



Trends and management implications of human-influenced life-history changes in marine ectotherms

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Abstract

Evidence is accumulating that many marine ectotherms are undergoing rapid changes in their life-history characteristics. These changes have been variously attributed to fisheries-induced evolution, inhibited adult growth rate due to oxygen limitation at higher temperatures, and plastic responses to density dependence or changes in ocean productivity. Here, we review the diverse underlying mechanisms by which plastic and evolutionary responses to climate change and fisheries are likely to produce similar life-history trends in harvested marine ectotherms, leading to faster life-histories with earlier maturation and smaller adult size-at-age. While mechanistically understanding these growth and maturation changes may be difficult, it is becoming clear that changing life-histories will lead to modified population dynamics, productivity and natural mortality of the affected species. We discuss how the observed and expected life-history changes could affect the assumptions and uncertainty within single and multispecies models currently used in marine ecosystem management, highlighting that models which allow for dynamic life-history traits often report significantly different estimates of stock biomass. Given that both climate- and harvest-induced life-history changes are likely to intensify and possibly amplify each other, there is an urgent need to adequately assess the implications of faster life-histories for marine ecosystem management. This is especially true for data-poor stocks, where growth and maturation are not regularly assessed. Targeted monitoring can be used to inform responsive management, but for improved sustainability outcomes, a precautionary approach to management that is robust to life-history trends is advised.

Keywords Climate change, evolution, fisheries, phenotypic response, physiology, plasticity

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Introduction

Most of the world's oceans are now believed to be affected by human activities at a medium to very high level (Chevin *et al.* 2010; Halpern *et al.* 2012). These anthropogenic pressures, such as fishing, climate change, pollution, and habitat degradation, are increasing in distribution and intensity (IPCC-AR5 2014; Merrie *et al.* 2014). Organisms exposed to such rapid changes in their environment and to new or intensified selective pressures are forced to adapt to new conditions through shifts in distributions, phenotypic plasticity and contemporary evolution (Hoffmann and Sgro 2011). Among other aspects, such adaptive responses will be strongly manifested through changes in growth and reproductive schedules, or life-histories.

Life-histories determine species energy allocation to growth and reproduction, and describe traits such as age and size of maturation, reproductive effort and maximum adult size and age. Some of the most rapid changes in life-history traits have been observed in commercially harvested fishes (Jørgensen *et al.* 2007; Devine *et al.* 2012), where the rate of change can be as high as 1–4% per year for size and age at maturity (Audzijonyte *et al.* 2013a) and 2.5% per year for growth (Morrongiello and Thresher 2015). The relative importance of genetic and plastic components in this change and the drivers have been intensely debated (e.g. Olsen *et al.* 2004; Kraak 2007; Rogers *et al.* 2011; Therkildsen *et al.* 2013; Baudron *et al.* 2014), yet regardless of the underlying mechanisms, the observed trends will have important implications for marine ecosystem management, including management of individual species.

Given that life-history parameters for harvested stocks will be affected by both fishing and climate change simultaneously, understanding the combined effects is an important but neglected priority (Perry *et al.* 2010; Planque *et al.* 2010).

This review aims to highlight how global environmental change and fishing are affecting life-histories of marine ectotherms. Naturally, responses to climate change or fishing involve many other features, such as changes in distributions, phenology or behaviour, but these have been discussed elsewhere (e.g. Brander 2013; Poloczanska *et al.* 2013). In contrast, while there have been important studies on how either harvesting or climate change is affecting life-histories separately (e.g. Heino *et al.* 2013, 2015; Holt and Jørgensen 2015), we believe that insufficient attention has been paid to the fact that both forces are likely to lead to convergent trends and possibly amplify each other. Hence, the main message of this review is that the diverse mechanisms caused by harvesting and climate change will, in many species, lead to faster ectotherm life-histories, with earlier maturation and smaller adult body sizes. To demonstrate this point, we first summarize the dominant trade-offs determining life-history strategy and explore how these trade-offs might be useful to predict likely changes in life-history traits. Second, we explore how the different contemporary environmental drivers, in particular climate change and fishing, are likely to produce similar life-history trends. Third, we describe how these trends might increase fluctuations in population abundance and hence reduce resilience to environmental change and exploitation. Finally, we discuss how contemporary life-history changes might affect the management advice and outcomes of

single and multiple species models, and suggest areas for further scientific investigation.

Plastic and genetic determinants of life-history strategies and important trade-offs

A study of directional life-history change in natural populations cannot avoid questions about the underlying nature (plastic, genetic or both) and hence reversibility of the observed trends. From an evolutionary perspective, life-histories are constantly being tuned to optimize fitness under a given juvenile and adult mortality regime; for example, different life-histories are expected in stable vs. highly stochastic environments (Roff 1992). Studies of heritability of life-history traits in aquaculture, laboratory experiments and wild populations typically estimate that about 20 to 40% of the phenotypic variability is genetically determined (Conover and Munch 2002; Carlson and Seamons 2008). Rapid evolutionary changes have also been demonstrated in wild populations and linked to ecological changes in aquatic systems (Reznick *et al.* 1997; Palkovacs *et al.* 2012). At the same time, growth rates and maturation schedules are highly plastic, showing rapid responses to changes in resource availability, temperature, or density (Enberg *et al.* 2012; Baudron *et al.* 2014; Morrongiello and Thresher 2015). While this plastic vs. genetic distinction is important when assessing possible reversibility of life-history trends, disentangling the two components in wild populations is notoriously difficult, because realized life-histories will depend on the combined effect of genetic background, maternal effects, and phenotypic plasticity (e.g. Gienapp *et al.* 2008; Kuparinen *et al.* 2009; Hansen *et al.* 2012). Nevertheless, the general trade-offs among life-history traits governing growth, maintenance and reproduction hold regardless of the driver causing the change (Charnov 1993; Jensen 1997), and this allows us to predict the general nature of correlated responses.

All organisms have limited amounts of energy that must be allocated to different body functions; increased energy allocation to reproduction takes energy away from somatic growth, and vice versa. Recognition of these trade-offs has led to the development of life-history theory (e.g. Roff 1992), which can be used, among other things, to infer age-at-maturation and energy-based life-history traits from individual growth trajectories (Brunel

et al. 2013). Assuming that a fixed amount of total energy is available, life-history trade-offs provide some general rules on how changes in one trait will lead to changes in other correlated traits (Fig. 1). For example, earlier maturity trades off with later reproductive output by reducing somatic growth and increasing natural mortality through survival costs of reproduction (Bell 1980). These reproductive costs include increased mortality due to reproductive changes in behaviour (competition for mates, nest guarding, spawning migrations), reduced feeding, energetic investment in gonads instead of somatic growth, and less energy allocation to immune functions (Jørgensen and Fiksen 2010; Jørgensen and Holt 2013). The trade-off between growth and maturation in animals with indeterminate growth is typically seen as a negative correlation between intrinsic growth rate against size at maturity and adult body size (Charnov 1993). Accounting for these trade-offs has a large impact on the outcomes of models aiming to predict population level consequences of life-history changes (see below).

The trade-offs in the energy allocation for different functions (growth, reproduction, maintenance) are also at the heart of correlations among species and population life-history parameters observed in broadly defined taxonomic categories. These correlations are known as life-history invariants, and provide some general rules about the expected relationships between asymptotic length (L_{∞}), age and size-at-maturation, growth rate, natural mortality, and length-fecundity relationship (e.g. Beverton 1992; Charnov *et al.* 2013). While these relationships encompass large variation, they nevertheless provide useful insights into population parameters in data-poor stocks and are used to inform ecological risk assessments (Patrick *et al.* 2010; Hobday *et al.* 2011a). They are also implemented in global databases, such as FishBase. A promising new approach to reduce variation and improve predictive value of life-history invariants is to derive these life-history ratios separately for species with different life-history strategies (Prince *et al.* 2015).

