

# Fisheries Resources as Diminishing Assets: Marine Diversity Threatened by Anecdotes

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## ABSTRACT

Fish stock dynamics are studied using fishery statistics which do not take into account the existence of the intraspecific diversity in fish populations. Populations are generally considered to be homogeneous and management considers each stock of a given species as a global entity. However recent genetic population studies reveal unsuspected intraspecific diversity. Examples of population collapses and local extinctions are presented which, in spite of restrictive measurements (limitation of the effort, quotas...), do not come back to their former abundance level (bluefin tuna, cod, herring, marine turtles, salmon...) resulting in decreasing catches from these stocks. At first sight, reports of fluctuations of such local populations may be viewed as anecdotal. The incorporation of fisheries history (anecdotes such as local extinctions) into models used by fishery scientists would help evaluate the true rate of disappearance of resource species and the ecological cost of fisheries. We present here a qualitative approach of fish behavior, based on earlier work of the first author to explain why the extinction of local populations may affect long-term overall fish productivity. The erosion of the marine intraspecific diversity could lead to a long-term decline in the productivity of the marine resources.

## RÉSUMÉ

La dynamique des populations de poisson est étudiée en utilisant des statistiques de pêches qui ne prennent pas en compte l'existence de la diversité intraspécifique. Les populations exploitées sont généralement supposées homogènes et la gestion considère les stocks comme des entités globales. Cependant de récentes études menées en génétique des populations révèlent une diversité intraspécifique inattendue. On présente des exemples d'effondrement de stocks et d'extinctions locales qui, en dépit de mesures d'aménagement (limitation de l'effort, des quotas...), ne se reconstituent pas pleinement (thon rouge, morue, hareng, les tortues marines, les saumons...) et aboutissent globalement à de moindres captures. A première vue, certaines fluctuations de populations locales peuvent être perçues comme des anecdotes. L'incorporation de l'histoire des pêches (anecdotes comme celles des extinctions locales) dans les modèles utilisés par les scientifiques pourrait aider à évaluer le réel impact de l'exploitation sur le taux de disparition de la diversité intraspécifique et son coût écologique. Nous présentons un cadre conceptuel basé sur un précédent travail du premier auteur qui permet d'expliquer pourquoi les extinctions locales peuvent conduire à long terme à un déclin des ressources marines. L'érosion de la diversité marine intraspécifique pourrait conduire à un déclin progressif de la productivité des ressources marines.

## 1. GLOBAL FISHERIES IN A NEW AND GLOBAL PERSPECTIVE

Almost all fish species have tiny eggs of one or a few millimeters, in diameter whatever are their adult sizes. Some life history traits of marine species have been apparently shaped by strong selective pressures. As a result, most fish populations have an enormous capacity of resilience due to the high batch fecundity and to the large populations they develop. This is part of what allows the impressive fish catches extracted from the oceans. However present global fisheries are not doing so well, not to say that fisheries are a global disaster (Pauly, 1995). The world marine fish catch have increased almost fivefold from around  $19 \cdot 10^6$  t in 1950 to  $100 \cdot 10^6$  t in 1992; this latter value was considered a threshold value; thus, in 1994 the FAO pointed out that 69% of the global fish stocks for which assessments are available, are either fully exploited, overfished, depleted or slowly recovering from depletion. Fisheries are in a new and global context. Will marine fish exploitation be viable under a persistent degraded ecological state? This certainly constitutes one of the most important challenge for the next decades of exploitation of renewable resources (Roberts, 1997).

Although fisheries assessment has been extensively developed over the last century, it has not hitherto considered the evolutionary consequences of fishing itself (Berry, 1995). The ever-increasing intensity of exploitation and the deterioration of fish stocks have generated an urgent need for a better understanding of evolution driven by harvesting and its implications for management (Stokes *et al.*, 1993). Intense fishing mortality could act as a new selective pressure producing genetic change, for example on heritable traits such as growth rate and age of first reproduction (Sutherland, 1990). Thus life histories of fish could be altered as a result of harvesting, inducing a risk of possible long-term decline in yields. Species are sometimes profitable at very low population levels and if a fishery targets a high-value species, it may reduce the stock to a level that leads to depletion and collapse. Fisheries-induced collapse of marine populations can have two consequences for biodiversity. First, the populations may not recover and/or re-colonize their ecological niche. Secondly, rare genes can be lost as a result of a drastic decrease in population number. To take a longer-term view and to rethink the way in which wild populations are harvested is needed.

