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Ecology of Marine Fish

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# Fisheries impact on marine fish populations

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## 17.1 Introduction

Global marine fisheries catch is estimated at around 80 million tons per year according to landings declarations recorded by the FAO (2022), and at more than 100 million tons when accounting for undeclared catches and discards (Pauly et al., 2020). Seventy-five percent of this production is intended for human consumption, which represents almost 7% of the world's nutritional intake of animal proteins. Thus fishery products play a decisive role in the food security of many developing countries, particularly in Asia, South America, and West Africa. Finfish alone represent almost 80% of sea fishing and therefore occupy a largely preponderant place.

The development of marine fisheries dates essentially to the 20th century and has been accompanied by increasing impacts on the sea's living resources (Gascuel, 2019). The first impacts that scientists became aware of, as early as the 1930s, were those directly affecting the demography of each of the exploited stocks (Beverton and Anderson, 2002). These impacts are indeed massive, leading to drastic declines in abundance and often to a reduction in the catches themselves. In the 1980s and 1990s, no doubt as a result of growing impacts and the gradual exploitation of an increasing number of species, it became clear that the reduction in abundance of species targeted by fishing had knock-on effects on their prey, competitors, and predators, and ultimately—via food webs—on all ecosystem compartments (IPBES, 2019). Scientists have also been interested in the impact of fishing gear on habitats, and in particular the impact of active gear such as bottom trawls and dredges on the seabed. Finally, over the last 20 years or so, rising attention has also been paid to the effects of fishing as a selection pressure, which has consequences for the genetic diversity of populations.

## 17.2 Demographic effects— Introduction to the dynamics of exploited marine populations

### 17.2.1 Less old fish and biomass in the sea

Contrary to what the general public often believes, the first impact of fishing is not to affect the renewal of the exploited populations, and therefore to reduce the number of young fish. It is to gradually make the oldest ones disappear (Beverton and Holt, 1957). Indeed, any fishing activity, even of low intensity, adds fishing mortality to natural mortality and therefore tends to reduce the life expectancy of fish and change the age structure of the population. This is an effect well known to fishermen themselves: as fishing intensifies, the average size of the catch decreases, along with that of the underlying population (Beverton and Holt, 1957). The main reason for this is the decrease in the abundance of old fish which are also the largest and heaviest specimens, even though the quantity of young, issued from reproduction, remains approximately constant, at least initially. Fishing thus has the effect of truncation of the age structure and rejuvenation of the exploited population (Jackson et al., 2001).

The decrease in abundance of the oldest year classes reduces the overall abundance of the population, and this is its total biomass. This drop can be very significant, even if the renewal of the population is still not affected. It is thus common for the biomass of a fish stock to be reduced by 3 or 5, or even by 10, solely due to changes in its age structure (Froese et al., 2008). This is the case, for example, of many populations of gadoids whose life expectancy in the absence of any fishing can exceed 20 years, and which can only include the first three or four age classes in the event of intense exploitation. In other words, fishing tends to empty

the sea of some of its fish, and initially, this impact is not linked to a decrease in the renewal of populations, but to a modification of their age structures at the expense of old fish.

### 17.2.2 Impacts on recruitment

The decrease in the abundance of the oldest fish induced by fishing reduces the reproductive potential of the population. However, in many species, the spawning biomass can be reduced by 4 or 5 times, or even by 10, compared to a no-fishing situation, without any significant effect being observed on recruitment (i.e., the number of young from reproduction). Therefore most models used in fisheries management admit that recruitment remains constant when fishing pressure increases and the overall abundance of the stock decreases, as long as the spawning biomass is above a threshold biomass (Blim) (Fig. 17.1). This recruitment stability, which does not exclude interannual variability, results from the absence of a statistically significant relationship between recruitment and the related reproductive potential. It is only below the Blim threshold when the abundance of spawners becomes very low, that recruitment can be affected.

This pattern is explained by the very high fecundity of marine species. Indeed, in the vast majority of fish, mollusks, and crustaceans, individual fecundity is several hundred thousand, or even several million eggs emitted at each spawning. In a way, the demographic strategy of these species is to saturate the environment with a very excess number of eggs. This huge fecundity is associated with a massive mortality in the first stages of life, the eggs, larvae, and postlarvae (cf. Chapter 3). Therefore the final quantity of recruits is very partly related to the initial quantity of

eggs, but rather to their survival rate. It is as if there were a carrying capacity of the environment to accommodate recruitment each year, which is thus determined by the environmental conditions of the year, and in particular by the availability of food resources (Le Pape and Bonhommeau, 2013). Consequently, it does not matter whether the quantity of spawners is strongly reduced; it is this carrying capacity that ultimately determines the abundance of recruitment.

Conversely, when the spawning biomass falls below the Blim threshold, due to fishing, recruitment may decline and the population abundance collapses. This situation, called recruitment overfishing, therefore reflects a very strong impact of fishing, and results in a decrease in the abundance of all age classes. This is typically what happened in some famous fisheries collapses, such as the Canadian cod in the 1990s. However, recruitment overfishing has also been observed in many less publicized situations in European fisheries. Logically, the risk of recruitment overfishing resulting from a given fishing pressure is higher for species with lower fecundity. Thus it can in particular affect species such as sharks and rays, or certain large hermaphroditic fish.

