Pacific coast rockfish (*Sebastes* spp.) have collectively experienced about 25 years of poor recruitment since 1977–1978 and *S. paucispinis* has a recruitment/stock ratio which varies by a factor of 1790 (Ralston, pers. comm.); northeast Atlantic rockfish have recruitment pulses every 5–10 years with almost nothing between.

For all these rockfish, annual natural mortality rates must be very low of order 0.05 or less (Koslow et al., 2000).

There are few data for open-ocean pelagic fish, but these (Fig. 4) also demonstrate the Murphy relationship in at least two ensembles—oceanic tuna (*Thunnus* spp.), and smaller pelagic predators, mostly *Caranx* and *Scomber*.

I infer that the observed relationships between longevity and recruitment variability reflect the adjust-

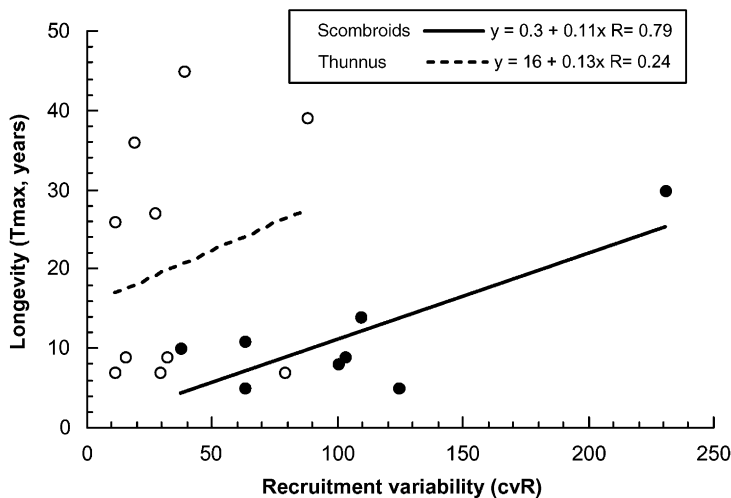


Fig. 4. Recruitment variability as a function of longevity among large pelagic species, exemplified by tuna and swordfish (*Thunnus*, *Katsuwonus*, *Istiophorus*, *Xiphias*) and some other pelagic genera (*Scomber*, *Scomberomorus*, *Trachurus*, *Seriola*).

ment of life history traits to the demands of reproductive ecology. I suggest too, that the findings explicitly support the concept that longevity of individual fish in the parent stock may be a crucial factor in sustaining recruitment wherever oceanographic variability is such that a match is not assured between the seasonal pulse of plankton growth and the date on which larvae need to start feeding.

The relatively low seasonality of many low latitude oceanographic regions induces relatively stable between-year recruitment variability. Batch spawning, with relatively weak seasonality in batch frequency, is commonplace among pelagic fish (Hunter et al., 1986) of warm seas, and some fish—such as tropical tuna—spawn almost continuously (Schaefer, 1998). Also typical are the shallow-water, demersal fish (Sciaenidae, Polynemidae) of the Gulf of Guinea, which are short-lived (5–7 years) and produce cohorts at about two monthly intervals during most of the year (Longhurst, 1964). Recruitment to these stocks is rather stable between years.

On the other hand, the long-lived fish of high latitudes tend often to exhibit recruitment variability of the kind observed by Hjort for Norwegian herring. When long recruitment time-series are available from high latitudes, these tend to show a background of small year-classes interspersed with occasional years, or small groups of years, when recruitment is significantly more successful. Here, seasonal plankton growth (if not always phytoplankton biomass accumulation) occurs as a vernal pulse during which primary production rate increases by a factor of 30–40, while the abundance of crustacean microplankton, the principal food of most larval fish, increases by about an order of magnitude. Although most teleosts here do spawn early in the year, there is no certainty that the occlusion of their larvae shall coincide with the increase of microplankton, the schedule of which responds directly to between-year variability in atmospheric forcing. This observation has been formalised as the “match–mismatch” hypothesis of recruitment variability (Cushing, 1982).

Under such conditions, longevity must confer a selective advantage. Since fecundity is a function of individual biomass, and because most species continue to grow throughout life, each year-class has the potential to sustain its annual egg production over a long period, even while progressively losing individuals to

natural mortality in the absence of a fishery (Longhurst, 1999). In this way, a stock may be able to sustain its spawning potential intact across long periods when “mismatch” is the rule.

But this model is not appropriate to all long-lived species. Some temperate reef fish have both great longevity and an unusual growth pattern; the pomacentrid *Parma microlepis* has a normal growth trajectory to about age 12, then puts on little more weight to the end of a 35–40-year life span (Tzioumis and Kingsford, 1999). Since *Parma* is territorial and population density on the reef varies little between years, fitness is bestowed by the holding of territories for extended periods; in this case, growth would be counter-productive once a territory is acquired. The growth pattern of pomacentrids is different from that of the larger hard-ground, warm-water lutjanids and serranids which grow slowly and continuously to much larger sizes; in these, territoriality is not so extreme.

The demersal stocks targeted by trawl fisheries on oceanic banks and the continental slope down to 1000 m have great longevity; these are the rockfish (*Sebastes*), orange roughy (*Hoplostethus*), rat-tails (*Macrourus*) and oreos (*Allocyttus*) which have, in the data discussed here, a mean longevity of 56 years. At the extreme, a specimen of *Sebastes aleutianus* has recently been quite confidently aged at 205 years (Kris Munk, pers. comm.).

