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Fishery-induced evolution provides insights into adaptive responses of marine species to climate change

Robin S Waples^{1*} and Asta Audzijonyte²

Climate change challenges marine species with seawater that is warmer, with less oxygen and lower pH. To date, most climate-change studies have focused on organisms' acclimation or shifts in distribution; relatively little is known about the capacity of marine species to respond through evolution. We propose that important insights can be gained from recent studies of fishery-induced evolution (FIE), which show that increased adult mortality from fishing leads to rapid changes in growth and reproduction schedules. These changes consistently involve evolution of "faster" life histories: earlier maturation at smaller sizes and shorter life spans. In the ocean, coupled effects of higher temperatures and reduced oxygen also differentially affect larger or older individuals, so expected evolutionary consequences of climate change are qualitatively similar to those of FIE. This general pattern will apply to large numbers of marine species and has important implications for conservation and management.

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Organisms faced with environmental challenges such as global climate change have three general coping mechanisms: (1) move to a location with more suitable environmental conditions, (2) exhibit phenotypic plasticity, or (3) evolve. Whereas evolution requires genetic change across generations, plasticity allows an organism to use existing genes to express different phenotypes in different environments. Marine species face special challenges, as the predicted velocity of climate change is several times higher in the ocean than on land for latitudes near the equator or in the subarctic (Burrows *et al.* 2011). This means that to maintain the same thermal niche, marine species must move much farther at those latitudes than do species on land. Climate-related

studies of marine species have primarily focused on these distributional shifts (option 1; Pinsky *et al.* 2013) or seasonal changes in the timing of key events such as migration and reproduction (option 2; Edwards and Richardson 2004). In contrast, our ability to predict the extent to which evolution can mitigate the effects of climate change remains limited (option 3; Munday *et al.* 2013).

This is unfortunate, given the importance of understanding patterns of evolutionary change in the sea. With marine ecosystems under increasing human pressure, ecosystem-based management should maximize the potential for species to exhibit adaptive evolutionary responses. Of particular interest is the evolution of life-history traits – those that determine optimal allocation of energy to growth versus reproduction. Life-history strategies determine fundamental properties of population dynamics, resilience to exploitation, and rates of adaptation (Audzijonyte *et al.* 2016). Furthermore, populations generally harbor considerable genetic variation for life-history traits and can respond quickly to altered selection regimes (Reznick *et al.* 1997; Walsh *et al.* 2006).

The paucity of interest in climate-change-induced evolution in life-history traits contrasts with the considerable attention given in recent decades to fishery-induced evolution (FIE) – evolutionary change promoted by increased mortality imposed by harvesting. We believe that important insights into marine species' adaptive responses to climate change can be gained from theoretical and empirical studies of FIE. Because harvesting increases adult mortality, it reduces the benefits of delaying reproduction and leads to earlier maturation and "faster" life histories, which involve shorter life spans and early maturation at smaller sizes. We suggest that similar life-history evolu-

In a nutshell:

- Evidence is mounting that increasing adult mortality through harvest has caused rapid evolution of life-history traits in fish populations
- Insights from this research can help predict evolutionary responses of marine species to climate-related stressors, especially warmer water with lower dissolved oxygen content
- Collectively, these stressors can be expected to select for earlier maturation at smaller size and for smaller adult body size; many cold-blooded (ectothermic) marine species will be affected
- These life-history changes will affect population productivity, will increase fluctuations in abundance, and should be accounted for in fisheries and marine ecosystem management

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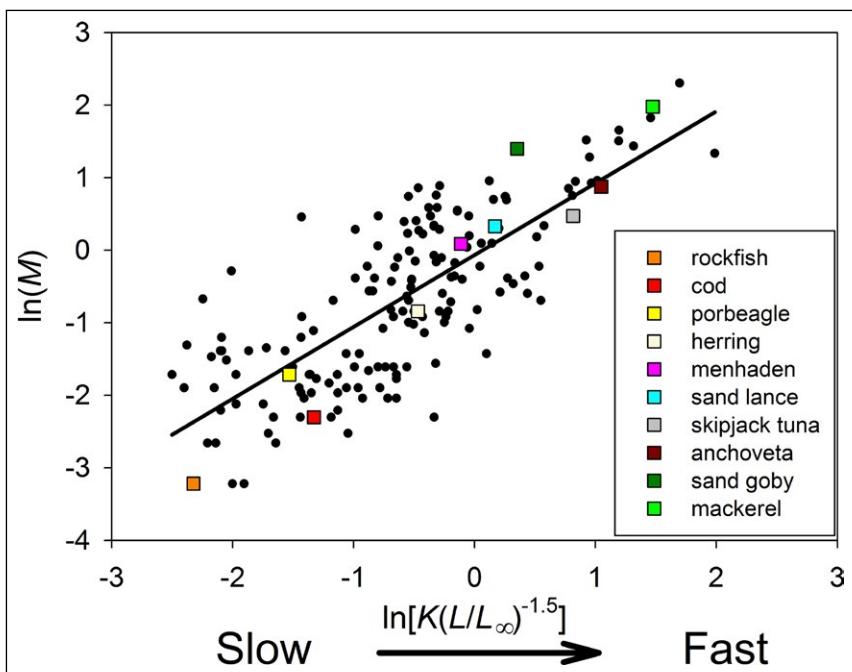


