Fish Stocks

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Abstract

Fishes occur in a wider range of habitats than any other vertebrate or invertebrate group, from the upper reaches of streams in high mountain ranges to the mouths of temperate and tropical rivers, and from the intertidal zone to the ocean's abyss. Fish grow in size, spawn and die, either from natural causes (predation, diseases, ageing) or from being caught in fishing nets if the population is exploited. These dynamical processes are expressed with mathematical equations and are used in population models to estimate fisheries reference points (stock assessment), which in turn provide the basis for fisheries management. Fish populations subjected to fisheries exploitation are called fish “stocks”. Fishing has been increasingly affecting fish stocks and ecosystems both directly and indirectly, and along with the human-induced climate change they pose major threats to fish biodiversity worldwide. Using the available data stored in local or global databases to assess the status of all stocks, even the data-poor fish stocks, and following an ecosystem approach to fisheries management that incorporates effort reduction through marine protected areas, may contribute to the sustainable exploitation of fisheries resources.

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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 through 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.

Key Points

Fish stocks are fish populations subjected to fisheries exploitation that may be regarded as an entity for management or assessment purposes. Although globally the number of depleted fish stocks has been increasing due to overexploitation, fishing effort restrictions may facilitate stock recovery.

Introduction

With few exceptions, fishes may be characterized as vertebrates that use gills for breathing in water and fins for moving. As in other groups of animals/organisms, fish species consist of populations inhabiting part of their overall geographical range, and usually having little genetic exchange with adjacent populations. The major adaptations of fishes, which determine their spatial distribution, pertain to their specific anatomy, reproductive biology, and respiratory physiology.

Fish populations subjected to fisheries exploitation are called fish "stocks". Fishing has been increasingly affecting fish biodiversity, either through its direct impacts (biomass removal, changes of population size and size/age structure), or indirectly by modifying the ecosystems in which fish are embedded. Research on fish biodiversity must interpret the huge amount of error-prone observational data in the context of the environmental preferences of the species and of their known native range. Climate change is also playing an increasingly important role in shaping fish biodiversity (population shifts, shrinking somatic sizes, migrations) but may also affect fish biomass, hence catch and fisheries operations.

Management regimes aiming at preserving fish biodiversity at the level of species, populations and genes, will have to include much stricter regulations of fishing as well as the establishment of marine protected areas to prevent overexploitation or rebuild already overfished stocks.

Fish Stock Dynamics

Fishes grow in size, spawn and die, either from natural causes (predation, diseases, ageing) or from being caught in fishing nets if the population is exploited. These dynamical processes are expressed with mathematical equations and are used in population models to estimate fisheries reference points (stock assessment), which in turn provide the basis for fisheries management. Russell (1931) was one of the firsts to describe the population dynamics processes with mathematical terms. He produced a mass balance equation which shows that the size of a closed population (i.e., assuming no emigration or immigration of individuals) will increase by recruitment (addition of young individuals to the exploited population) and by somatic growth (individual somatic gain in weight), while it will decrease by natural (deaths caused by natural causes such as predation and diseases) and fishing mortality (deaths caused by fishing) (**Fig. 1**). As in the earlier work of Baranov (1918), Russell maintained that rational exploitation should aim at maximum yields, and that maximum sustainable (or rational) yield occurs at the point of maximum population growth (Russell, 1931). Russell's mass balance equation is (**Fig. 1**):

$$B_{t+1} = B_t + (R + G) - (F + M)$$

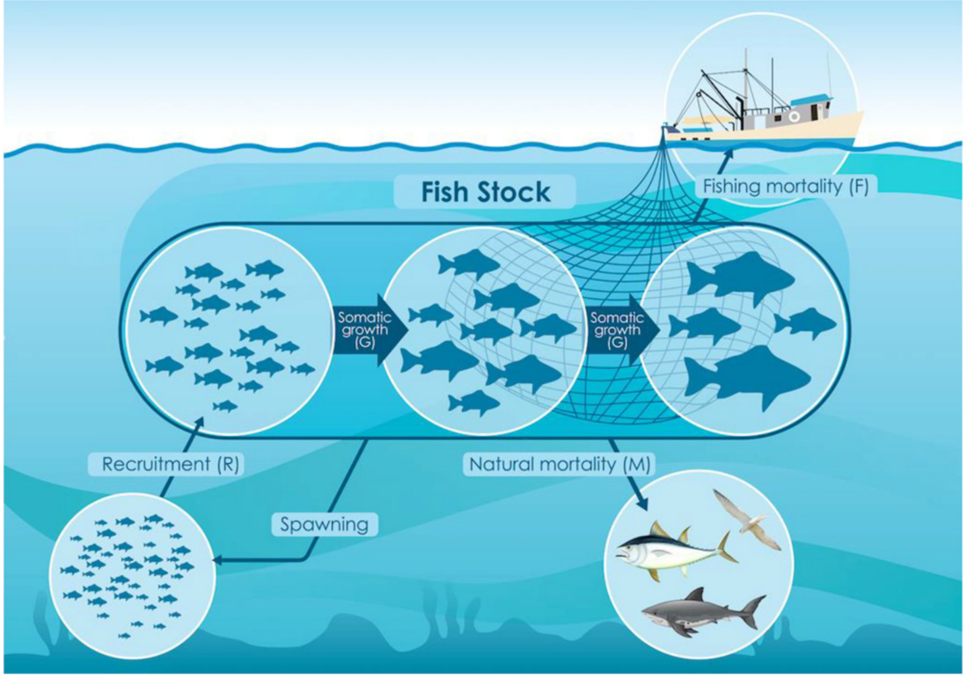


Fig. 1 Graphical representation of fish population dynamics according to Russell's mass balance equation (graphics by Louizos Verdaris).

where B_{t+1} is the biomass at time $t + 1$, B_t is the biomass at time t, R is recruitment, G is somatic growth, M is natural mortality and F is fishing mortality.