In this review, we focus on life-history and growth parameters and for illustration purposes, we use the von Bertalanffy (VB) growth model (von Bertalanffy 1957; see also Pardo *et al.* 2013) (Fig. 1). The two VB parameters of interest here are asymptotic length (L_{∞}) and the rate at which growth approaches the asymptote (k),

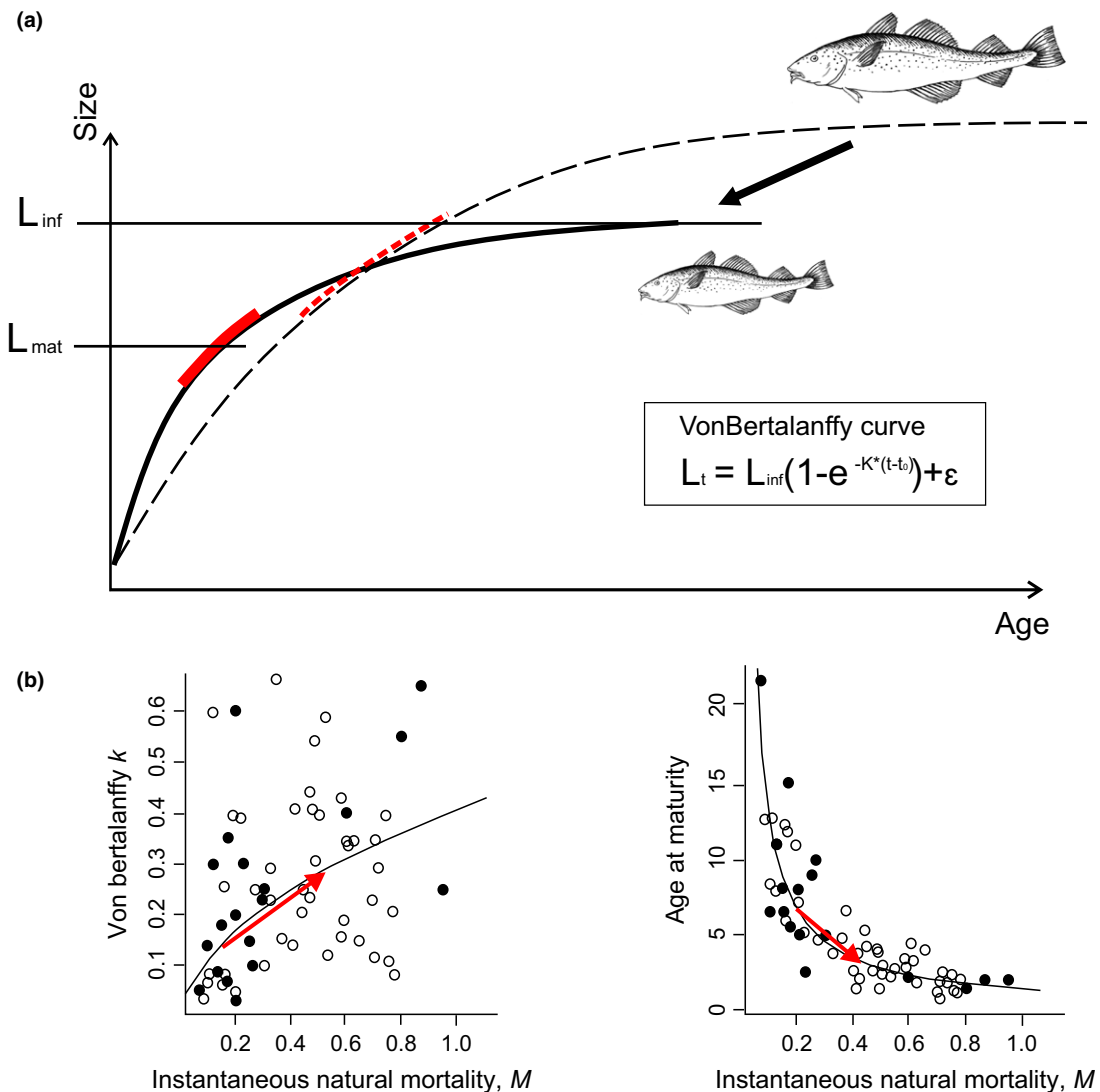


Figure 1 (a) Von Bertalanffy growth curves for slow (dashed line) and fast (thick solid line) life-histories. An arrow indicates the suggested general trend towards faster life-histories. Thickened lines indicate the length of maturity for the different life-histories. (b) Relationship between life-history parameters and natural mortality based on empirical and simulated data (modified from Carruthers *et al.* 2012).

which is often referred to as a growth coefficient. We should note that, as with any model, the VB model has its shortcomings. First, k is difficult to interpret ecologically, and cannot easily be compared across species (see Pauly 2010, who also offered a conversion of k to an ecologically meaningful growth performance index that is comparable across species). Second, in heavily fished stocks where few individuals survive to the older and larger age classes, the estimation of L_{∞} can be problematic (Haddon 2011). Yet, despite these limitations, the model is commonly used in fisheries, due to its flexibility and generality to sum-

marize somatic fish growth. The model is also used to describe many of the life-history invariants and correlations between L_{∞} and k with natural mortality (M), carrying capacity (K) and per-capita population growth rates (r), i.e. the key parameters defining population productivity and ability to sustain harvesting (Dulvy *et al.* 2004; Hobday 2011b). We nevertheless emphasize that our prediction on faster life-histories does not depend on the VB or any specific growth model, as the two key aspects of this prediction are simply earlier maturation and smaller adult body size.

Drivers and empirical evidence on life-history changes in marine ectotherms

Harvesting: short-term density-dependent growth changes

The effects of harvesting on age structure, population dynamics and density-dependent processes of fished stocks are at the core of basic fisheries models and stock-recruitment relationships, yet a lack of life-history data and poor understanding of interconnected processes remain a limitation of such models (Rose *et al.* 2001; Lorenzen 2016). Complex growth patterns are difficult to model explicitly, and most fisheries models that use growth models to predict body weight-at-length or -age either treat the growth parameters as fixed, or estimate the parameters within the model and assume they do not vary over time (Haddon 2011; Kuparinen *et al.* 2012; but see Whitten *et al.* 2013 for a case where cohort-specific growth is used to account for density dependence on adult growth). Typically, strong density dependence is assumed to operate during the juvenile stages and is modelled through stock-recruitment relationships. In contrast, density effects on the age groups captured by fisheries are usually considered to be weak (Rose *et al.* 2001; Lorenzen 2016).

There seems to be no consensus as to how density-dependent processes might affect life-history parameters (Prince *et al.* 2015). Lorenzen and Enberg (2002) found indications of density dependence on adult growth in many marine stocks and estimated that for species in a 20–45 cm size range, a 100% increase in stock biomass will lead to a 10% decrease in L_{∞} . In the evolutionary and physiological interpretation of the VB growth model presented by Charnov *et al.* (2013), L_{∞} , or maximum body size, is determined by both food availability and/or changes in maintenance and reproduction, whereas k , or early growth rate, is affected only by the allocation to maintenance and reproduction. In this formulation, increased food availability is expected to increase L_{∞} , but should not change k . Empirical data provide examples of both situations (Table 1). High abundance of certain age groups had negative effects on juvenile growth rates in sockeye salmon (*Oncorhynchus nerka*, Salmonidae) (Crozier *et al.* 2010) and has been linked to a decrease in L_{∞} from about 100 cm to 40 cm in the Baltic Sea cod (*Gadus morhua*, Gadidae) (Svedang and Hornborg 2014).

Reduced population sizes and thus lower density were correlated with increased k in southern Bluefin tuna (*Thunnus maccoyii*, Scombridae) (Polacheck *et al.* 2004), but decreased k and increased L_{∞} in southern king weakfish (*Macrodon atricauda*, Sciaenidae) in Southern Brazil (Cardoso and Haimovici 2011).

One limitation of these studies is that they do not statistically test alternative hypotheses that could explain the observed growth patterns, as in addition to density dependence they could include changes in reproductive investment, maturation age and length, maintenance costs and many environmental factors. This underscores the general difficulties in attributing empirically observed life-history changes to a specific driver. We suggest that, for many stocks, in the absence of long-term population trends, density-dependent processes will generally fluctuate over time in response to changes in harvesting levels and recruitment and will not be as important as the long-term trend towards faster life-histories caused by global warming or fisheries-induced evolution.

