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Managing Evolving Fish Stocks

Christian Jørgensen,[1*] Katja Enberg,[1,2] Erin S. Dunlop,[2,1] Robert Arlinghaus,[3,4] David S. Boukal,[2,1] Keith Brander,[5] Bruno Ernande,[6,7] Anna GŒrdmark,[8] Fiona Johnston,[7,3] Shuichi Matsumura,[7,3]Heidi Pardoe,[9,10] Kristina Raab,[11,10] Alexandra Silva,[12] Anssi Vainikka,[8] Ulf Dieckmann,[7] Mikko Heino,[2,1,7] Adriaan D. Rijnsdorp[13]

[1]Department of Biology, University of Bergen, N-5020 Bergen.
[2]Institute of Marine Research, Bergen, Norway.
[3]Department of Biology and Ecology of Fishes, Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Berlin.
[4]Humboldt-University of Berlin, Institute of Animal Sciences, Berlin, Germany.
[5]International Council for the Exploration of the Sea (ICES), Copenhagen, Denmark.
[6]Laboratoire Ressources Halieutiques, Institut Français de Recherche pour l'Exploitation de la Mer (IFREMER), Port-en-Bessin, France.
[7]Evolution and Ecology Program, International Institute for Applied Systems Analysis (IIASA), Laxenburg, Austria.
[8]Institute of Coastal Research, Swedish Board of Fisheries, Öregrund, Sweden.
[9]Marine Research Institute, Reykjavik;
[10]University of Iceland, Institute of Biology, Sturlugata 7, Reykjavik.
[11]Hólaskóli, Saudarkrókur, Iceland.
[12]INRB-IPIMAR National Institute for Agriculture and Fisheries, Lisboa, Portugal.
[13]Wageningen Institute for Marine Resources and Ecosystem Studies (IMARES), Ijmuiden, the Netherlands.

[*]Author for correspondence. E-mail: **christian.jorgensen@bio.uib.no**

Abstract:

Evolutionary impact assessment is introduced as a framework for quantifying the effects of harvest-induced evolution on the utility generated by fish stocks.

Darwinian evolution is the driving process of innovation and adaptation across the world's biota. Acting on top of natural selection, human-induced selection pressures can cause rapid evolution of our living environment. Sometimes such evolution has undesirable consequences for human societies, as is demonstrated by the quickly spreading resistance to antibiotics and pesticides, which incurs billion-dollar losses annually (*1*). Another anthropogenic selection pressure of comparable magnitude originates from fishing, which has become the major source of mortality in many fish stocks around the world, exceeding natural mortality by as much as 400% in heavily exploited populations (*2*). The notion that fishing mortality can induce adaptive evolution in exploited fish populations has, however, largely been ignored (*3*), even though studies based on fisheries data and controlled experiments have provided strong empirical evidence for fisheries-induced evolution over a range of species and regions (*4*). Moreover, these evolutionary changes unfold on decadal time scales – much faster than previously thought – and the resultant needs for mitigating actions have thus become compelling.

Life-history theory predicts that increased mortality generally favors earlier sexual maturation at smaller size, as well as elevated reproductive effort (*5*). Fishing that is selective with respect to size, maturity status, behavior, or morphology causes further evolutionary pressures (*6*). Evidence that harvesting can bring about genetic changes comes from breeding programs in aquaculture, which have demonstrated heritable genetic variation in numerous traits (*7*), and from experiments that have shown significant harvest-induced evolution in just a few generations (*8*-*12*). Furthermore, using time series of fisheries data spanning a few decades, new statistical methods have detected wide-spread changes in maturity schedules that are unlikely to be explained by environmental influences alone (*13-17*). While alternative causal hypotheses can be difficult to rule out, fisheries-induced evolution consistently arises as the most parsimonious explanation of the trends left unexplained after accounting for environmental factors. Fisheries-induced evolution is thus largely inevitable: the question is not whether it will occur, but how fast a given fishing practice brings about evolutionary change, and what the consequences of such a change will be.