Recently Pauly (1995) defined a 'shifting baseline syndrome' wherein a gradual accommodation of the creeping disappearance of resource species takes place due to inappropriate reference points: each generation of fisheries scientists accepts as a baseline the stock size and species composition that occurred at the beginning of their careers, and uses this to evaluate changes. Thus, Pauly (*op.cit.*), identified a lack of the use of fisheries history, to help us to understand and to overcome the shifting baseline syndrome and to evaluate the true social and ecological costs of fisheries. In this paper we would like to emphasize the importance of considering 'anecdotes' such as local populations extinctions for long term sustainable fisheries. Using an ecological framework, the relevance of the intraspecific level for fish stock management will then be considered.

## 2. HETEROGENEOUS MARINE FISH STOCKS

Field and genetic studies greatly modify any simplified view of population dynamics and structures. Hedgecock *et al.* (1989) report genetic heterogeneity within the central Californian northern anchovy stock (*Engraulis mordax*), previously regarded as a panmictic population. Thus, anchovy stocks that were thought to be homogeneous are in fact a mosaic of 'elementary' populations (Hedgecock, 1991). According to Mathisen (1989) the anchoveta stock off Peru consists of a large number of local subpopulations each of which is genetically adapted to 'home' to a different upwelling location and to spawn during a specific period of the year. European sardine populations are traditionally assigned to six different 'races'; however, further subdivisions have been made according to spawning seasons that are separated by several months and that may define sympatric populations (Wyatt *et al.*, 1991). As noted by Hedgecock (1991) for *Engraulis mordax* off California, the 'demonstration of sympatric, biologically distinct subpopulations within the main spawning area of the central stock is unexplained by current concepts of northern anchovy stock structure'. Electrophoretic analysis of stock structure in Northern Mediterranean anchovies, *Engraulis encrasicolus*, clearly illustrate the independence of anchovy stocks in the Northern Mediterranean and given a restricted level of migration, one would predict that regeneration of depleted stocks would be almost totally autochthonous (Bembo *et al.*, 1996). Recent genetic studies emphasize the fact that even high migrating fish populations are heterogeneous, even in an apparently homogeneous environment, and that this heterogeneity should play a fundamental role in population dynamics. Microsatellite DNA provide that Atlantic cod (*Gadus morhua*) overwintering in inshore Newfoundland are genetically distinguishable from cod overwintering offshore (Ruzzante *et al.*, 1996). Restriction analysis of mitochondrial DNA of swordfish (*Xiphias gladius*) revealed no

differentiation among samples from three sites in the Mediterranean Sea (Greece, Italy, Spain) but a high degree of differentiation between Mediterranean samples and a sample from the Gulf of Guinea (Kotoulas *et al.*, 1995). Another study indicated that the mtDNA haplotype frequencies were significantly different among samples from the Pacific Ocean, the Atlantic Ocean and the Mediterranean Sea (Bremer *et al.*, in press). Genetic analyses are generally very sensitive to gene flow. Relatively low levels of exchange between stocks, negligible from a management perspective, may be sufficient to ensure genetic homogeneity (Bembo *et al.*, 1996). These recent genetic analyses also clearly suggest that, under such integrity, recovery from collapse would be slow.

## 3. DIVERSITY AND EXPLOITATION

### 3.1. Generalities

Probably well over half of all vertebrate species are fishes as there are in excess of 22 000 described species of fish, and vertebrates as a whole comprise around 43 000 species (Anon., 1992). Thus fishes make up the most abundant class of vertebrates, both in terms of numbers of species and of individuals. It also appears that fish typically exhibit higher levels of variation both between and within populations than in other vertebrates (Ryman and Utter, 1987). More than 13 000 species are marine species, but the fisheries industry is based on a remarkably small number of species. Thus over one million tonnes each of 12 fish species (10 marine and 2 freshwater) were caught in 1989; together this comprised 34.7.10<sup>6</sup> t, or 35% of the total world catch (Anon., 1992).

