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Managing Evolving Fish Stocks

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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 also cause rapid evolution. Sometimes such evolution has undesirable consequences, one example being the spreading resistance to antibiotics and pesticides, which causes suffering and billion-dollar losses annually (*1*). A comparable anthropogenic selection pressure originates from fishing, which has become the main source of mortality in many fish stocks, and may exceed natural mortality by more than 400% (*2*). This has, however, been largely ignored, 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 (see table 1). These evolutionary changes are unfolding on decadal time scales—much faster than previously thought.

Life-history theory predicts that increased mortality generally favors evolution toward earlier sexual maturation at smaller size and elevated reproductive effort. Fishing that is selective with respect to size, maturity status, behavior, or morphology causes further evolutionary pressures (*3*). Evidence that harvesting can bring about genetic changes comes from breeding programs in aquaculture, which have shown heritable genetic variation in numerous traits (*4*), and from experiments showing harvest-induced evolution in just a few generations (table S1). Furthermore, analyses of fisheries data spanning a few decades have detected widespread changes in maturity schedules that are unlikely to be explained by environmental influences alone (table S2). Although alternative causal hypotheses can be difficult to rule out, fisheries-induced evolution consistently arises as the most parsimonious explanation after environmental factors have been accounted for. The question is not whether such evolution will occur, but how fast fishing practices bring about evolutionary changes and what the consequences will be.

Life-history traits are among the primary determinants of population dynamics, and their evolution has repercussions for stock biomass, demography, and economic yield (*5*, *6*). Fisheries-induced evolution may also be slow to reverse or even irreversible (*5*), with implications for recruitment and recovery (*7*). Consequently, predator-prey dynamics, competitive interactions, relative species abundances, and other ecological relationships will systematically change over time. Current management reference points are thus moving targets: Stocks may gradually become less resilient or may be erroneously assessed as being within safe biological limits. Some evolutionary trait changes will even have the potential to cause nonlinear ecological transitions and other unexpected outcomes (*8*). Fisheries-induced evolutionary changes are therefore pertinent beyond single-species management.

An evolutionarily enlightened management approach is needed (*5*, *6*, *9*). 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 ecological services generated by living aquatic resources (fig. S1). This perspective emphasizes that evolution underlies ecology and influences economies. An evolutionary perspective will, therefore, (i) support the ecosystem approach to fisheries management (*10*–*13*) by considering how evolution alters ecological relations and management reference points, (ii) comply with the precautionary approach (*14*) by accounting for uncertainty and risk, and (iii) respect the Johannesburg summit's commitment to the restoration of sustainable fisheries (*15*).

Environmental impact assessments are commonly used to evaluate the consequences of human activities for ecosystems and society. We propose evolutionary impact assessment (EvoIA) as a tool for the management of evolving resources. Conceptually, an EvoIA involves two major steps. The first relies on biological information and describes how human actions, such as fishing, lead to trait changes. 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 with stakeholder involvement. Evolutionary impact is then assessed as the change in utility of a stock as a result of fisheries-induced evolution.

Economically valuable stocks typically have a long history of exploitation; for such stocks, a natural starting point to help prioritize management efforts is a retrospective assessment of past evolutionary change [e.g., (*16*, *17*)]. Given suitable fisheries data, new statistical techniques can assess the extent to which evolutionary changes may have occurred (*18*).

A more detailed understanding will typically rely on evolutionary models. For example, Northeast Arctic cod was identified as being susceptible to large evolutionary changes in maturation, because offshore trawling, introduced in the 1920s, reversed earlier selection pressures (*5*).

An EvoIA goes a step further, linking evolution to an impact on utility. EvoIAs that look forward in time and compare alternative management options will have to rely on evolutionary models to provide quantitative predictions. In these prospective EvoIAs, projections of future utility depend not only on how fishing affects traits, but also on how trait changes alter ecological relations, which in turn affect utility (fig. S2). Empirical and theoretical studies have shown that many life-history traits are 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, because of nonlinear effects, as traits evolve further away from their historic distributions. Prospective EvoIAs will thus rely on life-history models that, ultimately, should address a broad range of mechanisms and traits influenced by fishing (*19*).

