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FISH STOCKS

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GLOSSARY

biomass Collective weight or mass of all the members of a given population or stock at a given time, or, on the average, over a certain time period.

bioquads Occurrence record of organisms, serving as key units for biodiversity research and consisting of four elements (species names, location, time, and source).

catches The fish (or other aquatic organisms) of a given stock killed during a certain period by the operation of fishing gear(s). This definition implies that fish not landed, that is, discarded at sea, or killed by lost gear ("ghost fishing"), should be counted as part of the catch of a fishery.

ecosystem Area where a set of species interact in characteristic fashion, and generate among them biomass flows that are stronger than those linking that area to adjacent ones.

recruitment Entry of juvenile fish into the (adult) stock. Recruitment is distinguished from reproduction, because the eggs and larvae that result from fish spawning usually suffer tremendous and largely unpredictable mortalities, thus uncoupling spawning from recruitment.

trophic level A number indicating the position of a species within an ecosystem though the number of steps linking it to the plants. By definition, plants are TL = 1, herbivores are TL = 2, and so on. Note that trophic levels do not need to be whole numbers; intermediate values occur among omnivorous consumers.

FISH STOCKS ARE POPULATIONS OF "FISH," THAT IS, VERTEBRATES WITH GILLS AND FINS, SUBJECTED TO EXPLOITATION BY HUMANS. Populations are components of species, inhabiting part of their overall range, and usually having little genetic exchange with adjacent populations. The major adaptations determining the spatial distribution of fish stock biomass pertain to the anatomy, reproductive biology, and respiratory physiology of the species to which the stocks belong. Also, fishing has become increasingly important to the biodiversity of fish, either through its direct impacts (changes of stock size and age structure, and overall biomass reductions, down to extirpation of populations), or by modifying the ecosystems in which they are embedded. Research devoted to monitoring the biodiversity of fish (or other organisms) must be able to handle large amounts of suitably formatted distributional information, here defined as consisting of "bioquads." Management regimes aiming at preserving fish biodiversity will have to include much stricter regulation of fishing and the establishment of no-take areas.

I. MAJOR ADAPTATIONS OF FISHES

A. Anatomy and Physiology

With about 25,000 recognized species in over 500 families, fish are the most diverse vertebrate group. However, their watery habitat, while failing to protect them from modern fishing gear, makes it difficult to fully appreciate this diversity, and the extent to which it is now threatened. It is even more difficult for us, as air breathers, to perceive the constraints under which fish, as water breathers, were forced to evolve.

Water is an extremely dense medium, 775 times heavier and 55 times more viscous than air. Also, water contains 30 times less oxygen than air, and this oxygen diffuses 300,000 times more slowly than in air. These physical constraints, which shaped all early life-forms, including the jawless predecessors of the fish, the agnathans, are best visualized by describing the major evolutionary trends leading from agnathans to modern fish (Fig. 1A).

The first of these trends was the evolution of jaws from the first upper and lower gill arches of agnathans. This built on the intimate connection, in the most primitive vertebrates, between the feeding apparatus (i.e.,

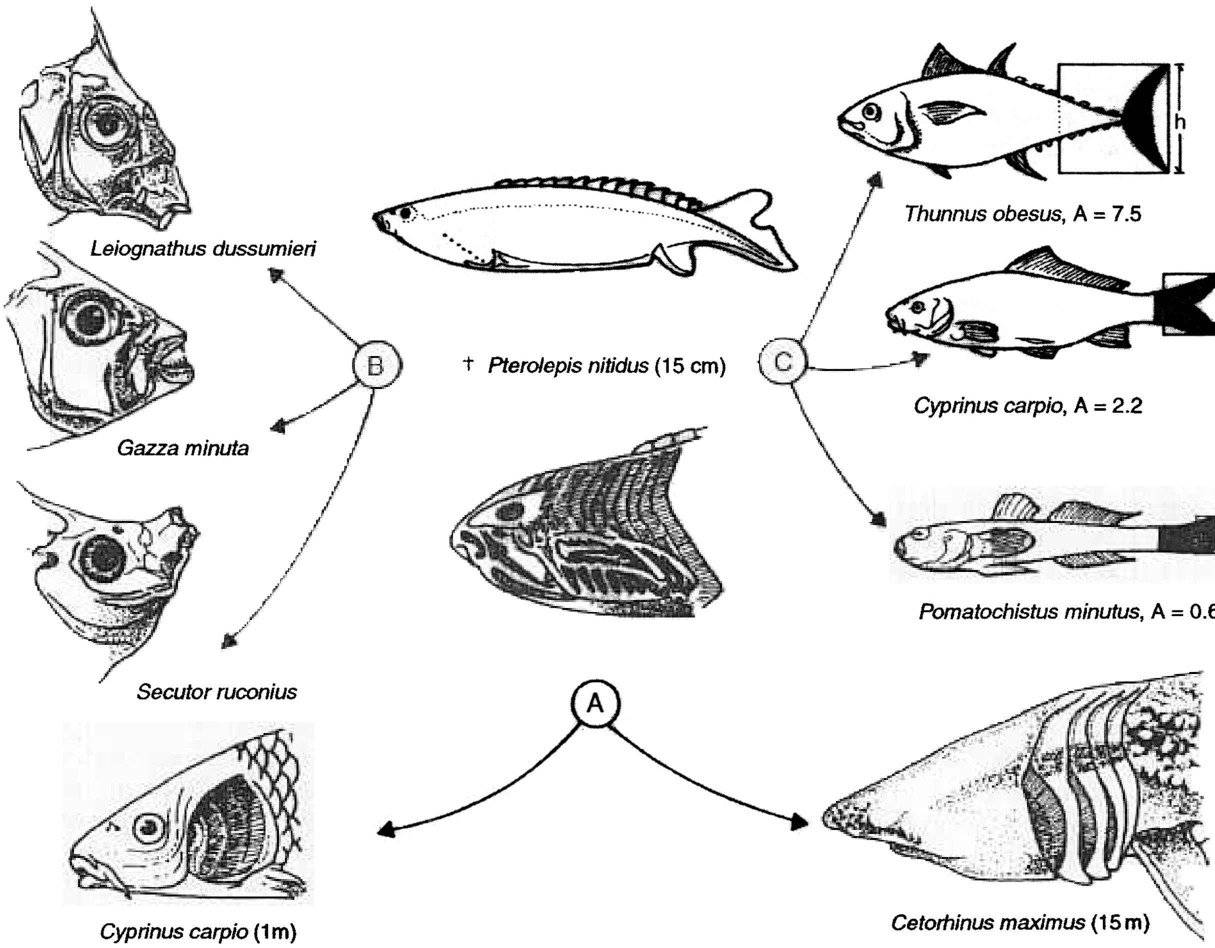

FIGURE 1 Major evolutionary trends from agnathans to extant fishes. (Note that no direct ancestor–descendant relationships are implied among the groups depicted.) (A) Trends toward larger gills; (B) trends toward efficient jaws; (C) trends toward effective paired and unpaired fins. [Note the aspect ratio of the caudal fin, defined by $A = h^2/s$, where h is the height and s the surface (in black) of the caudal fin, and of which high values define fast, large-gilled continuous swimmers, and conversely for low values.]

the mouth) and the respiratory apparatus (i.e., the gills adjacent to slits on both sides of the anterior part of the alimentary canal). Water-breathing invertebrates lack this close connection between feeding and breathing, one reason why even the largest among them (giant squids) cannot reach the mass of the largest fish (20 metric tons, for the whale shark *Rhincodon typus*).