The biological and economic consequences of fisheries-induced evolution are potentially severe. Life-history traits are among the primary determinants of population dynamics, and their evolution will have repercussions for stock biomass, demography, and economic yield (*9, 11, 18-20*). Such evolution may also be slow to reverse, or even turn out to be practically irreversible (*18, 21*), which has implications for recruitment and recovery (*22*). As a consequence, predator-prey dynamics, competitive interactions, production of offspring, and other ecological relationships will systematically change over time. Current management reference points are thus moving targets: stocks may gradually become less resilient, or be erroneously assessed as being within safe biological limits. In this way, knowledge based on past observations will become inadequate or insufficient for understanding current stock dynamics, with some evolutionary trait changes even having the potential for causing nonlinear ecological transitions and other unexpected outcomes (*23, 24*). Fisheries-induced evolutionary changes are therefore pertinent not only to single-species management but also to the ecosystem approach to fisheries management.

These insights call for an evolutionarily enlightened management approach (*11, 18, 25*). Here we define this as management of fishing activities based on knowledge and consideration of ecological and evolutionary dynamics, aiming at an optimum level of ecological services generated by fish resources. This definition emphasizes that a basic awareness of evolutionary processes and their impacts is fundamental if fisheries management is to achieve its long-term goals of sustainable exploitation and conservation of biodiversity. Although framed here in the context of fish stocks, harvest-induced evolution and its consequences also apply to other animals (*26*) and plants (*27*).

Environmental impact assessments are commonly employed for evaluating the consequences of human activities for ecosystems and society. Extending this concept to encompass evolution, we propose Evolutionary Impact Assessment (EvoIA) as an integral tool for the management of evolving resources. Conceptually, an EvoIA involves two major steps. The first step relies on biological information, and describes how human actions such as fishing lead to trait changes. A stock's *evolutionary susceptibility* is high if the evolutionary change in traits is rapid or large in magnitude. The second step addresses how trait changes affect the stock's utility to society. Any definition of utility has to reflect management objectives and needs to be developed in dialogue between fisheries managers, fishing communities, scientists, conservationists, and other stakeholders (Fig. 1). The *evolutionary impact* is then assessed by how the utility of a stock has changed or will change as a consequence of fisheries-induced evolution.

Economically valuable stocks typically have a long history of exploitation (*28, 29*); for such stocks, a natural starting point is a *retrospective* EvoIA, i.e., an assessment of past evolutionary change. Operational statistical techniques (*14, 15, 30*) can assess the extent to which evolutionary changes may have occurred, provided sufficient data are available. Where stock-specific data are lacking, inferences can be drawn from species with similar life histories and exploitation patterns. As a first approach, these simple EvoIAs can prioritize management efforts by identifying the most susceptible stocks.

A more detailed understanding of the evolutionary impact can be obtained by formally comparing management options. This will commonly require a forward-looking or *prospective* EvoIA. In contrast to retrospective EvoIAs, prospective EvoIAs will typically rely on dynamic models to provide quantitative predictions. This is because future utility projections depend not only on how fishing affects traits, but also on how trait changes might alter ecological relationships, which in turn affect utility (Fig. 2). Empirical and theoretical studies have singled out life-history traits as being particularly prone to rapid harvest-induced evolution. These traits are important because they influence a population's demography and harvestable biomass. However, life-history traits are also shaped by, and have implications for, density dependence, trophic interactions, geographical distribution, migration patterns, behavior, and sexual selection. Furthermore, the risk of adverse ecological consequences intensifies, due to nonlinear effects, as traits evolve further away from their historic distributions. Prospective EvoIAs will thus rely on life-history models that, eventually, should address a broad range of mechanisms and traits influenced by fishing.

A natural baseline is the continuation of a business-as-usual scenario with evolutionary and utility projections based on the current fishing regime. This allows the cost of inaction to be quantified for different time horizons. Thereafter, utility can be calculated for and compared between alternative management scenarios that differ in the intensity and selectivity of fishing mortality. In this way, one can determine which management strategies have the least negative, or potentially even positive, effects on utility. The cumulative utility and its net present value will depend on the choice of time horizon and discounting rates (*31*), both of which will require careful consideration (Fig. 2).