A population will be in equilibrium (balanced) when the total biomass production $(R + G)$ equals total mortality $(M + F)$. In order for a population to remain stable in biomass and abundance, fishing mortality (F) should not exceed the surplus production $(R + G - M)$, which is the biomass produced by the population through the processes of somatic growth (G) and recruitment of new individuals to the adult population (R) following a successful spawning act, minus the deaths from natural causes (M). In this equation, the biomass removal by fishing mortality (F) is the only anthropogenic parameter that can be controlled by fisheries management.

Spawning Dynamics

Maturity

Sexual maturity in fishes mainly depends on fish size, with small-sized species being shorter lived and earlier maturing compared to large-sized species. Gonad maturation is regulated by hormonal secretions of the pituitary gland and triggered, once a critical size has been reached, by external environmental (photoperiod, temperature) and other possibly exogenous factors that select for egg and larval survival and growth.

Several alternatives exist for defining length at maturity (L_m), but the generally accepted definition is the average size at which the individuals of a population mature for the first time or the average size at which 50% of the individuals in a population are sexually mature. Size at maturity is very important in fisheries management as it denotes the minimum size up to which fish should be allowed to grow so that they spawn at least once before being caught. The minimum conservation reference size (MCRS: the size below which fish should not be landed or traded – previously known as minimum landing size MLS) is a species-specific technical measure that is based on length at maturity and is applied to around 30 species in Europe aiming to avoid the catch of juvenile fish. The excessive exploitation of juvenile fish may lead to growth overfishing, which mostly affects slow growing, late maturing and long-lived species.

Size at maturity is estimated by plotting the proportion of mature individuals in the population per length class and expressing mathematically the resulting curve (usually logistic). This analysis requires sampling during the spawning period and identification of maturity stages. A wide range of sizes for both sexes needs to be collected during sampling, as the growth and maturation pattern may differ between males and females and because several fish species change sex during their life cycle (hermaphroditism).

Size at maturity is a function of the maximum attainable somatic (L_{max}) and asymptotic length (L_∞) of a population, with the corresponding ratios L_m/L_{max} and L_m/L_∞ being stable across populations of a species and species of a family. Therefore, when L_{max} or L_∞ are known for a population or a species, they can be used to derive L_m through empirical equations (Froese and Binohlan, 2000, 2003; Tsikliras and Stergiou, 2014; Pauly, 2021).

Fecundity

The energy available for fish spawning can be allocated in various ways and each species has developed a strategy that maximizes reproductive output with the least expenditure. There are species that produce numerous small oocytes or several and larger oocytes that are externally fertilized (oviparity), and others with internal fertilization – with the embryo being developed inside their body – that give birth to their offspring (viviparity). Although the range of reproductive strategies in fishes is very wide, two strategies prevail: the production of many small oocytes in actinopterygians and the production of large internally fertilized eggs in sharks and rays (Wootton, 1998). Species that produce numerous and small eggs are generally promiscuous, whereas those that offer some kind of protection (guarding, nest-building, mouth brooding, eggs deposition in cavities or burrows) are generally producing fewer eggs and have only one partner. Cohort dynamics in oviparous fishes is largely determined by the number of oocytes produced, which depends on species fecundity and the number of sexually mature females within a population. Egg and larval survival, as well as early stage natural mortality are important for annual recruitment (see next section) and future fisheries exploitation, especially in small pelagic fishes that are very susceptible to climatic and environmental changes.

Fecundity exhibits interspecific and intraspecific variability as a result of environmental adaptations and endogenous inherited factors that may also determine the quality of oocytes produced. The difficulty in measuring fertility in most marine fishes, mainly due to the external fertilization of their oocytes, has led to estimating the numbers of oocytes produced by each female fish. There are several definitions of fecundity in the literature arising from the various strategies fishes have employed for the maturation of eggs within the gonad and the frequency of their spawning (See "Relevant Website section"): absolute fecundity (total number of eggs in a female), annual fecundity (total number of eggs spawned by a female per year), batch fecundity (number of viable eggs usually released by a serial spawner in a pulse of spawning or number of hydrated oocytes released in one spawning).

In contrast to other vertebrates, parental care is very limited among the vast majority of fishes that exhibit very high fecundities but also experience vast mortalities in early life stages (eggs and larvae) until they grow in size. The high fecundity of actinopterygian fishes had led many scientists to believe that a heavily exploited fish population would be able to recover even from very low adult population densities (near extirpation) just because each female produces several hundred thousand or millions of eggs. This 'million-egg fallacy' led to the misperception of the effects of fishing on marine populations and to mismanagement, which caused the collapse of many stocks, including that of the emblematic Atlantic cod *Gadus morhua*. It has been estimated that, at low population densities, only 3–5 eggs per female survive to maturity despite the million of eggs that are shed and fertilized by males (Myers *et al*., 1999). When a population is not able to recover from very low population densities, then it characterized as having impaired recruitment. This phenomenon, known as "depensation", explains why many stocks fail to rebuild their populations despite being currently well managed.

Recruitment

Though many ancient fishes, such as sharks 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 (or 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 happen to have hatched within plankton-rich water layers. These layers are usually only 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 fresh waters and nutrients from deeper layers. 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 (Bakun, 1996). 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 sharks or ocean perches, genus *Sebastes*).

Another important feature of fish populations 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 (the genera *Oncorhynchus* and *Salmo*, respectively) and still under research due to technical challenges in the European eel (*Anguilla anguilla*), 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 (Cury, 1994). This reproductive strategy has proven successful in evolutionary time scales; however, it is not helpful in cases where climate change or pollution have impacted traditional spawning grounds, or where anthropogenic structures block the route to the parental streams or for stocks recovering from overfishing. In such cases, it is the fish making an "erroneous" choice to re-discover spawning sites that were abandoned during the depleted phase.

Growth and Mortality Dynamics

Somatic growth

Fish grow in somatic length and weight as they age. Contrary to warm blooded animals, fishes continue to grow throughout their lifespan, but growth rate slows down resulting in an asymptotic growth curve of length with age.