Global warming: response to productivity change

In this section, we focus on the life-history responses to changes in ocean productivity. The effects of global warming on marine organisms are multifaceted (Sarmiento *et al.* 2004; Doney *et al.* 2012), and also include ocean acidification, yet the impacts of ocean acidification on life-history traits remain speculative (Munday *et al.* 2013). We also do not discuss the global warming effects on the distributions of marine organisms, as they have been covered in a number of recent reviews (Poloczanska *et al.* 2013; Bates *et al.* 2014).

Changes in ocean temperature, circulation and mixing all affect nutrient supply and primary productivity (Poloczanska *et al.* 2008; Brown *et al.* 2009; Taucher and Oschlies 2011). A number of modelling studies find that climate change will lead to reduced ectotherm body size through nutrient limitation due to reduced mixing of water layers and smaller size of phytoplankton (e.g. Woodworth-Jefcoats *et al.* 2015). Yet, despite the important implications that productivity shifts are expected to have on marine ecosystem dynamics, our ability to model and forecast the magnitude or even direction of the productivity change is still limited (Doney *et al.* 2012; Polovina and Woodworth 2012). Even greater spatial

Table 1 Some literature examples on changes in life-history parameters: juvenile growth (JG, often assessed as k in the VB curve), maturation (MAT, assessed as either age at 50% maturation or probabilistic maturation reaction norms), and asymptotic length or adult size (AS, often assessed as L_{∞} in the VB curve). Increase/decrease in parameter values is shown with \pm , no change indicated with 0, parameters that were not assessed are shown with na. Uncertain inferences in parameter change are shown in parentheses. DD – density-dependent, T – temperature, FIE – fisheries-induced evolution. Species/stocks included in the review studies (e.g. Sharpe and Hendry 2009) are not listed separately.

Species	Area	MAT	JG	AS	Driver	Reference	Notes
Southern bluefin tuna	South Pacific	na	+	(–)	Relaxed DD	Polacheck <i>et al.</i> 2004	1960s–1990s, decrease in L_{∞} uncertain
Southern king weakfish	Southern Brazil	–	–	+	FIE, relaxed DD	Cardoso and Haimovici 2011	1976 to 2011; changes coincided with heavy exploitation
Cod	Baltic Sea	na	na	–	Increased DD	Svedang and Hornborg 2014	k values not reported
Cod	Baltic Sea	–	na	–	FIE, environment	Vainikka <i>et al.</i> 2009	1987–2003, condition corrected trend in maturation found only in females
Pike perch (<i>Sander lucioperca</i> , Percidae)	Baltic Sea	–	na	0	FIE, higher T	Kokkonen <i>et al.</i> 2015	Increased productivity may have increased growth, masking decrease in size due to FIE
The western blue groper (<i>Achoerodus gouldii</i> , Labridae)	Western Australia	na	+	na	Higher T	Rountrey <i>et al.</i> 2014	1952–2003, changes in growth for ages 1–20 years (maturation at ca 17 years)
Six commercial fish species	North Sea	na	na	–	Higher T	Baudron <i>et al.</i> 2014	16% change per 2C (ca 0.8%/year)
Western rock lobster (<i>Panulirus cygnus</i> , Palinuridea)	West Australia	–	na	na	FIE, higher T	Melville-Smith and De Lestang 2006	1975–2005, decrease in the carapace length-at-maturation
Banded morwong (<i>Cheilodactylus spectabilis</i> , Cheilodactylidae)	Tasman Sea	na	\pm	na	Higher T	Neuheimer <i>et al.</i> 2011	k decreased when T is above optimum
Three shallow water fishes (<250 m)	SW Pacific	na	+	na	Higher T	Thresher <i>et al.</i> 2007	Redfish, Jackass morwong, Banded morwong
Three deep water fishes (>1000m)	SW Pacific	na	–	na	Lower T	Thresher <i>et al.</i> 2007	Orange roughy, Smooth oreo, Warty oreo; no change at medium depth
Blacklip abalone (<i>Haliotis rubra</i> , Haliotidae)	Tasmania	–	+	–	Higher T	Helidoniotis and Haddon 2014	
Cod	E Atlantic	na	\pm	na	Higher T	Rogers <i>et al.</i> 2011	Increased T has + effect in spring, but – effect in summer (above optimum)
Chinook salmon (<i>Oncorhynchus tshawytscha</i> , Salmonidae)	W USA rivers	na	\pm	na	Higher T	Crozier <i>et al.</i> 2010	Increased T has + effect at low density, but – effect at high density (due to DD)
European plaice	North Sea	–	+	–	FIE	van Walraven <i>et al.</i> 2010	L_{∞} change at 1%/year for $F = 0.4$
Haddock (<i>Melanogrammus aeglefinus</i> , Gadidae)	Eastern Canada, Scotian Shelf	–	0	–	FIE	Neuheimer and Taggart 2010	Measures of temperature-corrected length-at-age
Pacific hake (<i>Merluccius productus</i> , Merlucciidae)	USA and Canada west coasts	na	+	–	Unclear	Stewart <i>et al.</i> 2011	Step change in k (0.1 to 0.5) and L_{∞} (80 to 60 m) between 1975–1990 and 1991–2010 inferred
Cod	NW Atlantic	–	na	na	FIE	Swain 2011; Therkildsen <i>et al.</i> 2013	Decrease in PMRN correlated to genetic change and fishing mortality

Table 1 Continued.

Species	Area	MAT	JG	AS	Driver	Reference	Notes
Sockeye salmon	Alaska	-	na	na	FIE	Kendall <i>et al.</i> 2014	Observed change corresponded to the estimated selection differentials
Tiger flathead (<i>Platycephalus richardsoni</i> , Platycephalidae)	SE Australia	na	±	na	Higher T	Morrongiello and Thresher 2015	<i>k</i> increased with temperature to a presumed optima, then declines
Estuary perch (<i>Macquaria colonorum</i> , Percichthyidae)	Victoria	na	+	na	Higher T and increased freshwater flow	Morrongiello <i>et al.</i> 2014	Juvenile growth strongly related to temperature with a lesser flow effect, but adult growth relatively unaffected by environmental change
37 commercial fish stocks	Mostly North Atlantic	-	na	na	FIE	Sharpe and Hendry 2009; Devine <i>et al.</i> 2012	Rate of change in PMRN correlated to fishing intensity
14 marine and freshwater fish stocks		na	na	-	FIE	Audzijonyte <i>et al.</i> 2013a	0.5–2%/year for $F = 0.5$

variability and uncertainty exist in coastal areas. In a semi-global analysis, Barange *et al.* (2014) predicted an overall minor increase in shelf productivity (<10%), with increased productivity at high latitudes and decreased productivity at low and mid latitudes, but considerable regional variation due to local circulation patterns and terrestrial inputs.

Changes in ocean productivity and hence food supply will operate on life-history traits in a broadly similar manner to the density-dependent effects discussed above, except that their combined effect is likely to be opposite – as productivity increases, density dependence is expected to decline, assuming the stock abundance remains at a similar level and there are no large changes in inter-specific interactions. Increased productivity is likely to amplify the temperature-induced trend towards faster growth and earlier maturation, whereas decreased productivity will lead to slower growth rates. In many cases, these effects might be difficult to separate from the response to increased temperature alone, especially in cold regions where higher temperatures often mean higher productivity. As with density dependence, rapid response to, for example, increased productivity through faster growth rates could mask long-term trends due to physiological or evolutionary factors (Fig. 1 in Crozier and Hutchings 2014; Thresher *et al.* 2014; Kokkonen *et al.* 2015). While there is great uncertainty in forecasting productivity changes, its monitoring is considerably easier and is routinely done (e.g. through chlorophyll *a* mapping via satellite images). Hence, up-to-date information on productivity could be a part of routine management (Pethybridge *et al.* 2015) and also incorporated into management decision processes (see Fig. 3).