The reorganization of the head of early fish allowed larger gills to evolve, which allowed the higher metabolic rates required for swimming in open waters. This transition was assisted by the gradual loss of the heavy armor protecting the slow, bottom-slurping agnathans. The fine "teeth" covering the bodies of sharks are vestiges of this armor.

Fast swimming in open water required better fins, both for propulsion and for steering. Propulsion is provided in most fish by oscillations of a caudal fin whose aspect ratio (Fig. 1C) gradually increased toward tunas and other derived, fast-swimming groups with very large gills. Steering, on the other hand, is provided by dorsal, pectoral, and anal fins. These fins are stiffened for precise action by hard, bony rays in the most derived fish, the teleosts, whose evolutionary success was further enhanced by a complexly built protrusile mouth that enables capture of a wide range of food items (Fig. 1B).

Subtle anatomical changes in fish can thus create more niches for increasing the numbers of specialists, which then occupy increasing numbers of closely packed niches. Ecosystems in which these changes have run for long periods, undisturbed by physical changes, therefore contain very large numbers of fish species. Their numbers are even larger in areas such as the Great Lakes of Africa and the tropical Indo-Pacific, where changes of water levels have repeatedly isolated basins and subpopulations, thereby accelerating species differentiation (Fig. 2).

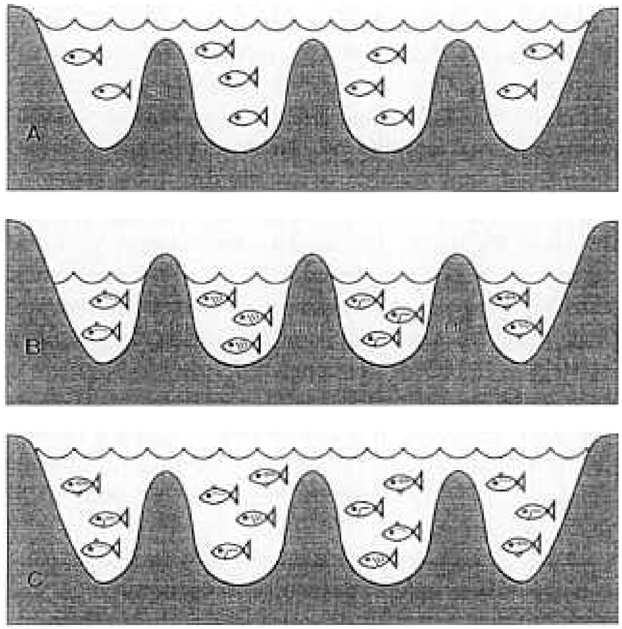

FIGURE 2 Schematic representation of how changes in water level can multiply, by creating isolated subpopulations, the number of species occurring in a given area. Such a mechanism, driven by repeated climatic changes, is thought to explain the large number of fish species in Southeast Asian marine waters and in the Great Lakes of Africa.

B. Reproduction and Recruitment

Though many ancient fishes such as sharks and rays or the coelacanth *Latimeria chalumnae* practice internal fertilization and produce few large eggs or live offspring, most recently evolved fishes produce numerous small eggs that are fertilized externally and develop as part of the plankton, without parental care. The larvae that emerge from those eggs, after less than one day in warm tropical waters and up to two weeks (and more for larger eggs) in cold temperate waters, are usually elongated, as befit small, finless zooplankton feeders.

The average zooplankton concentrations that these larvae encounter, even during spawning seasons attuned with zooplankton production cycles, are usually far too low to allow survival of fish larvae, and the overwhelming majority of such larvae perish. Those that tend to survive usually happened to have hatched within plankton-rich water layers. These layers are usually a few centimeters thick and last for only a few days of calm, between wind-driven or other mixing events, such as storms or upwelling pulses, that enrich surface waters with nutrients from deeper waters. This implies that large biomasses of fish can build up only when and where the local oceanographic conditions take the form of "triads" defined by (1) nutrient enrichment, such as generated by wind-driven mixing, (2) high plankton concentration, such as generated by various mechanisms including fronts, and (3) retention of larvae, required to prevent these weak swimmers from drifting away from suitable habitat. In pelagic fishes that build high biomass, for example, the anchovies and sardines in coastal upwelling systems off northwestern and southwestern Africa, Peru, and California, these triads occur only when the coastal winds range from 4 to 6 m per second. Weaker winds do not generate enough enrichment, and stronger winds disperse the larvae offshore.

Fish have developed several strategies to deal with the uncertain recruitment that results from the triad requirements. One is being small, short-lived, and capable of quickly building up large biomass under favorable environmental conditions. The other is being large, long-lived, and capable of weathering long series of recruitment failures through repeated spawning by old, large, and highly fecund adults. An example of the former strategy is provided by the Peruvian anchovy *Engraulis ringens*, whereas the northern cod, *Gadus morhua*, provides an example of the latter. Yet another strategy is to reduce the dependence on environmental conditions by various forms of parental care, such as nesting and guarding (e.g., in catfishes, family Clariidae), mouth-brooding (e.g., in cardinal fishes, family Apogonidae), and live-bearing (e.g., in ocean perches, genus *Sebastes*).

Another important feature of fish stocks is that, contrary to earlier assumptions of homogeneity, most appear to consist of well-differentiated individuals, each aiming to reproduce at the very place where it was hatched. Or, put differently: most migratory fish tend to "home." This behavior, well documented only in Pacific and Atlantic salmon (*Oncorhynchus* and *Salmo*, respectively), implies that individual fish, when reproducing, do not seek "optimal" sites, but rather spawn as close as possible to the site at which they hatched, and to which they are imprinted. This tendency to either stay in or return to a certain area makes it difficult for fish stocks to rebuild once they have been decimated by local overfishing or pollution.