The age of individual fish can be determined through the counting of permanent marks formed on their skeletal structures (scales, bones, spines). Where such aging is difficult -notably in the tropics- the relative ages of fish cohort can be inferred from their length-frequency distributions. Growth in time is then estimated by fitting an asymptotic curve on lengths-at-age, or to length-frequency data.

This allows the estimation of the three parameters of the von Bertalanffy Growth Function or VBGF (von Bertalanffy, 1938):

$$L_t = L_\infty(1 - e^{-K(t-t_0)})$$

where L_t is the length at age t, L_∞ is the asymptotic length (the average length the individual fish would attain if they were to live indefinitely), K is the average rate at which asymptotic length is approached (often erroneously reported as 'growth rate'), and t_o is the hypothetical age of zero length. The parameter t_o is required to adjust for the fact that fish larvae do not grow according to this equation.

Asymptotic length (L_∞) refers to a hypothetical length at a future indefinite age, which by definition should be larger than any maximum length (L_{max}) measurement available for a specific stock. However, L_∞ is also a mean, potentially lower than the largest fish observed in a population (L_{max}).

Maximum age (t_{max}) and maximum length (L_{max}) records that are available at a species or population level can be used to determine the growth parameters L_∞ and K through empirical equations that were derived from large datasets and include thousands of species and even more populations. Asymptotic length (L_∞) can be estimated using maximum observed or reported length (L_{max}) according to the following formula (Froese and Binohlan, 2000, 2003):

$$\log(L_\infty) = 0.044 + 0.984\log(L_{\max})$$

The rate at which asymptotic length is approached (K) can be indirectly estimated based on maximum reported or observed age (t_{max}) using the following equation:

$$K \approx \frac{3}{t_{max}}$$

Natural mortality

Natural mortality (M) is defined as the deaths by natural and other causes (predation, disease, cannibalism, ageing, pollution, parasitism) not associated directly or indirectly with fishing. Prior to becoming vulnerable to any fishing gear, fish are subject to natural mortality only, which, as far as predation is concerned, declines as the fish increase in size. The direct estimation of natural mortality is very difficult in open sea populations and it is usually estimated indirectly with the use of empirical equations that are based on growth parameters, especially K with which M covaries. The most commonly used empirical equation for estimating natural mortality is that of Pauly (1980), which uses the growth parameters L_∞ and K together with mean temperature of the water. According to Pauly's equation, smaller, tropical fish suffer higher mortality rates compared to larger fish of higher latitudes. Natural mortality has also been empirically estimated based on age at maturity, maximum lifespan (t_{max}) or the mean age of larger sized individuals, and length at maturity. All the aforementioned equations provide an average natural mortality for all individuals and sizes of a population. In general, all empirical methods have advantages and disadvantages and it is a common suggestion to use more than one method and use an average mortality value.

Relationships Between Growth, Mortality and Maturity

The growth of fishes is generally well described by the von Bertalanffy growth function (VBGF), including variants that account for seasonal growth oscillations. The VBGF for weight has an inflexion point where the increase in weight per unit time is maximum. This is also the area where the "expected body weight," i.e., the product of body weight and the probability of reaching that weight, has a maximum. Species such as anadromous Pacific salmon and catadromous eels which, for a single life-time spawning event (semelparous), transform a certain fraction of their body weight into gonads, maximize their expected reproductive output and thus their fitness if they mature, spawn and die at the size and age of maximum growth rate. Species with multiple spawning events (iteroparous), all of which are likely to have the same average success rate, maximize their fitness by maturing such that the maximum growth rate falls roughly into the middle of the mean duration of the reproductive phase. However, species for which successful reproduction depends on rare and unpredictable environmental conditions will maximize their fitness by a trade-off between reproductive output and number of spawning events, i.e., by maturing early.

These different strategies are shown schematically in **Fig. 2**. To maximize fitness, one-time spawners (A) will aim to mature at the peak of the blue curve, which represents the expected reproductive output. Bearers, nesters and guarders (B), whose parental

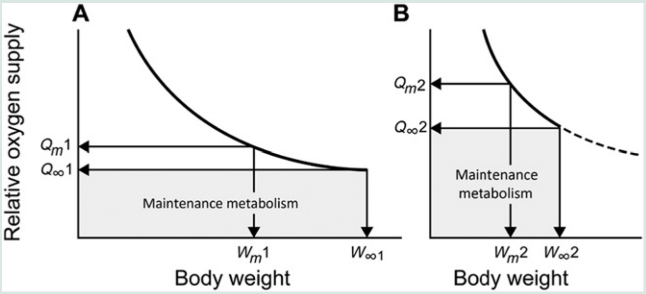
Box 1 Respiratory constraints to growth and related adaptations

Like other animals, fish grow by synthesizing new body mass, i.e. body tissues including gonads, a process that requires both food and oxygen. Oxygen is needed for consumed food to be oxidized ("burnt") and generate adenosine triphosphate (ATP), which acts as the energy used, e.g. for synthesis. In these water-breathing animals, water flows across the gills and between the lamellae, which extract most of the contained oxygen transferring it to the blood (Box Fig. 1).

Box Figure 1. Graphical representation of water flows across fish gills. Reproduced from Pauly, D., 2021. The gill-oxygen limitation theory (GOLT) and its critics. Science Advances 7, eabc6050.

Even though lamellae are arranged in 3D space, gills as a whole function as a surface, which implies that the metabolic and growth rate of fish are largely proportional to the surface area of their gills. Since the two-dimensional gill area cannot keep pace with the three-dimensional increase of body mass, as fish grow, the relative gill surface area declines down to a level when it suffices only for maintenance metabolism, and the gills end up delivering less oxygen per unit of body weight (Box Fig. 2A). This is why larger fish ultimately stop growing. Before that point and when the oxygen supply drops to 1.3–1.4 times the supply needed for maintenance and routine activities, the processes of gonad maturation and spawning are triggered (Box Fig. 2A). However, when the same fish are in a stressful environment shaped by environmental factors that increase oxygen demand for maintenance and thus metabolic rate, e.g., higher water temperatures, then the individuals are forced to mature and spawn at smaller sizes, while the maximum size they could potentially reach, is also reduced (Box Fig. 2B). This is illustrated in the fact that tropical fish have the tendency to be smaller than related species which inhabit cold waters.