Global warming: response to temperature change

A decline in average individual body size has been suggested as a ‘third universal ecological response to global warming’ (Daufresne *et al.* 2009; Cheung *et al.* 2013). For ectotherms, this ecological response is often based on the temperature-size rule (Atkinson 1994) that describes the tendency for increased juvenile growth (increase in *k* and hence faster approach towards asymptotic size) and developmental rates combined with the decreased adult body size (L_{∞}) at higher temperatures. Studies that have explicitly tested the tem-

Table 2 Pathways explaining the effects of temperature increase on ectotherm body size.

Pathway	Consequences	Examples
Oxygen concentration in water declines with temperature. Different surface area to volume ratios in small vs. large animals affect oxygen uptake	Large individuals with greater oxygen demands are more sensitive to temperature increases due to reduced relative surface area for oxygen diffusion. This results in disproportional mortality of oldest age classes, leading to smaller adult size-at-age and L_{∞}	Negative within-species relationship between size and temperature in aquatic species, especially in large-bodied taxa (Forster et al. 2012); increased mortality from acute high temperatures in large individuals of marine invertebrate species (Peck et al. 2009); loss of larger eel pout (<i>Lota lota</i> , Lotidae) in the North Sea due to heat stress (Portner and Krust 2007); assemblage-wide average body weights predicted to shrink in a warmer future due to oxygen limitation and the energetic costs of a large body size (Cheung et al. 2013)
Different response rate of anabolic and catabolic processes to temperature	Catabolic rates increase faster with temperature (and size, see above) than anabolic rates. As a result, increasing costs of catabolism at higher temperatures have a stronger effect on large individuals, leading to a cessation of growth at smaller sizes/younger ages, disproportionate mortality of oldest age classes, and to smaller adult size-at-age and L_{∞}	Increased relative catabolic rate in larger and older individuals reduces their growth potential (Kozłowski et al. 2004)
Different responses of growth and reproductive processes to temperature	Changes in temperature may advance maturation irrespective of growth, resulting in small adult body size due to earlier energy allocation to reproduction	Earlier age at maturation caused by higher temperature independent of growth rate and body size in stickleback (<i>Pungitius pungitius</i> , Gasterosteidae) males (Kuparinen et al. 2011); smaller body size and size at maturity at higher temperatures despite faster growth rates in blacklip abalone (Helidonotis and Haddon 2014)
Temperature-dependent differences in size-fecundity or size-reproductive rate relationships	Fecundity rate may increase with size faster under cool conditions than warm conditions. In such a case, the advantages of delayed maturation decrease as temperatures warm leading to earlier maturation and decrease in L_{∞}	The size-fecundity relationship of a freshwater snail is steeper in cooler environments, meaning that it is maladaptive to be a larger size at maturation in warm environments (Arendt 2015); size-specific clutch size is greater at cooler temperatures in a reef fish (Kokita 2003)
Increased temperature leads to higher predation rates and increased natural mortality	Mortality, regardless of size and age, increases with temperature. Increased natural mortality leads to evolutionary response maximizing earlier reproduction and decrease in L_{∞}	Active species have higher survival at elevated temperatures compared to sessile species, resulting in potential increases in predation at higher temperatures (Peck et al. 2009); predation rates on isopods are greater at warmer temperatures, likely causing the observed pattern of smaller size and age at maturity in warmer environments (Manyak-Davis et al. 2013)

perature-size rule in marine invertebrates indicate that one degree of warming results in a 0.5–4% decrease in body size (Daufresne *et al.* 2009; Irie and Fischer 2009). Similar patterns have been observed in marine fishes with, for example, L_{∞} declining by an average of 16% across eight North Sea fish stocks with around 2 °C of warming (Baudron *et al.* 2014). Different physiological and evolutionary mechanisms could produce this theoretically predicted and empirically observed pattern, but more importantly they have similar life-history consequences of earlier maturation and a decrease in L_{∞} (Table 2).

The physiologically related pathways in Table 2 are broadly grouped into the theory of oxygen- and capacity-limited tolerance, which states that growth and developmental rates are determined by the aerobic performance or oxygen supply to tissue and respiration rates that are strongly affected by temperature (Portner and Knust 2007). Growth rate is therefore expected to increase with temperature from a lower critical value to an optimum determined by aerobic scope, after which temperatures become increasingly too warm and aerobic performance declines (Portner and Knust 2007; Neuheimer *et al.* 2011). The aerobic scope curves are likely to be different for different life stages, and evidence is accumulating that juveniles of ectotherms have higher temperature optima than adults (Ohlberger 2013). While recent work suggests that the optimal temperature for growth is likely to be less than that for aerobic scope due to temperature-dependent costs of locomotion and digestion (Holt and Jørgensen 2015), performance still displays a dome-shaped relationship to temperature and the different effect on adults and juveniles still holds. Finally, growth and development are governed by different processes and scale differently to temperature, where developmental rates appear to be more sensitive to temperature than growth (Forster *et al.* 2011), and the size-fecundity relationship changes with temperature (Arendt 2011). In combination, these physiological responses lead to the general global warming-induced trend towards maturation at smaller size and age, and decreased lifetime reproductive output (Table 2), although specific conditions might alter the general trend. Modelling indicates that half of the predicted declines in marine fish body size can be attributed to changes in environmentally dependent physiology (Cheung *et al.* 2013).

Discussion on climate change effects would be incomplete without mentioning the evolutionary response to the strong selective force that rapid global warming represents (e.g. Hill *et al.* 2011; Pespeni *et al.* 2013). For example, Rummer *et al.* (2014) found that all six studied coral reef fish species had significantly reduced performance at temperatures 3 °C above ambient, leading the authors to conclude that many tropical reef species have little capacity for plastic responses to rising water temperatures. At higher temperatures, smaller individuals often perform better than larger ones (Portner and Farrell 2008), which results in selection for smaller body size. To some extent, adults might be able to avoid temperature increases by moving into deeper water layers (e.g. Dulvy *et al.* 2008). However, in many cases, these movements are limited by topography, suitable habitat and prey, and indeed globally most changes in species distributions are seen as poleward shifts (Poloczanska *et al.* 2013; Cheung *et al.* 2014). A strong correlation between temperature and lifespan of ectotherms, both at inter- and intra-specific level, suggests that a 3 °C increase in global temperatures is expected to shorten the lifespan by 8–42% (Munch and Salinas 2009). Shorter lifespan will decrease lifetime reproductive output, and that will lead to selection towards earlier reproduction and higher investment earlier in life, and consequently to smaller adult body sizes. Despite these predictions, empirical evidence for genetic adaptation to climate change is still very limited (Teplitsky and Millien 2014), which, as with fisheries-induced evolution, can mostly be attributed to the fact that convincingly demonstrating evolutionary change in wild populations is extremely difficult (Crozier and Hutchings 2014).

Harvesting: evolutionary response

Most fishing gear is selective with respect to size, age or behaviour of individuals (e.g. Kuparinen *et al.* 2009; Garcia *et al.* 2012). Over time, fishing will disproportionately increase mortality of selected phenotypes, which can lead to fisheries-induced evolution. For many stocks, fishing mortality of individuals recruited to fisheries can be considerably higher than natural mortality, which means that fishing will act as a stronger selective force than natural processes for that life stage (Darinmont *et al.* 2009). In some cases, these fishery-

selection differentials have been calculated from empirical data. For example, the fisheries-imposed selection differential on growth rate of two white-fish species in Swiss lakes was -7% to -9% per generation (Nusslé *et al.* 2011), selection for size-at-age of Alaska sockeye salmon was around -5 to -10 mm per year (Kendall *et al.* 2014), and selection for earlier migration dates of Columbia River sockeye salmon was around -1 day/year between 1950 and 2010 (Crozier *et al.* 2011). In each case, observed direction of change in the life-history trait matched expectations from the selection differentials, providing support for fisheries-induced evolutionary change.

