Life History Strategies for Marine Fishes in the Late Holocene

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ABSTRACT

Things change. Organisms flourish or flounder in response. This little essay is an attempt to utilize the rudiments of population biology acquired in three decades experience as a fisheries biologist to assess the likely patterns of response of a highly diverse taxa to the introduction of a single exotic species. Or, more directly, how will the marine fishes which survived the turbulence of the Pleistocene respond to ten thousand years of interaction with a marine primate ?

RÉSUMÉ

Les choses changent. En réponse les organismes prospèrent ou disparaissent. Ce petit essai constitue une tentative pour utiliser les rudiments en biologie des populations que j'ai acquis au cours de trois décennies d'expérience en tant que biologiste des pêches et qui ont été consacrées à évaluer les patterns probables de la réponse d'un taxon à l'introduction d'une seule espèce exotique. Ou, de façon plus explicite, comment les poissons marins qui ont survécu les turbulences du Pleistocène répondront à dix mille ans d'interaction avec un primate marin ?

INTRODUCTION

It is well known that fishes are the ancestors of all terrestrial vertebrates; however, it is not generally realized that mammals arose 80 million years before teleosts and that the teleosts which dominate today's seas evolved along with the modern mammals and birds following the massive extinction that brought the Cretaceous to a close about 65 million years ago (Table 1). Mass extinctions are followed by very extended periods with a depauperate fauna during which new forms evolve. Hobson (1994) has suggested that following the last mass extinction of marine fishes, at the end of the Cretaceous, the depauperate period lasted for about 10 million years (i.e., the Paleocene) and he notes that most forms of modern acanthopterygii arose during the Eocene.

Era	MYBP	Period	MYBP	Event
	-0.001	Late Holocene		Massive extinction
	0.0001	First modern fishing vessels		—
		Early Holocene		
	0.01			
		Pleistocene		
	1.8			Arctic glaciation begins
		Pliocene	3	Bering Sea opens to Arctic
	5			Isthmus of Panama closes
Cenozoic		Miocene		
	22			
		Oligocene	30	Most modern teleost families present
	35			
		Eocene		Rapid diversification of teleosts,
	55		55	mammals and birds
		Paleocene		
	65			Massive extinction
		Cretaceous	110	First diatoms
	140		145	First teleosts and birds
Mesozoic		Jurassic		
	210		225	Early mammals
		Triassic	245	First dinosaurs
	250			Massive extinction
		Permian		
	290		305	Early mammal-like reptiles
		Carboniferous	330	First reptiles
	360			
Paleozoic		Devonian	375	First sharks
	410		415	First bony fishes
		Silurian	425	First jawed fishes
	440			
		Ordovician		
	500		505	First agnatha
		Cambrian		
	590			

Table 1: The Evolution of Fishes. (MYBP= million years before present).

The descendants of the teleost fauna which evolved in the warm seas of the Paleocene and Eocene, when alligators were found north of the Arctic Circle (Dawson *et al.*, 1976) and temperatures at the bottom of the ocean were near 13°C (Crowley, 1983), today dominate the tropical and subtropical ocean. The largest component of today's marine fish fauna is the tropical Indo-Pacific fauna which is descendent from the Tethys fauna. The other two major faunas, i.e., the North Pacific and North Atlantic cold-temperate faunas, are descendant from the high latitude fauna of Panthalassa. These cold-temperate faunas were undoubtedly displaced from high latitudes to the mid-latitudes by the climatic deterioration which started with the build up of Antarctic glaciation in the Miocene (Berger, 1982), and accelerated in the late Pliocene and Pleistocene. Polar seas and deepwater regions are depauperate in marine fishes due to the small amount of time which has been available for fishes to evolve to the very cold marine climatic conditions which developed with the onset of extensive northern hemisphere glaciation about 2.4 million years ago (Shackleton *et al.*, 1984; Frakes *et al.*, 1993).

The recent or Holocene period started at the end of the last ice age, about 10 thousand years ago, and for the purposes of this paper I have divided it into the early Holocene and the late Holocene. The early Holocene - late Holocene boundary utilized in the paper coincides with the invention of the internal combustion engine. This boundary will, in the future, be easily noted in the increased lead and trace metal contents of estuarine and marine sediments. It is very clear that the early Holocene period was a period of mass extinction of large terrestrial vertebrates; however, there is no evidence of mass extinctions in marine vertebrates during this period. In fact, one of the major differences between the early and late Holocene is that humans had little effect on the marine environment in the early Holocene. The exception to this occurred near the end of the early Holocene when destructive land use practices resulted in massive sedimentation in the Mediterranean. The results can be seen at ancient sea ports such as Ostia in Italy and Utica in Tunisia which are now miles from the sea.