Through evolution, fish have developed various strategies and tactics to deal with the above-mentioned respiratory constraints. Such strategies that may mitigate or delay respiratory stress include (1) the evolution of large gills in pelagic species, such as tunas, but also in large plankton feeders, such as the basking shark; (2) the migration of juveniles to deeper, cooler waters as they become adults and the production of eggs that quickly float up to the warmer surface layers, thus avoiding the often cannibalistic adults, and are drifted to productive coastal nursery areas; (3) the storage of fat, which requires considerably less oxygen for maintenance and is partly used during the time of the year when food is scarce, and partly converted into other tissues, such as gonads (as a result, body mass is reduced and relative gill area increased during the warmer parts of the year); (4) the ontogenetic shifts in diet composition in which juveniles feed on small prey (e.g., zooplankton), whereas larger-sized adults are able to capture energy-richer prey at a lesser cost.



Box Figure 2. Graphical representation of the relationships between respiratory area (and thus metabolic rate) and maximum body size in fish. Reproduced from Pauly, D., 2021. The gill-oxygen limitation theory (GOLT) and its critics. Science Advances 7, eabc6050.

care ensures a certain success at every spawning event, increase their fitness by maturing such that their average reproductive phase (dotted line) maximizes the area under the blue curve. Highly-fecund non-guarders (C), for which most spawning events will be unsuccessful, maximize their fitness by maturing early and thus increasing the number of spawning events. This maturation framework is confirmed by the data on length at first maturity shown in Fig. 3: One-time spawners, bearers and guarders mature

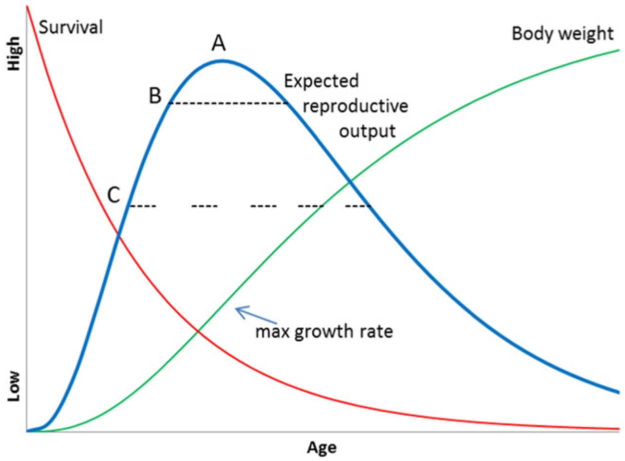


Fig. 2 Schematic representation of reproductive strategies in relation to probability of survival (red curve) and increase in body weight (green curve). The blue curve indicates the expected reproductive output. Strategy A represents single-spawners, such as Pacific salmon or eels. Strategy B represents multiple-spawners with parental investment, such as live-bearers, nesters or guarders. Strategy C represents highly-fecund non-guarders such as cods, sardines or tunas. The dotted horizontal lines indicate the necessary duration of the reproductive phase.

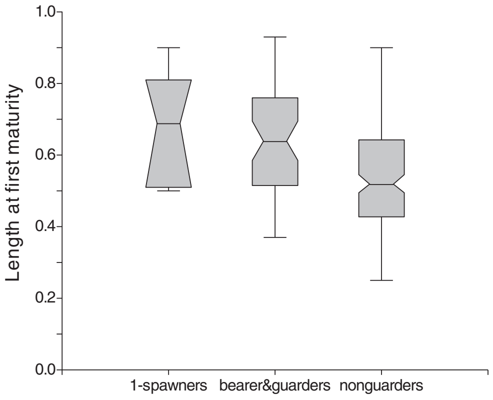


Fig. 3 Length at first maturity relative to asymptotic length for species that spawn only once in their lifetime (1-spawners, 5 studies), bearers or guarders (49 studies), and non-guarders (178 studies). The horizontal lines within the boxes present the median and the notched area the 95% confidence limits. The boxes contain 50% of the data and the extended lines indicate the spread of the data. The difference between bearers & guarders and non-guarders is significant. Data from FishBase 06/2011 (Froese and Pauly, 2011).

close to and slightly before 0.67 asymptotic length, which is the size range where the growth rate in weight and the expected reproductive output have their maximum. In contrast, non-guarders mature at a significantly smaller size.

These considerations are relevant for the biodiversity of fished stocks, because exploitation typically commences before maturation and high fishing mortality reduces the average duration of the reproductive phase to only one spawning event. From Fig. 2 it should be clear that this dramatically reduces the expected reproductive output of individuals and stocks, exerting unnatural selection for early maturation and provoking recruitment failures. Decreasing size and age at maturation and increasing recruitment failures are regularly observed in heavily exploited stocks.

Distribution of Exploited Fish Stocks

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., river loaches, Balitoridae) to the mouths of temperate and tropical rivers (e.g., gray mullets, Mugilidae). In the marine realm, fish range from the intertidal zone 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 about one to over 800 atmospheres experienced by some deep water fishes such as *Abyssobrotula galatheae*, which inhabits abyssal waters exceeding 8000 m in depth), temperatures (from −1.8°C in polar waters to about 40°C in hot springs, tolerated by some species of Cichlidae and killifish, Fundulidae), and salinities (from close to distilled water preferred by the discus fish, *Symphysodon discus*, of Amazonia to salinities of about 100 psu, 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 18 m reached by the largest fish, the whale shark (*Rhincodon typus*). These two species, incidentally, are exploited for food in the Philippines. The former, despite its high turnover rate, is in danger of extinction in the small lake where it is endemic because of overfishing, pollution, and the introduction of farmed tilapia. The latter is now legally protected, but enforcement remains problematic, which is the case for many legally protected sharks that are still targeted for their fins in many areas of the world.