Evidence of evolutionary change in life-history traits as a result of harvesting has been well demonstrated in experimental populations (Conover *et al.* 2003; Van Wijk *et al.* 2013; Uusi-Heikkilä *et al.* 2015), and subsequently in wild populations, where changes in frequencies of genes related to life-history traits matched expectations from life-history theory and were best explained by fishing (Jakobsson *et al.* 2012; Therkildsen *et al.* 2013). Nevertheless, evidence correlating life-history changes to fishing intensity still mostly comes from time series analyses of wild stocks. These consistently show decreasing size and age at maturity, smaller adult length-at-age, and to some extent also increasing reproductive investment (Sharpe and Hendry 2009; Devine *et al.* 2012) (Table 1). Rates of these trends vary between 0.1 to 4% per year and depend on fishing intensity, with an average rate of 1% per year for instantaneous long-term fishing mortality (F) of around 0.5 per year (Audzijonyte *et al.* 2013a). Age and size at maturation appear to be among the fastest changing traits, whereas increases in reproductive investment are considerably slower. Empirical phenotypic rates of change in life-history parameters in harvested stocks are on average four times faster than evolutionary rates inferred by simulations (Audzijonyte *et al.* 2013a), suggesting that around a quarter of the observed phenotypic change could be due to evolution; this estimate is consistent with the known heritability of life-history traits (0.2–0.4, Carlson and Seamons 2008).

Summary: climate change and fishing are likely to lead to faster life-histories

The theoretical predictions presented above, as well as empirical data, suggest that current

human impacts on marine ectotherms will often lead to synergistic effects on their life-history trends (Table 1, Fig. 1). First, growth rates in early life stages (including k in the VB curve) will tend to increase due to physiological responses to warming. This increase will be amplified in areas where primary productivity increases. The trend towards faster juvenile growth might be counteracted by the fisheries-induced evolution (FIE) towards slower growth, although empirical evidence on how FIE will affect juvenile growth is inconclusive. Second, in many stocks we expect to see decreased maturation age. This is indeed one of the best documented life-history trends (Table 1). Decrease in maturation age will be driven both by physiologically faster juvenile growth due to warming and by evolutionary response to elevated adult mortality caused by higher temperatures (Table 2) and fishing (irrespective of how FIE affects juvenile growth). Third, earlier maturation and costs of reproduction, increased reproductive investment, and susceptibility of large fish to decreased oxygen supply in warming waters can be expected to result in smaller adult body size, including smaller L_{∞} . Of these three predictions, the trends in the juvenile growth are most uncertain, but they will not have substantial effect on earlier maturation and decreased adult body size, as these are driven by several other mechanisms as well.

The majority of empirical examples reported in the literature confirm this expectation, regardless of the ultimate attribution of the causal factors (Table 1). Exceptions to this trend towards faster life-histories can occur in situations where climate change leads to temporary decrease in temperatures (e.g. some deep sea populations, Thresher *et al.* 2007) or where decreased productivity due to climate change will lead to food limitation in juveniles and hence outweigh the expected increase in early growth rates due to temperature and/or harvesting (e.g. some salmon streams, Crozier *et al.* 2011). Decadal-scale climatic oscillations can also override any warming trend on shorter time scales (e.g. Attrill and Power 2002). Finally, species interactions will alter these general trends through changes in natural mortality and resource availability (Ohlberger 2013). Different species will respond to fishing and climate differently, and the expected reductions in size will vary within the same geographic region. Subsequent shifts in species size composition, abundance and

distributions will modify predator-prey interactions, further affecting realized life-histories. We cannot make precise theoretical predictions for these second-order responses, but they should be considered and explored (Audzijonyte *et al.* 2013b).

Implications for population persistence: life-history changes will lead to increased stochasticity

The directional trend towards faster life-histories discussed above will result in changes to natural mortality and population growth rates. However, before we consider management implications, it is important to mention that, in addition to directional trends, climate change and harvesting are also likely to lead to reduced diversity of life-history strategies through both short-term demographic and long-term evolutionary mechanisms (Table 3).

A number of recent studies have demonstrated that the combination of age truncation through fishing and increased environmental variation through climate change will amplify fluctuations in fish stock abundance (Hsieh *et al.* 2008; Shelton and Mangel 2011; Rouyer *et al.* 2012). There is an emerging consensus that the presence of multiple age classes increases the diversity of egg sizes, and the spatial and temporal distribution of spawning events, and hence serves as a bet-hedging strategy to maximize resilience (Secor 2007; Hixon *et al.* 2014; Shelton *et al.* 2015). The trend towards faster life-histories discussed here now means that in addition to the demographic truncation effect we should also consider the consequences of the physiological and/or evolutionary trend towards earlier maturation and smaller adult size, an area that remains largely unexplored. It is possible that earlier maturation may somewhat counteract the demographic truncation effect, by allowing individuals to reproduce earlier. However, the effects of life-history changes on population stability in the presence of fishing and climate change may have many unexpected feedback mechanisms through changes in behaviour, age-specific mortality and fecundity (Jørgensen and Fiksen 2010; Audzijonyte *et al.* 2013b).

Directional selection from increased temperatures and size-selective fishing also means that we expect to see the narrowing of maturation and temperature reaction norms, and overall decrease

in phenotypic and genetic diversity (Table 3). These outcomes potentially have large implications for population persistence. Life-history diversity provides an important 'portfolio effect' (Schindler *et al.* 2010; Anderson *et al.* 2015), buffering stocks against environmental fluctuations. A population that is rich in genetic variation for life-history traits will be better able to mount an evolutionary response to changing conditions (Reed *et al.* 2011). The same concept applies to population complexes, such as in the salmon populations spawning in different rivers. The diverse life-history traits expressed by hundreds of sockeye salmon populations in Bristol Bay, Alaska, have possibly reduced the estimated fishery closure events by a factor of 10, compared to what would have occurred if populations had been homogeneous (Schindler *et al.* 2010). The short-term buffering due to the 'portfolio effect' can occur even in the absence of genetically based population differences; all that is required is different plastic responses to environmental and habitat heterogeneity. However, longer term benefits require inter-population genetic heterogeneity. The existence of a diverse portfolio of locally adapted populations greatly increases the probability that at least some will contain genetic resources that will allow them to persist under radically different future conditions and in this way reduce the biomass fluctuations. Notably, such locally adapted populations can be just as important in widespread marine species (Nielsen *et al.* 2012).

Management implications of changes in life-history characteristics and diversity

Effects of life-history changes on fish stock dynamics

Population parameters that will change with faster life-histories include, among others, natural mortality, steepness of the stock-recruitment relationship, growth model parameters, age at 50% maturity and maximum size. Changes in these parameters will have implications for fisheries stock assessment. Intuitive prediction and broad inter-species comparisons (Jennings *et al.* 1998; Hutchings *et al.* 2012) would suggest that faster juvenile growth, earlier maturation and lower asymptotic size lead to an increased per-capita population growth rate (r) and decreased carrying capacity (K) (Heino *et al.* 2013). In terms of fish-

Table 3 Mechanisms explaining how fishing and climate change can be expected to decrease life-history diversity in marine ectotherms.

Mechanism and potential consequences	How it works	Examples
Climate change: depletion of phenotypic/genetic variation due to directional selection on temperature reaction norms reduces the ability of populations and species to respond to additional change	Rapid and prolonged warming will result in strong selection against individuals with lower thermal tolerances or limited phenotypic plasticity	Decreased phenotypic variability in individual growth thermal reaction norms across 21 cohorts associated with warming waters in tiger flathead (Morrongiello and Thresher 2015)
Fishing: Depletion of phenotypic/genetic variation due to long-term directional selection of size-selective fisheries reduces the ability of populations and species to respond to additional change	Long-term size-selective fishing will produce strong selection against large-bodied fish	Decreased phenotypic variability in size-at-age of Atlantic cod (Olsen <i>et al.</i> 2009)
Fishing: Reduced average age of the spawning females increases variability in spawning events	Most fishing selects oldest individuals, leading to demographic population truncation. Young females are more likely to skip spawning if their energy reserves drop	Average individual age of fished populations goes down, increasing the likelihood of skipped spawning and reducing spawning season length (Jørgensen <i>et al.</i> 2006; Secor 2007; Hixon <i>et al.</i> 2014)
Fishing: Reduced average size and age of a spawning female leads to reduction in egg size and diversity	Fishing selectively removes larger and older females. Larger fish have more fat content per body weight, higher gonadal mass to somatic mass, and can divert relatively more energy into reproduction. Older individuals often produce larger eggs with higher energy reserves compared to the young females. Larger eggs from older females may perform better under poorer environmental conditions	Lower reproductive rates in 25 marine fish due to age truncation (Venturelli <i>et al.</i> 2009). Importance of large fish for population resilience (Hixon <i>et al.</i> 2014)
Fishing: Reduced diversity of spawning behaviour due to truncated age distribution in harvested stocks decreasing buffering capacity against variable environmental conditions and predation mortality in larval stages	Age distribution of fished stocks is usually truncated towards younger ages. Females of different ages often spawn at different places and times	European plaice, Atlantic herring, cod and others (reviewed in Secor 2007)

eries outcomes, this implies that biomass at maximum sustainable yield (B_{MSY}) may decrease ($B_{MSY} = K/2$), fishing mortality (F_{MSY}) needed to achieve the MSY should increase ($F_{MSY} = r/2$), while the actual sustainable yield may not change much, since it is the product of both r and K ($MSY = rK/4$).