The late Holocene period can be characterized by the presence of modern fishing vessels employing a diverse array of technological improvements which greatly increase their capacity to harvest fishes. Synthetic twines for nets, hydraulic power sources and technological advances in net design have fostered the development of specialized purse-seines, high-rise bottom trawls, midwater trawls, and huge gillnets. A wide range of electronic devices are used to increase fish catching efficiency (i.e., radio, radar, loran, depth recorders, sonar, lidar, satellite navigation and net mounted telemetry). Airplanes and helicopters are used to locate fish schools, sidescan and multibeam sonars are used to precisely map bottom topography, and remote sensing from aircraft and satellites is used to identify environmental conditions which relate to fishing success (i.e., location of fronts, real time sea surface temperatures and ocean color). This increase in fishing technology has allowed the world's marine catch to increase from a minimum estimate of about 18.10^6 t in 1948 to a peak of $86.3.10^6$ t in 1989. Estimates of the world's marine fish catch prior to the invention of the internal combustion engine are unavailable but probably did not exceed 3.10^6 t. The great increase in the world's catch during this century has primarily been due to the expansion of fishing to species, stocks and geographical areas which were previously unexploited or lightly exploited. Although the technology has continued to improve, the world's marine catch has declined since 1989. It is clear that in many regions fishery yields have approached, or even exceeded, levels that will be sustainable. Pauly and Christensen (1995) recently calculated that the percentage of the annual primary production required to support existing fisheries and bycatch has already reached 25% in the world's upwelling ecosystems and 35% in the world's non-tropical shelf ecosystems. The potential for fisheries expansion in the future appears to be limited primarily to oceanic regions.

The premise of the present paper is that humans have caused and will continue to cause large alterations in the populations and diversity of marine fishes in the late Holocene. Most projections of the effects of human exploitation of the sea deal with a time scale of less than a decade and are primarily concerned with population fluctuations. I am not evaluating what will happen if current trends are projected for the next decade or even the next century, when the human population may be more than four times today's value. Instead, I am addressing what will happen over the next small increment of time on a geological time scale (i.e., the next ten thousand years). At this time scale, the effect of humans on marine fishes will be both direct (fishing, sedimentation, pollution, and the filling of estuaries), and indirect (changes in food webs and interactions between natural climatic changes and the direct effects) and it will primarily be expressed not in population fluctuations but in extinctions.

The purpose of the present paper is to examine the life history strategies for marine fishes which were successful in the Pleistocene and early Holocene and to compare them with strategies which would appear to be advantageous or disadvantageous in the late Holocene. The major assumption made is that global human population will not be markedly smaller than it was at the start of the late Holocene.

1. Successful vertebrate life history strategies of the late Pleistocene

At the end of the Pleistocene there were a number of similarities between the successful life history strategies of marine and terrestrial vertebrates. One of the most conspicuous strategies was the reduction of mortality by acquisition of large size. This strategy has been utilized by a wide range of pelagic fishes (tunas, billfishes, sharks, molas, and some jacks), demersal fishes (halibuts, groupers and some scianids and skates) and marine mammals (whales, sea lions and porpoises). Terrestrial examples are best seen in the wildlife parks of Africa, in the Paleolithic cave paintings of France and in the La Brea tar pits of California. A second strategy, aggregation to reduce predation, was utilized by mobile, highly social, often migratory, lower trophic level animals. Species with this life-history strategy (i.e., terrestrial herding herbivores, flocking waterfowl, and marine schooling planktivores) dominated the vertebrate biomass of terrestrial and marine environments at the end of the Pleistocene. Two other strategies, (i.e., those utilized by small generalists and small specialists) were utilized by a large number of highly diverse species. Fishes with these strategies are often territorial and they generally do not achieve large population sizes.