Figure 1. Log-log relationship between instantaneous mortality at length (M) and Von Bertalanffy growth parameters (K = Bertalanffy growth constant; L = length when mortality is measured; L_∞ = asymptotic length) in marine and estuarine fishes. Selected common species along the continuum of “slow” to “fast” life histories are indicated by colored squares. Modified from Charnov et al. (2013) using data from Gislason et al. (2010).

tion can be anticipated for marine species responding to climate change, which can also generally be expected to increase mortality of adults.

This realization has several important consequences for conservation and management. First, the conceptual framework presented here provides a general paradigm for thinking about evolutionary responses of marine species to climate change. Second, the effects of evolutionary responses to climate change and harvesting will often be synergistic and hence larger in magnitude than effects that might occur from either phenomenon alone. Finally, parallel responses to harvesting and climate change suggest the possibility that species that have already experienced FIE might have evolved life histories that are more robust to climate-change impacts.

■ Life histories determine fundamental population dynamic processes

The life history of a species (its “game plan” for survival) includes a suite of phenotypic traits (eg size, age, fecundity) and behavioral/threshold traits (eg age at maturity, timing of seasonal migrations) that collectively guide an individual through successful completion of its life cycle. Although the number of possible combinations of life-history traits within a given species is essentially unlimited, only a fraction of these combinations are found in nature. This is because of inherent trade-offs, which are determined by the finite amount of energy available for growth,

maintenance, and reproduction. In this zero-sum game, more energy allocated to growth or maintenance reduces energy available to reproduction, and vice versa. Existence of these trade-offs has led to the theory of life-history invariants, which holds that only certain combinations of life-history traits produce an organism with high fitness (Charnov 1993).

Gislason et al.’s (2010) extensive dataset on life-history traits (including mortality) illustrates the fundamental trade-offs between instantaneous mortality (M) and parameters defining the maximum size and rate of growth in marine fish (Figure 1). The x axis represents the “slow” to “fast” life-history continuum. Species with “slow” life histories (eg rockfish [*Sebastes* spp], cod [*Gadus morhua*], porbeagle shark [*Lamna nasus*]) have delayed maturity and long life spans, whereas species with “fast” life histories (eg anchovetta [*Engraulis ringens*], mackerel [*Rastrelliger neglectus*]) are characterized by early maturation and short life spans. A “fast” life history is essential if natural mortality is high, as organisms rush to reproduce at least

once before they die. When adult mortality is low, it pays to invest more energy into early growth. Individuals following this strategy are evolutionarily favored because they are larger when they reach maturity and have higher reproductive output. Because of low adult mortality, they can also anticipate many reproductive seasons during which they reap the benefits of being large. Furthermore, relative costs of reproduction are smaller for larger individuals; this, in turn, increases longevity.

Note that no marine fish species have combinations of life-history traits that fall in the upper-left or lower-right quadrants of Figure 1. This is because those combinations do not represent evolutionarily stable strategies and hence would be vulnerable to replacement by combinations that promote higher fitness. For example, a species falling in the upper-left quadrant would delay maturity but would be unlikely to reap the benefits of doing so because of high adult mortality. Conversely, a species in the lower-right quadrant would expend a great deal of energy to mature and begin reproduction early, but would remain small and not capitalize on the benefits of increased fecundity that come with large body size and a long life span.