### 17.2.3 Overfishing and the debate on fisheries management

Fisheries management intends to ensure the long-term sustainability of marine resources and associated exploitations. A general consensus exists that recruitment overfishing has to be avoided in all cases, thanks to limitations in fishing pressure. This is in particular the aim of safe biological limits used in the frame of the European Common Fishery Policy (CFP). However, these limits are generally considered insufficient by fisheries managers and by the fishers themselves, as recruitment overfishing only occurs for already severely

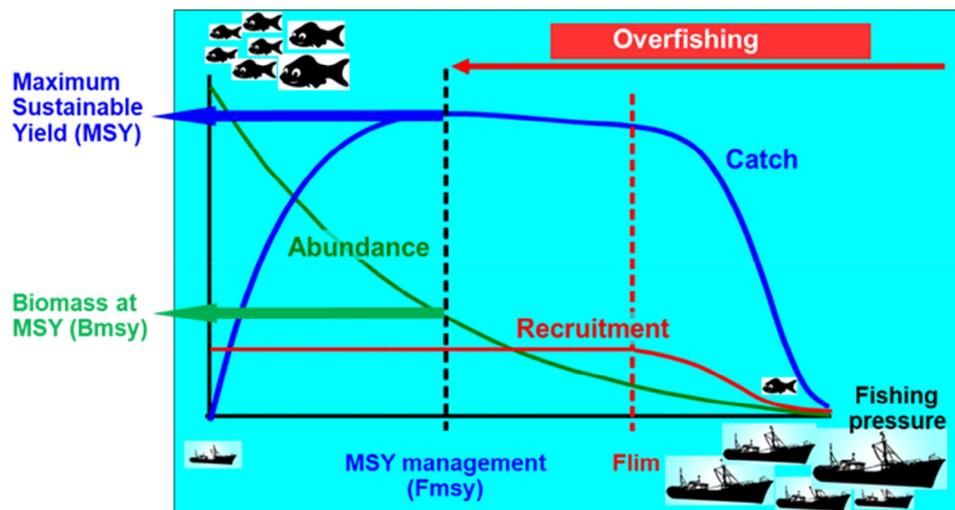


FIG. 17.1 Theoretical demographic effects of fishing of a fish population: changes in the abundance, catch, and recruitment as a function of fishing pressure (see text for explanation).

depleted resources, with remaining biomass typically lower than 20% of the nonfished population. In such a situation, population renewal is generally ensured but such very low abundances may affect the ecosystem functioning and lead to limited catches and poor fisheries profitability.

As a consequence, the current standard recognized worldwide, by the UN, most RFMOs (Regional Fisheries Management Organizations) or the European Common Fishery Policy, is to manage fisheries in order to get from each exploited population the maximum sustainable yield (MSY, i.e., the yearly highest catch that can be sustainably expected on average). MSY is obtained for an intermediate level of fishing pressure, just avoiding overfishing situations (also called growth overfishing situations, in order to distinguish from recruitment overfishing). It should be noted that overfishing is not defined on the basis of biological considerations; it is just a situation where high fishing pressure leads to decreasing catches, which is obviously an absurd situation from an economic point of view. This decrease is itself the result of a large impact of fishing on the abundance of the stock, linked to the previously mentioned changes in its age structure.

In other words, sustainable management usually aims at maximizing fisheries production from each exploited stock. In the absence of particular regulation on the mean fish size at first catch, the fishing pressure delivering the MSY results in a remaining biomass, which is around 25%–40% of the nonfished one (Beverton and Holt, 1957). Therefore the fishing impact is already very significant. The stock renewal is usually ensured (only low fecundity species are exceptions, and require a more precautionary management to avoid recruitment overfishing). However, such a management results from a single-species approach and there is no guarantee that the remaining population will be able to ensure all its role in the functioning of the ecosystem (Gascuel, 2019).

Therefore more precautionary targets are sometimes considered, in order to minimize the impacts of fishing while continuing to fish. In particular, countries such as Australia, Canada, or the United States often refer to the MEY target (or a proxy), as the maximum economic yield. This target requires a fishing pressure lower than the MSY, and thus induces less economic costs and lower ecological impacts, while theoretically maximizing the profitability of the considered fishery.

Increasing the mesh size of fishing gear and the sizes at first catch also leads to reduced impacts on the exploited population. In that perspective, several authors argue for new, more ecosystem-based management targets, implying that the remaining biomass should stay at least equal to 50% of the nonfished one (Froese et al., 2016). For many fish populations, a combination of lower fishing pressure and optimized size selectivity could allow current catches to be maintained, while greatly decreasing the impacts,

typically maintaining the exploited biomass around 60% or 70% of its unfished level.

### 17.3 Trend and diagnostic on stocks status and biomass—Where do we stand?

There are two primary sources of information used to estimate the status of fish stocks around the world (Rosenberg et al., 2018). The first source of information comes from the United Nations Food and Agriculture Organization (FAO) (FAO, 2022). In its biennial State of World Fisheries and Aquaculture (SOFIA), the FAO regularly classifies stocks into three categories based on expert opinions: underexploited, fully exploited, and overexploited. The second source comes from abundance estimates derived from stock assessments (Quinn and Deriso, 1999), compiled in the RAM Legacy database (Hilborn et al., 2020). In a recent version of the RAM Legacy database, 882 stocks were compiled, of which 635 have estimates of biomass or fishing pressure relative to biological reference points (Hilborn et al., 2020). The data requirements for doing the stock assessment that are in the database are substantial. Hence small-scale fisheries and those in developing countries are underrepresented (Rosenberg et al., 2018). The FAO stock status reviews include more stocks (almost three quarters of the world catches), but the applied methodology is more heterogeneous and less transparent than in the RAM Legacy database, where almost 50% of the world catches are accounted for (Rosenberg et al., 2018).

In the 2020 SOFIA report, the percentage of overfished stocks was estimated to be 35.4% in 2019, a substantial increase from 10% in 1974 (Fig. 17.2). Meanwhile, this also means that 64.6% of the fish stocks in the FAO database were within biological levels considered as sustainable. In terms of landings, this means that 82.5% of 2019 landings came from stocks that were within biologically sustainable levels.

Analyses of global trends in stock exploitation and the status of global fish stocks using the RAM Legacy database revealed that since the 1970s, average fishing pressure increased until 1995 while biomass declined (Hilborn et al., 2020, Fig. 17.3). After fishing pressure began to decrease in 1995, it took until 2005 for average biomass to increase. Averaged across all stocks in the database, biomass in 2016 was higher than BMSY, and fishing pressure was lower than FMSY. However, improvement is still needed for 24% of stocks, accounting for 19% of potential catch, which still have low biomass and high fishing pressure compared with MSY-based targets (Hilborn et al., 2020).