Adaptations to Open-Ocean Habitats

Fish have different strategies to deal with the low production of the oceans. Tunas 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 depth 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 mesopelagic 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).

Shelf Communities

Definition of neritic stocks

Most fish stocks are neritic, that is, they 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 neritic 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 exhibiting specialized fins and mouths, 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 recreational and commercial), which are rather selective gears that would have relatively minor impacts were it not for their excessive numbers.

Demersal fish stocks

The demersal fish living in, on, or just above shelf soft bottoms consist of specialized flatfishes, 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, apart from the horizontal expansion of fisheries in new previously unexploited regions, the latest trend in fisheries "development" is the vertical expansion in greater depths. One such example 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 sub-tropics and demersal fishes, cephalopods and crustaceans in temperate and sub-polar regions) plus a vast number of non-target 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. Non-target species and debris are then discarded, and it is therefore trawlers that contribute most to the global discarding problem. Presently, about 10 million metric tons of various fish species are reported to be discarded, down from nearly 30 million metric tons two decades ago. This is still a very high discard rate when compared to the 80 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.

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 and climate variability, 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 reduces their individual risk of capture by 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 tunas and dolphins. Large pelagics such as billfish (Xiphiidae and Istiophoridae) and tunas (Scombridae) 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 to rot, 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.

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 bottom fish, 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.

Ecosystem Impacts of Fisheries

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 species of 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 stocks 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 and technological equipment that allows the detection of every single fish. 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 of America) initiated costly stocking 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, unhappily).

Emergence of the Sustainability Concept

World War I put an end to most 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 World War II, 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 (for a review see Tsikliras and Froese, 2019). 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. Beverton, Holt, and Gulland in England, Ricker in Canada, and 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 did not become sustainable. As shared and unregulated systems, oceans and their fisheries resources have been freely exploited by individual users who have been acting independently according to their own self-interest, thus behaving contrary to the common good and depleting, in many cases, the shared resources through their collective action ("The tragedy of the commons"). As 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. Subsidization of expanding offshore and distant water fleets 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. Let's hope that there will be absolutely no need for a third World War to remind us that less fishing is a prerequisite for fish stocks to be rebuilt.

Biodiversity Trends in Global Catch Data

Since 1950, the Food and Agriculture Organization of the United Nations (FAO) has collected seafood catch data reported to them by the governments of the World. These data have been criticized as being incomplete, biased towards industrial fisheries, over-aggregated both spatially and taxonomically, and unreliable as exemplified by some countries continued reporting of high catches even after a typhoon had destroyed over half of their fishing fleet. Yet, this is the only available global data set on fisheries, and it forms the basis for global fisheries policy. In an effort to draw a more realistic picture of the biomass extracted from the marine environment, an international research initiative was launched in 1999 at the University of British Columbia, Canada. The "Sea Around Us" database includes freely available global and local catch data that are reconstructed combining officially reported landings data with comprehensive estimates of unreported landings, such as from recreational fisheries, as well as discards. The reconstructed global catch data revealed that global catches may be about 50% higher than reported data suggest for the past 60 years (**Fig. 4**).

Attempts to predict global trends from a few hundred stocks for which complete assessments are available are flawed because of their spatial and "survivorship" biases, i.e., the fact that such assessments are only available from developed countries for stocks that have withstood exploitation for decades and thus are more resilient to fisheries than the many stocks that have been quickly depleted, not meriting a full assessment anymore.

The nominal catches of seafood organisms have reached about 80 million tons in 1988 and fluctuated around that level since then (**Fig. 5**). This has been interpreted as a phase of stability, as if global fisheries had settled at a level that could be sustained indefinitely. A closer examination of the dynamics in the composition of these catches leads, however, to a very different interpretation, revealing severe impacts on global fish stock biodiversity.

The number of exploited stocks has increased continuously and has more than tripled since 1950, meaning that from the beginning the increase in global catches did stem not only from increased exploitation of existing stocks, but also from exploitation of new stocks. It also means that the impact of fishing on the biodiversity of fish stocks has tripled in half a century.

During the same period, the number of depleted stocks has increased from close to zero to about one third of all stocks in 2009. For the phase of perceived stability in total catches after 1988, this means that there is an underlying process where the loss in catch from stock depletion is made up by new catches from new stocks. But the number of new stocks suitable for exploitation is limited and if current trends continue, we can expect to see an accelerated increase in depleted stocks and an accelerating decrease in global catches. The only remaining option for halting this trend is the rebuilding of depleted stocks, a process that has started in New Zealand, Australia, the USA, and the EU, but which has yet to reach a level where it makes a difference in global statistics.

Managing Fish Biodiversity Information

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 Linnaeus created the taxonomic standards required for biodiversity research, after 120 years of applied fisheries research, and after at least 50 years of advances in ecosystem research. Rather,