A central challenge to all EvoIAs is to define operational management objectives that can be translated into unified utility metrics integrating disparate social values. Although some fish stocks will be managed primarily to maximize sustainable yield, successful management of fisheries-induced evolution will generally benefit from the recognition of a broader range of values and services (*32*) that are not inherent in the classic yield-maximizing management paradigm (*33*). In the context of fisheries-induced evolution, utility metrics might include yield and its variability and sustainability, conservation of genetic and phenotypic diversity, the role of a harvested species in ecosystem functioning, and its value for recreational fishing and tourism. The current state of each of these factors may be eroded directly through fisheries-induced evolution or indirectly through the ecosystem-level implications of such evolution (*34*) (Fig. 1).

Fisheries-induced evolution is likely to diminish yield and degrade ecological services within decades, impacting species, ecosystems, and societies. The sudden collapse and slow or absent recovery of many marine stocks (*35*) carry warnings that consequences can be nonlinear, rapid, and severe. Evolutionary effects come on top of, and may magnify, the ecological challenges that already threaten sustainable harvesting. Therefore, implementation of the international calls for the ecosystem approach to fisheries management (*36*), for the restoration of maximum sustainable yield by 2015 (*37*), and for the adoption of a precautionary approach (*38*) must embrace management of the evolutionary impacts of harvesting.

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37. The United Nations 2002 World Summit on Sustainable Development in Johannesburg, South Africa, declared that, as a universal goal, fish stocks shall be maintained or restored to levels that can produce the maximum sustainable yield (MSY) by 2015.
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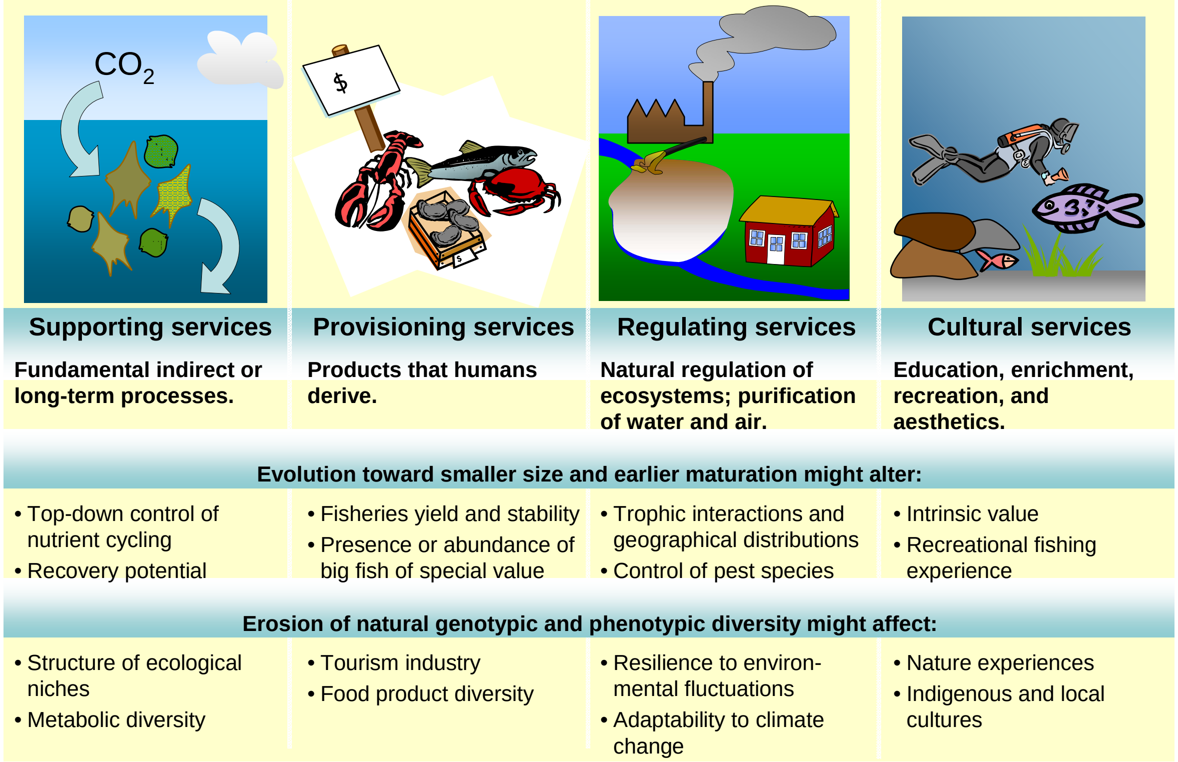
Figure captions:

Figure 1. Examples of utility components potentially affected by fisheries-induced evolution. Aquatic ecosystems produce four categories of ecological services of direct and indirect utility to society (*39-41*)**.** Using these definitions as a basic framework will facilitate discussions among stakeholders with different backgrounds, and assist in the prioritization of objectives and actions. Potential effects are shown for the two most ubiquitous effects of fisheries-induced evolution: *i)* reduction in body size, often due to earlier maturation, and *ii)* erosion of natural genotypic and phenotypic diversity.

Figure 2. Sketch of a prospective Evolutionary Impact Assessment (EvoIA) comparing two management scenarios. Using appropriate models, the consequences of fishing can be quantified using a utility function. In this hypothetical scenario of an EvoIA, the red solid lines refer to business-as-usual: moderate overfishing causes continued evolution at a constant rate (A), steadily declining regulating services (B), and reduced catches (C). In comparison (red dotted lines), a sufficiently strong reduction in harvest rate will in this example slowly reverse trends in trait evolution and improve regulating services, while also causing a significant short-term loss of yield. When evaluating management strategies, the difference in combined utility (D) depends on the time horizon considered. The cost of inaction (vertical arrow) is defined as the loss of utility, relative to its present value, if current fishing practices are continued. In this example, reduced fishing leads to a temporary loss of combined utility that is compensated for by a long-term gain, as indicated by the areas marked *Cost* and *Benefit* in (D).



Supporting services	Provisioning services	Regulating services	Cultural services
Fundamental indirect or long-term processes.	**Products that humans derive.**	**Natural regulation of ecosystems; purification of water and air.**	**Education, enrichment, recreation, and aesthetics.**

Evolution toward smaller size and earlier maturation might alter:

• Top-down control of nutrient cycling • Recovery potential	• Fisheries yield and stability • Presence or abundance of big fish of special value	• Trophic interactions and geographical distributions • Control of pest species	• Intrinsic value • Recreational fishing experience

Erosion of natural genotypic and phenotypic diversity might affect:

• Structure of ecological niches • Metabolic diversity	• Tourism industry • Food product diversity	• Resilience to environmental fluctuations • Adaptability to climate change	• Nature experiences • Indigenous and local cultures

