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

10 **Human-induced life-history changes in marine ectotherms: trends and management**
11 **implications**

12

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Running title: marine ectotherm life-history changes

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 multi-species 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, plasticity, physiology

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75

76 **Introduction**

77

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

86

87 Life-histories determine species energy allocation to growth and reproduction, and describe traits such as
88 age and size of maturation, reproductive effort and maximum adult size and age. Some of the most rapid
89 changes in life-history traits have been observed in commercially harvested fishes (Jørgensen *et al.* 2007;
90 Devine *et al.* 2012), where the rate of change can be as high as 1-4% per year for size and age at maturity
91 (Audzijonyte *et al.* 2013a) and 2.5% per year for growth (Morrongiello and Thresher 2015). The relative
92 importance of genetic and plastic components in this change and the drivers have been intensely debated
93 (e.g. Olsen *et al.* 2004; Kraak 2007; Therkildsen *et al.* 2013; Rogers *et al.* 2011; Baudron *et al.* 2014), yet
94 regardless of the underlying mechanisms, the observed trends will have important implications for marine
95 ecosystem management, including management of individual species. Given that life-history parameters
96 for harvested stocks will be affected by both fishing and climate change simultaneously, understanding
97 the combined effects is an important but neglected priority (Planque *et al.* 2010).

98

99 This review aims to highlight how global environmental change and fishing are affecting life-histories of
100 marine ectotherms. Naturally, responses to climate change or fishing involve many other features, such as
101 changes in distributions, phenology or behaviour, but these have been discussed elsewhere (e.g. Brander
102 2013; Poloczanska *et al.* 2013). In contrast, while there have been important studies on how either

103 harvesting or climate change are affecting life-histories separately (e.g. Heino *et al.* 2013; 2015; Holt and
104 Jørgensen 2015), we believe that insufficient attention has been paid to the fact that both forces are likely
105 to lead to convergent trends and possibly amplify each other. Hence the main message of this review is
106 that the diverse mechanisms caused by harvesting and climate change will, in many species, lead to faster
107 ectotherm life-histories, with earlier maturation and smaller adult body sizes. To demonstrate this point
108 we first summarize the dominant trade-offs determining life-history strategy and explore how these trade-
109 offs might be useful to predict likely changes in life-history traits. Second, we explore how the different
110 contemporary environmental drivers, in particular climate change and fishing, are likely to produce
111 similar life-history trends. Third, we describe how these trends might increase fluctuations in population
112 abundance and hence reduce resilience to environmental change and exploitation. Finally, we discuss how
113 contemporary life-history changes might affect the management advice and outcomes of single and
114 multiple species models, and suggest areas for further scientific investigation.

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

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

137 All organisms have limited amounts of energy that must be allocated to different body functions;
138 increased energy allocation to reproduction takes energy away from somatic growth, and vice versa.

139 Recognition of these trade-offs has led to the development of life-history theory (e.g. Roff 1992), which
140 can be used, among other things, to infer age at maturation and energy-based life-history traits from
141 individual growth trajectories (Brunel *et al.* 2013). Assuming that a fixed amount of total energy is
142 available, life-history trade-offs provide some general rules on how changes in one trait will lead to
143 changes in other correlated traits (Fig 1). For example, earlier maturity trades off with later reproductive
144 output by reducing somatic growth and increasing natural mortality through survival costs of reproduction
145 (Bell 1980). These reproductive costs include increased mortality due to reproductive changes in
146 behaviour (competition for mates, nest guarding, spawning migrations), reduced feeding, energetic
147 investment in gonads instead of somatic growth, and less energy allocation to immune functions
148 (Jørgensen and Fiksen 2010; Jørgensen and Holt 2013). The trade-off between growth and maturation in
149 animals with indeterminate growth is typically seen as a negative correlation between intrinsic growth
150 rate against size at maturity and adult body size (Charnov 1993). Accounting for these trade-offs has a
151 large impact on the outcomes of models aiming to predict population level consequences of life-history
152 changes (see below).

153
154 The trade-offs in the energy allocation for different functions (growth, reproduction, maintenance) are
155 also at the heart of correlations among species and population life-history parameters observed in broadly
156 defined taxonomic categories. These correlations are known as life-history invariants, and provide some
157 general rules about the expected relationships between asymptotic length (L_{∞}), age and size-at-
158 maturation, growth rate, natural mortality and length-fecundity relationship (e.g. Beverton 1992; Charnov
159 *et al.* 2013). While these relationships encompass large variation, they nevertheless provide useful
160 insights into population parameters in data-poor stocks and are used to inform ecological risk assessments
161 (Patrick *et al.* 2010; Hobday *et al.* 2011a). They are also implemented in global databases, such as
162 FishBase. A promising new approach to reduce variation and improve predictive value of life-history
163 invariants is to derive these life-history ratios separately for species with different life-history strategies
164 (Prince *et al.* 2015).

165
166 In this review we focus on life-history and growth parameters and for illustration purposes use the von
167 Bertalanffy (VB) growth model (von Bertalanffy 1957, see also Pardo *et al.* 2013) (Fig. 1). The two VB
168 parameters of interest here are asymptotic length (L_{∞}) and the rate at which growth approaches the
169 asymptote (k), which is often referred to as a growth coefficient. We should note that, as with any model,
170 the VB model has its shortcomings. First, k is difficult to interpret ecologically, and cannot easily be
171 compared across species (see Pauly 2010, who also offered a conversion of k to an ecologically
172 meaningful growth performance index that is comparable across species). Second, in heavily fished
173 stocks where few individuals survive to the older and larger age classes, the estimation of L_{∞} can be
174 problematic (Haddon 2011). Yet, despite these limitations, the model is commonly used in fisheries, due

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

181 182 **Drivers and empirical evidence on life-history changes in marine ectotherms**

183 184 ***Harvesting: short-term density-dependent growth changes***

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

196
197 There seems to be no consensus as to how density-dependent processes might affect life-history
198 parameters (Prince *et al.* 2015). Lorenzen and Enberg (2002) found indications of density dependence on
199 adult growth in many marine stocks and estimated that for species in a 20-45 cm size range, a 100%
200 increase in stock biomass will lead to a 10% decrease in L_{∞} . In the evolutionary and physiological
201 interpretation of the VB growth model presented by Charnov *et al.* (2013), L_{∞} or maximum body size, is
202 determined by both food availability and/or changes in maintenance and reproduction, whereas k , or early
203 growth rate, is affected only by the allocation to maintenance and reproduction. In this formulation,
204 increased food availability is expected to increase L_{∞} , but should not change k . Empirical data provide
205 examples of both situations (Table 1). High abundance of certain age groups had negative effects on
206 juvenile growth rates in sockeye salmon (*Oncorhynchus nerka*, Salmonidae) (Crozier *et al.* 2010) and has
207 been linked to a decrease in L_{∞} from about 100cm to 40 cm in the Baltic Sea cod (*Gadus morhua*,
208 Gadidae) (Svedang and Hornborg 2014). Reduced population sizes and thus lower density were
209 correlated with increased k in southern Bluefin tuna (*Thunnus maccoyii*, Scombridae) (Polacheck *et al.*

210 2004), but decreased k and increased L_{∞} in southern king weakfish (*Macrodon atricauda*, Sciaenidae) in
211 Southern Brazil (Cardoso and Haimovici 2011).