The primary difference in the community structures of Pleistocene terrestrial and marine vertebrates is that the bulk of terrestrial vertebrates are herbivores whereas only a small component of marine vertebrates subsist on plants. Marine food chains therefore tend to be longer and more complex than terrestrial food chains and the marine fauna is more dominated by predatory forms than is the terrestrial fauna. Another major difference is that the majority of marine fishes have reproductive strategies which include high to very high fecundity, very small larval stages and no parental care. The consequence of the above is that most marine fishes have very high mortality rates during their early life history.

1.1. Life history strategies at risk in the late Holocene

There are a number of life history strategies which will be particularly at risk in the late Holocene (Table 2). The marine fishes which are most likely to disappear quickly are high trophic level predators which have suddenly themselves become prey to modern fishing vessels. These predators have the dual problem that they are now experiencing mortality rates greatly in excess of those which occurred prior to their exploitation by humans and in addition their prey is now greatly reduced by the same predator that is preying on them. The most susceptible of the predaceous fishes are those which have relied on the king-of-the-reef strategy (i.e., large territorial fishes such as many of the serranids, lutjanids and lethrinids, and some of the sciaenids, sparids and scorpaenids). These fishes often have considerable longevity, a delayed age at maturity and their recruitment is often small in relation to population biomass.

Large to moderate sized, predaceous, territorial reef fishes and rockfishes which have late age at maturity, very low natural mortality rates and low recruitment rates vs. adult stock size:		
	Snappers	Lutianids
	Sea Basses	Serranids
	Scavengers	Lethrinids
	Rockfishes	Scorpaenids
	Sea Bream	Sparids
Large to moderate sized shelf dwelling, soft bottom predators which are susceptible to bottom trawling:		
	Cods	Gadids
	Flounders	Pleuronectids
	Soles	Bothids
	Rockfishes	Scorpaenids
	Croakers	Sciaenids
	Skates	Rajids
Large to moderate sized schooling midwater fishes susceptible to midwater trawling:		
	Hakes	Merluccids
	Rockfishes	Scorpaenids
	Armorheads	Pentacerolids
	Roughyes	Trachichthyids
Shelf dwelling, pelagic, estuarine dependent or anadromous fishes which home to restricted spawning grounds or have low fecundity:		
	Herrings, shads	Clupeids
	Capelin, eulachon	Osmerids
	Salmon	Salmonids
	Sharks	Carcharhinids, Squalids
Large to moderate sized shelf dwelling, schooling, pelagic fishes:		
	Bonitos, sierras	Scombrids
	Jacks, trevallies	Carangids
	Corvina, weakfish	Sciaenids
	Barracudas	Sphyraenids
	Salmon	Salmonids
Any species with exceptionally high monetary value:		
Bluefin tuna	Red snappers	Salmon
Halibuts	Groupers	Red mullets
Aquarium fishes	Medicinal fishes	Billfishes

Table 2: Obvious losers.

Fishes susceptible to capture by bottom trawls (such as the shelf dwelling gadids, pleuronectids, bothids, sparids and scorpaenids) are likely to have high extinction rates. Many of these species have a delayed age at maturity which is associated with their large size. In addition to the delayed maturity problem, skates and demersal sharks will be particularly at risk due to their low fecundity. Many of the smaller species which are presently not targeted by bottom trawl fisheries, but whose habitat is subject to trawling, are likely to face increased exploitation as the primary trawl species become less abundant and they also face increased mortality through incidental capture and decreased productivity through alterations in habitat caused by many centuries of trawling. Schooling midwater or epibenthic species which are susceptible to midwater trawling, such as hakes, armorheads, roughies and some scorpaenids, will also be at risk.