II. RESPIRATORY CONSTRAINTS TO GROWTH AND RELATED PROCESSES

A. Basic Geometrical Constraints

Fish growth, as in other animals, requires both food and oxygen, the latter being required to synthesize the substance (adenosine triphosphate or ATP) that serves as fuel to all organisms. For oxygen to be metabolically available, it must be inside the fish body, that is, it must have passed though its gills. Thus, since oxygen cannot be stored inside the fish body (contrary to food, which can be stored as gut contents and as fat), the metabolic and growth rate of fish are largely proportional to the surface area of their gills. So fish that quickly reach large sizes have gills with large surface areas (as in tunas), and conversely in slow-growing fishes (like groupers). Moreover, gill area per unit of body mass declines with size, because the two-dimensional gill area cannot keep up with the three-dimensional increase of body mass. Hence larger fish dispose of relatively less oxygen to supply their metabolism, the reason why they ultimately stop growing. Also, environmental factors that tend to increase metabolic rate—especially elevated temperatures, but also including other form of stress—have the effect of reducing the maximum size that the fish of a given population can reach (Figs. 3A and 3B). This is why tropical fish tend to be smaller than their respective cold-water relatives. A similar mechanism explains the nearly constant relationship in fish between size at first maturity and maximum size (Figs. 3C and 3D).

B. Adaptation to Respiratory Constraints

Fish have evolved various strategies and tactics to overcome respiratory constraints. One strategy, illustrated in Fig. 1B, is to evolve large gills, a route taken by numerous open-water ("pelagic") species, culminating in tunas (Fig. 4).

Another strategy is the evolution of life cycles in which the juveniles migrate to deeper, cooler waters as they grow and then, upon maturing, produce eggs that quickly float up to the warmer surface layers, out of reach of the often cannibalistic adults. Such typical cycles are completed by an onshore drift of the larvae to coastal areas, and productive shallow nurseries for the early, voracious juveniles, which again migrate into deeper waters as they grow.

A tactic to accommodate metabolic stress, which is particularly useful in areas with strong seasonal temperature oscillations, is for the feeding adults to store fat during the warmer part of the season (late summer to early fall). Fat requires far less oxygen for maintenance than protein of muscle and other tissues. As temperature declines, the accumulated fat is converted into other tissues, notably gonads, whose contents are shed in spring, thus reducing body mass when temperatures again start to increase. These cycles, which use fat as protection against respiratory stress, are the reason why temperate fish tend to contain more muscle and visceral fat than tropical species, where temperatures, although high, do not fluctuate much in the course of a year.

Another tactic that delays respiratory stress is associated with ontogenetic shifts in diet composition. Here, the young fish feed on a diffuse, small prey (e.g., invertebrate zooplankton), while the adults, via their sheer size, can capture energy-rich prey such as other fish, which are acquired at lesser cost by the predator.

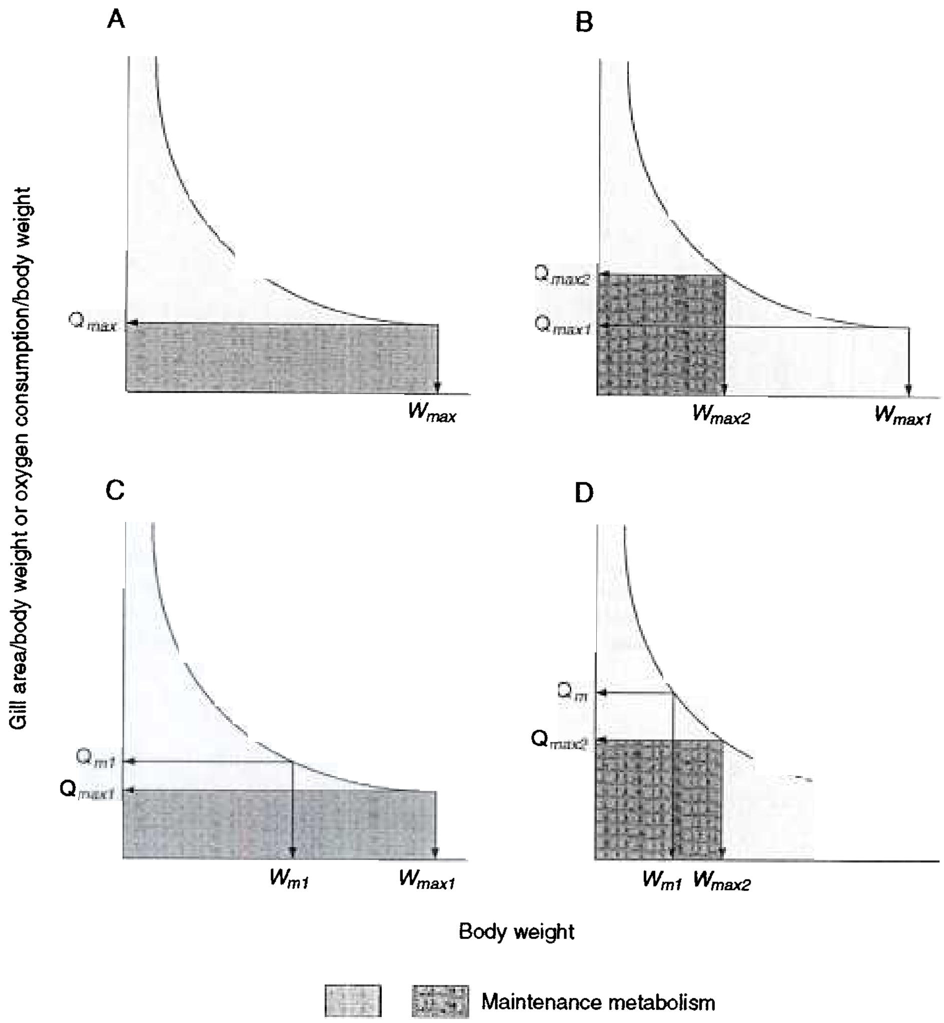

FIGURE 3 Schematic representation of the relationships linking, in fish, respiratory area (and hence metabolic rate), maximum body size, and size at first maturity. (A) As body size increases, gill area per body weight decreases, down to a level when it suffices only for maintenance metabolism. This defines the maximum size that can be reached. (B) Any environmental factor increasing oxygen demand for maintenance (such as elevated temperature) reduces the maximum size that fish can reach. (C) The relative metabolic rate at first maturity (Q_m) is necessarily higher than that associated with maximum size (Q_{max}). (D) An evolved, near constancy of the ratio Q_m/Q_{max} (about 1.4 from guppy to tuna) ensures that fish destined to remain small (as in case B) also spawn at smaller sizes.