212
213 One limitation of these studies is that they do not statistically test alternative hypotheses that could
214 explain the observed growth patterns, as in addition to density dependence they could include changes in
215 reproductive investment, maturation age and length, maintenance costs and many environmental factors.
216 This underscores the general difficulties in attributing empirically observed life-history changes to a
217 specific driver. We suggest that, for many stocks, in the absence of long-term population trends, density-
218 dependent processes will generally fluctuate over time in response to changes in harvesting levels and
219 recruitment and will not be as important as the long-term trend towards faster life-histories caused by
220 global warming or fisheries-induced evolution.

221 222 ***Global warming: response to productivity change***

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

229
230 Changes in ocean temperature, circulation and mixing all affect nutrient supply and primary productivity
231 (Poloczanska *et al.* 2008; Brown *et al.* 2009; Taucher and Oschlies 2011). A number of modelling studies
232 find that climate change will lead to reduced ectotherm body size through nutrient limitation due to
233 reduced mixing of water layers and smaller size of phytoplankton (e.g. Woodworth-Jefcoats *et al.* 2015).
234 Yet, despite the important implications that productivity shifts are expected to have on marine ecosystem
235 dynamics, our ability to model and forecast the magnitude or even direction of the productivity change is
236 still limited (Polovina and Woodworth 2012; Doney *et al.* 2012). Even greater spatial variability and
237 uncertainty exists in coastal areas. In a semi-global analysis, Barange *et al.* (2014) predicted an overall
238 minor increase in shelf productivity (<10%), with increased productivity at high latitudes and decreased
239 productivity at low and mid latitudes, but considerable regional variation due to local circulation patterns
240 and terrestrial inputs.

241
242 Changes in ocean productivity and hence food supply will operate on life-history traits in a broadly
243 similar manner to the density-dependent effects discussed above, except that their combined effect is
244 likely to be opposite – as productivity increases, density dependence is expected to decline, assuming the
245 stock abundance remains at a similar level and there are no large changes in inter-specific interactions.

246 Increased productivity is likely to amplify the temperature-induced trend towards faster growth and
247 earlier maturation, whereas decreased productivity will lead to slower growth rates. In many cases these
248 effects might be difficult to separate from the response to increased temperature alone, especially in cold
249 regions where higher temperatures often mean higher productivity. As with density dependence, rapid
250 response to e.g. increased productivity through faster growth rates could mask long-term trends due to
251 physiological or evolutionary factors (Fig. 1 in Crozier and Hutchings 2014; Thresher *et al.* 2014;
252 Kokkonen *et al.* 2015). While there is great uncertainty in forecasting productivity changes, its
253 monitoring is considerably easier and is routinely done (e.g. through chlorophyll *a* mapping via satellite
254 images). Hence, up-to-date information on productivity could be a part of routine management
255 (Pethybridge *et al.* 2015) and also incorporated into management decision processes (see Fig. 3).

257 ***Global warming: response to temperature change***

258 A decline in average individual body size has been suggested as a “third universal ecological response to
259 global warming” (Daufresne *et al.* 2009; Cheung *et al.* 2013). For ectotherms this ecological response is
260 often based on the temperature-size rule (Atkinson 1994) that describes the tendency for increased
261 juvenile growth (increase in k and hence faster approach towards asymptotic size) and developmental
262 rates combined with the decreased adult body size (L_{∞}) at higher temperatures. Studies that have
263 explicitly tested the temperature-size rule in marine invertebrates indicate that one degree of warming
264 results in a 0.5–4% decrease in body size (Daufresne *et al.* 2009; Irie and Fischer 2009). Similar patterns
265 have been observed in marine fishes with, for example, L_{∞} declining by an average of 16% across eight
266 North Sea fish stocks with around 2°C of warming (Baudron *et al.* 2014). Different physiological and
267 evolutionary mechanisms could produce this theoretically predicted and empirically observed pattern, but
268 more importantly they have similar life-history consequences of earlier maturation and a decrease in L_{∞}
269 (Table 2).

271 The physiologically-related pathways in Table 2 are broadly grouped into the theory of oxygen- and
272 capacity-limited tolerance, which states that growth and developmental rates are determined by the
273 aerobic performance or oxygen supply to tissue and respiration rates that are strongly affected by
274 temperature (Portner and Knust 2007). Growth rate is therefore expected to increase with temperature
275 from a lower critical value to an optimum determined by aerobic scope, after which temperatures become
276 increasingly too warm and aerobic performance declines (Portner and Knust 2007; Neuheimer *et al.*
277 2011). The aerobic scope curves are likely to be different for different life stages, and evidence is
278 accumulating that juveniles of ectotherms have higher temperature optima than adults (Ohlberger 2013).
279 Whilst recent work suggests that the optimal temperature for growth is likely to be less than that for
280 aerobic scope due to temperature-dependent costs of locomotion and digestion (Holt and Jørgensen
281 2015), performance still displays a dome-shaped relationship to temperature and the different effect on

282 adults and juveniles still holds. Finally, growth and development are governed by different processes and
283 scale differently to temperature, where developmental rates appear to be more sensitive to temperature
284 than growth (Forster *et al.* 2011), and the size-fecundity relationship changes with temperature (Arendt
285 2011). In combination, these physiological responses lead to the general global-warming-induced trend
286 towards maturation at smaller size and age, and decreased lifetime reproductive output (Table 2),
287 although specific conditions might alter the general trend. Modelling indicates that half of the predicted
288 declines in marine fish body size can be attributed to changes in environmentally-dependent physiology
289 (Cheung *et al.* 2013).

290
291 Discussion on climate change effects would be incomplete without mentioning the evolutionary response
292 to the strong selective force that rapid global warming represents (e.g. Hill *et al.* 2011; Pespeni *et al.*
293 2013). For example, Rummer *et al.* (2014) found that all six studied coral reef fish species had
294 significantly reduced performance at temperatures 3°C above ambient, leading the authors to conclude
295 that many tropical reef species have little capacity for plastic responses to rising water temperatures. At
296 higher temperatures smaller individuals often perform better than larger ones (Portner and Farrell 2008),
297 which results in selection for smaller body size. To some extent, adults might be able to avoid
298 temperature increases by moving into deeper water layers (e.g. Dulvy *et al.* 2008). However, in many
299 cases these movements are limited by topography, suitable habitat and prey, and indeed globally most
300 changes in species distributions are seen as poleward shifts (Poloczanska *et al.* 2013; Cheung *et al.* 2014).
301 A strong correlation between temperature and lifespan of ectotherms, both at inter- and intra-specific
302 level, suggests that a 3°C increase in global temperatures is expected to shorten the lifespan by 8-42%
303 (Munch and Salinas 2009). Shorter lifespan will decrease lifetime reproductive output, and that will lead
304 to selection towards earlier reproduction and higher investment earlier in life, and consequently to smaller
305 adult body sizes. Despite these predictions, empirical evidence for genetic adaptation to climate change is
306 still very limited (Teplitsky and Millien 2014), which, as with fisheries-induced evolution, can mostly be
307 attributed to the fact that convincingly demonstrating evolutionary change in wild populations is
308 extremely difficult (Crozier and Hutchings 2014).