■ Life histories can evolve rapidly in response to change in mortality

Harvest-induced mortality can greatly exceed natural mortality in many marine fish and invertebrate populations

(Darinmont *et al.* 2009). For instance, natural mortality estimates for adult Atlantic cod (*Gadus morhua*) are about 10–20% per year, whereas annual mortality from fishing is commonly 50% or higher. Humans have thus created a massive, worldwide, unintentional “experiment” on how changes in mortality regimes will affect life histories. The selective pressures and expected responses associated with increases in adult mortality are schematically illustrated

in Figure 2a (Panel 1). If increased adult mortality does not affect baseline natural mortality, the expected evolutionary response follows the solid horizontal red arrow. If anthropogenic mortality increases natural mortality in a positive feedback loop (eg Jørgensen and Holt 2013), the trajectory could follow the oblique, upward-trending arrow. On the other hand, if members of the population exhibit behavioral or physiological responses that reduce

Panel 1. Adult mortality and life history in marine fish

We replotted the relationships in Figure 1 to better illustrate the evolutionary pressures created by a sudden increase in adult mortality. First, we changed the scale on the y axis from instantaneous mortality (M) to the more intuitive annual mortality rate (v), which is the fraction of the population that dies each year; the two are related by $v = 1 - e^{-M}$, where e is the base of the natural logarithm. Second, because our focus is on adult mortality, we trimmed the dataset to remove samples for juveniles; as a result, Figure 2 is based on data for $n = 119$ presumably adult samples for which body size was at least 60% of asymptotic length L_∞ . An anthropogenic increase in overall adult mortality from level “A” to level “B” (arrow from green circle to red circle in Figure 2a; eg from fishing or climate change) moves the population into the “no-man’s land” of low viability in the upper-left quadrant. Red arrows show possible trajectories of evolutionary response, depending on whether anthropogenic mortality affects the baseline level of natural mortality (see main text for discussion).

Empirical data for two species that have experienced many decades of elevated mortality from fishing illustrate these phenomena (Figure 2b). In Pacific hake (*Merluccius productus*), fishing rapidly increased total adult mortality more than threefold, which has greatly reduced asymptotic size (L_∞ for females decreased from 80 cm in 1975–1989 to 50 cm in 1990–2010) (Stewart *et al.* 2011). Total adult mortality in North Sea plaice (*Pleuronectes platessa*) increased only twofold by fishing, but reduction in asymptotic size has been even more pronounced (90 to 48 cm). Although the earliest data for plaice are a century old, most of the life-history changes in this species are also believed to have occurred in the past few decades (van Walraven *et al.* 2010). The exact trajectories of life-history change over time in hake and plaice are not known (curved arrows in Figure 2b are possible scenarios), but the net result is clear: in response to elevated adult mortality, each species now has a much faster life history, which is consistent the theoretical response to selection (Figure 2a).