Pelagic, schooling fishes are particularly susceptible to capture by modern purse-seines and gillnets. Prior to exploitation by fisheries, small and mid-sized pelagic fishes (sardines, anchovies, herrings, mackerels and jack mackerels) achieved real reductions in mortality by aggregating in dense schools. This behavioral pattern, which was highly successful in the early Holocene, now results in greatly increased mortality when these species are targeted by a fishing fleet using modern fishing technology. Aggregation of fishes into dense schools allows a modern purse-seiner to kill all, or nearly all, of the fish in a school in a single set. While schooling is likely to be a very poor strategy for the late Holocene; shoaling (i.e., when numerous fish schools are in close proximity) is even worse. When shoaling occurs in some species (i.e., clupeids and engraulids) a modern fishing fleet can kill several hundred thousand tons (i.e., more than 10 billion fish) in just a few days. In most small pelagic fishes the survivors from one day of fishing re-aggregate in schools which are less numerous but essentially of the same size as the original schools. This behavioral trait is particularly mal-adapted for the late Holocene as it results in a situation where mortality rates due to fishing do not decrease as the population size decreases. The behavioral traits which allowed many small schooling fishes to reduce their mortality rates from predation in the early Holocene now often result in greatly increased mortality rates from modern fishing fleets. On the positive side, there will be a reduction in predation rates for many of the small pelagic fishes as fishing will reduce the numbers and diversity of their predators. The trade-off between increased fishing mortality and decreased predation mortality may allow some small pelagics to increase both their ranges and population sizes while others will be at risk of extinction (Beverton, 1990). Generally the tropical small pelagics will be the most likely to have population and range increases as pre-exploitation predation rates tended to be higher in the tropics due to the highly diverse tropical fauna. Also tropical species are more likely mature at an early age and to be indeterminate spawners, which may allow them to maintain or even increase their fecundity under the altered physical environments, species composition and age structures of the late Holocene. Cold-temperate and subpolar small pelagics are the most likely to be at risk as they have higher ages at maturity and tend to spawn only once per year at established locations.

The mid-sized and larger coastal, pelagic predators such as the barracudas, bonitos, Spanish mackerels, salmons, and carangids which aggregate in schools are also at risk during the late Holocene. Many of these species have fast absolute growth rates and delayed ages at maturity, which makes them susceptible to recruitment overfishing.

Some fishes will be at risk of extinction in the late Holocene simply due to the fact that they have exceptionally high value to fishers. Examples include bluefin tuna, red snappers, groupers and aquarium fishes.

How will extinctions actually occur? Many species will simply fade away as a result of a life history strategy which does not produce enough new adults to replace those lost in the altered environments that will occur in the future. Many of those lost will be species which were relatively uncommon even before the rapid increase in exploitation by fisheries. It is likely that the changes in the populations of fishes will lead to large alterations in the invertebrate marine fauna and some fishes will disappear due to changes in the species composition of invertebrates which result in the destruction of their niches. Direct loss of habitat as well as physical or chemical alteration of habitats will remove some species, particularly fishes which utilize freshwater or estuarine habitats as part of their life history. Shallow reef and rocky bottom ecosystems, which contained the most complex and diverse marine fish communities in the Pleistocene, are likely to be highly altered by fishing, reef destruction, and sedimentation. The simple increase in mortality rates due to fishing will cause some species to go extinct. This is not likely in the next few decades; however, the effects of centuries of increased mortality will eventually take its toll. Many species will be stressed, but still viable under present climatic conditions but many of these will be lost during periods with different climatic conditions.

1.2. Life history strategies likely to be successful in the late Holocene

The late Holocene ocean will differ from that of the early Holocene in two major ways: a great reduction in the abundance of large and moderate-sized predators, caused by the increase and diversification in fishing power and an extensive physical, chemical and biological alteration of estuarine and nearshore environments. Many species will have greatly reduced population size and distribution and many stocks will eventually go extinct. Changes which will cause many stocks to decline and disappear will allow other types of fishes to increase both their ranges and populations (Table 3). A number of life history characteristics which occur in the present marine fish fauna appear to be particularly advantageous for the environment that is developing in the late Holocene (Table 4). Factors which will be of importance in determining which species will be favored include population rates, behavioral traits, genetic stock structures and habitat preferences. Obviously, avoidance of fishing mortality will be of high importance in the determination of which species will be successful in the late Holocene.

Population dynamics factors will be critical in the determination of which species will be successful during the late Holocene. Fishes which have low absolute growth rates (i.e., small maximum size) but high relative growth rates (i.e., they reach adult size quickly) will be favored. Fishes with an early age at maturity, high fecundity rates, and a high recruit to adult ratio will be favored. Fishes which have a relatively plastic age at maturity and/or indeterminate spawning (factors which allow excess energy to be readily used to increase annual fecundity) will have an advantage over those with a set age at maturity and set annual fecundity. Fishes able to persist under high mortality rates (i.e., those with a low natural mortality rate relative to their age at maturity or to their recruit-adult ratio) will also be favored. Fishes whose population size and or range has been limited by large or schooling predators could have great increases in their distribution and abundance as the abundance and distribution of predators is reduced.