309 310 ***Harvesting: evolutionary response***

311 Most fishing gear is selective with respect to size, age or behaviour of individuals (e.g. Kuparinen *et al.*
312 2009; Garcia *et al.* 2012). Over time, fishing will disproportionately increase mortality of selected
313 phenotypes, which can lead to fisheries-induced evolution. For many stocks, fishing mortality of
314 individuals recruited to fisheries can be considerably higher than natural mortality, which means that
315 fishing will act as a stronger selective force than natural processes for that life stage (Darimont *et al.*
316 2009). In some cases these fishery-selection differentials have been calculated from empirical data. For
317 example, the fisheries-imposed selection differential on growth rate of two whitefish species in Swiss

318 lakes was -7% to -9% per generation (Nussle *et al.* 2011), selection for size-at-age of Alaska sockeye
319 salmon was around -5 to -10 mm per year (Kendall *et al.* 2014), and selection for earlier migration dates
320 of Columbia River sockeye salmon was around -1 day/year between 1950 and 2010 (Crozier *et al.* 2011).
321 In each case, observed direction of change in the life-history trait matched expectations from the selection
322 differentials, providing support for fisheries-induced evolutionary change.

323
324 Evidence of evolutionary change in life-history traits as a result of harvesting has been well demonstrated
325 in experimental populations (Conover and Munch 2002; Van Wijk *et al.* 2013; Uusi-Heikkilä *et al.* 2015),
326 and subsequently in wild populations, where changes in frequencies of genes related to life-history traits
327 matched expectations from life-history theory and were best explained by fishing (Jakobsdóttir *et al.*
328 2012; Therkildsen *et al.* 2013). Nevertheless, evidence correlating life-history changes to fishing intensity
329 still mostly comes from time series analyses of wild stocks. These consistently show decreasing size and
330 age at maturity, smaller adult length-at-age, and to some extent also increasing reproductive investment
331 (Sharpe and Hendry 2009; Devine *et al.* 2012) (Table 1). Rates of these trends vary between 0.1 to 4%
332 per year and depend on fishing intensity, with an average rate of 1% per year for instantaneous long-term
333 fishing mortality (F) of around 0.5 per year (Audzijonyte *et al.* 2013a). Age and size at maturation appear
334 to be among the fastest changing traits, whereas increases in reproductive investment are considerably
335 slower. Empirical phenotypic rates of change in life-history parameters in harvested stocks are on average
336 four times faster than evolutionary rates inferred by simulations (Audzijonyte *et al.* 2013a), suggesting
337 that around a quarter of the observed phenotypic change could be due to evolution; this estimate is
338 consistent with the known heritability of life-history traits (0.2-0.4, Carlson and Seamons 2008).

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

341 The theoretical predictions presented above, as well as empirical data, suggest that current human impacts
342 on marine ectotherms will often lead to synergistic effects on their life-history trends (Table 1, Fig. 1).
343 First, growth rates in early life stages (including k in the VB curve) will tend to increase due to
344 physiological responses to warming. This increase will be amplified in areas where primary productivity
345 increases. The trend towards faster juvenile growth might be counteracted by the fisheries-induced
346 evolution (FIE) towards slower growth, although empirical evidence on how FIE will affect juvenile
347 growth is inconclusive. Second, in many stocks we expect to see decreased maturation age. This is indeed
348 one of the best documented life-history trends (Table 1). Decrease in maturation age will be driven both
349 by physiologically faster juvenile growth due to warming and by evolutionary response to elevated adult
350 mortality caused by higher temperatures (Table 2) and fishing (irrespective of how FIE affects juvenile
351 growth). Third, earlier maturation and costs of reproduction, increased reproductive investment, and
352 susceptibility of large fish to decreased oxygen supply in warming waters can be expected to result in
353 smaller adult body size, including smaller L_{∞} . Of these three predictions, the trends in the juvenile growth

354 are most uncertain, but they will not have substantial effect on earlier maturation and decreased adult
355 body size, as these are driven by several other mechanisms as well.

356
357 The majority of empirical examples reported in the literature confirm this expectation, regardless of the
358 ultimate attribution of the causal factors (Table 1). Exceptions to this trend toward faster life-histories can
359 occur in situations where climate change leads to temporary decrease in temperatures (e.g. some deep sea
360 populations, Thresher *et al.* 2007) or where decreased productivity due to climate change will lead to food
361 limitation in juveniles and hence outweigh the expected increase in early growth rates due to temperature
362 and/or harvesting (e.g. some salmon streams, Crozier *et al.* 2011). Decadal-scale climatic oscillations can
363 also override any warming trend on shorter time scales (e.g. Attrill and Power 2002). Finally, species
364 interactions will alter these general trends through changes in natural mortality and resource availability
365 (Ohlberger 2013). Different species will respond to fishing and climate differently, and the expected
366 reductions in size will vary within the same geographic region. Subsequent shifts in species size
367 composition, abundance and distributions will modify predator-prey interactions, further affecting
368 realised life-histories. We cannot make precise theoretical predictions for these second-order responses,
369 but they should be considered and explored (Audzijonyte *et al.* 2013b).

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

372
373 The directional trend towards faster life-histories discussed above will result in changes to natural
374 mortality and population growth rates. However, before we consider management implications, it is
375 important to mention that, in addition to directional trends, climate change and harvesting are also likely
376 to lead to reduced diversity of life-history strategies through both short-term demographic and long-term
377 evolutionary mechanisms (Table 3).

378
379 A number of recent studies have demonstrated that the combination of age truncation through fishing and
380 increased environmental variation through climate change will amplify fluctuations in fish stock
381 abundance (Hsieh *et al.* 2008; Shelton and Mangel 2011; Rouyer *et al.* 2012). There is an emerging
382 consensus that the presence of multiple age classes increases the diversity of egg sizes, and the spatial and
383 temporal distribution of spawning events, and hence serves as a bet-hedging strategy to maximise
384 resilience (Secor 2007; Hixon *et al.* 2014; Shelton *et al.* 2015). The trend towards faster life-histories
385 discussed here now means that in addition to the demographic truncation effect we should also consider
386 the consequences of the physiological and/or evolutionary trend towards earlier maturation and smaller
387 adult size, an area that remains largely unexplored. It is possible that earlier maturation may somewhat
388 counteract the demographic truncation effect, by allowing individuals to reproduce earlier. However, the
389 effects of life-history changes on population stability in the presence of fishing and climate change may

390 have many unexpected feedback mechanisms through changes in behaviour, age-specific mortality and
391 fecundity (Jørgensen and Fiksen 2010; Audzijonyte *et al.* 2013b).