There is difference in view on the state of the world's stocks. The FAO reports an increase in the fraction of overfished stocks since 2000, while analysis of the RAM Legacy

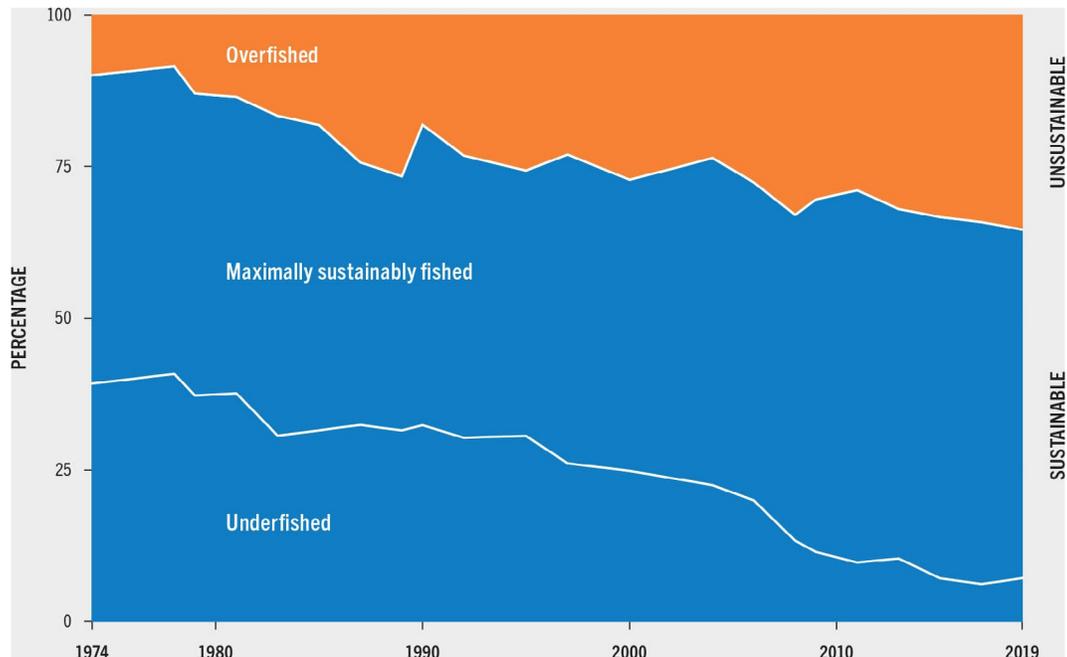


FIG. 17.2 Global trends in the state of the world's marine fishery stocks 1974–2019 as estimated by FAO. The methodology used for the assessment is described in Annex 1 of FAO, 2011 ([www.fao.org/3/i2389e/i2389e02.pdf](http://www.fao.org/3/i2389e/i2389e02.pdf))

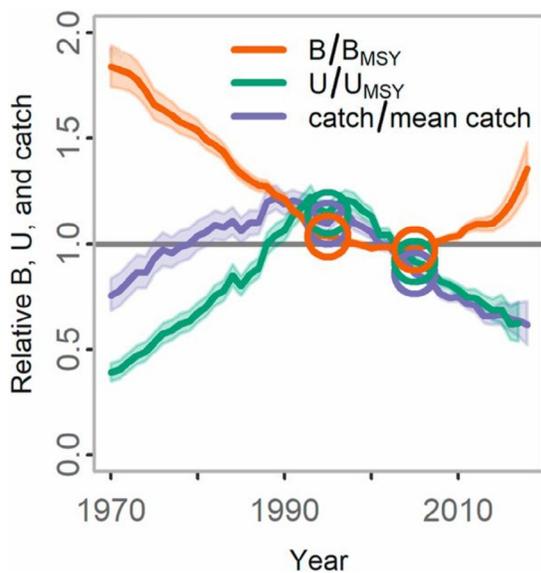


FIG. 17.3 State-space model estimates of geometric mean  $B/B_{MSY}$  (relative stock biomass),  $U/U_{MSY}$  (relative fishing mortality) and catch/(mean catch) from 1970 to 2016, rescaled to the median in years of high coverage, using the RAM Legacy database. All stocks are given equal weight. Circles denote years 1995 and 2005. Shaded regions denote 95% finite population corrected confidence bounds. From Hilborn, R., Amoroso, R.O., Anderson, C.M., Baum, J.K., Branch, T.A., Costello, C., De Moor, et al., 2020. *Effective fisheries management instrumental in improving fish stock status. Proc. Natl. Acad. Sci. USA* 117(4), 2218–2224.

database suggests that an increase in stock biomass is likely due to differences in stock coverage (Hilborn et al., 2020) and differences in the classification methodology (Rosenberg et al., 2018). The RAM Legacy database only

includes stocks with reliable quantitative stock assessments, constituting approximately half of the world's catches. The other half of the world's catches come from stocks with limited data of stock trends, from regions with low intensity of fisheries management (Hilborn et al., 2020). Stocks in data-limited regions, better accounted for in FAO stock status than from stock assessment, face lower fisheries management, and are often in poorer condition than stocks in data-rich regions (Costello et al., 2012).

Indeed, there are large differences among different regions in the world. FAO distinguishes 16 regions, with the Southeast Pacific having the highest percentage (66.7%) of stocks fished at unsustainable levels, followed by the Mediterranean and Black Sea, where 63.4% of the stocks fished at unsustainable levels. For all other regions, the majority of the stocks were fished at sustainable levels (FAO, 2011). Analysis of the RAM Legacy database concluded that, with the exception of the Mediterranean and NW Africa, fishing pressure around the world in 2016 was lower than target levels (Hilborn et al., 2020). The biomass levels in the EU waters outside of the Mediterranean declined in the period 1970–2005, but the decline in exploitation levels since approximately 1995 has resulted in a gradual increase in SSB (Hilborn et al., 2020).