Behavioral traits which will be favored in the late Holocene include nearly any trait which spreads out the population or makes it difficult for fishers to locate or harvest them. For example, it will be advantageous to be solitary or to live in small groups, to have an age-dependent habitat distribution, to be non-territorial, to be nomadic but to have little seasonal pattern in migrations.

Some habitats will be less affected by fishing and environmental alteration than others. Oceanic fishes will be less at risk than estuarine and neritic fishes; mesopelagic and bathypelagic fishes will be less at risk than epipelagic, benthic, and reef fishes.

It is possible that certain stock structure types will be favored. A species with a widely dispersed but relatively viscous stock structure (i.e., a stock which intermixes on a time scale of more than a decade) would be favored over a species with geographically restricted multiple genetic stocks each with fluid stock structure. The reason is that geographically restricted, multiple stocks can be decimated one by one whereas a single viscous stock can constantly recolonize areas from which it has disappeared. A fishery which only occurs over part of a stocks' range can drive a highly fluid stock to commercial extinction where a highly viscous stock would be maintained in the unexploited or less exploited part of its range.

Marine fishes have a broad spectrum of life history and behavioral characteristics some will be advantageous and others disadvantageous in the late Holocene. Species which have many characteristics which place them at risk may survive or even be abundant if the net effect of their life history strategy is favorable. The yellowfin tuna, *Thunnus albacares*, is a good example of a species with a mixture of favorable and unfavorable characteristics. On the negative side they are large, juveniles and young adults aggregate in schools which are susceptible to purse-seines, and they have a high value as food. They have a very high absolute growth rate and a low growth rate in relation to either their size at maturity or maximum size. The majority of yellowfin do not reach maturity until they are more than 120 cm; however, some reach maturity at 90 cm when they are about three years old. They are heavily exploited before they reach maturity and thereafter. Yellowfin tuna also have a number of characteristics which are favorable. They are oceanic and have a single, highly viscous genetic stock which is dispersed over the entire tropical ocean. The larger adults are too fast to be caught by trawls, too deep and too dispersed to be heavily exploited by purse-seines, and their catch rates appears to be directly density dependent. In addition they are indeterminate spawners with very high fecundity and they appear to be rather plastic in their age at maturity.

POPULATION RATES

- Low absolute growth rate.
- Small maximum size.
- High relative growth rate (vs. asymptote or maximum size).
- Small size at maturity.
- Early age at maturity.
- Indeterminate spawning.
- High recruit: adult ratio.
- Compensatory spawner-recruit relationship.
- Low natural mortality rate (relative to the von Bertalanffy parameter K).
- Ability to sustain a high natural mortality rate.

BEHAVIOR

- Solitary (as opposed to schooling).
- Mobile (as opposed to sedentary).
- Little pattern to movement (i.e. no set migrations)
- Non-territorial
- Age dependent habitat distribution.
- Avoidance of spawning concentrations

STOCK STRUCTURE

- Single widely dispersed genetic stock.
- Viscous stock (a fluid stock is available to more fishers).

HABITAT

- Oceanic (as opposed to coastal)
- Meso-pelagic
- Bathy-pelagic
- Neustonic
- Abyssal
- Non-benthic

BEST STRATEGY

- Be small, bony, ugly and unpalatable to primates

Table 3: Advantageous life-history strategies for the late Holocene.

Small offshore, non-schooling, meso-pelagic or epipelagic fishes:	
Lanternfishes	Myctophids
Cyclothone	Gonostomatids
Deepsea smelts	Bathylagids
Flying fish	Exocoetids
Small, solitary, ugly, shore fishes:	
Blennies	Blennids
Sculpins	Cottids
Poachers	Agonids
Prickbacks	Stichaeids
Kelpfish	Clinids
Small unpalatable, reef and slope bottomfishes:	
Lizardfish	Synodontids
Sandlance	Ammodytids
Gobies	Gobiids
Leatherjackets	Balistids
Toadfish	Batrachoidids
Small , reef and slope dwelling generalists:	
Cardinalfish	Apogonids
Damselfish	Pomacentrids
Soldierfish	Holocentrids
Wrasses	Coridids
Butterflyfish	Chaetodontids
Small, early maturing pelagics with indeterminate spawning:	
Tropical anchovies	Engraulids
Tropical herrings	Clupeids
Round herrings	Dussumierids
Scads, Jacks	Carangids
Frigate mackerel	Auxis

Table 4: Obvious winners.