392
393 Directional selection from increased temperatures and size-selective fishing also means that we expect to
394 see the narrowing of maturation and temperature reaction norms, and overall decrease in phenotypic and
395 genetic diversity (Table 3). These outcomes potentially have large implications for population
396 persistence. Life-history diversity provides an important “portfolio effect” (Schindler *et al.* 2010;
397 Anderson *et al.* 2015), buffering stocks against environmental fluctuations. A population that is rich in
398 genetic variation for life-history traits will be better able to mount an evolutionary response to changing
399 conditions (Reed *et al.* 2011). The same concept applies to population complexes, such as in the salmon
400 populations spawning in different rivers. The diverse life-history traits expressed by hundreds of sockeye
401 salmon populations in Bristol Bay, Alaska, have possibly reduced the estimated fishery closure events by
402 a factor of 10, compared to what would have occurred if populations had been homogenous (Schindler *et al.*
403 *et al.* 2010). The short-term buffering due to the “portfolio effect” can occur even in the absence of
404 genetically-based population differences; all that is required is different plastic responses to
405 environmental and habitat heterogeneity. However, longer-term benefits require inter-population genetic
406 heterogeneity. The existence of a diverse portfolio of locally-adapted populations greatly increases the
407 probability that at least some will contain genetic resources that will allow them to persist under radically
408 different future conditions and in this way reduce the biomass fluctuations. Notably, such locally adapted
409 populations can be just as important in widespread marine species (Nielsen *et al.* 2012).

411 **Management implications of changes in life-history characteristics and diversity**

412 413 *Effects of life-history changes on fish stock dynamics*

414 Population parameters that will change with faster life-histories include, among others, natural mortality,
415 steepness of the stock-recruitment relationship, growth model parameters, age at 50% maturity and
416 maximum size. Changes in these parameters will have implications for fisheries stock assessment.
417 Intuitive prediction and broad inter-species comparisons (Jennings *et al.* 1998; Hutchings *et al.* 2012)
418 would suggest that faster juvenile growth, earlier maturation and lower asymptotic size lead to an
419 increased per capita population growth rate (r) and decreased carrying capacity (K) (Heino *et al.* 2013). In
420 terms of fisheries outcomes, this implies that biomass at maximum sustainable yield (B_{MSY}) may decrease
421 ($B_{MSY}=K/2$), fishing mortality (F_{MSY}) needed to achieve the MSY should increase ($F_{MSY}=r/2$), while the
422 actual sustainable yield may not change much, since it is the product of both r and K ($MSY=rK/4$).

423
424 Heino *et al.* (2013) described how faster life-histories caused by fisheries-induced evolution (FIE) may
425 affect r , K and fisheries reference points. They argued that if FIE increases a stock’s reproductive

426 potential through earlier maturation and shorter generation time, it will lead to increased steepness of the
427 stock-recruitment relationship, meaning that higher recruitment occurs at lower biomass. Yet, if FIE
428 reduces pre-recruit survival, through e.g. lower egg quality from smaller females, then the steepness of
429 the stock-recruitment relationship will decrease. Similarly, FIE might change the ratio of spawning stock
430 biomass (SSB) to total biomass. If fish mature earlier, then overestimation of maturation age will
431 underestimate the SSB. However, if FIE reduces the weight of mature fish, then SSB might actually be
432 overestimated if an old age-weight relationship is used (Fig. 2). Earlier maturation means that a cohort's
433 biomass will peak earlier. This would lead to higher fishing mortality on older individuals in cases where
434 selectivity remained unchanged (see the Baltic Sea cod case for a similar result due to density dependence
435 effects; Svedang and Hornborg 2014).

436
437 These general predictions should apply regardless of whether faster life-histories are caused by fishing or
438 global warming. However, it is essential that studies exploring the population level consequences of life-
439 history changes account for the trade-offs between growth and reproduction (see section 2). While there is
440 a general consensus that faster life-histories are likely to decrease carrying capacity (a decrease in adult
441 body size of 5-20% led to a 5-30% decrease in K , see Enberg *et al.* 2009, 2010; Audzijonyte *et al.* 2013b;
442 Kuparinen *et al.* 2014), the modelled effect of earlier maturation on r strongly depends on the
443 assumptions about the survival costs of reproduction. As an example, a model of Atlantic cod (*Gadus*
444 *morhua*, Gadidae) used by Enberg *et al.* (2010) predicted that FIE will increase the ratio of SSB to total
445 biomass, simultaneously increasing the steepness of the stock-recruitment relationship. The authors
446 argued that populations adapted to fishing would produce more recruits for a given level of total biomass,
447 which is likely to increase r . In contrast, modelling studies that included some version of reproduction
448 costs suggest that a combination of earlier maturation (1 to 3 years earlier) and smaller adult body size (ca
449 20% decrease in L_{∞} and L_{mat}) is likely to decrease r by 20-50% (Hutchings *et al.* 2005; Kuparinen *et al.*
450 2014; Audzijonyte and Kuparinen 2016). These simulations are also corroborated by empirical studies
451 exploring r among closely related populations of iteroparous species, showing that natural mortality
452 rather than maturation age is the major determinant of population growth rate (squirrels: Mcadam *et al.*
453 2007; gadoid fishes: Wright 2014). Hence if the benefits of earlier reproduction are outweighed by
454 increased natural mortality (Fig. 1B) the overall effect of faster life-histories on population productivity
455 (r) can be negative.

456
457 There are two ways in which the simulation studies presented above may still be too conservative. First,
458 some of them considered the effects of FIE alone, yet our argument is that life-history effects of climate
459 change and fisheries can often be synergistic and amplify each other. Second, these studies generally
460 assumed that egg quality is independent of female age or population context, and that egg production is
461 linearly related to female weight. This assumption means that the total egg production is equivalent to the

462 SSB. While it is a standard assumption in fisheries, often justified by the absence of time series of
463 reproductive traits (Saborido-Rey and Trippel 2013), it ignores the importance of “Big Old Fat Fecund
464 Female Fish” to the stock’s reproduction (Secor 2007, Hixon *et al.* 2014). If relative egg production
465 and/or quality increases with female age or size, reducing the average age of the spawning stock will even
466 further *decrease* the steepness of the stock-recruitment curves; the effect will be stronger for long-lived
467 species (Venturelli *et al.* 2009). In a number of cases, allowing for time-variable total egg production that
468 takes into account age structure and growth led to different inferences about stock biomasses and
469 recommended fishing rates (Spencer and Dorn 2013). These findings suggest that routine monitoring of
470 reproductive parameters is an important consideration in a precautionary approach to fisheries
471 management.

472 473 ***Impact of life-history trends in single species management***

474
475 With respect to this review, the main question of interest to fisheries management is – what are the
476 consequences of basing harvesting decisions on assessments that ignore possible trends in life-history
477 parameters? If stocks are monitored and assessed routinely, would the management be self-correcting
478 even without taking into account possible changes in growth and maturation? The answers to these
479 questions all depend on the rate of change in life-history parameters - a change of 0.5% per year will be
480 less risky than a change of 5% per year. Empirical studies (Table 1) often report rates of phenotypic
481 change in the range of 0.5-2% per year, with age-at-maturation among the fastest changing traits.
482 Assuming a conservative estimate of *ca* 0.5% change per year, this would lead to *ca* 5% change over 10
483 years (see also van Walraven *et al.* 2010). For age-at-maturation, a more realistic value might be *ca* 1%
484 per year (Sharpe and Hendry 2009; Audzijonyte *et al.* 2013a). Given that it is common for stock
485 assessments to use 10-year-old maturation data (e.g. Stewart *et al.* 2011; ICES Advice 2014) and, when
486 growth models are used, an average growth curve for the entire assessment period is assumed, it would be
487 important to ascertain the likely errors in the stock assessment and management recommendations if the
488 actual age-at-maturation is overestimated by 1 (or 2) years and length-at-age of adult individuals is
489 overestimated by *ca* 5% (10%). To answer these questions specific simulations are needed. Some harvest
490 strategies or management plans (combinations of monitoring, assessment and decision rules) may be
491 relatively robust to ignorance about life-history changes, while others may be quite sensitive. Results
492 from a few studies that specifically looked at the consequences of mis-specifying life-history parameters
493 in fisheries models are provided below.