Heino *et al.* (2013) described how faster life-histories caused by fisheries-induced evolution (FIE) may affect r , K and fisheries reference points. They argued that if FIE increases a stock's reproductive potential through earlier maturation and shorter generation time, it will lead to increased steepness of the stock-recruitment relationship, meaning that higher recruitment occurs at lower biomass. Yet, if FIE reduces pre-recruit survival, through e.g. lower egg quality from smaller females, then the steepness of the stock-recruitment relationship will decrease. Similarly, FIE might change the ratio of spawning stock biomass (SSB) to total biomass. If fish mature earlier, then overestimation of maturation age will underestimate the SSB. However, if FIE reduces the weight of mature fish, then SSB might actually be overestimated if an old age-weight relationship is used (Fig. 2). Earlier maturation means that a cohort's biomass will peak earlier. This would lead to higher fishing mortality on older individuals in cases where selectivity remained unchanged (see the Baltic Sea cod case for a similar result due to density dependence effects; Svedang and Hornborg 2014).

These general predictions should apply regardless of whether faster life-histories are caused by fishing or global warming. However, it is essential that studies exploring the population level consequences of life-history changes account for the trade-offs between growth and reproduction (see section 2). While there is a general consensus that faster life-histories are likely to decrease carrying capacity (a decrease in adult body size of 5–20% led to a 5–30% decrease in K , see Enberg *et al.* 2009, 2010; Audzijonyte *et al.* 2013b; Kuparinen *et al.* 2014), the modelled effect of earlier maturation on r strongly depends on the assumptions about the survival costs of reproduction. As an example, a model of Atlantic cod (*Gadus morhua*, Gadidae) used by Enberg *et al.* (2010) predicted that FIE will increase the ratio of SSB to total biomass, simultaneously increasing the steepness of the stock-recruitment relationship. The authors argued that populations adapted to fishing would produce more recruits for a given level of total

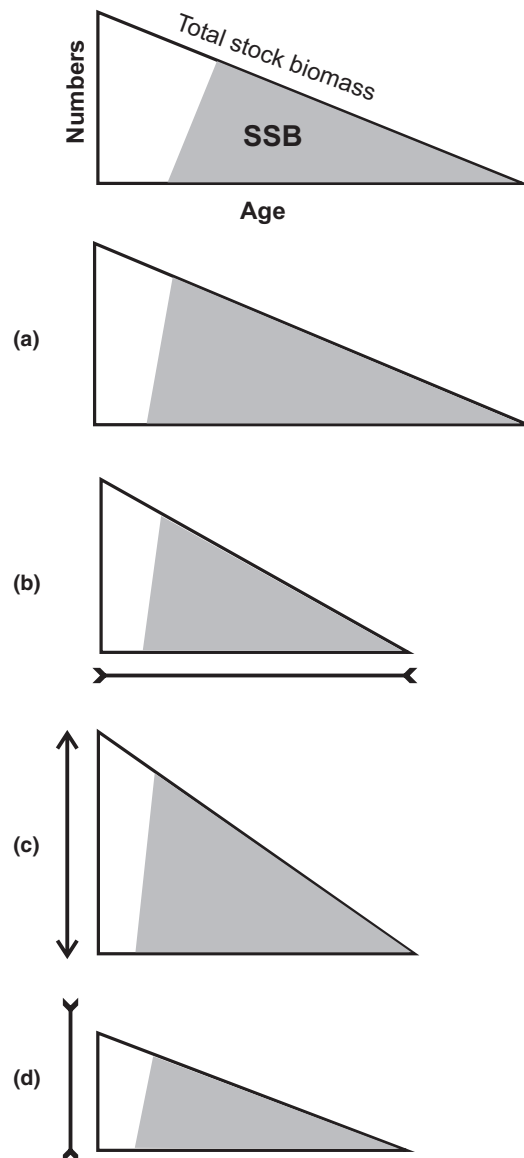


Figure 2 Implications of faster life-histories for stock biomass and productivity: four possible scenarios. (a) Earlier maturation increases spawning stock biomass and productivity, compensating for smaller adult size; total biomass and carrying capacity remain unchanged. (b) Earlier maturation leads to shorter lifespan as survival costs of reproduction reduce longevity. In combination with reduced adult size, this leads to decreased carrying capacity. (c) Earlier maturation increases the spawning stock biomass, egg production and recruitment, leading to increased productivity. (d) Decreased size of an average female leads to lower egg production and recruitment, and to lower productivity.

biomass, which is likely to increase r . In contrast, modelling studies that included some version of reproduction costs suggest that a combination of

earlier maturation (1 to 3 years earlier) and smaller adult body size (ca 20% decrease in L_{∞} and L_{mat}) is likely to decrease r by 20–50% (Hutchings 2005; Kuparinen *et al.* 2014; Audzijonyte and Kuparinen 2016). These simulations are also corroborated by empirical studies exploring r among closely related populations of iteroparous species, showing that natural mortality rather than maturation age is the major determinant of population growth rate (squirrels: Mcadam *et al.* 2007; gadoid fishes: Wright 2014). Hence, if the benefits of earlier reproduction are outweighed by increased natural mortality (Fig. 1b), the overall effect of faster life-histories on population productivity (r) can be negative.

There are two ways in which the simulation studies presented above may still be too conservative. First, some of them considered the effects of FIE alone, yet our argument is that life-history effects of climate change and fisheries can often be synergistic and amplify each other. Second, these studies generally assumed that egg quality is independent of female age or population context, and that egg production is linearly related to female weight. This assumption means that the total egg production is equivalent to the SSB. While it is a standard assumption in fisheries, often justified by the absence of time series of reproductive traits (Saborido-Rey and Trippel 2013), it ignores the importance of 'Big Old Fat Fecund Female Fish' to the stock's reproduction (Secor 2007; Hixon *et al.* 2014). If relative egg production and/or quality increases with female age or size, reducing the average age of the spawning stock will even further decrease the steepness of the stock-recruitment curves; the effect will be stronger for long-lived species (Venturelli *et al.* 2009). In a number of cases, allowing for time-variable total egg production that takes into account age structure and growth led to different inferences about stock biomasses and recommended fishing rates (Shelton *et al.* 2012; Spencer and Dorn 2013). These findings suggest that routine monitoring of reproductive parameters is an important consideration in a precautionary approach to fisheries management.