Overfishing seems to be a major threat to biodiversity as it depletes resources, and thus can lead to loss of genetic integrity, local populations and even species. Moreover, the important catches of immature fish prevent the stocks from renewing themselves. In the North Sea, only 2 to 3% of cod and haddock reach maturity (60 cm, 4 years) and more than 90% of cod and 65% to 80% of grouper caught (between the Gulf of Biscay and West Scotland) are composed by juveniles. For fixed species (giant clams *Tridacnidae*), low densities and erratic recruitment make such populations prone to overfishing, inducing local extinctions (Lucas, 1994). Natural environment changes, and especially for species which inhabit or migrate in area in vicinity of human activity numerous causes (such as habitat degradation, anthropogenic changes, deterioration of water quality, etc.) often lead to a local disappearance of a species. In Chichiawan stream, Taiwan, the salmon cohort born in 1987 has been destroyed by the typhoon Lynn which occurred during the breeding season. Some fishing methods such as the use of dynamite, chemicals (bleach and cyanide), bottom trawling or bottom-set net can damage or destroy habitat, reducing the survival of organisms. Introduction of fishes was thought to be a solution to various problems: introduction of fast-growing fish for fish culture, introduction of predatory fishes to control fish production in ponds, 'improvement' of sport fisheries, 'control' of unwanted organisms (aquatic weed, snails, mosquitoes, etc.), to fill seemingly 'empty' ecological niches. But such introductions generally create major problems (Moreau *et al.*, 1988), through predation or competition. The introduced fishes can reduce or cause local extinction of some endemic species (Lodge and Hill, 1994).

Most examples of collapses are due to multiple causes and are the result of interaction between various factors. Generally, for marine species it is the consequence of a natural disturbance such as environmental changes, associated with intense exploitation (Beverton, 1990).

## 3.2. Facts and numbers

### 3.2.1- Herring (*Clupea harengus*)

Herring are known for their tendency to return to the spawning ground where they themselves have been hatched. Fecundity data show that herring hatched in the Southern North Sea and the English Channel probably are genetically distinct from those in the Central and Northern North Sea (Zijlstra, 1973). The subpopulations of each spawning site tend to maintain their integrity over the years. Thus, when several of these subpopulations were destroyed by overfishing in the 1960s, they did not re-appear after the recovery of the total North Sea stock from 75 000 t in 1975 to  $1.4 \cdot 10^6$  t in 1992. The size of the actual spawning sites hardly decreased during this period and the former spawning sites that were fished out in the 1960s were not reoccupied since (Corten, 1993). The herring stock recovered during the 1980s owing to the closure of the herring fishery in the late 1970s - early 1980s and subsequent increases in recruitment. However the spawning-stock biomass which used to range between 2 and  $5 \cdot 10^6$  t in the 1950s, hardly reaches 1 million t in the 1990s. (Serchuk *et al.*, 1996). Generally, during their feeding migration, fish appear to follow the same route from one year to another, and like the choice of the spawning and overwintering grounds, it is probably also determined by tradition (Corten, op.cit.). Thus, it may be that the recolonization of a feeding ground requires the presence of older, experienced herring to guide new generations to the former, traditional feeding ground (Corten, op. cit.). Herring adapt their feeding ground with local conditions: for example in the 1980s, their feeding grounds during June to July changed from the Western North Sea to Northeastern North Sea, and they extended their migration and changed their vertical distribution (Corten and Van de Kamp, 1992). Another change in migration involved Baltic herring, which in 1986 changed from the Kattegat and Skagerrak into the North Sea (Anon, 1991).

Herring have been caught in Norway since time immemorial. The history of the herring fisheries can be traced back hundreds of years, but data on stock assessment are only available since the 1950s. The adult herring stock was estimated to range from 7 to  $10 \cdot 10^6$  t in the 1950s, but declined in the 1960s and since then remained below  $2 \cdot 10^6$  t (Hamre, 1994). The Norwegian spring-spawning herring showed a steady pattern in its feeding migration for many decades until the collapse of the stock in the late 1960s. After this local extinction, herring remained in the vicinity of the Norwegian coast throughout the year (Corten, 1993). These fishes now extend their feeding ground over the Norwegian Sea east of  $5^{\circ}$ W, but they have not yet rediscovered their old feeding grounds. In 1963 and 1964, heavy exploitation of both immature and mature herring by Norwegians in Norwegian waters led to a collapse of the overwintering stock. It is only in 1984, after the recruitment of the first strong North Sea class, that herring reappeared in the Norwegian zone.