494
495 A model with cohort-specific growth rates in an age-structured assessment of southeast Australia’s blue
496 grenadier (*Macruronus novaezelandiae*, Merlucciidae) showed that a 5-15% misspecification of length-
497 at-age led to *ca* 5-20% difference in inferred stock biomass (Whitten *et al.* 2013). A similar result was

498 found in a study of Baltic Sea herring (*Clupea harengus*, Clupeidae), where growth was modelled as a
499 time-variable parameter in a Bayesian framework, using information on zooplankton abundance, sea
500 surface temperature and small prey fish biomass as priors (Mantyniemi *et al.* 2013). Wells *et al.* (2013)
501 showed that overestimation of L_{∞} (expected in cases of faster life-histories) will overestimate fishing
502 mortality rates, because the absence of large individuals in stocks with smaller adult length-at-age would
503 bias fishery mortality estimates for older age groups upwards. Bias in selectivity estimates can occur if
504 data are pooled from stocks that have different responses to temperature (e.g. increased and decreased
505 growth as temperature increased up to and above the optimum) (Punt *et al.* 2014). A 20% underestimate
506 in VB k will lead to *ca* 20% reduction in the estimation of yield-per-recruit biomass at fishing mortality
507 $F_{0.1}$ (year⁻¹) (the F value where the curve of production against fishing mortality has a gradient of 10%)
508 (Pardo *et al.* 2013). Concerns about changes in growth may be less important for assessment models
509 (such as some cohort analyses) that use annual empirical information about weight at age rather than
510 fitted and assumed growth curves (but data quality and quantity are critical, see Kuriyama *et al.* 2015).
511 However, even for stocks managed using such models and data, projections about future stock dynamics
512 may become biased if possible trends in growth and maturation are not considered. Also the drawback of
513 such empirical fitting is that no insight into the processes governing growth is gained (Lorenzen 2016).
514 Finally, one of the major ways in which faster life-histories will affect stock productivity is through an
515 expected increase in natural mortality (Fig. 1B). Broad empirical and theoretical comparisons suggest that
516 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
517 from 5 to 4 years would increase M from 0.2 to 0.3 (e.g. Carruthers *et al.* 2012) (Fig. 1B). Jørgensen and
518 Fiksen (2010) suggest that, due to harvest induced evolution in life-histories and behaviour, natural
519 mortality rates increase proportionally to harvest, such as “fishing two fish kills three”. When studied in
520 an ecosystem modelling framework, a decrease in body length of *ca* 4% led to 10-50% increase in
521 predation mortality in four out of five studied species (Audzijonyte *et al.* 2013b).

522
523 Given the evidence for dynamic life-histories in marine species, is it then reasonable to use simplifying
524 assumptions about life-history, such as fixed age or length at maturation, fixed growth curves, fixed *a*
525 *priori* assumed size independent natural mortality, and fixed steepness of the stock-recruitment
526 relationship, in stock assessment models (see also Lorenzen 2016)? For example, although age at
527 maturation is shown to be one of the most rapidly changing life-history traits (Table 1, Sharpe and
528 Hendry 2009; Devine *et al.* 2012; Audzijonyte *et al.* 2013a), this parameter is often fixed in stock
529 assessments. This is true even in cases where trends in maturation have been demonstrated (e.g. for North
530 Sea plaice (*Pleuronectes platessa*, Pleuronectidae), see van Walraven *et al.* 2010 and ICES Advice 2014).
531 Mangel *et al.* (2013) state that the standard practice of assuming fixed values for steepness of the stock-
532 recruitment relationship and natural mortality will *a priori* determine fisheries reference points in a
533 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 realised growth rates. Nevertheless, there is a growing realisation 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 recognised 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; Miethe *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 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, multi-species 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-

570 history characteristics can undermine management relevant information from single species models, so
571 too the omission of shifting life-history parameters in ecosystem models has the potential to lead to
572 erroneous conclusions about the implications of stressors and management for the long term status of the
573 system and its sub-components (Collie and Gislason 2001; Audzijonyte *et al.* 2013b, 2014).

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

576
577 Given the evidence for the changes in life-history of exploited marine species, and the compounding
578 effects of climate change, scientists and marine managers have a range of options in terms of life-history
579 research and subsequent application to management issues (Fig. 3). Scientists involved in stock
580 assessments should acknowledge that trends in life-history traits are likely to be happening and consider
581 what implications this has for the marine populations and ecosystem management arenas in which they
582 work. The framework proposed in Fig. 3 would consider the interaction and relative strength of density
583 dependence, physiological and evolutionary processes. If there is evidence for strong year classes due to
584 relaxed density dependence (top box in Fig. 3) or improved food supply due to increased productivity
585 (second top box in Fig. 3), it is likely that the trend towards decreased adult body size might be masked. It
586 is important to highlight that the underlying physiological and evolutionary processes would still be
587 operational during the periods of faster growth due to improved food supply.

588
589 The realisation of the importance of life-history trends is evident in several resource management
590 working groups (Piet *et al.* 2010), but wider investigation is needed. To support management, improved
591 monitoring strategies are required to provide up-to-date life-history characteristics (e.g. Hollowed *et al.*
592 2013), such as maturation data, growth rate and natural mortality. We acknowledge the difficulties of
593 collecting such data, especially on suitable spatial scales, yet the importance has never been greater. Size-
594 at-age and size-at-maturity could be one of the most important measures determining organism responses
595 to thermal conditions (Ohlberger 2013), and is also one of the main parameters showing rapid response to
596 fisheries-induced population dynamics and productivity (Brander 2010).

597
598 Since life-history information for many stocks is missing, we suggest that as the first step, assessment
599 scientists could explore the sensitivity of model outcomes to misspecification of the life-history
600 parameters using simulations (Szuwalski and Punt 2013; Deroba *et al.* 2014). The next step could be to
601 make better use of existing information, such as in otolith collections, to infer life-histories and possible
602 trends. Otolith data have been used to infer individual-level variation of growth (Morrongiello and
603 Thresher 2015), larval growth rates and the age at which juveniles settle into adult habitats (Fowler and
604 Jennings 2003; Hale and Swearer 2008), differential selection on size-at-age imposed by fisheries (Swain
605 *et al.* 2007; Kendall *et al.* 2014), and the age at sexual maturity, either directly through observing a

606 transition zone (Francis and Horn 1997) or through use of energy-based modelling that recognises the
607 main trade-offs between growth, maintenance and reproduction (Brunel *et al.* 2013). Otolith-based bio-
608 chronologies can provide long-term datasets to aid the investigation of the impacts of environmental
609 variability and fishing pressure on fish stocks (Morrongiello *et al.* 2012). The repeated measures nature of
610 otolith-derived growth data also means that more sophisticated statistical techniques can be employed to
611 decompose population-level patterns into their within and among individual components. This is very
612 important from a climate change perspective as the likelihood of species being able to respond to
613 warming depends on the levels of phenotypic plasticity (Nussey *et al.* 2007).