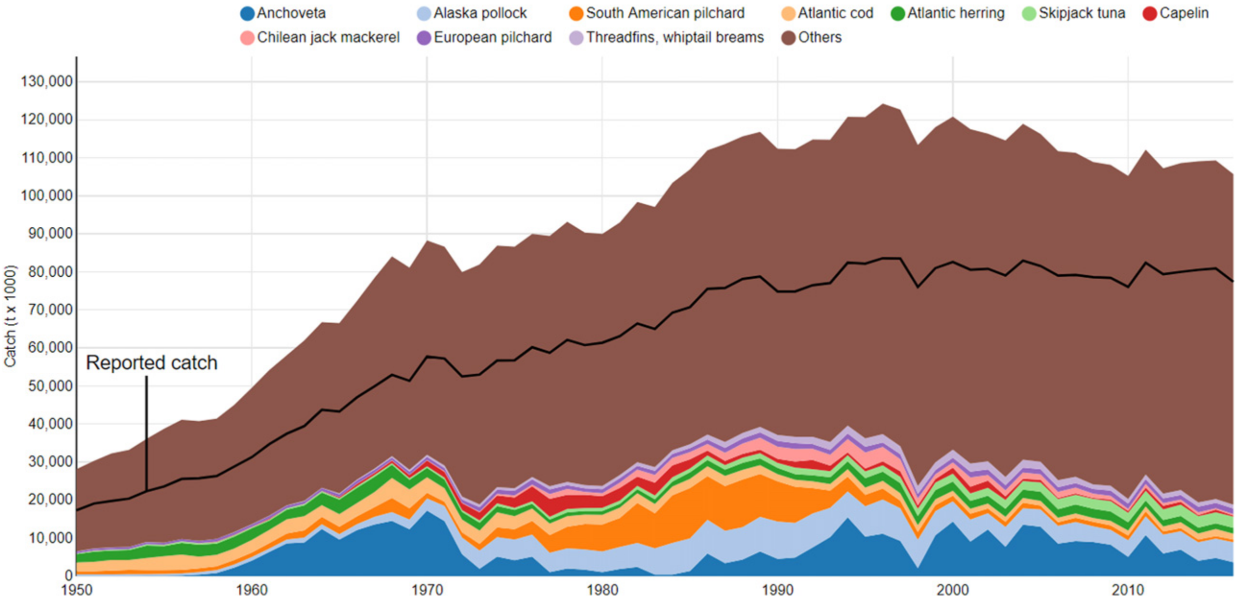


Fig. 4 Global catches from 1950 to 2016 as presented in the Sea Around Us database. The reconstructed data combine official reported data and reconstructed estimates of unreported data (including major discards). Official reported data are mainly extracted from the Food and Agriculture Organization of the United Nations (FAO) FishStat database. The "Reported catch" line overlaid on the catch graph represents all catches deemed reported (including foreign).

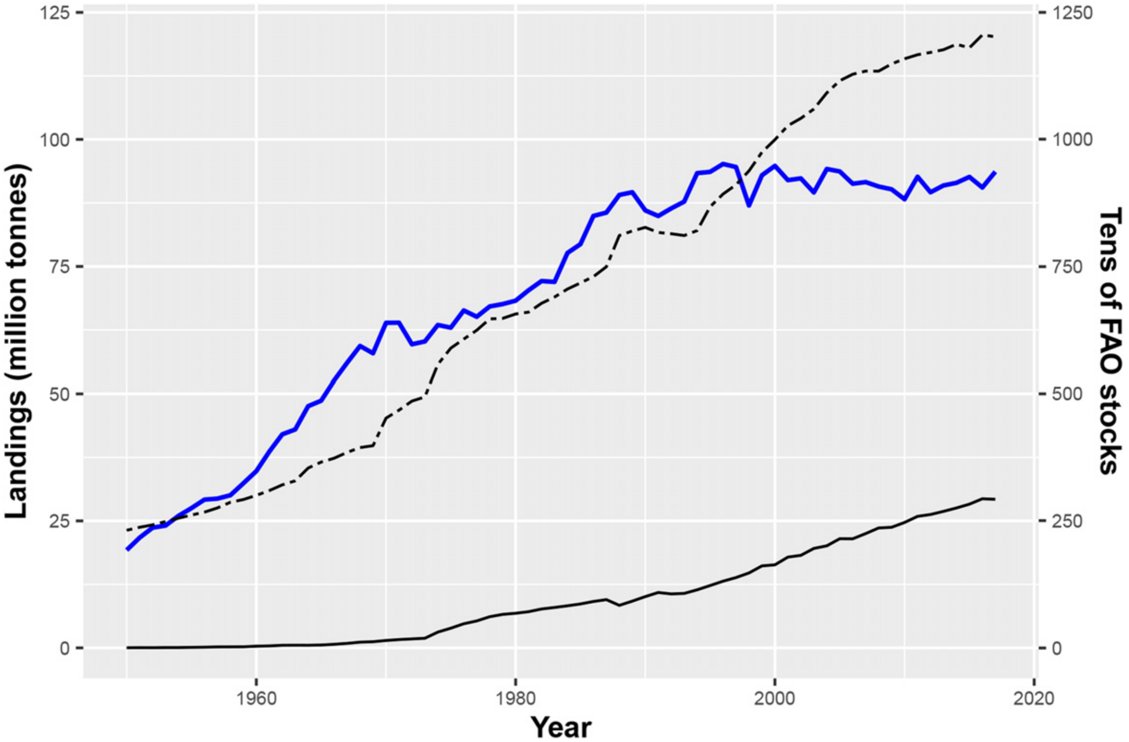


Fig. 5 Underlying trends in global catch statistics. The bold blue curve shows the reported FAO (Food and Agriculture Organization of the United Nations) landings of seafood organisms from 1950 to 2017. The number of exploited stocks, defined here as species by statistical marine area, is indicated by the black dashed curve. The number of depleted stocks, defined here as those producing less than 10% of their maximum contribution in the time series, is indicated by the lower black line.

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.

Bioquads as Primary 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). A standard for scientific names (a) has been developed by the Catalogue of Life initiative (See "Relevant Website section"), which provides an authoritative index of scientific names for over 1.4 million species of the 1.8 million species that are thought to have been formally described by taxonomists during the past 250 years. Standards for (b)-(d) have been set by the Global Biodiversity Information Facility (GBIF) and applied so far to over 250 million bioquads, which are freely accessible from the GBIF portal (See "Relevant Website section"). The number of bioquads is expected to increase rapidly as observations of lay persons are integrated into the system. The challenge now is to interpret these large amounts of data and to derive insights on marine biodiversity and the diversity of fish stocks. This task has been taken on by the AquaMaps initiative (See "Relevant Website section"), which has published the first comprehensive global map of marine biodiversity (**Fig. 6**). Although the map is based on only 33,500 of the estimated 250,000 species living in the oceans, it already shows the expected trends in global species richness, such as exponential decline in species numbers from the equator to the poles, higher diversity on the continental shelves, and the center of marine biodiversity in the Malaysian-Indonesian-Philippine triangle.