C. Relationships between Growth and Mortality

Whichever strategy and tactic fish use to grow, more time will be needed in large species than in small fish for the size at first reproduction to be reached. Large sizes thus imply, other things being equal, more time during which the growing fish may become the prey of some predator. Hence the evolution of large fish was coupled with a reduction of their relative vulnerability to various predators, mainly by their ability to grow quickly through "small-size" stages in which mortality is highest. Fish capable of reaching large size and that have a high longevity also have low rates of natural mortality (Fig. 5). Hence fishing tends to have a stronger impact on species with low natural mortality, such as sharks or rockfishes. Because these are often the top predators, their reduction tends to disrupt the food webs in which they are embedded.

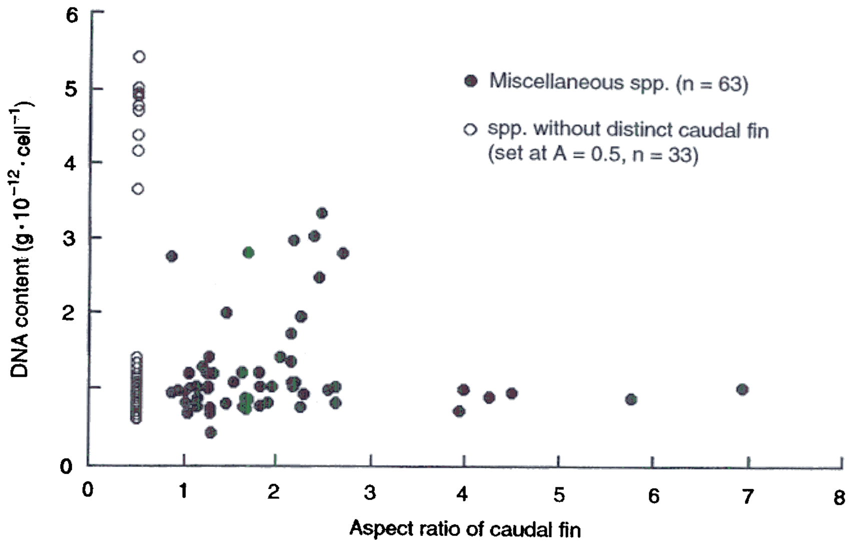

FIGURE 4 Relationship between DNA contents of body cells (a measure of cell size) versus caudal fin aspect in fish. Note triangular patterns, indicating that active fish with high aspect ratios are limited to small cells (which are metabolically more active than large cells), whereas more sluggish fish may have either small or large cells. Based on records in *FishBase 98*.

III. DISTRIBUTION OF EXPLOITED FISH STOCKS

A. Overall Distribution Ranges

Although mostly confined to water, fish occur in a wider range of habitats than any other vertebrate or invertebrate group. Thus, fish range from the upper reaches of streams in high mountain ranges (e.g., many river loaches, Balitoridae) to the mouths of temperate and tropical rivers (e.g., many gray mullets, Mugilidae). In the marine realm, fish range from the intertidal to the ocean's abyss, both as predators in their desert-like expanses (e.g., skipjack tuna, *Katsuwonus pelamis*) or as components of the rich, newly discovered deep-sea vent ecosystems (e.g., some live-bearing brotulas, Bythitidae). Environmental adaptations include the ability to deal with an enormous range of pressures (from

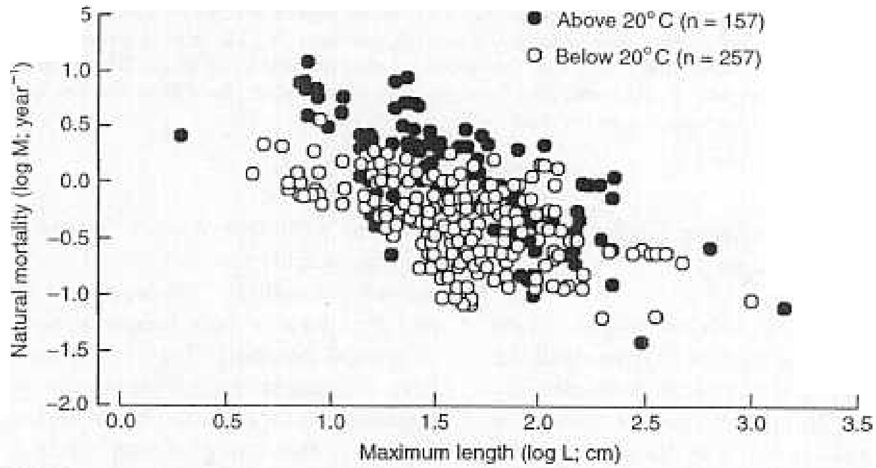

FIGURE 5 Relationships between maximum length, temperature, and rate of natural mortality (*M*) in fish, based on records in *FishBase 98*.

about one to hundreds of atmospheres), temperatures (from −1.8°C in polar waters to about 40°C in hot springs, tolerated by some tilapias), and salinities (from close to distilled water preferred by the discus fish, *Symphysodon discus*, of Amazonia to about 10%, e.g., in West African hypersaline coastal lagoons inhabited by the blackchin tilapia, *Sarotherodon melanotheron*), to list only three environmental factors. No single fish species or family, however, spans more than small fractions of these ranges. Rather, these various adaptations are exhibited by a bewildering variety of forms, ranging from minute gobies that are fully grown at close to 1 cm (e.g., *Mystichthys luzonensis*) to the 15 m reached by whale sharks (*Rhincodon typus*). These two species, incidentally, are exploited for food in the Philippines. The former, despite its turnover rate, is in danger of extinction in the small lake where it is endemic because of overfishing and pollution. The latter will be extirpated if the new directed, export-oriented fishery for this slow-growing fish continues.

B. Adaptations to Open-Ocean Habitats

Fish have different strategies to deal with the low production of the oceans. Tuna have adopted a high-energy strategy, wherein their tightly packed schools quickly move from one food patch to the other, essentially hopping from one "oasis" to the next and minimizing the time spent in the intervening desert-like expanses. Others, notably the lantern fishes (Myctophidae), occur in scattered populations that, at dawn, migrate from 1000 m down to the surface waters, and back again at dusk. These different strategies imply very different biomasses: tens of millions of metric tons for the major tuna species (prior to their recent depletion by various longline, purse seine, and other fisheries) against an estimated global biomass of one billion metric tons for the lantern fish and associated communities. The latter number is often viewed as a promising figure, from which various estimates of potential yields have been derived. Most of these estimates, however, do not consider the extremely dilute nature of this biomass (usually less than 1 g per metric ton of water).

C. Shelf Communities

1. Definition of Neritic Stocks

Most fish stocks are neritic, that is, occur above the continental shelves, the productive areas of shallow waters (down to 200 m) around the continents, from which about 90% of the world marine fisheries catches are extracted. Shelves may have rocky or soft (sandy or muddy) substrates, and usually support two weakly connected fish communities, one species-rich and consisting of bottom or "demersal" fishes, the other consisting of fewer species of open-water or "pelagic" fishes. The fish of demersal communities are those exhibiting the specialized fins and mouths mentioned earlier, enabling utilization of distinctive food sources, particularly on reefs in both temperate and tropical regions.