Atlantic herring (*Clupea harengus harengus* L.) was, before its collapse in 1977 (probably due to overfishing, Moeller, 1984) supported on the Georges Bank, the largest herring fishery in the Northwest Atlantic. After almost a decade herring have reappeared. An analysis of age composition, isozyme characteristics, time of the reappearance, shows that the reappearance of this population would have resulted from resurgence of a residual Georges Bank population (Stephenson and Kornfield, 1993) rather than recolonization from other areas located nearby, i.e., Jeffreys Ledge and S.W. Nova Scotia.

Herring stocks are composed of different subpopulations adapted to local areas. Thus, a concentration of fishing effort on certain subpopulations can lead to the extinction of these components before the total stock shows signs of overfishing (Corten, 1993). This characteristic make herring stocks prone to local extinction even if, generally, they will recover; thus, the depleted British Columbia stock recovered as soon as fishing stopped (Saville, 1980). However in general, once the spawning site has been abandoned by the population, it is not easily re-occupied by later generations. Thus, there is

evidence of extinction, such as that of Pacific herring, *Clupea barengus pallasii* or that of the Hokkaido-Sakhalin herring, which has disappeared since 1946 (Tanaka, 1983). Certain races have never recovered from earlier overfishing: the spring-spawning stock of Icelandic herring is now effectively extinct, though Jakobsson (1985) believes that the failure of this stock to recover may be associated with a sharp decline in the level of primary production in the area. Corten (1990) mentions the recolonization of the Aberdeen Bank spawning ground in 1983 after an absence of 15 years. Bergstad *et al.* (1991) noticed that the traditional spawning ground off Karmoy in Southern Norway has been recolonized in 1989, 30 years after the stock was depleted.

### 3.2.2- Northern cod (*Gadus morhua*)

The Sami Fjord Cod in Northern Norway is of three types, all different from the Norwegian Arctic cod, which spawns off Lofoten (Eythorsson, 1993). These three types are: The Algae-cod (in Sami: *tararunuk*) which is brown in color, never leaves the fjord. This type of cod seems to be disappearing, along with the brown algae belt that it lives in. The Fjord cod (Sami: *vuotnaguolli*), which spawns in the fjord and does not migrate out of it. It starts spawning before the migrating cod. The migrating cod (Sami: *buoiddesguolli*), which spawns in the fjord in winter, but lives in the open sea the rest of the year. Similarly, the analysis of mtDNA provided evidence that Atlantic cod overwintering in offshore Newfoundland are genetically distinguishable from cod overwintering offshore (Ruzzante *et al.*, 1996).

The commercial extinction of northern cod off Newfoundland and Labrador in 1992 was a social and economic disaster for the region. The high rates of exploitation in the late 1980s and early 1990s are thought to be responsible for the collapse of the six major cod stocks in Eastern Canada by 1993. The hypothesis that the primary cause of the collapse was environmental has been proposed (climate change, seal predation, changes in the ecosystem) (Lear and Parsons, 1993; Mann and Drinkwater, 1994). Against this speaks the fact that two declines in annual survival probabilities in the 1980s appear at the same time inshore and offshore as fishing effort increased (Hutchings and Myers, 1994). Indeed, even if an increase of natural mortality in the first half of 1991 occurred, overfishing was high enough to cause a collapse of the cod population (Myers and Cadigan, 1995b). It has also been claimed that the collapse was due to overfishing alone (Hutchings and Myers, 1994; Myers and Cadigan, 1995a,b). Results of studies on three of these stocks (Southern Labrador/North-East Newfoundland, St-Pierre Bank, and Northern Gulf of St-Lawrence) attribute the collapse of these stocks to overfishing (Myers *et al.*, 1996). Because of errors on the estimations of population abundance and fishing mortality (the first one was overestimated and the second was underestimated), quotas were too high. The over capacity of fishing fleet allowed to increase the fishing mortality and the discarding of juveniles. As a consequence, the number of fish entering the fishery was reduced and the extremely low levels of spawners inhibited the recovery of the population (Myers and Barrowman, 1994). All of this lead to a declining long-term catch rate, even under a fishing effort that switched from inshore to offshore (from areas of low to high catch rates).