A baseline for comparison 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. Further, utility can be calculated for alternative management scenarios. This identifies management regimes that have the least negative, or even positive, effects on utility (fig. S2). Cumulative utility and its net present value will depend on the choice of time horizons and discounting rates (*20*).

A central challenge to all EvoIAs is to define evolutionarily enlightened management objectives that can be translated into unified utility metrics integrating disparate social values. Pragmatically, such objectives are more likely to be implemented if they harmonize with the pressing short-term goals of traditional fisheries management (*21*). 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 implications for recreational fishing and tourism. The current state of each of these factors may be eroded either directly through fisheries-induced evolution or indirectly through the ecosystem-level implications of such evolution.

Fisheries-induced evolution is likely to diminish yield and degrade ecological services within decades, having an impact on species, ecosystems, and societies. Evolutionary effects could magnify the ecological challenges that already threaten sustainable harvesting. Successful management, therefore, will require the ecological and evolutionary consequences of fishing to be evaluated and mitigated. Adopting EvoIAs will enable fisheries managers to rise to this challenge.

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Table 1:

Harvest-induced evolutionary changes in marine and freshwater fish.			
Evolutionary change	No. of species	No. of studies	Change in % (n)
Maturation at lower age	6	10	23-24 (1)
Maturation at smaller size	7	13	20-33 (3)
Lower PMRN midpoint	5	10	3-49 (13)
Reduced annual growth	6	6	15-33 (3)
Increased fecundity	3	4	5-100 (3)
Loss of genetic diversity	3	3	21-22 (2)

Supporting Online Material for

Managing Evolving Fish Stocks

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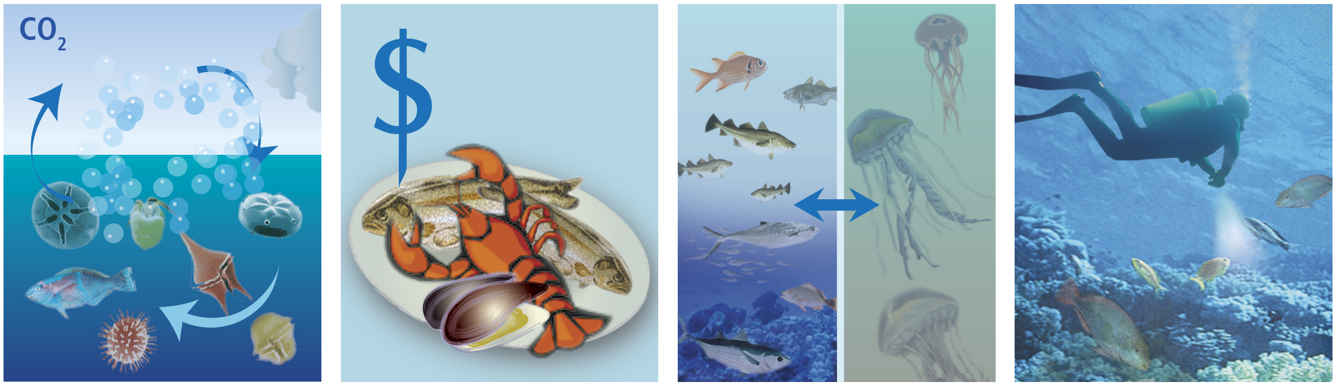

Supporting services	**Provisioning services**	**Regulating services**	**Cultural services**
Fundamental indirect or long–term processes	Products that humans derive	Benefits from natural ecosystem regulation	Values for education, recreation, enrichment and aesthetics
Evolution toward smaller size and 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 • Pest and invasion control	• Intrinsic value of species and ecosystems • Recreational fishing experience
Erosion of natural genotypic and phenotypic diversity might affect:			
• Structure of ecological niches	• Benefits to tourism industry • Food product diversity	• Resilience to environmental fluctuations • Adaptability to climate change	• Enjoyment of nature • Indigenous and local culture

Fig. S1. 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 (ref. *S1*, *S2*). 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) reductions in body size and maturation age; and (ii) erosion of natural genotypic and phenotypic diversity.