On coral reefs, this fine partitioning of resources culminates in hundreds of fish species sharing a single reef, with dozens of specialists for each of its food resource types, from the filamentous algae consumed, for example, by damselfishes (Pomacentridae), the encrusting algae consumed by parrot fishes (Scaridae), the coral themselves, consumed by butterfly fishes (Chaetodontidae), to the small invertebrates consumed by, for example, wrasses (Labridae). A vast array of predators such as groupers (Serranidae) and sharks (Carcharhinidae) regulate the number of these smaller fishes. Hard-bottom shelves and, in tropical areas, the coral reefs that occur down to 30 m are also exploited wherever they occur. The fishing gear used over hard bottoms are mainly traps and handlines (the latter both sport and commercial), which are rather selective gears that would have relatively minor impacts were it not for their excessive numbers.

2. Demersal Fish Stocks

The demersal fish living in, on, or just above shelf soft bottoms consist of specialized flatfishes and rays and numerous generalized teleosts feeding on bottom invertebrates (the zoobenthos) and smaller fishes. The complex communities thus formed can reach very high biomass, at shallow depth in the tropics (20–50 m) and deeper in colder waters. In the warm waters of the tropics, bacteria induce a quick remineralization of the dead organic matter (detritus) falling out of the lighted part of the water column. This allows very little detritus to become available for consumption by the zoobenthos. In cold water, on the other hand, the short but intensive burst of algal production occurring in the spring is consumed only partly by the zooplankton of the upper water layers. Most of the remainder is consumed as detritus after falling down to the sea bottom as "marine snow." Thus, cold-water soft-bottom communities can occur in very deep waters, down to the shelf slopes (200–300 m) and well beyond. Indeed, the latest trend in fisheries "development" is the exploitation of deep-sea stocks of cod-like fish (order Gadiformes), orange roughy (*Hoplostethus atlanticus*), and other fish, down to depths of 1000 m or more, through ventures that even in principle could never be managed so as to achieve sustainability.

Wherever they occur, soft-bottom shelves are nowadays invariably subjected to bottom trawling, a very unselective fishing method that is environmentally damaging. This involves dragging a heavy, chain-studded net over the sea bottom and "catching," that is, removing all that it encounters. Not surprisingly, this procedure has often been compared to harvesting crops with a bulldozer. Trawler catches thus consist of targeted species (usually shrimps in the tropics and subtropics) plus a vast number of nontarget species, often the juveniles of demersals with large adult sizes, and literally parts of the habitat of bottom-fishes, notably sessile invertebrates and chunks of reefs lifted from the sea bottom. Nontarget species and debris are then discarded, and it is therefore trawlers that contribute most to the global discarding problem. Presently, about 30 million metric tons of various fish species are discarded; this is a very high discard rate when compared to the 90 million metric tons that appear in global landing statistics.

The contribution of trawlers to habitat destruction, including conversion of richly structured bottom habitats into featureless expanses of mud, is well recognized, and can only be compared in terms of scale with global deforestation and the ensuing trend toward desertification. Only recently has the impact on biodiversity of this mode of fishing begun to be evaluated in systematic fashion. The information so far available indicates high impacts and a tendency for small generalized fish and invertebrates to replace larger specialized fish, a trend that amplifies the food web effects to be described later.

3. Pelagic Fish Stocks

The pelagic communities over most shelf areas previously consisted of both major and minor stocks and stocklets of herrings, sardines (Clupeidae), anchovies (Engraulidae), and their relatives, and of their predators, notably mackerels and tunas (Scombridae) and various jacks (Carangidae). In many parts of the world, pelagic fisheries have eliminated the minor stocks and stocklets, and now depend wholly on annual recruitment to the remaining major stocks. The overfishing of old, highly fecund adults in these remaining stocks explains much of their volatility. Indeed, the present emphasis of much fisheries research on "variability" is thus devoted largely to a secondary phenomenon created by the fishery itself. It is true, however, that pelagic stocks, feeding lower in the food web, often closely track environmental changes, such as the decline of the Peruvian anchovy *Engraulis ringens* during El Niño events, and their subsequent rebuilding, mainly from recruits produced off northern Chile.

Pelagic fish tend to form tightly structured, dense schools, which protects them from predators and facilitates detection and herding of scattered food patches. The fisheries rely on this behavior when deploying purse seines, which can surround and catch such schools in one go, often with associated predators such as dolphins. Large pelagics such as billfish (Xiphiidae and Istiophoridae) are caught by arrays of longlines, set by the thousands along shelf edges, which also capture, besides the target species, large amounts of by-catch (notably sharks). These sharks were previously left on the spot, but are now finned before the carcasses are discarded. Longlines are indeed as unselective as the now banned giant driftnets that, in the 1980s, erected "walls of death" that were hundreds of kilometers long across the migratory routes of fish in the North Pacific and the Atlantic.

4. Overall Status of Neritic Stocks

When combined, the demersal and pelagic fisheries of shelves and adjacent waters represent major threats to fish biodiversity. Particularly endangered are groupers and other slow-growing bottomfish, and pelagics such as bluefin tuna and various species of sharks and billfish.

Besides the fisheries, one factor contributing to this endangerment is the traditional separation of research devoted to fisheries management ("stock assessments") from that devoted to conservation and to ecosystem research. Both lines of research are separated institutionally, in terms of their methods and publication outlets, and in terms of what they perceive as their mandates. Overcoming this separation is crucial if fish biodiversity is to be maintained in the face of the onslaught by fisheries. Key needs are the development of tools and concepts for integrating information on fish biodiversity and ecosystem function with the knowledge gained through a century of applied, single-species fisheries research. Before considering these, however, evidence for fisheries impacts on ecosystems will be presented.

IV. ECOSYSTEM IMPACTS OF FISHERIES

A. Historical Trends

The earliest fishing gear so far identified by archeologists are bone harpoons that were recovered, along with other evidence of systematic fishing, from a site 90,000 years old, in the present-day Democratic Republic of Congo (formerly Zaire). Tellingly, the main species that was targeted appears to have been a now extinct, very large freshwater catfish.

This pattern of fisheries exterminating the stocks upon which they originally relied, then moving on to other species, is now understood to be common. This contradicts earlier perceptions of the ocean's quasi-inexhaustible resources, as expressed among others by such Victorian grandees as the geologist Charles Lyell and the zoologist Thomas Huxley. They were misled by the then prevailing abundance of various stocks of coastal fish (notably herring, *Clupea harengus*), and by what may be called "Lamarck's Fallacy": the notion that "animals living in the waters, especially in sea-water ... are protected from the destruction of their species by Man. Their multiplication is so rapid and their means of evading pursuit or traps are so great that there is no likelihood of his being able to destroy the entire species in any of these animals."