AquaMaps can also be used to depict changes in catches on fish stocks, which in many cases are driven by changes in abundance. For example, **Fig. 7** shows catches of Atlantic cod (*Gadus morhua*) in 1968 and in 2007. Available stock assessment data confirm that the visible strong decline in catches is a result of the strong decline in biomass, which itself is a result of previous overfishing.

Species Databases as Tools for Management of Biodiversity Information

Knowing the correct scientific name and the native range is a minimum requirement for a species to be included in one of the two biological databases available for marine organisms, FishBase (See "Relevant Website section") for fishes and SeaLifeBase (See "Relevant Website section") for all other organisms. Both databases extract and standardize key information from the scientific literature, such as diet composition, growth, reproduction, morphology and physiology. They also record human use and the resilience of species. FishBase has been utilized extensively for understanding and management of fish biodiversity, with over 13,000 citations in the scientific literature, and about 700,000 visits per month to the FishBase portal. Recent changes in legislation, e.g., in the USA, require fisheries managers to provide reference points and assessments for all fished stocks, including many cases where no stock specific data are available. In order to fill these gaps, FishBase uses Bayesian methods to derive priors from related stocks and species. It also provides empirical equations for preliminary estimates of, e.g., resilience or size at first maturity. Following a general trend to preserve scientific data, FishBase is considering storing primary life history data, such as weight- at-age or fecundity-at-length, in addition to the published models fitted to such data. This will enable the re-use of such data with other models and for different questions.

Preserving Fish Biodiversity

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

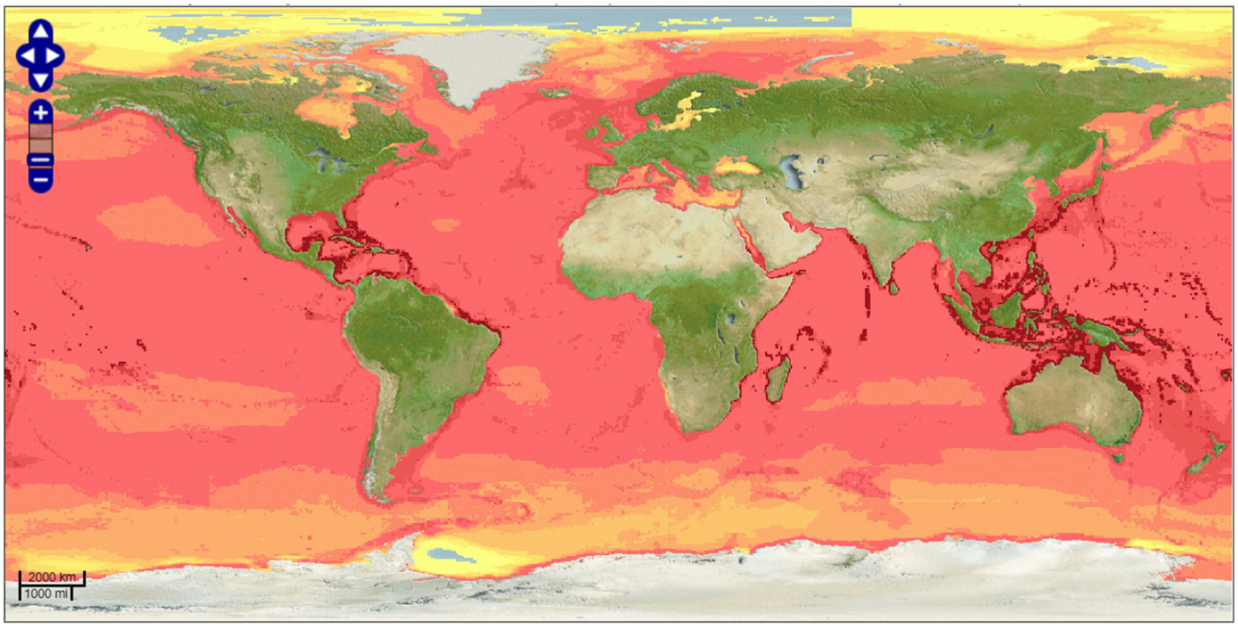


Fig. 6 Marine species richness based on individual range maps for over 33,500 species of fishes, marine mammals, and invertebrates. Species richness is depicted on a log scale from low (= yellow) to high (= dark red). *Source*: AquaMaps 10/2019 (Kaschner *et al.*, 2019).

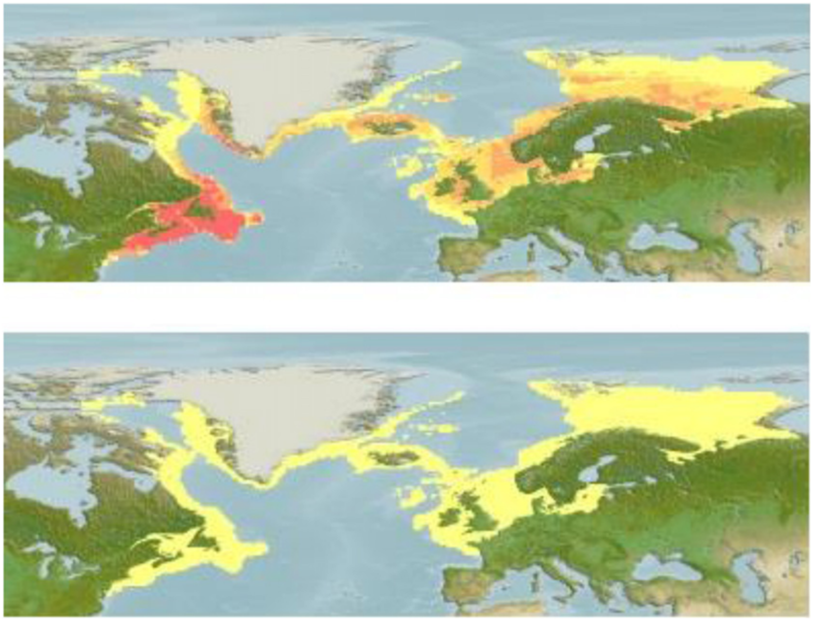


Fig. 7 Catches of Atlantic cod distributed according to the large statistical areas from which they were reported and the suitability of habitat. The upper map refers to 1968 while the lower map refers to 2007. Light yellow indicates catches of 1 - 400 tonnes whereas dark-red areas yielded 1600 - 2100 tonnes per year and half-degree cell.