614
615 Finally, molecular analyses of life-history traits also provide an increasingly valuable source of
616 information. Genes and markers responsible for life-history traits have now been identified in some fishes
617 (Van Wijk *et al.* 2013; Therkildsen *et al.* 2013; Uusi-Heikkilä *et al.* 2015). If these markers are
618 consistently correlated to life-history traits in different species, they can be used for targeted genetic
619 monitoring. Even when monitoring data are collected for other purposes, it should be imperative to
620 preserve material in ways that will be suitable for retrospective genomic analyses, particularly given the
621 rapid decrease in analysis costs (Hayden 2014). Currently the main costs typically come from the
622 subsequent bioinformatics analyses, but here also better tools are being developed every year.
623 Nevertheless, careful analytical design will be needed to provide information relevant to the time and
624 spatial scales useful for assessments.

625
626 With regard to management decisions underpinning sustainable use of marine resources exposed to life-
627 history changes, a combination of precautionary and learning through adaptive management is
628 recommended to maximise species resilience to climate change. For example, based on evidence that age
629 truncation will lead to increased recruitment variability (Secor 2007), precautionary management might
630 seek to increase resilience by increasing the number of age classes contributing to reproductive output.
631 This might be achieved with lower fishing mortality rates, or by using spatial protection for low mobility
632 species (Plagányi *et al.* 2013), or with upper size limits or dynamic spatial management for more mobile
633 species (Hobday *et al.* 2014). Adaptive management would mean that management strategies would be
634 flexible and could respond rapidly as new information is received (e.g. on the status of the stock, realised
635 mortality rates, or in the context of this review assessments could be continuously updated with new life-
636 history information). Notably, when a positive effect of maternal age is taken into account, reducing
637 harvest rates on older, larger individuals may actually increase catch compared to the *status quo*, as
638 productivity increases and more young fish offset the foregone harvest on older fish (Shelton *et al.* 2015).
639 Spatial management may offer protection to some proportion of a population in no-take reserves, which
640 may also help to maintain genetic diversity and demographic structure of the population, increasing
641 adaptive potential and resilience to fluctuations. Clearly, the effectiveness of any measures will vary

642 across stocks, and predictions are difficult as processes determining stock resilience are not well
643 understood. Overall, because it is unclear what exploitation rate is sustainable and maintains the adaptive
644 potential and demographic resilience of marine populations to rapid environmental change, the best
645 precautionary management option will be the one that protects life-history diversity and maintains larger
646 stock biomass (Froese 2004). Without further study, we cannot recommend a single biomass reference
647 point, but it is likely to be higher than the biomass leading to maximum sustainable yield. Further work
648 would be necessary to explore whether more conservative target reference points, such as the biomass
649 leading to maximum economic yield (or its proxy of 48% of the unfished level ($B_{0.48}$)), which has been
650 adopted by fisheries management in places such as Australia (Rayns 2007), is sufficient.

651
652 As human influence on marine ecosystems is increasing, a return to baseline conditions is unlikely in
653 most habitats and management based on the past will fail to account for new patterns (Merrie *et al.* 2014).
654 Hence, adaptive management informed by monitoring is a suitable pathway to follow. Because resources
655 will always be limited, calls for monitoring should be clear about the specific variables that can provide
656 the information to assess the effectiveness of the management approach - we suggest that up-to-date
657 information on life-history characteristics, such as age-at-maturity and growth rate is essential for
658 implementing adaptive management strategies.

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1076 **Table 1.** Some literature examples on changes life-history parameters: juvenile growth (JG, often assessed as k in the VB curve), maturation (MAT,
1077 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
1078 VB curve). Increase/decrease in parameter values is shown with +/-, no change indicated with 0, parameters that were not assessed are shown with na.
1079 Uncertain inferences in parameter change are shown in parentheses. DD – density dependent, T – temperature, FIE – fisheries-induced evolution.
1080 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	Polachek et al. 2004	1960s-1990s, decrease in L_{∞} uncertain
Southern king weakfish	Southern Brazil	-	-	+	FIE, relaxed DD	Cardoso & Haimovici 2011,	1976 to 2011; changes coincided with heavy exploitation
Cod	Baltic Sea	na	na	-	increased DD	Svedang & Hornborg, 2014	k values not reported
Cod	Baltic Sea	-	na	-	FIE, environment	Vainikka et al. 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 et al. 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 et al 2014	1952–2003, changes in growth for ages 1-20y (maturation at ca 17 y)
Six commercial fish species	North Sea	na	na	-	higher T	Baudron et al. 2014	16% change per 2C (ca 0.8% /year)
Western rock lobster (<i>Panulirus cygnus</i> ,	West Australia	-	na	na	FIE, higher T	Melville-Smith & de Lestang, 2006	1975-2005, decrease in the carapace length at maturation

Palinuridea)

Banded morwong (<i>Cheilodactylus spectabilis</i> , Cheilodactylidae)	Tasman Sea	na	+/-	na	higher T	Neuheimer et al. 2011	<i>k</i> decreased when T is above optimum
Three shallow water fishes (<250m)	SW Pacific	na	+	na	higher T	Thresher et al. 2007,	Redfish, Jackass morwong, Banded morwong
Three deep water fishes (>1000m)	SW Pacific	na	-	na	lower T	Thresher et al. 2007,	Orange roughy, Smooth oreo, Warty oreo; no change at medium depth
Blacklip abalone (<i>Haliotis rubra</i> , Haliotidae)	Tasmania	-	+	-	higher T	Helidoniotis & Haddon 2014	
Cod	E Atlantic	na	+/-	na	higher T	Rogers et al. 2011	Increased T has + effect in spring, but - effect in summer (above optimum)
Chinook salmon (<i>Oncorhynchus tshawytscha</i> , Salmonidae)	W USA rivers	na	+/-	na	higher T	Crozier et al. 2010	Increased T has + effect at low density, but - effect at high density (due to DD)
European plaice	North Sea	-	+	-	FIE	Walraven et al. 2010	L_{∞} change at 1%/year for F=0.4
Haddock (<i>Melanogrammus aeglefinus</i> , Gadidae)	Eastern Canada, Scotian Shelf	-	0	-	FIE	Neuheimer & Taggart 2010	measures of temperature-corrected length-at-age
Pacific hake (<i>Merluccius productus</i> , Merlucciidae)	USA and Canada west costs	na	+	-	unclear	Stewart et al. 2011	Step change in <i>k</i> (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 et al. 2013	decrease in PMRN correlated to genetic change and fishing mortality

Sockeye salmon	Alaska	–	NA	na	FIE	Kendall et al. 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 et al. 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 & Hendry 2009; Devine et al. 2012	Rate of change in PMRN correlated to fishing intensity
14 marine and freshwater fish stocks		na	na	–	FIE	Audzijonyte et al. 2013a	0.5-2% /year for F=0.5