Figure 1

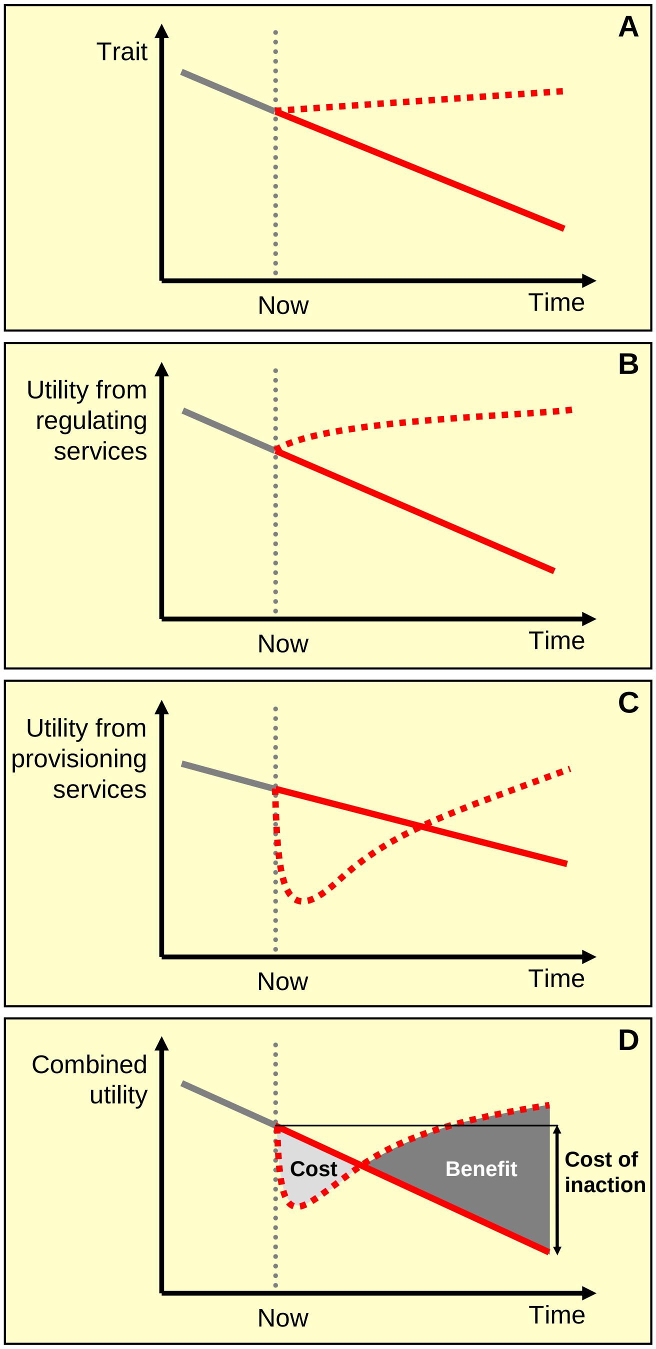

A
Trait
Now
Time
B
Utility from regulating services
Now
Time
C
Utility from provisioning services
Now
Time
D
Combined utility
Cost
Benefit
Cost of inaction
Now
Time

Figure 2

Supporting online material

1. Table S1. Studies suggesting evolutionary changes in life-history traits caused by fisheries in wild populations.
2. Table S2. Experimental studies where harvestings has caused evolutionary trait changes in aquatic animals.
3. References cited in tables S1 and S2.

Table S1. Empirical studies suggesting evolutionary changes in life-history traits caused by fisheries in wild fish populations.

Species	Population or stock	Data period	Reference
Trend towards maturation at earlier age and/or smaller size			
American plaice	Labrador and NE Newfoundland	1973 – 1999	Barot et al. 2005
Hippoglossoides platessoides	Grand Bank	1969 – 2000	
	St. Pierre Bank	1972 – 1999	
Atlantic cod	Northeast Arctic	1932 – 1998	Heino et al. 2002
Gadus morhua	Georges Bank	1970 – 1998	Barot et al. 2004
	Gulf of Maine	1970 – 1998	
	Northern	(1977 –)1981 – 2002	Olsen et al. 2004
	Southern Grand Bank	1971 – 2002	Olsen et al. 2005
	St. Pierre Bank	1972 – 2002	
	Baltic	1984 – 1997	Cardinale & Modin 1999
		1989 – 2003	Vainikka et al. 2006
	North Sea and West of Scotland	1969 – 1970, 2002 – 2003	Yoneda & Wright 2004
Atlantic herring *Clupea harengus*[1]	Norwegian spring-spawning	1935 – 2000	Engelhard & Heino 2004
Atlantic salmon *Salmo salar*	Goodbout River, Quebec	1859 – 1983	Bielak & Power 1986
Brook trout *Salvelinus fontinalis*	17 Canadian lakes	1984, 1999, comparative	Magnan et al. 2005
Chinook salmon *Oncorhynchus tschawytscha*	British Columbia	1951 – 1975	Ricker 1981

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[1] Weak trend.

Species	Population or stock	Data period	Reference
Grayling *Thymallus thymallus*	Several lakes in Oppland, Norway	1903 – 2000 (ca. 15 years)	Haugen & Vøllestad 2001
Plaice *Pleuronectes platessa*	North Sea	1957 – 2001	Grift et al. 2003, 2007 Rijnsdorp 1993a, b
Sole *Solea solea*	Southern North Sea	1958 – 2000	Mollet et al. In press
Red porgy *Pagrus pagrus*	South Atlantic Bight	1972 – 1994	Harris & McGovern 1997
Trends toward increased fecundity / reproductive investment			
Atlantic cod *Gadus morhua*	North Sea and West of Scotland	1969 – 1970, 2002 – 2003	Yoneda & Wright 2004
Haddock *Melanogrammus aeglefinus*	North Sea	1976 – 1978, 1995 – 1996	Wright 2005
Plaice *Pleuronectes platessa*[2]	North Sea	1900 – 1910, 1947 – 1949, 1977 – 1985	Rijnsdorp 1991 Rijnsdorp et al. 2005
Trends towards decreased size at age			
Atlantic cod *Gadus morhua*	Southern Gulf of St Lawrence	1971 – 2001	Swain et al. 2007
Atlantic salmon *Salmo salar*	Goodbout River, Quebec	1859 – 1983	Bielak & Power 1986
Pink salmon *Oncorhynchus gorbuscha*[3]	British Columbia	1951 – 1975	Ricker 1981

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[2] Only for females with smaller body size.
[3] Only size at maturation decreased, not age.