The industrialization of the fisheries, first in Northern Europe and then in North America at the end of the nineteenth century, quickly showed these predictions to be wrong. Most coastal stocklets of herring and other small pelagics were extirpated, and faded even from memory, therein soon followed, after the introduction of bottom trawling, by coastal stocks of demersal fishes.

The practical response to this was the introduction of bigger boats with bigger engines, fishing farther offshore. Another response was the creation of research bodies (such as the International Council for the Exploration of the Sea, founded in 1902) to assess the reason why the resources were declining. Also, several countries (notably Norway and the United States) initiated costly programs wherein juvenile cod and other fish were raised in hatcheries and then thrown into the sea, in the vain hope that they would replenish the stocks rather than be eaten by happy predators (which they were).

B. Emergence of the Sustainability Concept

The First World War put an end to the stocking programs. It also established that a strong reduction of fishing effort, as caused by the drafting of fishers and vessels into the war effort, and the spiking of major fishing grounds by underwater mines (thus creating the first marine protected areas), would lead to a recovery of depleted fish stocks. Yet the Second World War, and another demonstration of stocks rebuilding themselves when subjected to less fishing, was required for the notion of sustainable fishing to establish itself. This notion implies that some appropriate level of fishing effort (number of vessels or gear, mesh size) exists such that catches (or "yield") can be maintained at high levels—hence the concept of "maximum sustainable yield" or MSY. This led to the emergence of "fish population dynamics" and "stock assessments," wherein mathematical models of single-species fish stocks and of their response to targeted fishing became the mainstay of fisheries research. R. J. Beverton, S. J. Holt, and J. A. Gulland in England, W. E. Ricker in Canada, and W. E. Schaefer in the United States proposed most of these still-used models during an extremely creative period lasting from the early 1950s to the mid-1970s.

Yet in spite of these advances, the fisheries never became sustainable. One obvious reason was that, given a resource to which access was essentially open, the fisheries never could limit their collective effort at the level supposed to generate MSY. Rather, effort levels increased well beyond that, permitting some fleet owners to increase their stakes even as the aggregate "rent" from the fisheries declined. Recent trends toward subsidization of offshore and distant water fleets, driven by international competition, have aggravated these economic issues, enabling commercial profits to be gained even from strongly overexploited stocks. These developments are so widespread that they have rendered obvious the impacts which fisheries have on ecosystems.

C. Fishing Down Marine Food Webs

The ecosystem impacts of fisheries are due mainly to the fact that the targeted fish function as part of food webs, both as consumers and as prey. Within food webs, the fish of different species occupy distinct trophic levels (TL), each defining a step away from plants, which have a definitional TL of 1. Thus, fish feeding on planktonic algae have TL = 2, fish feeding on herbivorous zooplankton have TL = 3, and so on. It is important here to recognize that most fish tend to have intermediate TL values (2.7, 3.5, 4.1, etc.), reflecting the catholic nature of their diet.

Fisheries, by removing biomass from one of several fish stocks, necessarily modify food webs, thus forcing predators of the targeted species to shift toward available alternative prey, if any. Such adjustments were previously not distinguishable from natural fluctuations. They have gradually become highly visible, however, because they change the mean trophic level of the landings extracted from different stocks. Moreover, the changes induced by fishing are not of a random nature, with decreases in one area matched by increases in another. Rather, they are directed, with a clear downward trend (Fig. 6A), due to the link between growth and natural mortality mentioned in Section II. Thus, in large fish, even a low level of fishing mortality generated by a well-managed fishery will quickly exceed the low level of total mortality (i.e., natural + fishing mortality) that can be accommodated by the stock. By-catch species are even more endangered because the fishing will not stop as their numbers dwindle until they are eradicated, as has happened with rays in the Irish Sea. The trend of mean trophic level resulting from this (see Fig. 6A), reflecting a phenomenon now known as "fishing down marine food webs," provides a clear indication that, globally, fisheries generate levels of effort well past those required for sustainability, however defined. Indeed, other indices can be used to indicate that global changes have occurred in the composition of global fisheries landings, and in the structure of the ecosystems from which these landings are extracted (Fig. 6B).

Fisheries-induced modification of the structure of marine and freshwater ecosystems has strong indirect impacts on fish biodiversity, in addition to the direct impacts of reducing the biomass of the target and associated stocks by a factor of 10 or more, as is usually the case. Incorporating these indirect effects in fisheries stock assessments has proven to be difficult so far. This is true for objective reasons (ecosystems are complex, and their behavior under exploitation, due to the large number of stocks to be considered, is difficult to simulate) and for subjective reasons (notably a perceived lack of suitable field data on these many stocks).

The recent development of robust ecosystem simulation tools should allow the first of these issues to be addressed. Overcoming the second not only involves pointing out the existence of suitable data, often lost in the "gray literature," but in making such data available in suitable format to all who are aware of the need for a transition from single-species to ecosystem-based fisheries assessments. This brings us to the issues related to the standardization, dissemination, and uses of biodiversity information.

V. MANAGING FISH BIODIVERSITY INFORMATION

A. Biodiversity as a Conceptual Challenge

There is a widespread perception that the main obstacle to the conservation of fish stocks and of fish biodiversity is "lack of data," a notion strengthened by public statements of biologists worried about the lack of funding for relevant research. However, simple lack of data cannot be the problem, not after the 250 years since Lin-

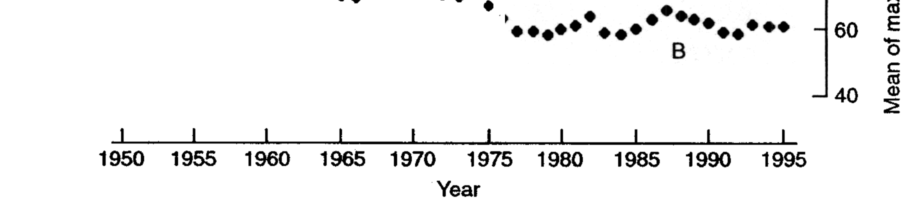

FIGURE 6 Trend, for the Northeast Atlantic from 1950 to 1996, of two indices of sustained fishing, based on landings originally compiled by the Food and Agriculture Organization of the United Nations, and other data in *FishBase 98*. (A) Trend in the mean trophic level of fisheries landings. (B) Trend in the mean maximum size of fish species in the landings. Note parallel declines, indicative of structural changes in the ecosystem from which the landings are extracted. Similar trends occur throughout the marine and freshwater fisheries of the world.

naeus created the taxonomic standards required for biodiversity research, 100 years of applied fisheries research, and at least 50 years of advances in ecosystem research. Rather, the problem here is the fragmentation of the database collected so far. Indeed, many studies conducted in recent years on the status of various stocks fail to consider previous knowledge on their relative abundance and distribution, and thus contribute to shifting baselines, wherein only the most recent and usually low estimates are used as reference for conservation or rebuilding efforts.