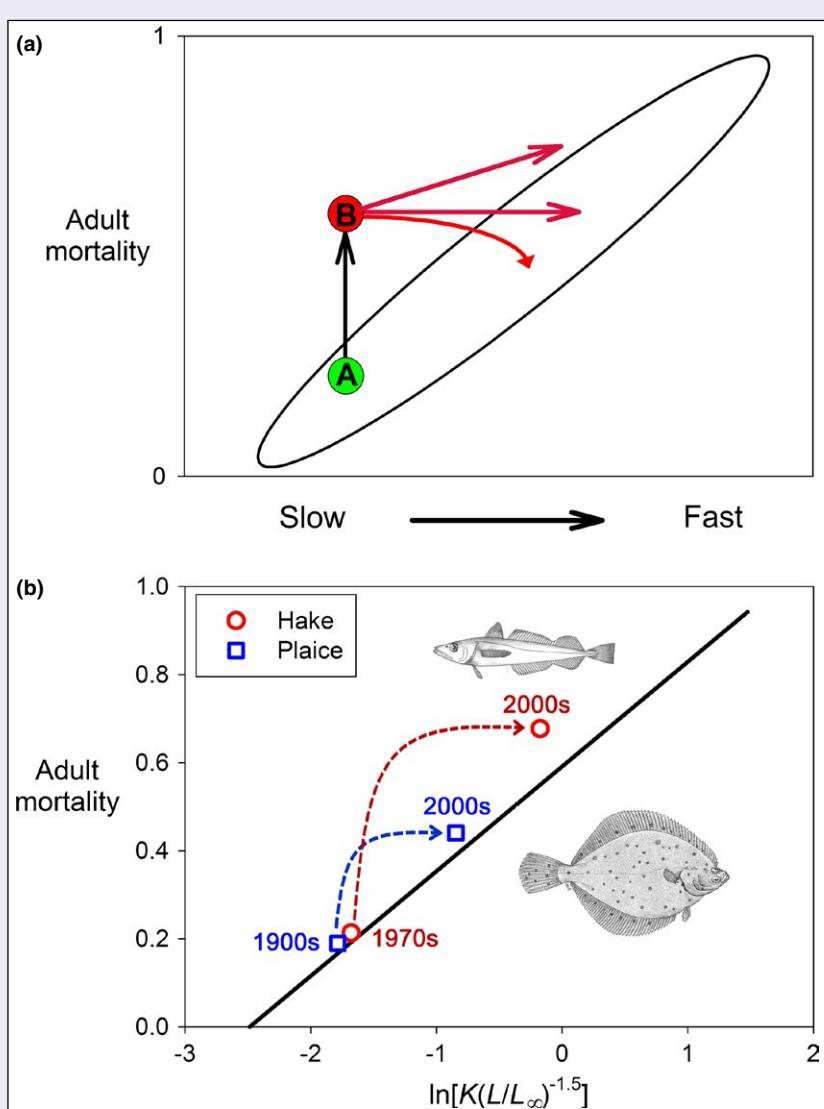


Figure 2. Theoretical and empirical responses by marine fish to sudden increases in adult mortality. (a) Schematic representation of the relationship shown in Figure 1, after filtering out data for juveniles and converting instantaneous M to annual adult mortality. The ellipse represents the regression of adult mortality on $\ln[K(L/L_\infty)^{-1.5}]$ for the filtered dataset. (b) Empirical rates of change in adult mortality and Von Bertalanffy growth parameters in Pacific hake and North Sea plaice. Color-coded dates and symbols indicate starting and ending decades covered by the data, and the solid line is the regression represented by the ellipse in (a). Images in (b) are reproduced with permission from the Food and Agriculture Organization of the United Nations (Species Fact Sheets; Rome, Italy; www.fao.org).

overall mortality, the trajectory could follow the downward-curving arrow. In any case, however, the expected direction of response to higher adult mortality is evolution toward a “faster” life history that gives each individual a better chance of reproducing at least once before dying. Although not illustrated here, a sudden reduction in adult mortality could be expected to have a mirror-image effect. The population would be shifted to the “no-man’s land” in the lower-right quadrant, which would exert selective pressure to evolve a slower life history characterized by delayed maturity and large adult body size that could take better advantage of the increased life span (eg Reznick *et al.* 1997).

And what are the empirical results of the large “experiment” involving increases in human-induced mortality to harvested species? General patterns of reduced body size and age at maturity observed in wild fish populations (see two examples in Figure 2b in Panel 1) are consistent with theoretical expectations and with empirical results for experimental manipulations of model species (Reznick *et al.* 1997; Walsh *et al.* 2006). The rate of life-history change in wild populations is positively correlated with fishing intensity; for an annual fishing mortality of 40%, the mean rate of change in life-history traits is 1% per year (Sharpe and Hendry 2009; Audzijonyte *et al.* 2013). Furthermore, when the strength of selection imposed by fisheries has been estimated quantitatively, the observed life-history responses agreed with expectations (Kendall *et al.* 2014).

Although FIE has often been associated with size-selective fishing, evolution toward faster life histories does not require selective harvesting; all that is required is that adult mortality be artificially elevated as compared with the mortality regime under which the population’s life history evolved (Ernande *et al.* 2004; Hutchings 2009). Of course, selectively removing larger or older individuals can magnify the life-history response, but this generally will be less important than the overall magnitude of increase in adult mortality (Kuparinen and Hutchings 2012; Kuparinen *et al.* 2016).

■ Climate change and marine ectotherms

The principal environmental consequences of climate change that are relevant to marine ectotherms can be characterized as a three-pronged “syndrome” of increasing water temperature, decreasing concentration of dissolved oxygen (DO), and increasing carbon dioxide (CO_2) concentration (Figure 3). Below we discuss how these factors can influence adult mortality and thereby impose selective evolutionary forces on ectotherm life histories. Note that here we focus on evolutionary responses of life histories to climate change. Substantial phenotypic changes in growth and maturation are also expected through purely physiological responses to global warming (eg Baudron *et al.* 2014) or changes in ocean productivity, but these are outside the scope of this article.