Species	Population or stock	Data period	Reference
Red porgy *Pagrus pagrus*	South Atlantic Bight	1972 – 1994	Harris & McGovern 1997
Whitefish *Coregonus clupeaformis*	Lesser Slave Lake	1941 – 1975	Handford et al. 1977
Whitefish *Coregonus lavaretus*	Lake Constance	1947 – 1997	Thomas & Eckmann 2007
Loss of genetic diversity			
Atlantic cod *Gadus morhua*	North Sea	1954, 1970, 1998	Hutchinson et al. 2003
Brook trout *Salvelinus fontinalis*	9 Canadian lake-stream population pairs	1996 and 1997 (comparative)	Jones et al. 2001
Orange roughy *Hoplostethus atlanticus*	New Zealand	1982 – 83 and 1988	Smith et al. 1991
Snapper *Pagrus auratus* (=*Chrysophrys auratus*)	Tasman Bay, New Zealand	1950 – 2000	Hauser et al. 2002

Species	Population or Stock	Data period	Evolutionary response	Reference
Other life history trends				
Atlantic cod *Gadus morhua*	Newfoundland and Labrador	1977 – 2002	Maturation at lower condition	Baulier et al. 2006
Altantic salmon *Salmo salar*	Rivers Asón, Pas, Nansa, and Deva, Spain	1988 – 2000	Later smolting, lower sea-age, smaller body size	Consuegra et al. 2005
Bluegill *Lepomis macrochirus*	Lakes in Minnesota	1989 – 1995 (Comparative)	Slower growth, earlier maturation, more cuckolders	Drake et al. 1997

Species	Population or stock		Data period	Reference
Common carp *Cyprinus carpio carpio*	Aquaculture races from China and Europe	Comparative between regions	Seine harvesting (China) selected for viability, lean body, escapement, early maturation.	Wohlfarth et al. 1975
Sockeye salmon *Onchorhynchus nerk*a	Bristol Bay, USA	1969 – 2003	Earlier run timing	Quinn et al. 2007
Whitefish *Coregonus clupeaformis*	Lesser Slave Lake	1941 – 1975	Decreased condition	Handford et al. 1977

Table S2. Experimental studies demonstrating evolutionary changes in life-history traits caused by harvesting in aquatic animals.

Species	**Time frame**	**Trait changes**	**Reference**
Atlantic silverside *Menidia menidia*[4]	4 generations (4 years)	Decreased growth rate Decreased fecundity, egg volume, larval size at hatching, larval growth rate, larval survival, food consumption, growth efficiency, food conversion efficiency, willingness to forage under threat of predation, and number of vertebrae	Conover & Munch 2002 Walsh et al. 2006
Water flea *Daphnia magna*[4]	37 generations (148 days)	Decreased growth rate and delayed maturation	Edley & Law 1988
Guppy *Poecilia reticulata*[5]	11 years (30 – 60 generations)	Smaller size and age at maturation, higher number of offspring, smaller offspring size, higher reproductive allocation, shorter time interval between successive litters	Reznick & Ghalambor 2005 Reznick et al. 1990
Largemouth bass *Micropterus salmoides*[6]	4 generations	Reduced parental care, reduced resting metabolic rate, poorer swimming performance	Cooke et al. In press
Tilapia mossambica	75 months	Decreased growth rate	Silliman 1975

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[4] Effects are for lines where large individuals had been harvested.

[5] Compares fish from high and low mortality environments (high and low predation pressure, respectively), effects are for fish experiencing high mortality rates.

[6] Effects are when fish vulnerable to harvesting are removed from the population.

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