Like *Parma*, the growth rate of these long-lived fish may flatten after maturity. *Hoplostethus*, for example, grows very slowly and matures after 20–30 years having a potential lifetime of order 125–150 years (Fenton et al., 1991). After maturity, these fish put energy preferentially into fecundity rather than growth, a strategy apparently matched to the exigencies of their habitat, because retention of larvae may be the key to a successful year-class. Reproduction of *Hoplostethus* occurs at 800–900 m over or around isolated oceanic banks, and the rather large planktonic eggs rise through the water column perhaps to be retained above the bank during the brief 15-day planktonic phase. The extremely episodic recruitment of these fish suggest that this is a relatively rare outcome, as has also been suggested for haddock (*Melanogrammus aeglefinus*) on Rockall Bank. This stock recruits strongly only in exceptional years when an anticyclonic Taylor column above the bank remains continuously in situ for a sufficiently long period to

retain haddock larvae during their entire planktonic phase (Dooley, 1984).

The evidence seems overwhelming that the life history traits of each species are tuned to match the problems posed by its natural habitat, and logic demands that this fact should not be ignored. And, by extension, logic also surely demands that a fishery for a species having intermittent recruitment must somehow eschew the common practice of truncating the age-structure so as to induce compensatory growth?

It is perhaps only among species whose habitat yields a reliable return of planktonic larvae to recruit to the juvenile population that we may expect a stock of teleosts to sustain a modern fishery indefinitely if managed by contemporary population models. Note that the eastern Pacific yellowfin tuna stock has yielded a total catch and a catch rate that has been sustained with very minor fluctuations since 1962.

By extension from this conclusion, it is quite likely that marine mammals could be exploited indefinitely because their recruitment success is well insulated from variability in the physical environment. So the stochastic population models developed by the Scientific Committee of the International Whaling Commission (Holt, 1998) would perform as predicted if whaling once again becomes fashionable or necessary. And if incidental catches could be controlled, selachians—sharks and rays—could also be successfully managed with the same models, since these fish likewise avoid the uncertainty of a planktotrophic larval period; each female produces only a few, large young each year.

In making this case, I should also offer a retraction of a letter I wrote to 'Nature' long ago from our laboratory in Sierra Leone (Longhurst, 1961): "In general, the tropical West African demersal fisheries depend on only a small number of year-classes, and this may be expected to have important consequences in any management policy—variations in the brood strength from year to year will have far greater effect on availability than is the case in cold water species, where the landings may depend on 10- or 20-year classes". I now think I got it backwards, as have others more recently; under comparable fishing pressure, a good case can be made that it is the warm-water fish which can best accept truncation of their age-structure while continuing to maintain a satisfactory level of recruitment varying little between years.

If the thesis that age-truncation by fishing is apparently unavoidable and yet, may be ecologically unsustainable for some species, then what follows? Fisheries science, collectively, is probably not easily for turning so that changes will come very slowly, and the models welded into the routines of management agencies will continue to be deployed *faute de mieux* for many years. It may be difficult to persuade these agencies to support a search for alternative solutions.

But a lot could be done with the tools already in hand. For a start, even if it is undefined, perhaps, the precautionary principle should be invoked even further in fishery management. Perhaps, a formal watch should be kept on the evolution of the age-structure of each stock, routinely to compare it with that of the pristine population. I emphasise 'pristine' because the longevity that is assumed for many stocks today is the maximum age that was observed when the fishery was already well established and the age-structure probably already truncated.

With the aim of maintaining a more stable age-structure that characterises many cold-water fisheries today, it should be possible to establish a code of conduct so that progressive and long-term truncation of the age pyramid, such as the one that occurred in the Newfoundland cod stocks, could be identified. A warning signal could then be used to justify an easing-off of fishing pressure and a progressive reduction in catch-quotas until the trend should be reversed. In fact, I believe that such "Traffic Lights" are even now being discussed in relation to management of the eastern Canadian fisheries.

There is also encouraging evidence from just a few regions that deliberate re-building of stocks is feasible if management agencies are clear-headed about what needs to be done; one such exceptional case appears to be the Alaskan fishery now managed under the strictures of the Magnuson-Stevens Act of 1996 which requires that fishery management plans should explicitly consider the state of essential fish habitat (Witherell et al., 2000). The Alaskan exception, where all groundfish stocks are still considered healthy after 20 years of sustained exploitation suggests that management agencies must carefully control by-catches and the fishing gear appropriate to each fishery, marine protected areas must be established to encompass significant parts of the habitat of particularly sensitive species, monitoring of stock status on scientifically

sound principles should be established and that zero-tolerance enforcement both at sea aboard the fishing vessels and in fish-plants ashore must become the norm. It also goes without saying that industry (and their bankers) must discover ways of operating with a variable resource, since allowable landings will certainly fluctuate significantly from year to year in almost any fishery in cold seas. Political pressure from owners of fish-plant and boats to maintain undiminished their supply of raw material was a major factor in the collapse of the Newfoundland cod.

Perhaps, if all this can be accomplished, we may yet hope for some renewal of the lost fisheries, but never again should we believe that recourse to numerical stock assessment models alone will serve for management as has been almost universally assumed in the past.

Acknowledgements

I am grateful to many friends who have helped me, either by locating data or by discussing these problems, and especially for their criticisms of earlier drafts. I wish to thank Crispina Binohlan, Bill Doubleday, Paul Fanning, Sidney Holt, Tony Koslow, Milton Love, Ransom Myers, Dan Pauly, Steve Ralston, Scott Parsons, Kurt Schaefer, Peter Shelton and Mike Sinclair.

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