Temperature and dissolved oxygen

In marine ecosystems, the effects of increased temperature and reduced DO are closely linked: oxygen is less soluble in warmer water, and changes in ocean circulation associated with global warming are expected to lead to greater thermal stratification and reduced opportunity for air-sea gas exchange (Keeling *et al.* 2010). Therefore, we consider the effects of temperature and DO jointly. One of the best documented examples of climate change is the differential response of small and large individuals to increased water temperature and reduced DO. Large individuals are more sensitive to temperature increases due to (1) a reduced surface area-to-volume ratio, which limits oxygen uptake, and (2) a faster increase in catabolic versus anabolic rates with elevated temperature (Kozłowski *et al.* 2004). As a consequence, at higher temperatures larger individuals suffer increased mortality, creating evolutionary pressure toward smaller body size; this applies to marine invertebrates (Peck *et al.* 2009) as well as to fish (Pörtner and Knust 2007). Pressures to reduce adult body size are particularly strong for aquatic species because of the greatly reduced oxygen availability, and the much greater effort required to increase oxygen uptake in water as compared to air (Forster *et al.* 2012). Climate-induced changes in water temperature and DO can therefore be expected to produce age-specific changes in mortality (eg reduced survival of larger, older fish as compared with smaller, younger ones) that mimic the patterns already documented to result from size-selective harvest of many fish populations.

In addition to the direct effect of increased mortality for large individuals, processes involving growth, maintenance, and reproduction change with temperature at different rates, resulting in a steeper size–fecundity relationship in colder waters (Arendt 2011). This relationship provides an evolutionary explanation for the commonly observed temperature–size rule, which states that ectotherms in colder environments have slower growth and larger body size (Atkinson 1994). Steeper size–fecundity relationships in colder waters translate into greater benefits of delayed maturity, and this promotes a slower life history. Benefits of delayed maturity are diminished as water temperatures increase, adding to the evolutionary pressure to mature earlier and at a smaller size.

Is it possible to quantify the expected contribution of increased water temperature to increased adult mortality? Regression equations developed by Pauly (1980) in a large meta-analysis of marine fish suggest that the contribution of temperature to increased natural mortality is rather modest (about 1–2% per $^{\circ}\text{C}$). However, this relationship reflects patterns that have developed over evolutionary time scales (thousands or millions of years) and is not a reliable predictor of short-term fitness consequences of rapid increases in temperature. More relevant are