2. Discussion

It is relatively easy to pick out life-history and behavioral characteristics which will place marine fishes at risk of extinction over the next several thousand years; anyone with local fisheries knowledge could add their favorite candidates to the lists of obvious winners and losers. However, it should be recognized that we have little real knowledge of the interactions between species, little information on crucial environmental interactions, and little ability to predict what will happen when the species composition of an ecosystem is highly altered. Some species which have a number of life-history and behavioral characteristics which put them at risk may become dominant species due to other of their characteristics which give them an advantage in the altered ecosystems of the future. In contrast some species which have life history characteristics which would appear to be advantageous in the late Holocene will become extinct due to alterations in food webs or interactions with species which have suddenly become abundant or scarce.

It is possible that some ecosystems will have more biomass of fishes than they have at present while others may become dominated by invertebrates. Rapid increases and decreases in the abundance and distribution of species should be expected as the marine biota reacts to anthropogenic alterations of their habitat. This type of occurrence may have already happened in several ecosystems; for example the 'gadoid outburst' in the North Sea, the sparid outbreak off of northwest Africa, the gobid outbreak in the Benguela current. The best - excuse me: the worst - example is the present situation in the Black Sea (See Daskalov *et al.*, this vol.) where environmental alteration has resulted in an incredible change of the community structure.

3. Fisheries management

One of the early fisheries science concepts is that prior to exploitation there was some sort of an equilibrium state and that the fisheries would be able to achieve an equilibrium maximum, or 'optimum', yield from a population if we could just get fishing mortality at the right level (Roedel, 1975). In many areas of the world we currently have the knowledge to tell when stocks are over harvested and depleted; but very few areas of the world have political regimes capable of managing a stock at a fishing mortality rate which would even approach 'optimum' levels.

The political and fisheries regimes that I am most familiar with, those of the USA, are examples of fisheries management at the beginning of the late Holocene. Both the Pacific and Atlantic coasts of the USA have bellwether fisheries which have been exploited for several centuries, have great economic and cultural importance, many decades of well funded multidisciplinary research and extensive state-of-the-art fishery management regimes. The bellwether fishery on the Atlantic Coast is the George's Bank groundfish fishery and on the Pacific Coast it is the salmon fishery. The fisheries regimes for both fisheries are based on the concept of achieving the 'optimum yield' of the individual regulated species. The groundfish fishery harvests a mixture of marine fishes whereas the salmon fishery harvests just a couple of anadromous species but each species has/had many isolated genetic stocks. Evidence was available for each fishery which clearly showed that the principal stocks were being overharvested and that the populations were in an extended state of decline. The management regimes in each of these fisheries can only be credited with overseeing the collapse of its fishery. In discussing the collapse of the George's Bank fishery, Apollonio (1995) suggested that part of the problem was that "we don't know in fact how to control fishing mortality in multi-species groundfish fisheries". He even questioned the very concept that the management regime was based on "what is optimum yield (OY) anyway?" The situation with the Pacific Coast salmon fishery of the Washington to California region has had equally bad success in reducing mortality; which in this case includes extensive alteration of the river systems utilized for reproduction and early life history. This fishery is now only maintained by fish hatcheries, a large number of genetic stocks have already been driven to extinction and many more are endangered (Nehlsen *et al.*, 1991).

Most current fisheries management regimes operate on concepts based on equilibrium states. John Issacs has suggested that the marine fauna is never at equilibrium and that it is constantly recovering from environmental perturbations on a wide range of time scales (Behrman, 1992). If one takes Issacs' view and includes anthropogenic impacts (i.e., increasing fishing pressure and environmental alteration), one is led to the conclusion that the expected pattern which will occur over the next few thousand years in most fisheries ecosystems is a series of extensive but unpredictable changes.

It is possible that a fisheries management regime based on long-term preservation of species diversity will someday prevail. Fishery management regimes are of course primarily dependent upon political regimes which, history teaches us, are very ephemeral. One should therefore not be led to the conclusion that any fishery management regime will last longer than the political regime it was based on. In my opinion a strategy of reliance on fisheries management appears to be inferior to one based on being a small, quick growing, early maturing, non-schooling, offshore fish which is unpalatable to primates.

I would place my bet that the late Holocene will be a myctophid heaven.

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