#### 17.4 Adaptation/selection—Fisheries-induced evolution

The exploitation of living resources in general, and fishing in particular, can be seen as “a large-scale experiment on

life-history evolution” (Rijnsdorp, 1993). Fishing mortality is a major source of mortality in commercial fish species, often exceeding natural mortality. Aside from directly altering the demography of exploited populations illustrated in Sections 17.1 and 17.2, this additional mortality is likely to induce adaptive responses to their life-history traits (LHTs).

### 17.4.1 Fishing-induced selection pressures on fish life-history traits

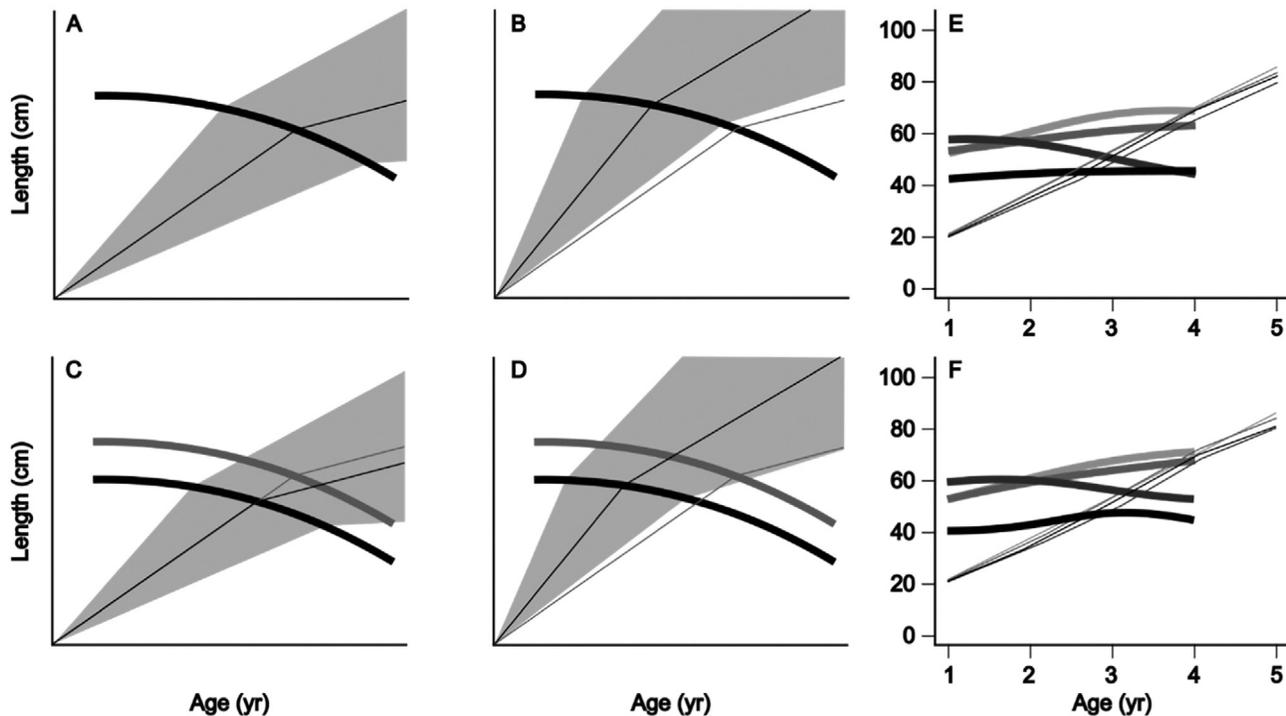
Predictions from life-history theory suggest that elevated mortality, even uniformly across age and size classes, selects for earlier sexual maturation but also increased reproductive effort at the expense of postmaturation growth and less investment in longevity (Stearns, 1992). Selection pressures are due to the micro-evolutionary trade-offs that mortality generates between age classes. For instance, delaying maturation or limiting current reproduction to favor energy allocation in somatic growth for the benefit of future reproduction and survival pays little dividends when the probability of reaching the oldest age classes is low. In other words, an increase in mortality selects for an acceleration of life histories because of the low likelihood of reaching old ages and thus their low contribution to an individual’s fitness. Such low likelihood in exploited fish stocks is testified by the disappearance of the oldest age classes highlighted in Section 17.2.1. Fishing mortality will therefore generate selection pressures not only on some LHTs (maturation, reproductive effort, growth) as described previously but also on other traits either correlated with these LHTs or affecting catch probability, such as morphological, physiological, or behavioral traits (Hollins et al., 2018).

Beyond selection generated by simply elevated mortality, fishermen selectively remove individuals due to fishing practices and their regulation, which also induces selection pressures on traits more specifically related to the selectivity criteria of the fishery (Kuparinen et al., 2009). Fishing mortality is most often size-selective, with regulations often protecting smaller (and thus younger) individuals and fishermen targeting larger individuals. The shape of the selectivity curve according to fish size differs according to the fishing gears used: a selectivity that increases as a sigmoid function of size is observed for active gears such as trawls, whereas passive gears such as gillnets operate a bell-shaped selectivity, capturing intermediate sizes. The size selectivity of fisheries generates not only direct selection pressure on body growth but also indirect selection pressure on maturation and reproduction since the latter affects growth through the bioenergetic trade-off between growth and reproduction.

### 17.4.2 Evidence of changes in maturation: Demography, plasticity or evolution?

Following a precursor book in the 1990s (Stokes et al., 1993), studies on fishery-induced adaptive changes developed mainly in the 2000s (e.g., Olsen et al., 2004). These focused primarily on temporal trends in age and size of sexual maturation as (i) the most ubiquitous temporal trend in fish stock LHTs is a trend toward earlier maturity (Law, 2000) and (ii) concomitant methodological developments, namely the concept of probabilistic maturation reaction norms (PMRNs, Barot et al., 2004; Heino et al., 2002), allowed their analysis. Beyond simply documenting temporal trends in maturity, these studies aimed at identifying the nature of the processes behind the trends. Temporal changes in LHTs in general, and in age and size at maturation in particular, might actually arise from demography, phenotypic plasticity, and/or evolution in response to fishing (Dieckmann and Heino, 2007). Regarding demography, the rejuvenation of the population caused by fishing implies that younger mature individuals are observed as the older ones have disappeared. As for phenotypic plasticity, the reduction in population biomass brought by fishing may lessen trophic competition so that fish grow faster and thus mature earlier since maturation depends strongly on size in most fish. Concerning evolution, if the maturation process is partly heritable, which is the case for most LHTs (Friars and Smith, 2010), the fisheries-induced selection pressures for an acceleration of life history translate into evolutionary changes toward maturation at younger ages. The relative contributions of these three components to changes in LHTs constitute an important issue for fisheries management because the degree and speed of their reversibility, and thus of their consequences, are very different: demographic effects and phenotypic plasticity can theoretically be reversed within a generation, whereas evolution can only be counteracted on the scale of several generations, and may even prove irreversible (Marty et al., 2015). This affects the time horizon of potential management actions for mitigating LHT changes.