1081

1082 **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 Knust 2007); assemblage-wide average body weights predicted to shrink in a warmer

		<p>future due to oxygen limitation and the energetic costs of a large body size (Cheung et al. 2013)</p>
<p>Different response rate of anabolic and catabolic processes to temperature</p>	<p>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_{∞}</p>	<p>Increased relative catabolic rate in larger and older individuals reduces their growth potential (Kozłowski et al. 2004)</p>
<p>Different responses of growth and reproductive processes to temperature</p>	<p>Changes in temperature may advance maturation irrespective of growth, resulting in small adult body size due to earlier energy allocation to reproduction</p>	<p>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 (Helidoniotis and Haddon, 2014)</p>
<p>Temperature-dependent differences in size-fecundity or size-reproductive relationships</p>	<p>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_{∞}</p>	<p>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)</p>

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 maximising 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)

1083

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 et al. 2008)
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

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

season length (Jørgensen et al. 2006; Secor 2007; Hixon et al. 2014).

Lower reproductive rates in 25 marine fish due to age truncation (Venturelli et al. 2009). Importance of large fish for population resilience (Hixon et al. 2014).

Fishing: Reduced diversity of spawning behavior 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)

1084 **Figure legends**

1085

1086 **Fig. 1. A:** Von Bertalanffy growth curves for slow (dashed line) and fast (thick solid line) life-histories.
1087 An arrow indicates the suggested general trend towards faster life-histories. Thickened lines indicate the
1088 length of maturity for the different life-histories. **B.** Relationship between life-history parameters and
1089 natural mortality based on empirical and simulated data (modified from Carruthers et al. 2012).

1090

1091 **Fig. 2.** Implications of faster life-histories for stock biomass and productivity: four possible scenarios. **A:**
1092 Earlier maturation increases spawning stock biomass and productivity, compensating for smaller adult
1093 size, total biomass and carrying capacity remain unchanged. **B:** Earlier maturation leads to shorter
1094 lifespan as survival costs of reproduction reduce longevity. In combination with reduced adult size this
1095 leads to decreased carrying capacity. **C:** Earlier maturation increases the spawning stock biomass, egg
1096 production and recruitment, leading to increased productivity. **D:** Decreased size of an average female
1097 leads to lower egg production and recruitment, and to lower productivity.

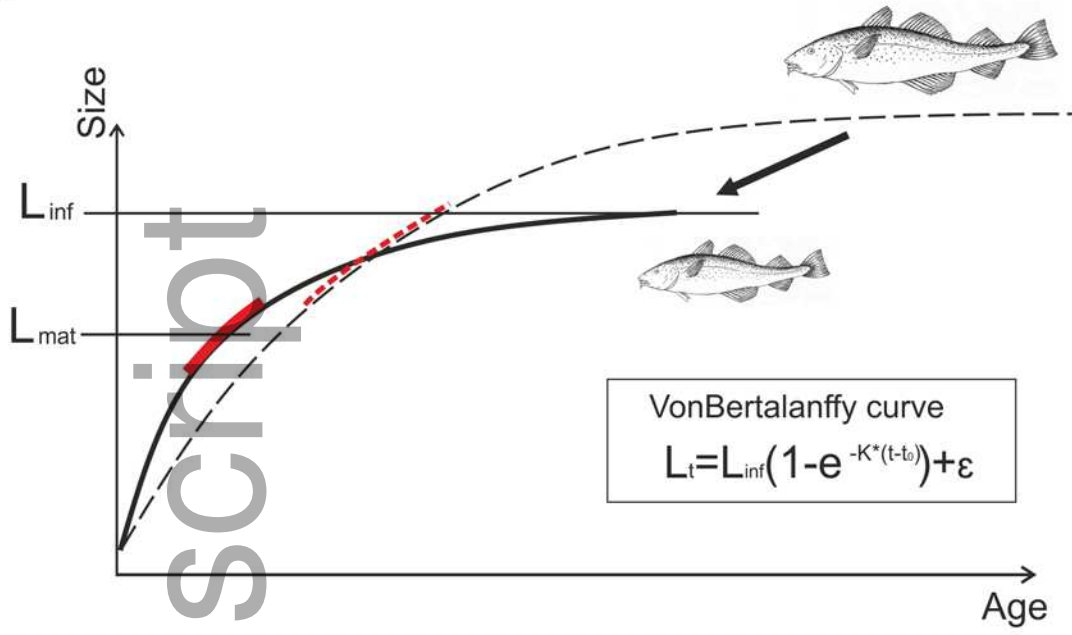
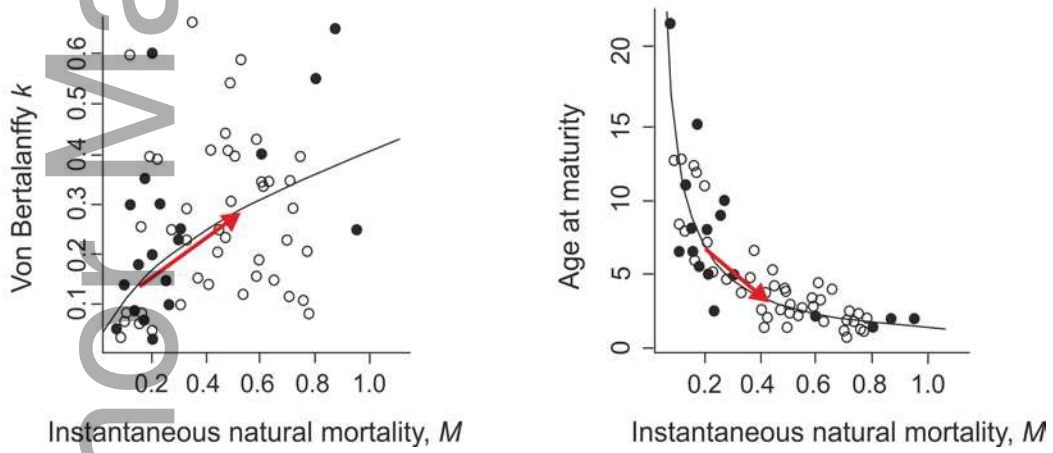
1098

1099 **Fig. 3.** Suggested framework for precautionary and adaptive management that evaluates different factors
1100 that are likely to affect life-history traits and for which monitoring could be established. A trend towards
1101 faster life-histories (from dashed to thick solid line) is shown with a red arrow.