One reason for this reluctance of biologists to consolidate existing data into comprehensive, global databases may be due in part to the perception that biological data are too difficult to standardize, or are useless once standardized. Addressing these issues will be a key task of biodiversity research, and we now present a few ideas related to this.

There is consensus that the objects of biodiversity research are genes, populations, species, and ecosystems. However, there is little consensus as to what distinguishes biodiversity from the existing disciplines of fisheries biology, ecology, biogeography, population genetics, or taxonomy. As a result, the array of data being claimed to be essential for biodiversity studies reads like a composite list of the data traditionally used in the older disciplines, with few attempts at integration or prioritization. Such integration and prioritization are possible, however, by giving emphasis, in biodiversity studies, to data that are: (1) relevant to current research issues (e.g., richness, rarity, distinctiveness, representativeness, threat, function, and utility of species); (2) part of the data traditionally collected in taxonomy, biogeography, population genetics, and ecology; (3) widely available, in sufficient quantity; (4) pertinent to past, present, and most likely future trends; (5) easy to collect; (6) easy to standardize; (7) easy to verify; and (8) suggestive of new lines of research.

B. Bioquads as Key Biodiversity Data Sets

A minimum core of biodiversity information that fulfills these eight criteria is provided by "bioquads" (from "quads," short for quadriads), consisting of: (a) the scientific name of a taxon, usually a biological species or other evolutionarily significant unit; (b) the locality where a specimen of this taxon has been encountered; (c) the date (time) of the encounter; and (d) the authority or source reporting (a)–(c).

Of the research items mentioned under criterion (1), richness (number of species encountered) is derived directly from the bioquads from a given area. Distinctiveness (how much the species encountered differ from each other) is derived from the classification of these species into higher taxa such as families, orders, and classes. Representativeness (how closely an area represents a predefined ecosystem type) is derived by comparing observed species composition with the typical composition of the ecosystem type under study. The utility of species to humans can be derived from published, or local knowledge, or from catches in the case of fish. Status of threat can be derived from trends in the distribution area defined by bioquads. Rarity can be estimated from the number of bioquads available for a species in a given area, standardized by sampling effort.

Taxonomists have made a conscious effort to systematically compile data of this sort in specimen collections, and to publish them in original species descriptions and revisions. As a result, bioquad-type data are readily available in enormous numbers (about 10 million for fish alone) in museum collections, survey reports, historical photos and films, and other forms (criterion 3). While museum collections go back over 200 years, some literature contains verifiable records that date back to antiquity (criterion 4). Also, archeological data reach back to the dawn of modern humanity (see the earlier record pertaining to giant catfish).

Numerous scientific surveys and projects also continuously collect contemporary bioquads. Other sources are the commercial fisheries and the many laypersons whose hobby is to observe and sometimes to collect fish and other wildlife. These activities are most likely to continue in the foreseeable future (criterion 5). An increasing number of the preceding data sources are available in computer-readable form (criteria 3, 5, and 6).

Efforts do exist to standardize the elements of the bioquad (criterion 6). For example, the Species 2000 Initiative has embarked on the task of providing a standard reference list of the valid names of the known 1.75 million species sharing Earth with humans (see the website www.sp2000.org). Geographical coordinates and the international date and time format are obvious standards for items (2) and (3), although there remains a need for a global gazetteer to deal efficiently with localities reported without coordinates, and there is a need for standards to deal with date and time ranges. On the other hand, standards exist for sources such as printed publications, databases, photos, films, and personal communications. Many of these were considered when developing FishBase, a computerized database on the biology, ecology, and uses of fish containing a vast number of bioquads (see the following).

The necessary verification (criterion 7) of millions of data points can only be done automatically. Basically, a computer can verify a scientific name against a standard list, compare the indicated locality and date against the established range of a species, and judge the reliability of a source, for example, by the number of outliers it has reported previously. Procedures will have to be established, however, on how to deal with the different types of outliers, some of which may represent valid new information.

An important consideration is how fast a research agenda based on bioquads will be exhausted (criterion 8). Important here is the ability of well-structured relational databases to interlink independently developed data sets. Thus, the scientific name links to all available information on a species, including taxonomy, systematics, genetics, biology, ecology, and human uses. The locality connects to all available information on surrounding environments, including province, country, continent, habitat, ecosystem, and tectonic plate. The combination of species, locality, and date points to a population or stock. Date and time in connection with the locality can be used to infer a wide range of environmental conditions, from local temperatures to current fisheries legislation. The source relates to the human dimension, such as persons and institutions working on certain species groups or in a certain area, representing the scientific interface between humans and the other species (Fig. 7).

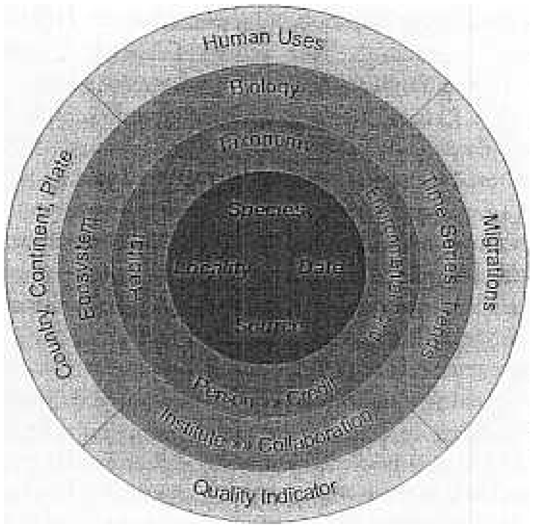

FIGURE 7 Interrelationships of the elements of biodiversity, articulated through the four elements of bioquads (species, location, times, and source).

bioquads as defined previously. Important here is that a new original of this graph is generated on the fly, from currently available bioquads, every time the relevant routine of FishBase is evoked, and that each of its "dots" can be clicked to verify the four elements of the underlying bioquad.

C. Databases as Tools for Management of Biodiversity Information

Two major initiatives presently exist to assemble and make widely available, for research on fish biodiversity, the information presently held by various institutions (notably museums). One is NEODAT, which makes accessible on the Internet about 400,000 bioquad records pertaining to freshwater fish of the Neotropics (NEODAT; www.fowler.acnatsci.org). The other is FishBase, an ongoing international collaborative project dedicated to assembling the estimated 10 million existing fish bioquads and to combining them with other, standardized biological information on fish. The intention here is to provide a global relational database, addressing head-on the data fragmentation issue mentioned earlier (see www.fishbase.org).