PMRNs describe, for a given cohort, the probability of an individual to mature according to its age and size. They have been precisely designed to remove the confounding effects of demography and growth-related phenotypic plasticity, thus retaining the maturation process only. It results that temporal changes in PMRNs can be interpreted as suggestive of fisheries-induced evolution (FIE) in maturation (Fig. 17.4A). Luckily, cohort-wise time series of PMRNs can be estimated using data on individuals’ age, length, sex, and maturity stage that are routinely collected for fish stock assessment (Barot et al., 2004). One of the first applications of PMRN analysis dealt with the emblematic Northern cod off the coasts of Labrador and Newfoundland (Canada) that collapsed in the mid-1990s (Olsen et al.,



**FIG. 17.4** PMRN analyses. (A)–(D) Principle. Thick lines in shades of gray represent the PMRN midpoint curves, i.e., combinations of ages (x-axis) and body sizes (y-axis) at which the probability of maturation reaches 0.5. Thin lines in shades of gray represent the corresponding average growth trajectories in the population. The spread of growth trajectories in the population, represented by gray areas, determines the portion of the PMRN that is effectively expressed, and the intersection between the average growth trajectory with the PMRN midpoint curve gives the average age and body size at which maturation probability reaches 0.5. Using scenario A as a reference, an acceleration of growth (scenario B) leads to a leftward shift of the growth trajectories (thin black versus gray line for the average and gray area for the entire range of growth curves) and thus to earlier maturation (leftward shift of the portion of the PRMN expressed), while the PMRN remains unaffected. In the case of an evolutionary change towards earlier maturation at smaller sizes (scenarios C and D), the PMRN is shifted downward relative to the reference scenario (thick black versus gray line). As a result, earlier maturation at smaller sizes is observed (leftward shift of the expressed portion of the PMRN), whether without (scenario C) or with (scenario D) growth acceleration. Thus, PMRNs can be used to disentangle changes in maturation ages and sizes due to growth acceleration and maturation evolution. (E)–(F) Application to the North Sea cod case (from Marty et al., 2014). Temporal trends in PMRN midpoint curves and average growth trajectories are shown for males (E) and females (F). PMRN midpoint curves are averaged over cohorts 1974 to 1980 (thick light gray curve), 1981 to 1990 (thick medium gray line), 1991 to 2000 (thick dark gray line) and 2001 to 2006 (thick black line). Thin lines of the same color represent the mean length-at-age of both immature and mature individuals for the corresponding cohort groups. (A) From Olsen, E.M., Heino, M., Lilly, G.R., Morgan, M.J., Brattey, J., Ernande, B., Dieckmann, U., 2004. Maturation trends indicative of rapid evolution preceded the collapse of northern cod. *Nature* 428, 932–935., suppl. mat. (B) From Marty, L., Rochet, M.-J., Ernande, B., 2014. Temporal trends in age and size at maturation of four North Sea gadid species: cod, haddock, whiting and Norway pout. *Mar. Ecol. Prog. Ser.* 497, 179–197.

2004). It showed that, from cohort 1979 to 1992, the size at 50% probability of maturing of females aged 5 and 6, the ages at which most mature, decreased by 5.2 to 15.6 cm depending on the age and the portion of the stock considered. North Sea cod, another emblematic cod stock, exhibited similar rates of changes between cohort 1974 and 2006, with the size at 50% probability of maturing decreasing by 23.5 cm for both males and females aged 3 (Marty et al., 2014, Fig. 17.4B). This shift in PMRNs resulted in a decrease of the average age at 50% probability of maturing from 3.9 to 2.7 years and 4.1 to 2.8 years for males and females, respectively. Despite a minor contribution of water temperature increase for the North Sea case, these results are suggestive of an evolutionary response to fishing as the main explanation of observed trends toward earlier maturity in these two stocks.

Similar conclusions have been reached for 23 exploited marine fish stocks out of 28 analyzed (reviewed in Heino et al., 2015). Thirteen of these studies focused on Atlantic cod, including the two examples above, 12 on other demersal fish species and only 3 on small pelagics. Among the five cases inconclusive for FIEs, four correspond to the three small pelagics and one to North Sea Norway pout, a small short-lived early-maturing gadoid. Together with some earlier theoretical findings (Ernande et al., 2004) and within-taxonomic family comparison (Marty et al., 2014), this suggests that large-bodied, late-maturing, (relatively) low-fecundity, long-lived species are more prone to FIE toward earlier maturation at smaller sizes than small-bodied, early-maturing, highly fecund, short-lived species. In other terms, the susceptibility of exploited fish species to FIE is likely to decrease with their position along the

slow-fast life-history continuum. This aspect could be leveraged for the conservation and evolutionary-enlightened management of fisheries resources.

Adaptive changes in the two other major life-history processes, reproductive investment and growth, have been much less studied, likely because of the lack of proper methodological approaches to disentangle the respective effects of demography, phenotypic plasticity, and evolution for these (but see [Swain et al., 2007](#) for growth). Consequently, the results obtained are equivocal and only two studies, on growth, report FIE (reviewed in [Heino et al., 2015](#)).