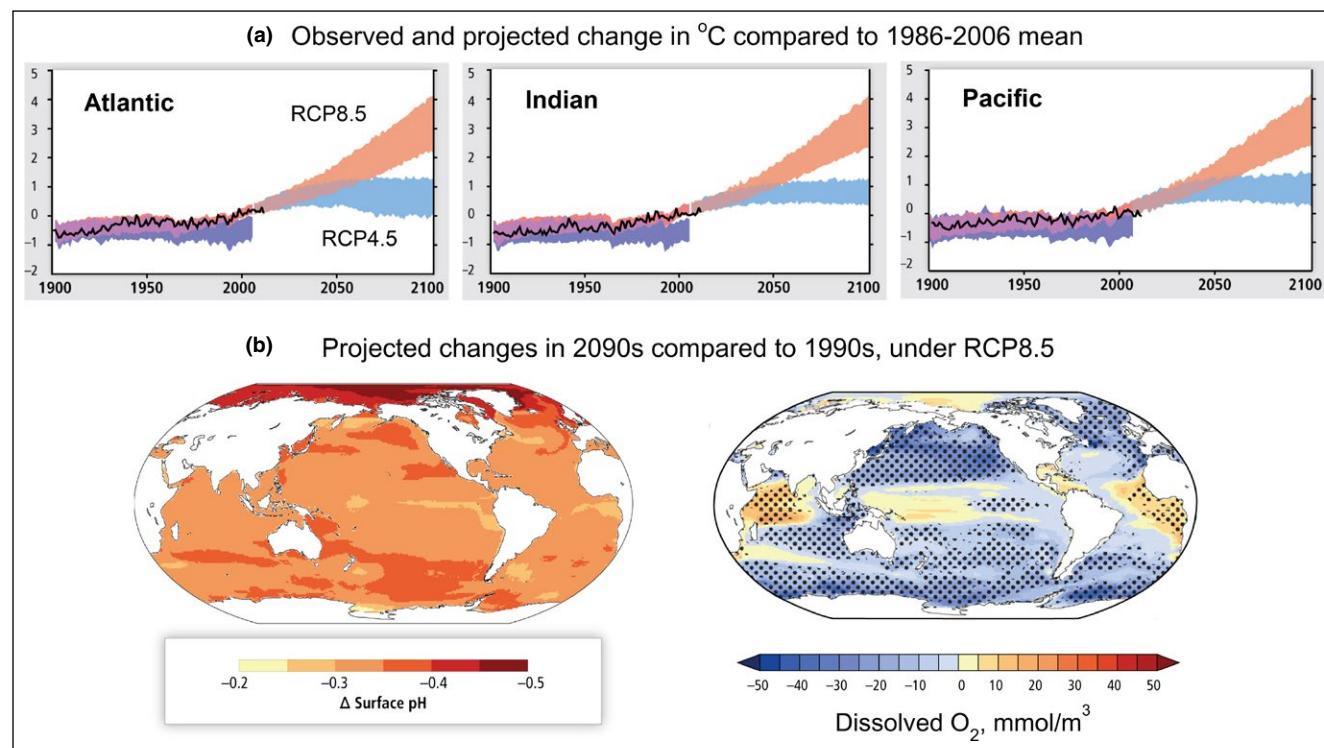


Figure 3. The climate-change “syndrome” faced by marine ectotherms. (a) Changes in sea-surface temperature in three major ocean basins (>300 km from coast). Black lines are historical means; shading indicates the 90% confidence intervals for historical data (pink) and simulated historical data assuming no anthropogenic elevation of atmospheric CO₂ (purple). Blue and orange shadings show 90% confidence intervals for projections under moderate (RCP4.5) and relatively high (RCP8.5) emission scenarios. (b) Projected changes under RCP8.5 for pH of surface water (left) and dissolved oxygen (O₂) in the main thermocline (200–600 m depth; right). Stippled areas in the dissolved O₂ plot are regions where ≥80% of models agree on the sign of change. mmol/m³ = millimoles per cubic meter. Images modified from Hoegh-Guldberg et al. (2014).

experimental data from studies like Rummer et al. (2014), who calculated reaction norms for aerobic scope (a measure of the capacity for maximum energy expenditure to exceed basal metabolic rate) for six coral reef fish species. All of those species had substantially reduced performance at temperatures 3°C above ambient, leading the authors to conclude that many tropical reef species are already living close to their thermal maxima and have little capacity for plastic responses to rising water temperatures. Similarly, Muñoz et al. (2015) found little capacity of Chinook salmon (*Oncorhynchus tshawytscha*) challenged with elevated temperature to maintain some key aspects of cardiac function, through either plastic or evolutionary responses. So, although responses to warming ocean temperatures will undoubtedly be species specific, these recent empirical studies show that they can be more pronounced than might be expected based on general patterns that reflect adaptations that have developed over evolutionary time frames.

Ocean acidification

Most evaluations of ocean acidification (OA) have focused on species (eg corals, mollusks, crustaceans,

echinoderms) that build calcareous structures, construction of which becomes more difficult as pH drops. More generally, OA can increase physiological maintenance costs for marine species, leaving less energy to devote to growth and reproduction. Key processes that can be affected in marine fish include fertilization, sensory capacity and behavior, and disease and immune responses. In contrast to harvesting effects, increased temperature, and reduced DO (all of which primarily affect adult mortality), OA often affects larvae or juvenile stages most strongly. Empirical results to date are highly variable, ranging from negligible to strongly detrimental; some topics have received little attention, and direct effects on adults are largely unstudied (reviewed by SCBD 2014). Because they have well-developed mechanisms for acid-base regulation, fish are thought to be more resilient than other marine species to direct effects of OA (SCBD [Secretariat of the Convention on Biological Diversity], 2014). Thus, although it is challenging to forecast how OA might affect life-history traits of marine fish, the effects of OA (for adults at least) are expected to be smaller in magnitude than those of temperature and DO. For example, in a study

Table 1. Summary of effects of fishing and climate change on mortality patterns in marine species

	Fishing	Climate change	
		Water temperature and dissolved O ₂	Ocean acidification
Effects on mortality	Increased; generally greater than natural mortality. Often higher for larger or older individuals.	Increased. Energetic demands and low surface area-to-volume ratio differentially affect larger or older individuals.	Direct effects on adults are largely unstudied, but likely to be small for fish, which have efficient acid-base regulation. Can adversely affect settlement or homing in some species.
Notes	Effects are more easily quantified than those related to climate change.	These two factors are tightly coupled in the marine environment.	Best-documented effects are on species that must form calcium carbonate structures (crustaceans, mollusks, corals, echinoderms).

of a coral reef fish, the combined effects of OA and elevated temperature reduced reproductive performance, but the effects of OA were small compared with the effects of temperature (Miller *et al.* 2015). That being said, because synergistic effects of multiple stressors are difficult to predict with certainty, some marine species will likely exhibit unexpected responses to climate change that depart from the general patterns outlined here.