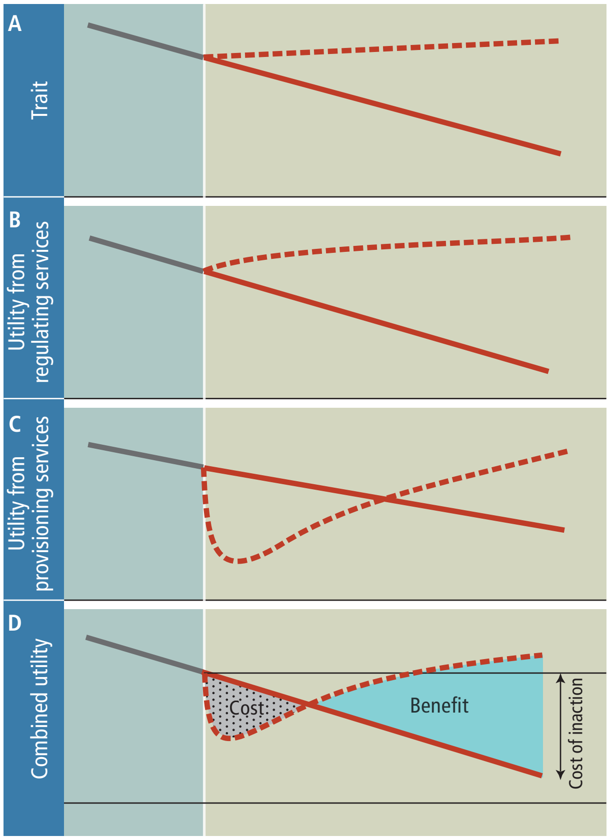

Fig. S2. Sketch of a prospective Evolutionary Impact Assessment (EvoIA) comparing two management scenarios. Using appropriate models, the consequences of fisheries-induced evolution can be quantified using a utility function. In this hypothetical scenario of an EvoIA, the red solid lines refer to business-as-usual: moderate overfishing causes continued evolution at a constant rate (A), resulting in steadily declining regulating services (B) and reduced catches (C) (see Fig. S1 for terminology and examples of how ecological services might be affected). In comparison (red dotted lines), a sufficiently strong reduction in harvest rate will in this example slowly reverse trends in trait evolution and thereby 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).

Table S1. Experimental studies demonstrating evolutionary changes caused by harvesting in aquatic animals.

Species	Data period	Evolutionary change	Reference
Atlantic silverside *Menidia menidia**	4 generations (4 years)	Decreased growth rate	*S3*
		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	*S4*
Water flea *Daphnia magna**	37 generations (148 days)	Decreased growth rate and delayed maturation	*S5*
Guppy *Poecilia reticulata§*	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	*S6*, *S7*
Largemouth bass *Micropterus salmoides#*	4 generations	Reduced parental care, reduced resting metabolic rate, poorer swimming performance	*S8*
Tilapia mossambica	75 months	Decreased growth rate	*S9*

*Effects are for lines in which large individuals were harvested. §Effects are for fish experiencing high predation pressure. #Effects are for treatments in which fish vulnerable to recreational fishing were removed.