### 17.4.3 Which consequences of fishing-induced evolution for fish stock dynamics and fisheries productivity?

LHTs are among the first determinants of population dynamics. Beyond its direct demographic effect, fishing mortality will therefore affect fish stock dynamics through the evolutionary changes in LHTs it generates. Although FIE is a priori adaptive as it reduces fisheries-induced selection, it may be detrimental to fish stock demography with harmful consequences for fisheries productivity. This is because adaptive evolution is beneficial for individual fitness but may, due to density- and frequency-dependent processes and trade-offs between traits, lead to negative effects for some population characteristics such as total fecundity or biomass.

For instance, fishing mortality increasing with body size as imposed by many industrial fisheries is predicted to favor slow-growing, early-maturing individuals at small sizes and with high reproductive investment (e.g., [Enberg et al., 2009](#)). These changes in different LHTs can interact and, depending on their respective magnitudes, compromise, for example, the renewal capacity of a stock if the reduction in fecundity due to a smaller adult size is greater than the gain in fecundity due to a higher reproductive investment. These changes could even become maladaptive if fishing pressure were to be relaxed. Notably, in the hypothetical case of a moratorium declared after a population has adapted to fishing, some demographic characteristics are expected to increase to values equal or higher than the unexploited stock, such as total population size or total population fecundity. However, others are not expected to be restored to their virgin values, notably total biomass and spawning biomass, and thus the stock's exploitable fraction ([Marty et al., 2015](#)).

Conversely, a population that evolves in response to exploitation is expected to maintain a higher total biomass than an unadapted population under the same fishing (e.g., [Enberg et al., 2009](#)). For realistic fishing intensities, all the demographic properties of stocks described previously are predicted to fall when exploitation on a virgin stock starts due to the direct demographic effect of fishing. However, a rebound is expected to occur in a second period, due to the adaptive evolutionary changes in LHTs that partially

mitigate the direct demographic effects. Similarly, several models predict that populations that have evolved in response to fishing can tolerate higher fishing pressure than nonadapted populations (e.g., [Enberg et al., 2009](#)), and that the slope underlying their stock-recruitment relationships increases ([Enberg et al., 2010](#)).

### 17.4.4 Toward global erosion of genetic diversity and adaptive potential in fish?

In addition to affecting the average LHTs, FIE can also erode their genetic variability. Contemporary adaptive evolution proceeds on the basis of extant genetic variability by reducing the frequency of alleles that move LHTs away from the values favored by selection and by promoting those that push LHTs closer to these values. If this process is not counterbalanced by gene flow from other populations (or mutation rates, but these are inconsequential at the timescales considered), genetic variability decreases over generations.

LHTs' genetic variability is all the more important in that it determines a population's evolutionary potential and thus controls fish stocks' ability to adapt to other selection pressures acting on the same LHTs but also their evolutionary restoration in case of a decrease of the fishing selection pressure. A number of modeling studies (e.g., [Enberg et al., 2009](#)) showed that evolutionary changes in LHTs are expected to be reversed when fishing stopped, but that the evolutionary restoration is much slower than FIE itself. This is because natural selection pressure, which becomes dominant again once exploitation is stopped, is lower than that generated by exploitation. However, this slowness is predicted to be amplified by a strong reduction in genetic variability of LHTs, related to maturation mostly ([Marty et al., 2015](#)), if it is not replenished by gene flow from neighbor populations. In such a case, even under a complete moratorium, evolutionary restoration of LHT to their original value is expected to be extremely slow, if not impossible. It should be noticed, however, that the phenotypic values of the LHTs are predicted to be partially restored through phenotypic plasticity. This partial phenotypic restoration, although positive for fish stocks and fisheries, also partly explains the expected lack of evolutionary restoration: it reduces the gap between the phenotypic values of the LHTs and those favored by natural selection after the cessation of fishing, and thus decreases the selection pressures toward the initial genetic values of the LHTs.

## 17.5 Ecosystem effects

### 17.5.1 Fishing preys and bottom-up effects (supporting habitats, primary production)

When trawling the seabed and killing or damaging living organisms laying on the seafloor (the benthic communities),

fishing activities can induce unexpected outcomes on marine ecosystems by affecting their biological, physical, or geochemical environment. Hence a repeated disturbance of marine habitats or changing fishing pressure affects the balance among species occurrences and/or abundance. These effects sometimes propagate to the marine food webs by reducing the biomass, diversity, and body size of the affected organisms and the dependent ones in the short term. For example, one outcome could be increasing the availability of benthic prey for benthivorous fishes that survived the fishing (Hinz et al., 2017). Another outcome could be increasing the occurrence of more opportunistic species, small-bodied species with high turnover, or less fragile morphology rates (Blanchard et al., 2004).

These effects could also propagate and change the level of carrying capacity of the marine ecosystem in the long term, which may eventually translate into lower commercial fish production (bottom-up control). For example, intensive trawling provokes siltation of muddy areas, changing sediment biogeochemistry and eventually influencing primary production. By affecting habitat-forming or “engineer” species (that are, deep mud shrimp, *Polychaeta*, etc.), fishing can induce long-term change in marine ecosystems. Populations such as *Amphiura* spp. can grow (Sköld et al., 2018), or the sea urchin can proliferate (Guidetti et al., 2005) when predators keeping the density of these species low have disappeared. By altering nutrient fluxes on the bottom, fishing activities impact the marine food web with an increased accumulation of dead biomass in the detrital compartment. Such an accumulation responds to intensive fishing when not enough benthos biomass of scavenger invertebrates is left to process the primary production (Tillin et al., 2006). On the contrary, favoring the infaunal and scavenger invertebrates decreases overall productivity and redirects the resource to the microbial loop (Tillin et al., 2006). The consequences of such changes on fisheries productivity at the ecosystem level are difficult to predict (Reiss et al., 2009).