Summary

The joint effects of temperature and DO are well documented in the marine environment, and abundant evidence indicates that climate change can be expected to produce effects on marine ectotherms that mimic those of FIE: namely, increased mortality, especially of adults, and consequently selective pressure to evolve faster life histories (Table 1). In contrast with the strong and predictable effects of elevated temperature and reduced DO are uncertain consequences of OA for marine fish. If OA has any direct influence on marine fish survival, it is likely to be detrimental; however, it is unclear for how many species this will be an important factor. Therefore, in response to the previously described climate-change syndrome – increased temperature and reduced DO and pH – we expect the overall result to be an increase in adult mortality, modulated for some species to an unknown degree by various effects related to OA. The stressors related to climate change will be more severe in certain geographic areas, and some species will be able to respond by moving (Pinsky *et al.* 2013), by acclimation (Miller *et al.* 2012), or by evolving greater tolerance (Munday *et al.* 2013). However, rapid environmental change will outpace the ability of many species to implement any of these coping strategies (Devine *et al.* 2012; Muñoz *et al.* 2015), in which case they could experience selective pressure to evolve faster life histories – just as occurs under FIE.

Although we have stressed the many similarities between expected life-history responses to fishing and climate change, there is at least one important difference:

whereas FIE only directly affects target (and potentially bycatch) species, essentially every marine organism could be affected by global climate change. The most pronounced effects are expected for species that currently have low adult mortality and long life spans (such as those shown in Figure 4). These considerations apply primarily to cold-blooded species, given that marine mammals and seabirds have greater capacity to control their functional temperature. Most examples of FIE are for fish, but the same evolutionary principles apply to invertebrates as well. Therefore, we predict that large numbers of marine ectotherms will experience considerable evolutionary pressure to adopt faster life histories as a result of climate change.

Consequences for conservation and management

What are the practical consequences of increased pressure to evolve faster life histories in marine species? Species that grow rapidly and mature early can be highly productive; they also play major roles in all marine food webs, and some (such as sardines and anchovies [Clupeidae]) are targets of large fisheries. Species with fast life histories are therefore not inherently at high risk. However, truncating age structure within a population typically leads to larger fluctuations in abundance, so factors that favor early maturity and short life span are likely to produce more “boom or bust” cycles within marine ecosystems. Furthermore, rapid changes in life history can be expected to produce other transient instabilities within and among species. In species that persist within dynamically stable ecosystems, the entire life cycle, including biotic interactions with other species, can be fine-tuned and integrated by evolution over long periods of time (thousands to millions of years). In contrast, climate change could easily cause rapid evolution in some life-history traits of “slow” species at rates that outpace the ability of other key traits (eg temperature tolerance, cardiac function) to keep up. The result can produce populations that initially have a mosaic of traits that do not interact in an optimal fashion to promote high viability. Evolutionary honing of the species’ overall game plan