Impact of life-history trends in single species management

With respect to this review, the main question of interest to fisheries management is – what are the consequences of basing harvesting decisions on

assessments that ignore possible trends in life-history parameters? If stocks are monitored and assessed routinely, would the management be self-correcting even without taking into account possible changes in growth and maturation? The answers to these questions all depend on the rate of change in life-history parameters – a change of 0.5% per year will be less risky than a change of 5% per year. Empirical studies (Table 1) often report rates of phenotypic change in the range of 0.5–2% per year, with age-at-maturation among the fastest changing traits. Assuming a conservative estimate of ca 0.5% change per year, this would lead to ca 5% change over 10 years (see also van Walraven *et al.* 2010). For age-at-maturation, a more realistic value might be ca 1% per year (Sharpe and Hendry 2009; Audzijonyte *et al.* 2013a). Given that it is common for stock assessments to use 10-year-old maturation data (e.g. Stewart *et al.* 2011; ICES Advice 2014) and, when growth models are used, an average growth curve for the entire assessment period is assumed, it would be important to ascertain the likely errors in the stock assessment and management recommendations if the actual age-at-maturation is overestimated by 1 (or 2) years and length-at-age of adult individuals is overestimated by ca 5% (10%). To answer these questions, specific simulations are needed. Some harvest strategies or management plans (combinations of monitoring, assessment and decision rules) may be relatively robust to ignorance about life-history changes, while others may be quite sensitive. Results from a few studies that specifically looked at the consequences of mis-specifying life-history parameters in fisheries models are provided below.

A model with cohort-specific growth rates in an age-structured assessment of southeast Australia's blue grenadier (*Macruronus novaezelandiae*, Merlucciidae) showed that a 5–15% mis-specification of length-at-age led to ca 5–20% difference in inferred stock biomass (Whitten *et al.* 2013). A similar result was found in a study of Baltic Sea herring (*Clupea harengus*, Clupeidae), where growth was modelled as a time-variable parameter in a Bayesian framework, using information on zooplankton abundance, sea surface temperature and small prey fish biomass as priors (Mantyniemi *et al.* 2013). Wells *et al.* (2013) showed that overestimation of L_{∞} (expected in cases of faster life-histories) will overestimate fishing mortality rates because the absence of large individuals in stocks

with smaller adult length-at-age would bias fishery mortality estimates for older age groups upwards. Bias in selectivity estimates can occur if data are pooled from stocks that have different responses to temperature (e.g. increased and decreased growth as temperature increased up to and above the optimum) (Punt *et al.* 2014). A 20% underestimate in VB k will lead to *ca* 20% reduction in the estimation of yield-per-recruit biomass at fishing mortality $F_{0.1}$ (year⁻¹) (the F value where the curve of production against fishing mortality has a gradient of 10%) (Pardo *et al.* 2013). Concerns about changes in growth may be less important for assessment models (such as some cohort analyses) that use annual empirical information about weight-at-age rather than fitted and assumed growth curves (but data quality and quantity are critical, see Kuriyama *et al.* 2015). However, even for stocks managed using such models and data, projections about future stock dynamics may become biased if possible trends in growth and maturation are not considered. Also, the drawback of such empirical fitting is that no insight into the processes governing growth is gained (Lorenzen 2016). Finally, one of the major ways in which faster life-histories will affect stock productivity is through an expected increase in natural mortality (Fig. 1b). Broad empirical and theoretical comparisons suggest that a change in k from 0.1 to 0.2 would increase M from 0.1 to 0.3 (year⁻¹), and a change in maturation age from 5 to 4 years would increase M from 0.2 to 0.3 (e.g. Carruthers *et al.* 2012) (Fig. 1b). Jørgensen and Fiksen (2010) suggest that, due to harvest-induced evolution in life-histories and behaviour, natural mortality rates increase proportionally to harvest, such as 'fishing two fish kills three'. When studied in an ecosystem modelling framework, a decrease in body length of *ca* 4% led to 10–50% increase in predation mortality in four out of five studied species (Audzijonyte *et al.* 2013b).

Given the evidence for dynamic life-histories in marine species, is it then reasonable to use simplifying assumptions about life-history, such as fixed age- or length-at-maturation, fixed growth curves, fixed *a priori* assumed size independent natural mortality, and fixed steepness of the stock-recruitment relationship, in stock assessment models (see also Lorenzen 2016). For example, although age-at-maturation is shown to be one of the most rapidly changing life-history traits (Table 1, Sharpe and Hendry 2009; Devine *et al.* 2012;

Audzijonyte *et al.* 2013a), this parameter is often fixed in stock assessments. This is true even in cases where trends in maturation have been demonstrated (e.g. for North Sea plaice (*Pleuronectes platessa*, Pleuronectidae), see van Walraven *et al.* 2010 and ICES Advice 2014). Mangel *et al.* (2013) state that the standard practice of assuming fixed values for steepness of the stock-recruitment relationship and natural mortality will *a priori* determine fisheries reference points in a standard stock assessment that uses two-parameter (Beverton-Holt or Ricker) stock-recruitment relationships. The resulting estimates from a stock assessment 'can provide a false sense of precision and information because an important source of uncertainty is hidden'. We believe that acknowledging and explicitly including important sources of uncertainty in fisheries models will reflect the state of affairs about our knowledge and encourage better monitoring (Kuparinen *et al.* 2012; Evans *et al.* 2013).

Life-history trends in multi-species models

The number of parameters and interactions in multispecies models means that the life-history traits of individual species (and hence their temporal change) may not dominate their dynamics in the way they do in population models used in fisheries. Yet, individual size remains one of the key characteristics defining functional groups in most complex ecosystem models (e.g. OSMOSE, Shin and Cury 2004; Atlantis, Fulton 2011) and forms the basis of size- and trait-based models (Andersen and Beyer 2006; Blanchard *et al.* 2009). As tractable complexity is only possible in a few dimensions at a time (e.g. either in food web structure, spatial resolution, or life-history detail), most models do not consider spatial or temporal variation in size or any other life-history parameters beyond what is produced by physiologically mediated responses, or where spatial forage fields are non-uniform and result in changes to realized growth rates. Nevertheless, there is a growing realization that non-stationary and spatially varying life-histories may be essential to simulate effects of directional pressures such as climate change (e.g. Brännström *et al.* 2012).

Life-history change is recognized mechanistically in some ecological models (single and multispecies) through the use of multiple growth curves per species (e.g. Little *et al.* 2007). Such models allow for

changes in aggregate average life-history characteristics if there is differential catchability or gear selectivity. Models that explicitly consider evolution are typically constrained to small species complexes (DeAngelis and Mooij 2005; Mithé *et al.* 2009) or explore evolution of food webs (e.g. Rossberg *et al.* 2005) rather than life-history traits. However, where ecosystem models have been modified to allow for trends in size-at-age, they

showed that even small changes in body sizes can get amplified or dampened through species interactions (Audzijonyte *et al.* 2013b) and have large effects on the trophic dynamics, diets and recovery of harvested species (Audzijonyte *et al.* 2014).

Brännström *et al.* (2012) state that further development of models which consider evolution in the context of food webs is critically important for addressing (i) the biological adaptive capacity