### 3.2.3- Bluefin tuna

The bluefin tuna (*Thunnus thynnus thynnus*) has a temperate distribution. It is supposed to have a 'natal homing' strategy, which brings it back to spawn either in the South Central Mediterranean Sea or in the Gulf of Mexico (Cury *et al.*, in press). This migrant fish which has been fished in Mediterranean Sea since the 8th millennium BP (Desse and Desse-Berset, 1994) is much sought after for the quality of the flesh, or for sport fishing (mostly in the Eastern USA).

Bluefin tuna has disappeared from some areas (Norway, N-E Brazil, Black Sea, etc.) where they were feeding during the 1960s. The disappearances may have various causes: change in fishing pattern for Norway, overfishing off Brazil (Cury *et al.*, op cit.). But the hypotheses would not explain entirely the depletion of stocks of bluefin tunas. This is also true for other causes that must be taken into account such as climatic changes or variations on the main prey biomass (anchovies in the Black Sea).

Fish catch statistics may help track migration patterns and particularly reproductive migration as these fish tend to aggregate when they spawn. Bluefin tuna is certainly the tuna species that is fished in the Atlantic Ocean since most ancient times. Archeological studies reveal that 8th millennium BP age, bluefin was found in a coastal pre-ceramic Neolithic site of Cape Andres Kastros in Cyprus (Desse and Desse-Berset, 1994). It was also exploited more than 3 000 years ago by the Greeks. Then Phoenicians, and subsequently Romans, initiated active fisheries using large traps all around the Straits of Gibraltar. This exploitation was developed until the early XXth century all around the Mediterranean Sea. Since 1950, new fishing gear (hand-lines made of nylon thread, pole and line, purse seine, longline) offered possibilities of development for new coastal fisheries in the Eastern and the Western Atlantic. Bluefin tuna supplied national markets of fresh fish and a low demand market for canning. By 1960, the bluefin fisheries reached their maximal geographical extension. Then, at the end of the 1960s, two major fisheries disappeared. Bluefin tuna entirely vanished from the Brazilian area (centered on the Equator between 25 and 35°W) (Cury *et al.*, in press), a major fishing zone during the early sixties (producing 64% of the West Atlantic bluefin catch between 1963 and 1965). The North East Atlantic bluefin fishery off Norway was also a major one during the 1950s (an average 20% of the bluefin catch between 1951 and 1962); this fishery had collapsed by 1965.

### 3.2.4- Many others

Many more examples may extend the list of natural or human induced disappearance of marine populations. Over the last century, Pacific salmon (*Oncorhynchus* spp.) have totally or partially disappeared from about 40% of their breeding ranges in the states of Washington, Oregon, Idaho, and California (Comm. on Protection and Management of Pacific Northwest Anadromous Salmon, 1995). The European sea sturgeon (*Acipenser sturio*), once numerous along western coastal Europe and Scandinavia, has today only marginal populations in the Gironde River, France, and possibly in the Black Sea. The Adriatic sturgeon (*Acipenser dabryanus*) limited to the Yangtze River, the Adriatic sturgeon (*Acipenser naccarii*), or the Amu-Dar shovelnose sturgeon (*Psuedoscaphirhynchus kaufmanni*) of the Amu-Darya River are all in sharp decline or near extinction (Waldman, 1995). Not only fishes are subject to local extinctions. Marine turtles, coconut crabs and giant clams (long-lived and slow-growing species) are endangered in most of the South Western Pacific islands region (Zann, 1994). Not only overfishing but also the increasing pressure from rapidly rising human populations, urbanization, agricultural, industrial development, result in a significant loss of coastal habitats, pollution and eutrophication of coastal lagoons and reefs; the consequence are local extinctions of various populations. Green turtle (*Chelonia mydas*) migrate between tropical and subtropical feeding and a local specific nesting ground. The females probably return to nest at their natal rookery (Carr, 1967). For thousands of years green turtles have been fished, but in the last four centuries, increasing exploitation of green turtle marketing has driven several populations to extinction and has greatly diminished others (Parsons, 1962). Former rookeries such as Grand Cayman, Bermuda, Alto Velo, have not been re-colonized by natural recruitment (Parsons, 1962). Because of natal homing, overharvesting of nesting assemblages is not compensated by recruitment from other rookeries (Bowen *et al.*, 1992).