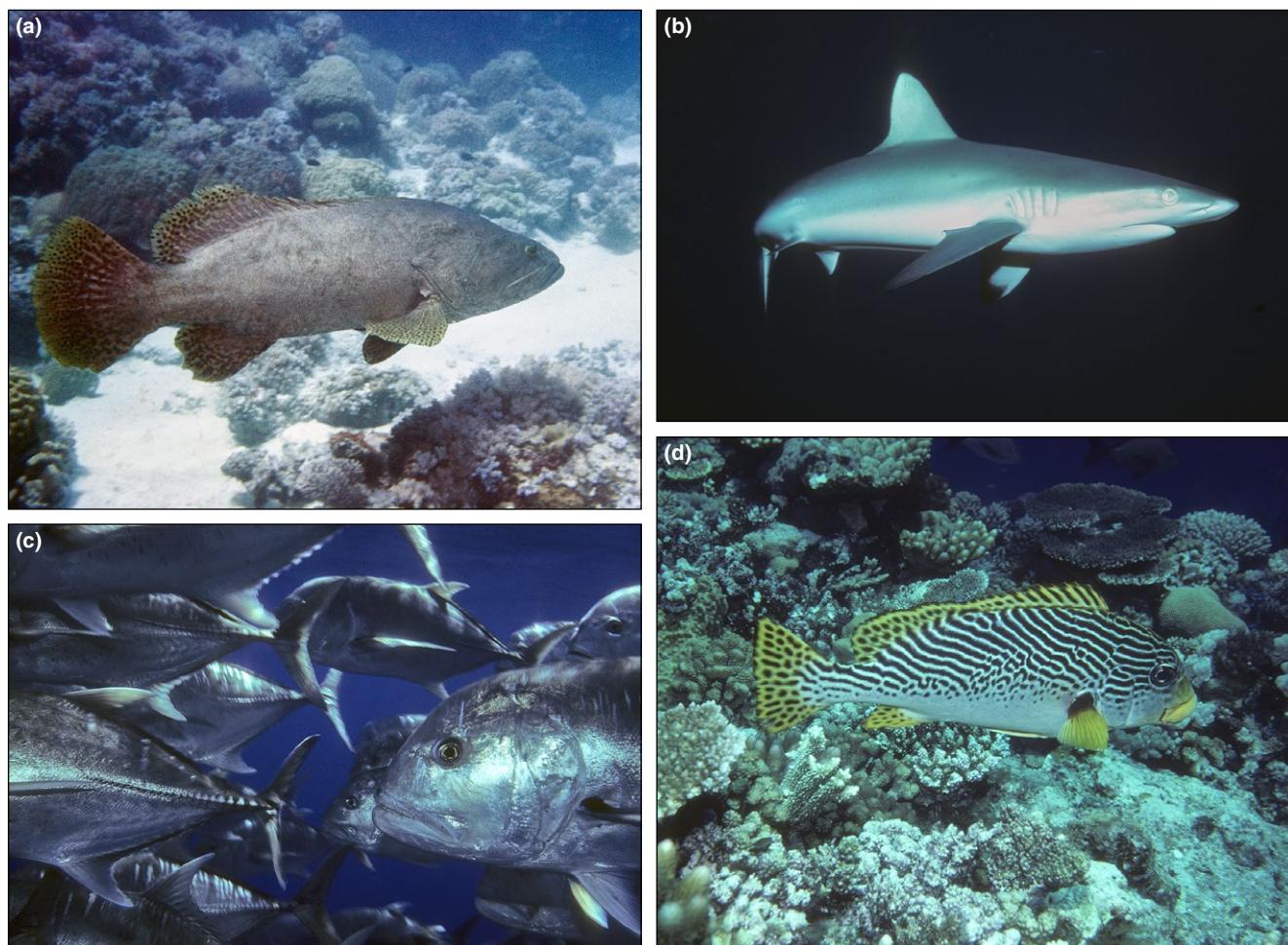


Figure 4. In Australia's Great Barrier Reef, selected tropical fish with slow life histories could face pressure to evolve faster life histories under climate change. Clockwise from upper left: Queensland grouper (*Epinephelus lanceolatus*), gray reef shark (*Carcharhinus amblyrhynchos*), yellowbanded sweetlip (*Plectorhinchus lineatus*), and giant trevally (*Caranx ignobilis*).

to function effectively with a faster life history may take a long time. During this transition period, the species is likely to be at increased risk. Finally, because many interacting species will also be similarly affected, ecosystems will be altered in unpredictable, and perhaps chaotic, ways.

These considerations have important implications for managers and conservation practitioners. First, slow life histories provide a buffer against consequences of unpredictable environments, as longevity increases the chances of at least one successful reproduction event. It will be important to account for decreased buffering capabilities due to faster life histories. Second, a shift to faster life histories will have a strong influence on per-capita population growth rate (r), which is a key parameter in stock assessments and risk assessments. Also, harvested species will experience synergistic effects of fishery-induced and climate-change-induced mortality, with consequences for the species' life history that will exceed those caused by either factor alone. Therefore, the assumption of many harvest models that key life-history parameters of target species remain constant over time needs to be reassessed.

Similarly, ecosystem-based models that assume life-history characteristics of component species are fixed will produce increasingly unreliable results as cumulative effects of climate change on marine species continue to mount. The qualitative predictions outlined here provide a general guide to the types of changes to be expected, but monitoring developments in key life-history parameters over time will be necessary to provide quantitative information to ensure that these models produce robust results.

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