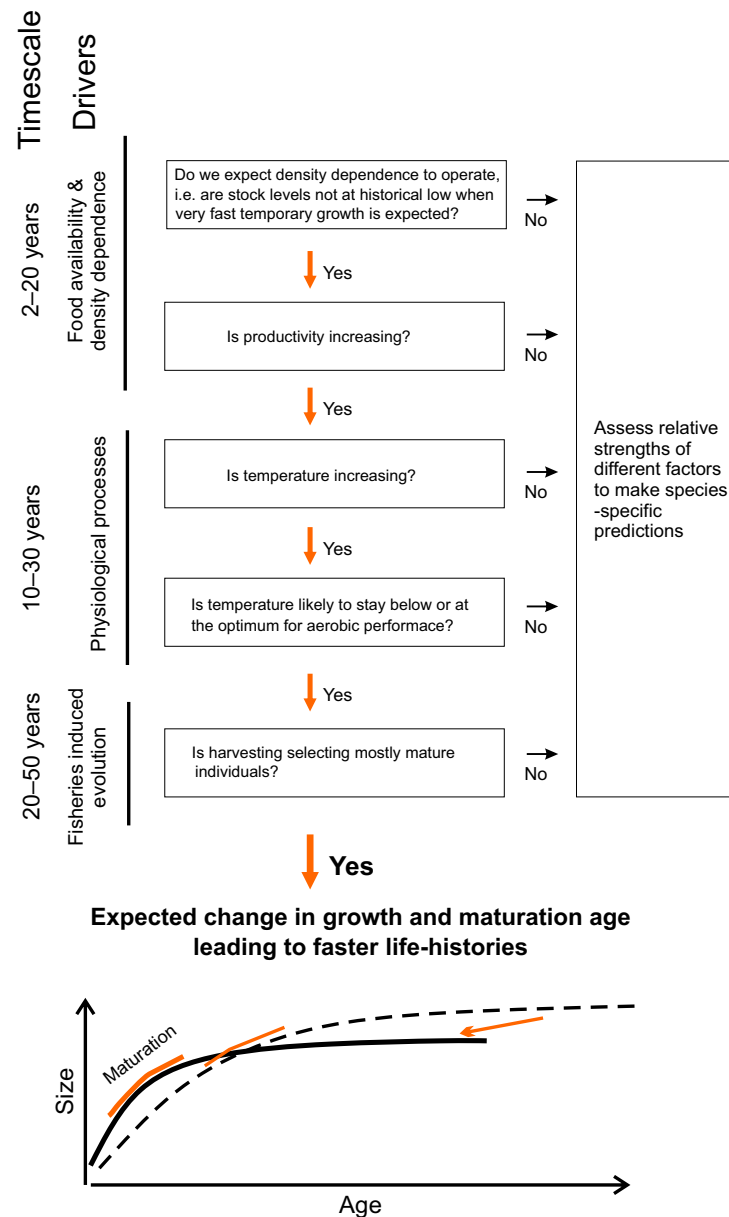


Figure 3 Suggested framework for precautionary and adaptive management that evaluates different factors that are likely to affect life-history traits and for which monitoring could be established. A trend towards faster life-histories (from dashed to thick solid line) is shown with a red arrow.

of ecosystems and (ii) the vulnerability of these systems to stock and food web collapse as a result of secondary extinctions due to trophic cascades. Allowance for plasticity in growth, consumption and reproductive rates is similarly important. Moreover, multispecies and ecosystem models are beginning to provide strategic ecosystem-based management advice, assessing ecosystem and food web implications of management decisions (e.g. Fulton *et al.* 2014). Consequently, just as overlooking the potential for changing life-history characteristics can undermine management relevant information from single species models, so too the omission of shifting life-history parameters in ecosystem models has the potential to lead to erroneous conclusions about the implications of stressors and management for the long-term status of the system and its sub-components (Collie and Gislason 2001; Audzijonyte *et al.* 2013b, 2014).

How to address changes in life-histories of marine organisms – a plan of action

Given the evidence for the changes in life-history of exploited marine species, and the compounding effects of climate change, scientists and marine managers have a range of options in terms of life-history research and subsequent application to management issues (Fig. 3). Scientists involved in stock assessments should acknowledge that trends in life-history traits are likely to be happening and consider what implications this has for the marine populations and ecosystem management arenas in which they work. The framework proposed in Fig. 3 would consider the interaction and relative strength of density dependence, physiological, and evolutionary processes. If there is evidence for strong year classes due to relaxed density dependence (top box in Fig. 3) or improved food supply due to increased productivity (second top box in Fig. 3), it is likely that the trend towards decreased adult body size might be masked. It is important to highlight that the underlying physiological and evolutionary processes would still be operational during the periods of faster growth due to improved food supply.

The realization of the importance of life-history trends is evident in several resource management working groups (Piet *et al.* 2010), but wider investigation is needed. To support management, improved monitoring strategies are required to provide up-to-date life-history characteristics (e.g.

Hollowed *et al.* 2013), such as maturation data, growth rate, and natural mortality. We acknowledge the difficulties of collecting such data, especially on suitable spatial scales, yet the importance has never been greater. Size-at-age and size-at-maturity could be one of the most important measures determining organism responses to thermal conditions (Ohlberger 2013), and is also one of the main parameters showing rapid response to fisheries-induced population dynamics and productivity (Brander 2010).

Since life-history information for many stocks is missing, we suggest that as the first step, assessment scientists could explore the sensitivity of model outcomes to mis-specification of the life-history parameters using simulations (Szuwalski and Punt 2013; Deroba *et al.* 2014). The next step could be to make better use of existing information, such as in otolith collections, to infer life-histories and possible trends. Otolith data have been used to infer individual-level variation of growth (Morrongiello and Thresher 2015), larval growth rates and the age at which juveniles settle into adult habitats (Fowler and Jennings 2003; Hale and Swearer 2008), differential selection on size-at-age imposed by fisheries (Swain *et al.* 2007; Kendall *et al.* 2014), and the age at sexual maturity, either directly through observing a transition zone (Francis and Horn 1997) or through use of energy-based modelling that recognizes the main trade-offs between growth, maintenance, and reproduction (Brunel *et al.* 2013). Otolith-based bio-chronologies can provide long-term datasets to aid the investigation of the impacts of environmental variability and fishing pressure on fish stocks (Morrongiello *et al.* 2012). The repeated measures nature of otolith-derived growth data also means that more sophisticated statistical techniques can be employed to decompose population-level patterns into their within and among individual components. This is very important from a climate change perspective as the likelihood of species being able to respond to warming depends on the levels of phenotypic plasticity (Nussey *et al.* 2007).

Finally, molecular analyses of life-history traits also provide an increasingly valuable source of information. Genes and markers responsible for life-history traits have now been identified in some fishes (Therkildsen *et al.* 2013; Van Wijk *et al.* 2013; Uusi-Heikkilä *et al.* 2015). If these markers are consistently correlated to life-history traits in

different species, they can be used for targeted genetic monitoring. Even when monitoring data are collected for other purposes, it should be imperative to preserve material in ways that will be suitable for retrospective genomic analyses, particularly given the rapid decrease in analysis costs (Hayden 2014). Currently, the main costs typically come from the subsequent bioinformatics analyses, but here also better tools are being developed every year. Nevertheless, careful analytical design will be needed to provide information relevant to the time and spatial scales useful for assessments.

With regard to management decisions underpinning sustainable use of marine resources exposed to life-history changes, a combination of precautionary and learning through adaptive management is recommended to maximize species resilience to climate change. For example, based on evidence that age truncation will lead to increased recruitment variability (Secor 2007), precautionary management might seek to increase resilience by increasing the number of age classes contributing to reproductive output. This might be achieved with lower fishing mortality rates, or by using spatial protection for low mobility species (Plagányi *et al.* 2013), or with upper size limits or dynamic spatial management for more mobile species (Hobday *et al.* 2014). Adaptive management would mean that management strategies would be flexible and could respond rapidly as new information is received (e.g. on the status of the stock, realized mortality rates, or in the context of this review assessments could be continuously updated with new life-history information). Notably, when a positive effect of maternal age is taken into account, reducing harvest rates on older, larger individuals may actually increase catch compared to the *status quo*, as productivity increases and more young fish offset the foregone harvest on older fish (Shelton *et al.* 2015). Spatial management may offer protection to some proportion of a population in no-take reserves, which may also help to maintain genetic diversity and demographic structure of the population, increasing adaptive potential and resilience to fluctuations. Clearly, the effectiveness of any measures will vary across stocks, and predictions are difficult as processes determining stock resilience are not well understood. Overall, because it is unclear what exploitation rate is sustainable and maintains the adaptive potential and demographic resilience of

marine populations to rapid environmental change, the best precautionary management option will be the one that protects life-history diversity and maintains larger stock biomass (Froese 2004). Without further study, we cannot recommend a single biomass reference point, but it is likely to be higher than the biomass leading to maximum sustainable yield. Further work would be necessary to explore whether more conservative target reference points, such as the biomass leading to maximum economic yield [or its proxy of 48% of the unfished level ($B_{0.48}$)], which has been adopted by fisheries management in places such as Australia (Rayns 2007), is sufficient.

As human influence on marine ecosystems is increasing, a return to baseline conditions is unlikely in most habitats and management based on the past will fail to account for new patterns (Merrie *et al.* 2014). Hence, adaptive management informed by monitoring is a suitable pathway to follow. Because resources will always be limited, calls for monitoring should be clear about the specific variables that can provide the information to assess the effectiveness of the management approach – we suggest that up-to-date information on life-history characteristics, such as age-at-maturity and growth rate is essential for implementing adaptive management strategies.

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