## 4. FISHERIES RESOURCES AS DIMINISHING ASSETS

Due to extension and openness of seas and oceans, the extinction through overfishing of a marine species rarely occurred until recent times. Today many fish species are known to have been brought to the verge of extinction and are added to the red list by the Species Survival Commission of the World Conservation Council (IUCN) (Grain, 1995). The need to protect biodiversity has become increasingly apparent over the past two decades (Ryman *et al.*, 1995). Gould (1996) recently discussed the importance of preserving the diversity of life as the loss of one species is forever. He argued that the same arguments can not be done when considering the intraspecific diversity. Moreover, local extinctions may not be considered as important as the great majority of the stocks shows sign of recovery. It seems that populations reduced to 1/1000th or so of their peak sizes for long time periods (e.g., more than 20 years in the case of the California sardine), can form a nucleus of a revival when conditions become favorable (Beverton, 1990). In this sense, reducing intraspecific diversity does not represent the same kind of threat as species extinctions. However, reducing intraspecific diversity of marine populations could affect the long-term productivity of the fisheries. There are several reasons for that. The first one is that long-term stocks sustainability should not be taken for granted: reviewing collapse and recovery of pelagic fish stocks, Beverton (*op. cit.*) noted "the possibility that the collapsed population may never be able to fully regain its former status in the ecosystem"; among nine documented stocks which experienced a collapse, only one has fully regained its original size. Then, at the subpopulation scale, the extinction of one or few populations can pass unnoticed if the others have a great productivity and a subpopulation may become extinct before signs of overfishing are noticed in the total stock. Finally, even if regulation of fisheries is established, the biomass of the total stock will fluctuate at a long-term lower level. The second reason is that ecological frameworks are now being developed that can help to incorporate fisheries history (anecdotes such as the local extinction documented in this paper) into models for fisheries scientists. These models may help us evaluate the true disappearance of resource species and their ecological cost to fisheries. In ecology, it is common to consider a demographic exchangeability of individuals (two individuals are then equivalent) and this is used to define populations in most models of population and community ecology (Templeton, 1989). Recently Cury (1994) proposed a generalization of 'natal homing' within which homing is viewed as part of a continuum of reproductive strategies, all relying on imprinting. This generalization postulates that a newborn individual memorizes early environmental cues, which later determine the choice of its reproductive environment. This way of looking at fish population dynamics implies that inertia is the driving force in the functioning of natural systems. Because every individual is able to explore a specific environmental possibility and in some way to transmit it to its descendants, it makes each of these individuals unique in terms of their reproductive behavior. In other words, once a spawning site has been abandoned or fished out, it takes a long period of time to reoccupy it by later generations. As noted in the Introduction, the resilience of marine fish population is potentially enormous and allows the fisheries to be so successful. On the other hand, various behavioral mechanisms that lead to the discrete population concept thwart the renewal process in its duration and intensity dimensions (see also Parrish, this vol.). Thus, the disappearance of subpopulations can have a detrimental effect on long-term marine fish catch (Fig. 1).