Table S2. Empirical studies suggesting evolutionary changes caused by fisheries in wild populations. *Inclusion criteria:* Studies were included that (i) documented changes in a quantitative trait over time or between populations that experienced different fishing regimes, (ii) attempted to account for environmental factors that could have caused the trend in the trait, and (iii) concluded that fisheries-induced evolution was a likely cause for the observed changes. We thus omitted negative findings, as well as reports of changes that might have been evolutionary but where the authors concluded otherwise or did not discuss evolution as a potential cause. Studies may be listed under more than one trait. The statistical procedures for estimating probabilistic maturation reaction norms are reviewed in ref. *S10*. *Quantification of evolutionary change:* For studies that included time series or compared different periods and contained quantitative information on the evolutionary change, we used either estimates from reported linear regressions with respect to time, or means of several years at the beginning and end of the data periods. Adjusted phenotypic trends were used where changes in environmental conditions were accounted for. Evolutionary changes in probabilistic maturation reaction norms were quantified as the mean displacement of the reaction norm midpoint (L_{P50}) for all ages for which the midpoint had been quantified at both the beginning and the end of the data periods. The magnitude m of evolutionary change was then calculated as $m = |z_2 - z_1| / z_1$ where z_1 and z_2 denote the considered quantitative trait at the beginning (t_1) and end (t_2) of the data period, respectively. The rate r of evolutionary change, in the standard unit 'darwin,' was calculated as $r = |\ln(z_2) - \ln(z_1)| / (t_2 - t_1)$, where $t_2 - t_1$ was measured in millions of years. Unless otherwise noted, we assumed linear trends throughout the data periods.

Species	Population or stock	Data period	Evolutionary change: Magnitude	Rate*	Reference
Maturation at younger age					
Atlantic cod *Gadus morhua*	Northeast Arctic	1932–1998	23–24%	4.0–4.1	*S11*
	North Sea, West of Scotland	1969–1970, 2002–2003			*S12*
	Baltic	1984–1997			*S13*
Bluegill *Lepomis macrochirus*	Lakes in Minnesota	1989–1995, comparative			*S14*
Brook trout *Salvelinus fontinalis*	17 lakes in Canada	1984, 1999, comparative			*S15*
Grayling *Thymallus thymallus*	Several lakes in Norway	1903–2000 (ca. 15 years)			*S16*
Plaice *Pleuronectes platessa*	North Sea	1957–2001			*S17–S19*
Red porgy *Pagrus pagrus*	South Atlantic Bight	1972–1994			*S20*
Maturation at smaller size					
Atlantic cod *Gadus morhua*	Northeast Arctic	1932–1998	22–24%	3.9–4.4	*S11*
	North Sea, West of Scotland	1969–1970, 2002–2003			*S12*
	Baltic	1984–1997			*S13*
Brook trout *Salvelinus fontinalis*	17 lakes in Canada	1984, 1999, comparative			*S15*
Coho salmon *Oncorhynchus kisutch§*	British Columbia	1951–1975	24–26%	10–11	*S21*, *S22*
Grayling *Thymallus thymallus*	Several lakes in Norway	1903–2000 (ca. 15 years)			*S16*
Pink salmon *Oncorhynchus gorbuscha*	British Columbia	1951–1975	20–33%	8.3–14	*S21*, *S22*
Plaice *Pleuronectes platessa*	North Sea	1957–2001			*S17–S19*
Red porgy *Pagrus pagrus*	South Atlantic Bight	1972–1994			*S20*

Table S2 (continued).