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 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 non-target species. Limits on nominal fishing effort are subverted by technological developments (creep), 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 benefits, 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.

Current fisheries management is globally based on fishing mortality and biomass reference points that correspond to Maximum Sustainable Yield (MSY), which is the largest average catch that can continuously be taken from a stock under existing environmental conditions. The first reference point is fishing mortality or fishing pressure (F_{MSY}) that, if applied over a time span similar to generation time, will eventually result in a catch equal to MSY where F describes the part of the total mortality rate that is caused by fishing. For a stock to be sustainably exploited, current F should be lower than F_{MSY} ($F < F_{MSY}$). The other related reference point is the biomass at MSY, B_{MSY}, which is the smallest stock size that can support catches equal to MSY. For a stock to be in good status, current B should be higher than B_{MSY} ($B > B_{MSY}$).

New Methods for Assessing Data-Poor Fisheries

Traditional age-based stock assessment methods are data hungry and require detailed biological data on growth, maturity, mortality per age class, as well as age-specific fisheries independent dataset from surveys for each stock to be assessed. These methods have been developed and applied in fisheries data-rich areas (e.g., North Atlantic) and are used by countries with a long tradition in fisheries science, long time series of scientific surveys and consistent catch data records. However, the vast majority of global fish stocks (over 80% but nearly 100% for developing countries) remain un-assessed or are being irregularly and sporadically assessed.

In data-poor fisheries and stocks, for which the required data to estimate the maximum sustainable yield (MSY) and fisheries reference points are unavailable (such as the majority of Mediterranean fisheries), the need for appropriate stock assessment models led to the development of novel methods specifically designed for data-poor areas. Recently, a new method (CMSY) that can assess the exploitation pattern and status of stocks using only time-series of catch and species resilience has been developed (Froese *et al.*, 2017, 2018a). The improved CMSY appears to outperform data-moderate stock assessment methods when tested against data-rich stocks. When catch data are missing, for example for non-target species, a time-series of abundance (AMSY: Froese *et al.*, 2020) or length frequency distribution data (LBB: Froese *et al.*, 2018b, 2019) can be used.

These new data-poor methods, especially CMSY, allow the assessment of all commercial stocks for which at least catch data are available and are expected to fill in the gap in the number of stocks assessed globally, and particularly in developing countries. All these methods rely on surplus production models (e.g., Schaefer, 1954), which are based on the intrinsic rate of population increase (r) and carrying capacity (k) of a population and can be compatible with Ecosystem Based Fisheries Management (EBFM) in estimating the average carrying capacity of an area (Pauly and Froese, 2021).

Ecosystem Based Fisheries Management (EBFM) for Preserving Biodiversity

The historical fisheries management pathway originated with single-species approaches and with most scientific agencies worldwide traditionally giving advice on a stock-by-stock basis. This has proved to be problematic as it disregards the mixed-species aspect of fisheries and of course the multispecies nature of ecosystems. As a result, various fisheries management approaches have been developed through the years, forming a continuum that starts with a single-species focus and then extends the scope of interest to also include ecosystem considerations, thus building towards a more systemic and multi-sector perspective (Dolan *et al.*, 2016).

EBFM requires that decision making should be based not only on the characteristics of particular commercial stocks, but on all components of the ecosystem. As a result, it takes into consideration environmental and ecological factors that have an impact on the population dynamics of a particular stock and examines multiple or even all fisheries that exploit an ecosystem in order to follow a coordinated approach to incorporating ecosystem considerations into management decisions and providing the greatest benefit to society. Ecological models, food web models such as Ecopath with Ecosim (EwE: Pauly *et al.*, 2000) serve as important tools for EBFM and are nowadays considered as one of the most robust and powerful approaches used to understand the structure and functioning of marine ecosystems, and predict the consequences of human-induced and climate-driven changes on the natural environment. Apart from the dynamics of fish stocks, such models may incorporate environmental and anthropogenic driving factors, as well as multispecies feeding interactions covering the entire trophic spectrum of the ecosystem, from primary producers and zooplankton, to top predators such as large pelagic fish and marine mammals (Dimarchopoulou, 2020).

Marine Protected Areas

There is an emerging consensus among fisheries scientists and conservationists that an important fisheries management tool that will allow the recovery of damaged stocks 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

Total Allowable Catches (TACs). Also, technology-driven increases of fishing effort (i.e., technological creep) 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. Indeed, to achieve the highest benefits of protection, MPAs would need to be accompanied by a parallel reduction in total fishing effort, rather than a mere redistribution of fishing activities that would just move the pressure on the boundaries of the protected areas (the "fishing-the-line" phenomenon), causing a local increase of catches owing to the beneficial results of protection.

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 if these limits are ignored. 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.

Conclusion

Research on fish stock dynamics and adaptions, as well as on the distribution of exploited stocks has been going on for decades. The resulting in-depth knowledge of several such processes and facts has allowed researchers to highlight the ecosystem impacts of fisheries and climate change, and engage managers and stakeholders to managing and preserving fish biodiversity globally. As healthy stocks produce more fish, increasing fishing mortality will lead to decreasing stock biomasses, hence decreasing future catches. In contrast, less fishing will allow the stock biomass and population structure to rebuild, and marine ecosystems to regain their functional roles, thus returning closer to pre-overexploitation, pristine levels.

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