The paradigm underlying most fisheries regulation is to prevent undersized fish from being caught and/or to allow a sufficient number of fishes to escape harvest to ensure a sufficient adult spawning stock, so as to maintain high recruitment levels. The two principal forms of regulation are to control the size of organisms taken and the amount of harvesting effort applied (Bohnsack and Ault, 1996). Rarely are the effects of fishing on the genetic or stocks composition considered. Management has led to an ultimate pathology of less resilient and more vulnerable ecosystems, more rigid and

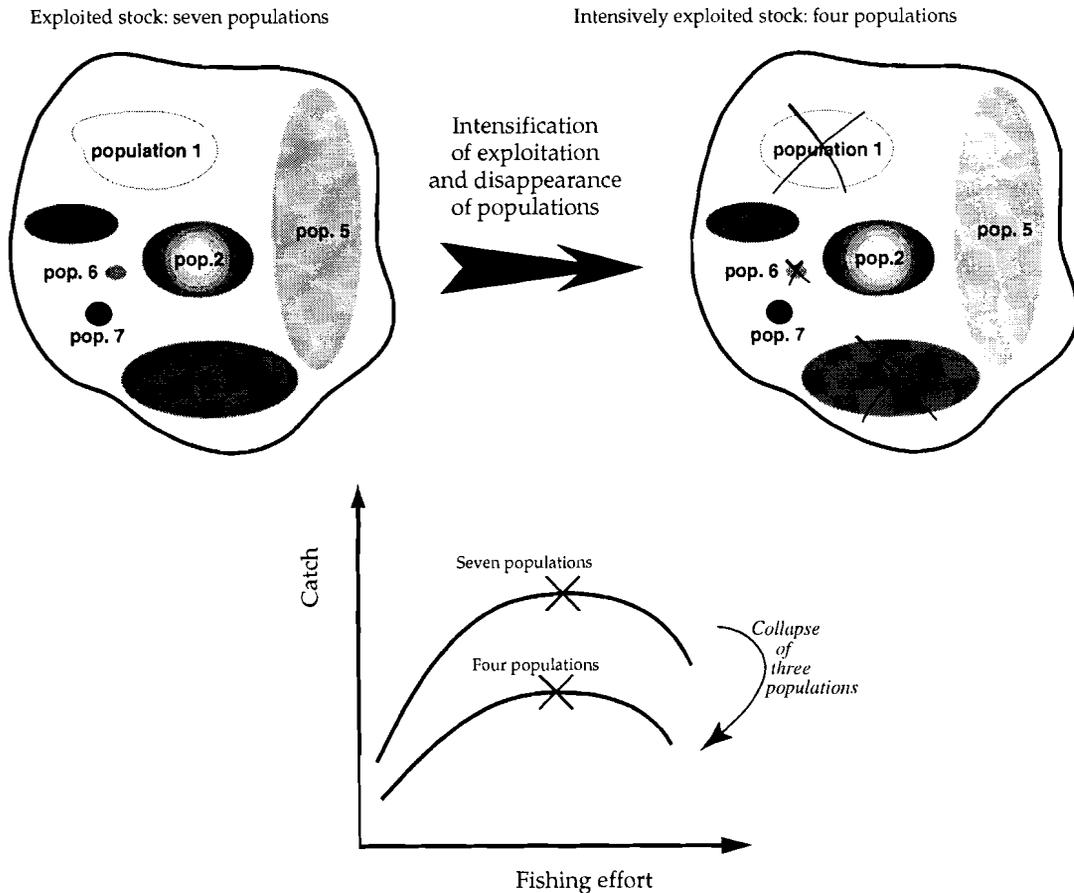


Fig. 1: Schematic representation of how the erosion of the intraspecific diversity may affect the productivity of fisheries. The disappearance of three populations under intense exploitation can have a detrimental effect on long-term marine fish catch. Productivity declines as a result, as suggested in the catch-effort diagram where two catch levels are possible for a given fishing effort according to the composition of the two stocks.

unresponsive management agencies and more dependent societies (Gunderson *et al.*, 1995) A new objective is to change from single species management to ecosystem management aimed at protecting marine biodiversity and at promoting its viable use. This constitute a chance to integrate biodiversity into fish population dynamics and to develop frameworks to understand and promote new concepts on the functioning and the dynamics of renewable resources (Cury, 1994). As mentioned by Franck and Leggett (1994), a greater consideration of the implications of ecological and evolutionary theory could lead to significant advances in the understanding of processes of population regulation in marine fishes. Because fish are the only major food source harvested from natural populations, a knowledge of the structure of these populations is essential for proper resource management. The need for better understanding of biodiversity among fishes is particularly needed below the species level (Ryman *et al.*, 1995).

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