Species	Population or stock	Data period	Evolutionary change: Magnitude	Rate*	Reference
Reduction in the probabilistic maturation reaction norm midpoint					
American plaice *Hippoglossoides platessoides*	Labrador, Newfoundland	1973–1999	22–47%	12–31	*S23*
	Grand Bank	1969–2000	19–49%	10–32	*S23*
	St. Pierre Bank	1972–1999	14–42%	7.1–26	*S23*
Atlantic cod *Gadus morhua*	Northeast Arctic	1932–1998	12%	2.1	*S11*
	Georges Bank	1970–1998	26–41%	15–26	*S24*
	Gulf of Maine	1970–1998	25–26%	14–15	*S24*
	Northern†	(1977–)1981–2002	–	7–19#	*S25*
			11–27%	11–21	*S26*
	Southern Grand Bank†	1971–2002	18%	9.3–9.6	*S26*
	St. Pierre Bank†	1972–2002	25–32%	15–20	*S26*
	Baltic	1988–2003	21%	16	*S27*
Atlantic herring *Clupea harengus*	Norwegian spring-spawning	1935–2000	3%	0.7	*S28*
Plaice *Pleuronectes platessa*	North Sea	1957–2001	13%	4.7	*S19*
		1957–2001	14%	4.6	*S29*
Sole *Solea solea*	Southern North Sea	1958–2000	11%	4.1	*S30*
Maturation at lower condition					
Atlantic cod *Gadus morhua*	Baltic	1988–2003			*S27*
	Northern, St Pierre Bank, Southern Grand Bank	1977–2002			*S31*
Bluegill *Lepomis macrochirus*	Lakes in Minnesota	1989–1995, comparative			*S14*
Brook trout *Salvelinus fontinalis*	17 lakes in Canada	1984, 1999, comparative			*S15*
Whitefish *Coregonus clupeaformis*	Lesser Slave Lake	1941–1975			*S32*
Reduced annual growth					
Atlantic cod *Gadus morhua*	Southern Gulf of St Lawrence	1971–2002			*S33*
Atlantic salmon *Salmo salar*	Godbout River, Quebec	1859–1983			*S34*
Coho salmon *Oncorhynchus kisutch*‡	British Columbia	1951–1975	24–26%	10–11	*S21*, *S22*
Pink salmon *Oncorhynchus gorbuscha*‡	British Columbia	1951–1975	20–33%	8.3–14	*S21*, *S22*
Whitefish *Coregonus clupeaformis*‡	Lesser Slave Lake	1941–1975			*S32*
Whitefish *Coregonus lavaretus*¤	Lake Constance	1947–1997	15%	3.8	*S35*
Increased fecundity					
Atlantic cod *Gadus morhua***	North Sea, West of Scotland	1969–1970, 2002–2003	25%	8.2	*S12*
Haddock *Melanogrammus aeglefinus***	North Sea	1976–1978, 1995–1996	33%	15.5	*S36*
Plaice *Pleuronectes platessa*§§	North Sea	1900–1910, 1947–1949, 1977–1985	5–100%	0.5–21	*S37*, *S38*
Loss of genetic diversity					
Brook trout *Salvelinus fontinalis*	9 lake–stream population pairs in Canada	1996, 1997, comparative	##	–	*S39*
Orange roughy *Hoplostethus atlanticus*	New Zealand	1982/1983–1988	22% ##	–	*S40*
Snapper *Pagrus auratus* (=*Chrysophrus auratus*)	Tasman Bay, New Zealand	1950–2000	21% ††	–	*S41*
Other trends					
Atlantic salmon *Salmo salar*	Rivers Asón, Pas, Nansa, and Deva, Spain	1988–2000	Later smolting, lower sea-age		*S42*
Common carp *Cyprinus carpio carpio*	Aquaculture lineages from China and Europe	Comparative between regions	Seine harvesting (China) selected for viability, lean body, escapement, early maturation		*S43*
Sockeye salmon *Oncorhynchus nerka*	Bristol Bay, USA	1969–2003	Earlier run timing		*S44*
Whitefish *Coregonus clupeaformis*	Lesser Slave Lake	1941–1975	Decreased condition		*S32*

*In 10^3 darwins, absolute values. §Assuming no change in maturation age. #Numbers from ref. *S25*. †Estimates based on pre-moratorium years only. ‡Weight. ¤Length. **Standardized by length and condition. §§Standardized by length. ##Heterozygosity loss. ††Allele loss.

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