Figure 8 shows the geographic distribution of Nile tilapia, *Oreochromis niloticus*, through dots representing

VI. PRESERVING FISH BIODIVERSITY

A. Traditional Approaches to Stock Management

None of the foregoing considerations will help, however, if fisheries are allowed to continue undermining their resource base, which they will if fisheries management continues to rely on the panoply of approaches so far deployed. These traditional approaches include, among other things: (1) mesh size restriction; (2) restriction on the amount and/or species of fish that may be legally landed; (3) effort limitation, for example, through caps on the vessel tonnage that may deployed; and (4) seasonal closures.

Besides being extremely hard to enforce, these approaches—which are invariably conceived in the context of single-species assessments—fail to address the ecosystem effects mentioned earlier. Thus, mesh sizes

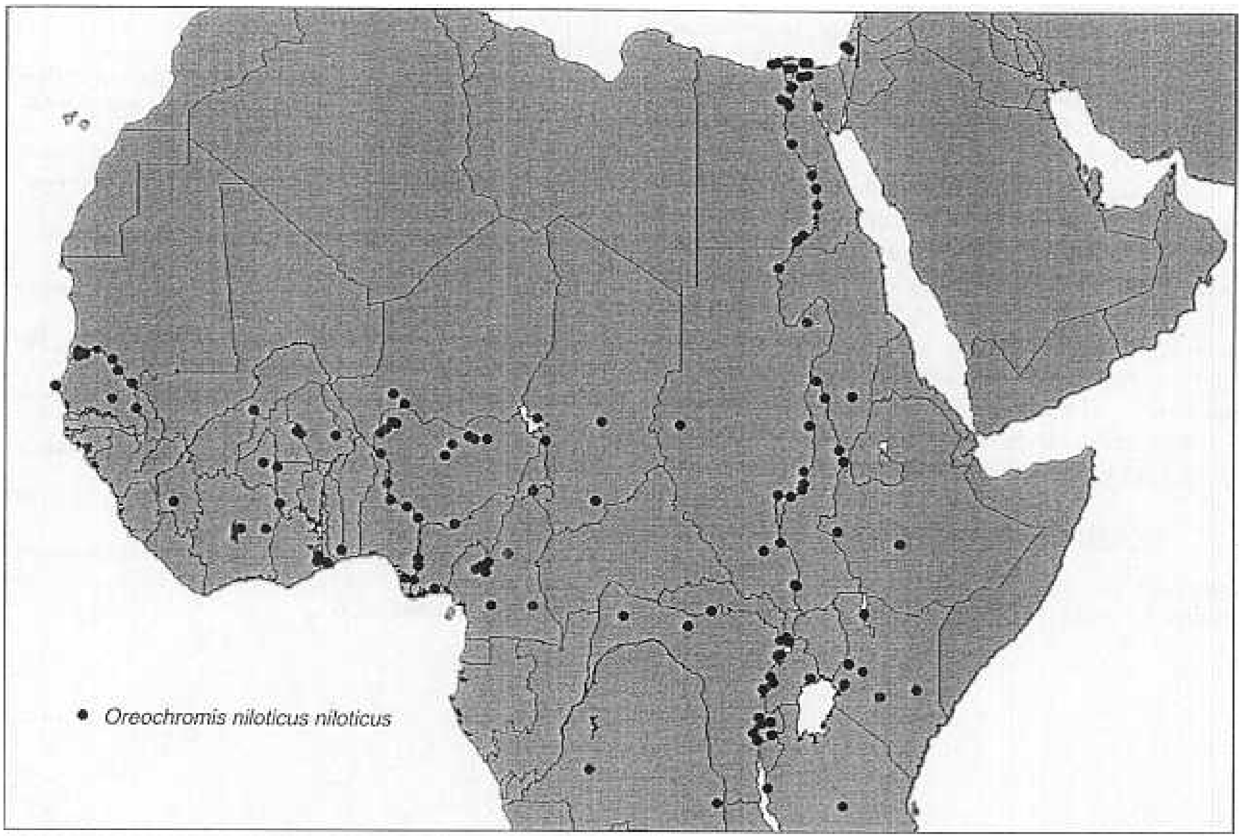

FIGURE 8 Distribution of Nile tilapia (*Oreochromis niloticus*) based on 425 bioquads contributed by the Musée Royal de l'Afrique Centrale, Tervuren, Belgium, and other sources. In the computerized version of this graph, each dot can be "clicked" to reveal the four elements of the underlying bioquad, thus allowing identification of outliers, temporal trends, etc.

above a certain limit, meant to protect the young of a given species, do not prevent associated species form being caught. Indeed, when combined with restrictions on total allowable catch (TAC), and on the landing of bycatch (as is often the case), mesh size restrictions become the very reason for discarding both the young of targeted species and the nontarget species. Limits on nominal fishing effort are subverted by technological developments, such as improved gears and navigation instruments (e.g., GPS), which increase the catching power of fishing vessels. Thus, government-run vessel retirement schemes often end up subsidizing the modernization of fishing fleets. Finally, seasonal closure of various areas usually has negligible ecological impacts, because the fishing effort expended during the open season is sufficient for the sea bottom to be scraped up numerous times by trawlers, and for the stocks of long-lived fishes to be severely impacted.

B. Marine Protected Areas

There is an emerging consensus among fisheries scientists and conservationists that the only fisheries management tool that will allow the recovery of damaged stock and ecosystems is the establishment of Marine Protected Areas (MPAs), including permanent No-Take zones as their core. Such core zones are easy to enforce—at least relative to the task of enforcing mesh sizes or TACs. Also, technology-driven increases of fishing effort can be ignored, and there is assurance that the long-lived organisms of seafloors and their associated fish communities can gradually return to a semblance of their original configurations. However, much research will have to be devoted to identifying the optimal size and location of MPAs, particularly for migratory stocks.

Still, traditional fisheries management, aimed at limiting effective fishing effort, will have to continue around MPAs, lest they become marine larders or fish-attracting rather than fish-producing zones from which resources are drained by fisheries operating at their very periphery.

Finally, the social context of fisheries will have to change: fisheries do not harvest crops they have sown. Rather, they exploit the natural productivity of wildlife; thus there are inherent limits to global fish catches, and future fisheries will not meet the demand of an ever-increasing human population. Indeed, the massive ecosystem changes already described indicate that these limits have been reached in most parts of the world, and that sustainable fisheries must be embedded in some form of ecosystem management.

See Also the Following Articles

ADAPTATION • FISH, BIODIVERSITY OF • FISH CONSERVATION • MARINE ECOSYSTEMS

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