1102

1103 Fig. 1

1104

A**B**

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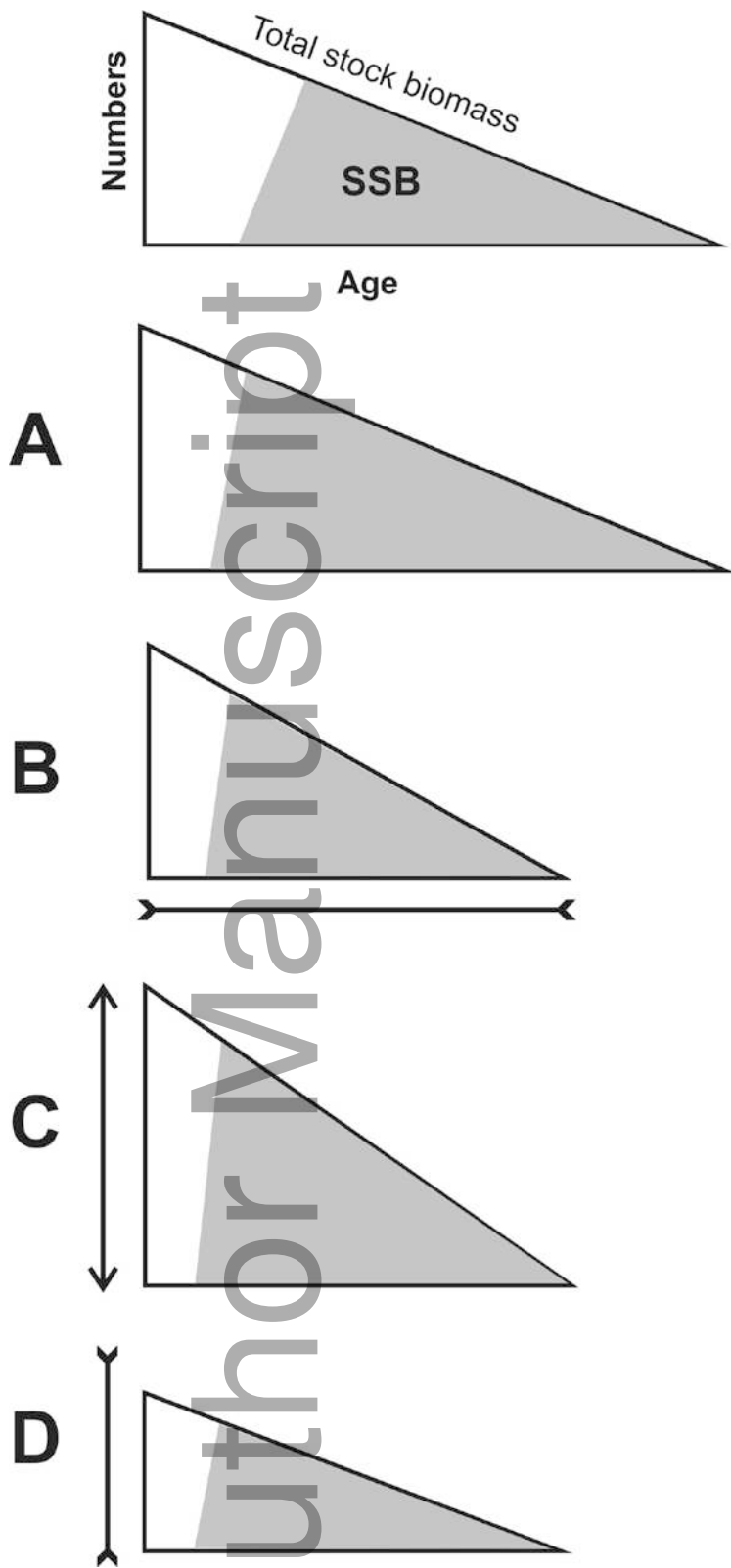
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1109 Fig. 2

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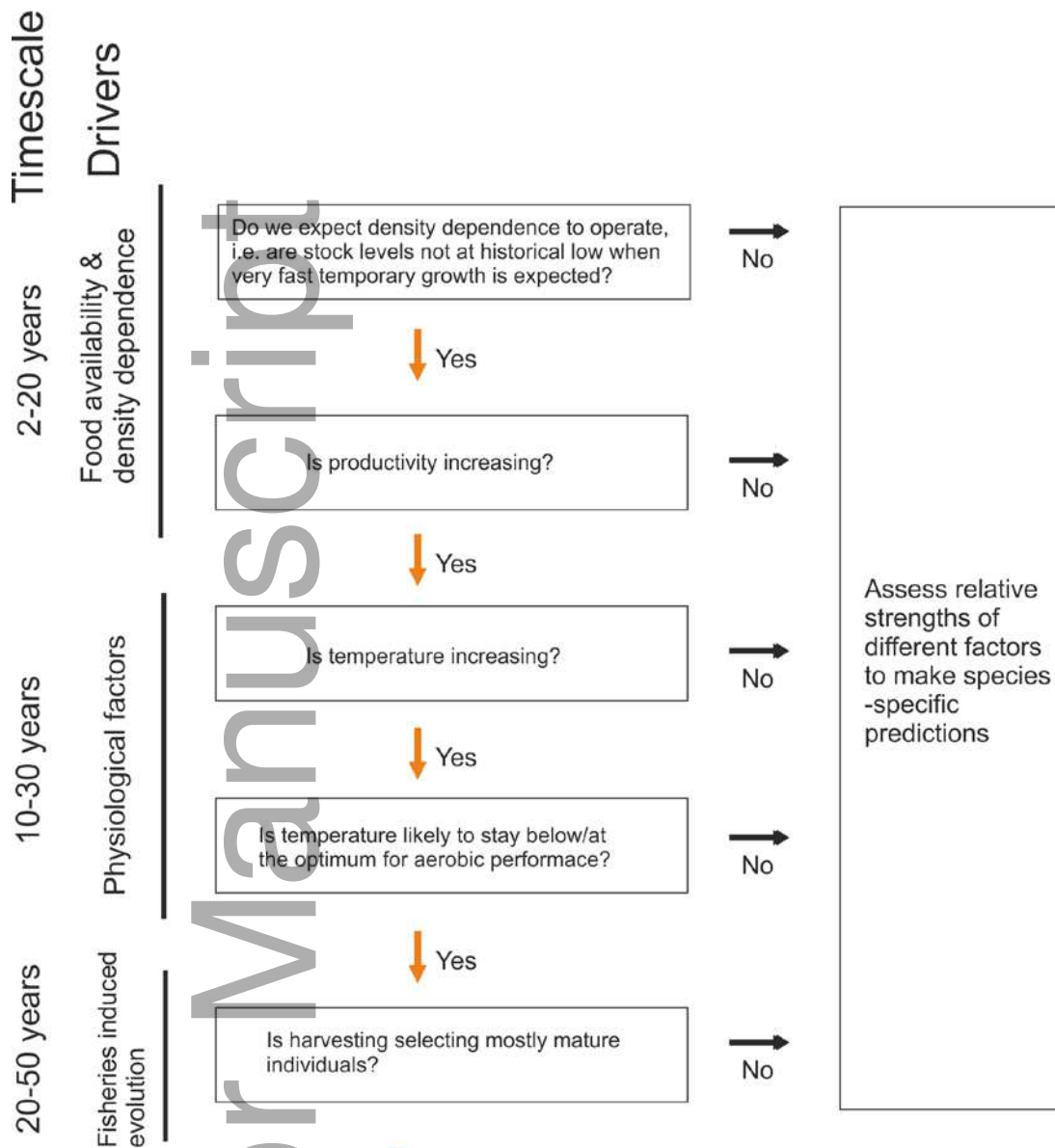
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1114

1115 Fig. 3



Yes

Yes

Yes

Yes

Yes

Expected change in growth and maturation age leading to faster life-histories