At worst, successive disturbance events can lead to a loss of functional redundancy on the seabed, ultimately resulting in a regime shift toward a permanently altered state. In particular, seabed impacted by extreme situations could see the deposit or filter feeder function effectively removed, leading to a permanent change in the functioning of the benthic ecosystem. The North Sea is a well-studied example where biogeographical fishing-induced changes from the beginning to the end of the 20th century occurred in 27 of 48 taxa, and the most profound changes in the epibenthos appear to have taken place before the 1980s (Callaway et al., 2007). Since then, there has been a further change, but the communities of recent decades probably reflect faunal assemblages adapted to long-term impacts (Callaway et al., 2007). Hence an increase in water column diatom biomass could have occurred in the North Sea

ecosystem because of less grazing pressure due to reduced filter-feeder biomass, which may promote a general shift favoring the pelagic system (van der Molen et al., 2013). This chronic disturbance may prevent the re-establishment of the abundance of depleted populations, prevent recolonization from adjacent areas, and may be exacerbated by a lack of redundant species available locally or in adjacent areas.

Fishing activities can also impact some ecosystem components more heavily, such as vulnerable cold-water or deep-water coral or deep-sea fishes, with a radical change to them, but with species-specific impacts that are highly variable (Godbold et al., 2013). Vulnerable habitats (VMEs) are often high fish concentration areas associated with seamounts, making them very attractive to fisheries. Unfortunately, understanding the observed patterns in biomass in response to the deep-sea fishery requires a further detailed understanding of the behavior and ecology of individual species, which is, by nature, challenging to attain in such remote areas. Hence recovery from any disturbance or damage could take several years or is even irreversible. Benthic seamount communities, including cold-water corals, are extraordinarily long-lived and grow very slowly, making them particularly vulnerable to the impact of fishing. Therefore biogenic habitats that may accumulate over thousands of years can be rapidly reduced by fishing, whereas recovery from this severe destruction may span decades or even centuries. It is also uncertain whether systems will ever recover to their original ecological structure.

On shallow waters, fishing can impact essential fish habitats, for which many coastal and offshore fish species are highly dependent on specific habitat types for population maintenance. There are shallow, productive habitats in the coastal zone such as wetlands, vegetated flats/lagoons, and sheltered bays, as well as more exposed rocky and sandy areas. Fish utilize these habitats across many life history stages including spawning, juvenile development, feeding, and migration (Kraufvelin et al., 2018). In the Northeast Atlantic, 44% of all ICES species that contribute to 77% of the commercial landings, i.e., species assessed and advised by the International Council for the Exploration of the Sea, utilize coastal habitats as spawning, feeding, nursery, or migration areas (Seitz et al., 2014). Unfortunately, active fishing gear can alter the suitability of persistent spawning habitats or habitats suitable for early life stages as the estuarine habitats or the kelp forests. A change in suitable habitats is also a challenge when affecting keystone species preyed on by marine mammals and species of commercial interest.

Affecting forage fish abundance fluctuations may also often have complex and unanticipated consequences on other commercially and/or ecologically important species (Lynam et al., 2017). As there are strong interactions

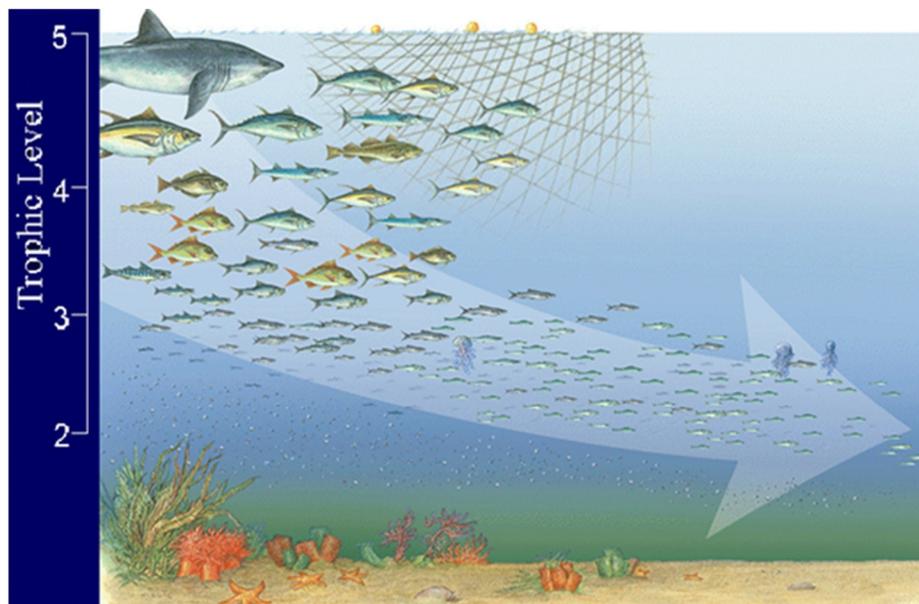
between the forage fish species, both interspecific competition and intraspecific mechanisms such as density-dependence and cannibalism mechanisms, or even interactions through shared parasites or disease, come into play linking bottom-up and top-down effects in the marine ecosystems. Affecting the plankton indirectly can cascade up to impact demersal fish and predatory seabirds. The exploitation of forage fish for purposes other than human consumption also removes large amounts of fish biomass from ecosystems and may well “force” predatory fish species critical to human consumption fisheries to target suboptimal prey with a lower calorific value. Suboptimal preying leads to reduced growth and conditions likely to impair reproduction and survival chances (Dickey-Collas et al., 2014). Ironically, the far-reach consequences might go through up to the fishery economy of the entire fleet. For example, restricting the exploitation of forage fish in the North Sea region might actually result in increased revenue at the scale of the entire fishing fleet, making it economically suboptimal to catch more forage species (Dickey-Collas et al., 2014).

### 17.5.2 Fishing predators and top-down effects (trophic cascade, instability)

Fishing can change the productivity of the marine ecosystem because fishing often targets the largest, highest trophic level fish, which would result in declining trends for big fish over time (Bell et al., 2018). It has been shown

that “fishing down the food web” could occur leading to landings increasingly dominated by smaller species from lower trophic levels (Fig. 17.5; Pauly et al., 1998). Decreases in the trophic level of landings are assumed to reflect those in fish communities because size-selective mortality causes decreases in the relative abundance of larger species and in mean body size within species. By selecting species, fishing activities exert a “top-down effect” that can change trophic interactions with possible far-reach indirect changes with cascading effects from a change in species composition of the marine ecosystem, a removal of particular functional groups, and a change in species size-structure (Bell et al., 2018). For example, removing apex predators releases predation pressure that can result in better survival of small species, while eliminating entire functional groups of predators could cascade, affecting primary producers. Fisheries could also alter the abundance ratio of species and thereby alter or emphasize the biotic interactions in the community, possibly inducing biomass fluctuations or, on the contrary, stabilizing species biomass.

As a result, a marine ecosystem can switch to an alternative stable state dominated by small pelagics and marine mammals (Bell et al., 2018). Prey-switching, such as seals under different cod population sizes and spatial overlap, makes it variable how this top predator could affect the exploited stocks. In contrast, in communities regulated by interspecific interactions, high predation intensity can alter the strength of competitive interactions and allow for



**FIG. 17.5** Symbolic representation of the Fishing down the marine food web process (Pauly et al., 1998). In this process, high trophic levels are most impacted when fisheries develop, due to their lower turnover and therefore higher sensitivity, and due to the cumulative effects of fishing along food webs. Gradually, the exploitation targets the prey, which is impacted in turn, then the prey of the prey and so on toward the lower trophic levels. The bottom part of the graph also illustrates the impact of fishing on the seabed, with a decrease in the abundance of algae and benthic invertebrates as fishing pressure increases.

increased coexistence of competitive species (Blanchard et al., 2004). Those effects are mediated by a multitude of other environmental factors. It results that two stocks of one species in a fishery may respond differently under specific or changing environmental conditions. Hence the trophic relationships between species and life stages are often unknown, especially in the local context and for species with no immediate economic value.

### 17.5.3 Minimizing the impact of fishing— Toward an ecosystem approach to fisheries management

The exploitation of targeted commercial species can lead vulnerable species to extinction by degrading some ecosystem components that make its biodiversity. Bycatch or destructive fishing practices exert pressure on vulnerable species and habitats caused by unselective fishing (e.g., catching juvenile fish or disturbing fish when they aggregate to spawn) and unsustainable fishing practices (e.g., when fishing gears penetrate the seafloor and resuspend sediments). Bycaught species are the result of mixed fisheries and technical interactions between them. Because of an imperfect selection of the fishing, the high spatial co-occurrence of target and incidental species makes them very sensitive to overexploitation (Milessi and Defeo, 2002). For commercially exploited species, it is often argued that the economic extinction of exploited populations will occur before biological extinction, and therefore the exploitation would cease before it is too late. However, this is not the case for bycatch species caught in multispecies fisheries. Hence bycatch fish species decline along with the overexploitation of target species, even if the target species may decline first and incidental ones later. A collapse pattern would be sequential, starting with the most valuable resources (Milessi and Defeo, 2002).

If not regulated, fishing impacts will lead the marine ecosystem toward a stable equilibrium of less vulnerable species left in the seas and lower ocean productivity. Hence the ecosystem approach to fisheries management (EAFM) recognizes that it is necessary to manage to preserve other species and ecosystem components in the long-term perspective because fisheries exploitation affects not only target species populations but can also affect the fish and their habitats with low or no immediate commercial interest (Bastardie et al., 2021). This recognizes the supportive role of these components in maintaining healthy and productive marine ecosystems (IPBES, 2019). This is also because various pressures accumulate in the oceans and the seas and affect ocean productivity, conditioned by its biodiversity and the maintenance of marine food webs and seafloor integrity. Cumulative pressure from climate change, pollution and eutrophication, and other industrial sectors exploiting the seas combines to alter the dynamic of the

marine ecosystems. European oceans will also be subject to massive development of marine infrastructure soon, exposing the marine ecosystems to various environmental and anthropogenic stressors, including habitat modification from coastal development, invasive species, pathogens, sport fishing, etc. Such a combination of pressure affects biological, physical, and geochemical conditions, including different biological interactions between functional diversity groups, altering the species' vital rates and essential life history aspects along with different vulnerability and exposure, therefore possibly restraining future fishing opportunities.

## 17.6 Concluding remarks and perspectives

According to FAO's guidelines and to a variety of international commitments, including resolutions from UN World summits on sustainable development, the ecosystem approach to fisheries management is now recognized worldwide as a necessity. The challenge is notably to reinforce the productivity and resilience of marine ecosystems, especially in the context of the expected impacts of climate change (cf. Chapter 18). Incidentally, this approach should restore many fish populations, often depleted due to overfishing, thus contributing to maintain or strengthen the place and role of fishes in the functioning of marine ecosystems.

However, EAFM implementation is a long process, currently on the way, and probably still in its infancy at global scale, with progress occurring primarily in developed countries. In Europe, EAFM is the practical set of management actions and policy instruments deployed to resolve the historical divide between environmental protection and fisheries management. Hence the last reform of the Common Fishery Policy adopted in 2013 introduced the possibility of making fisheries management in Europe coherent with its environmental protection objectives defined in some major European Directives (Marine strategy framework directive, Habitats, and Birds directives).

Such new legislations, also observed in countries such as the US, Canada, Australia, or South Africa, come to reinforce the management with technical measures that contribute to the EAFM. In particular, these new EAFM-oriented measures intend to address issues on biodiversity conservation. They especially aim to preserve sensitive species using more selective fishing gears and practices, to maintain the seafloor integrity using less impacting gears or closed areas, and to reducing the impact on targeted species while maintaining the structure of the marine food webs, by protecting juveniles and monitoring trophic guilds. As an ultimate goal, and as notably claimed by the CFP itself, EAFM aims to minimize, i.e., reduce as much as possible, all adverse impacts of fishing on marine ecosystems.

In the process of implementing EAFM, new needs emerge for research to better understand the functioning of the ecosystem and the complexity of fishing impacts, from marine fish populations to species assemblages, and to the entire ecosystem, including benthic or pelagic habitats as well as the various components of biodiversity. In particular, challenge to minimize fishing impact relies on understanding the resilience drivers and adaptative capacities of fish populations and ecosystems.

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