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Impacts of climate change on the complex life cycles of fish

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Abstract :

To anticipate the response of fish populations to climate change, we developed a framework that integrates requirements in all life stages to assess impacts across the entire life cycle. The framework was applied on plaice (*Pleuronectes platessa*) and Atlantic herring (*Clupea harengus*) in the North Sea, Atlantic cod (*Gadus morhua*) in the Norwegian/Barents Seas and European anchovy (*Engraulis encrasicolus*) in the Bay of Biscay. In each case study, we reviewed habitats required by each life stage, habitat availability, and connectivity between habitats. We then explored how these could be altered by climate change. We documented environmental processes impacting habitat availability and connectivity, providing an integrated view at the population level and in a spatial context of potential climate impacts. A key result was that climate-driven changes in larval dispersion seem to be the major unknown. Our summary suggested that species with specific habitat requirements for spawning (herring) or nursery grounds (plaice) display bottlenecks in their life cycle. Among the species examined, anchovy could cope best with environmental variability. Plaice was considered to be least resilient to climate-driven changes due to its strict connectivity between spawning and nursery grounds. For plaice in the North Sea, habitat availability was expected to reduce with climate change. For North Sea herring, Norwegian cod and Biscay anchovy, climate-driven changes were expected to have contrasting impacts depending on the life stage. Our review highlights the need to integrate physiological and behavioural processes across the life cycle to project the response of specific populations to climate change.

Keywords : anchovy ; Cod ; Connectivity ; eco-physiology ; habitat ; herring ; plaice

45 INTRODUCTION

46 The effect of a changing climate on fish resources has been documented at
47 different levels of biological organization (Pörtner and Peck, 2010), from individual
48 physiological and behavioural responses to effects at the population level (Rijnsdorp *et*
49 *al.*, 2009), to changing species proportions in fish assemblages (Engelhard *et al.*, 2011a)
50 and to ecosystem re-organization (Beaugrand, 2004). Yet, the impact of climate change
51 on the links in the life cycle has received little attention, especially considering that they
52 could represent additional mechanisms and vulnerabilities of relevance to physiological
53 tolerance envelopes that might explain observed changes in the spatial distribution of
54 species. For instance, when predicting changes in the distribution of species using bio-
55 climate envelopes (e.g., Cheung *et al.*, 2008) the life cycle is greatly simplified as the
56 requirements of the different life history stages are rarely considered nor are the
57 connectivity pathways between their habitats. Here we develop a generic life cycle
58 framework to analyse how climate variability and change may impact marine fish
59 populations.

60 Fish have complex life cycles that comprise different stages exploiting a variety of
61 habitats (Rijnsdorp *et al.*, 2009). For life cycle closure, larval dispersal and fish
62 movements are often necessary to connect spatially-separated habitats utilized by
63 successive life stages (Harden-Jones, 1968; Sinclair, 1988). Each life stage has
64 particular habitat requirements that are based, in part, on stage-specific physiological
65 requirements. The availability of habitats with the required abiotic and biotic
66 characteristics will undoubtedly change both spatially and temporally as a result of
67 short-term (weeks to years) environmental variability and longer-term (years to
68 decades) climate variability and change. Thus, it is critical to characterize the life cycle
69 of species in terms of specific habitat requirements, habitat availability, and
70 connectivity.

71 To illustrate changes in habitat availability and connectivity occurring at the
72 species-level, the migration triangle originally depicting life cycle closure (e.g., Harden-
73 Jones, 1968) was redrawn in a climate change context (Fig. 1), which shows the need to
74 integrate climate impacts occurring during all life stages. To explore the usefulness of
75 this life cycle approach in assessing the potential effects of climate change on fish
76 populations, we study the habitat requirements of successive life history stages in
77 relation to the availability of suitable habitats and the connectivity between them.
78 Particular attention is paid to whether certain life stages are bottlenecks in the life cycle

79 and can thus be considered to be critical to understanding climate impacts on
80 populations.

81 As such, this study provides an integrated approach to assess the aggregate
82 population level response to potential climate impacts on selected, commercially
83 important marine fish species in European waters.

84

85 **ANALYSIS FRAMEWORK AND SPECIES CONSIDERED**

86 To achieve some generality in the analyses, case study species and populations
87 were chosen to represent a range of life history types (Table 1) and which are known to
88 occupy habitats possessing varying degrees of complexity over a latitudinal range of
89 ecosystems. Species/stocks chosen were 1) European anchovy *Engraulis encrasicolus*
90 in the Bay of Biscay, 2) Atlantic herring *Clupea harengus* in the North Sea, 3) European
91 plaice *Pleuronectes platessa* in the North Sea, and 4) Atlantic cod *Gadus morhua* in the
92 Norwegian/Barents Seas (Northeast Arctic cod). Habitat requirements were considered
93 at the species level while habitat availability and connectivity were considered at the
94 population level within particular regions. Based on literature reviews, qualitative
95 categorizations were argued for each life stage, including eggs, larvae, juveniles,
96 feeding and spawning adults (Tables 2 to 5). Where appropriate, sub-stages were
97 considered, e.g., pelagic larvae / juveniles versus demersal juveniles.

98 Each case study was reviewed using a similar template. For each life stage, (i)
99 physiological habitat requirements, (ii) habitat availability, and (iii) connectivity to the
100 next life stage were examined, followed by (iv) an assessment of the likely impact of
101 climate variability and climate change on each of these factors. *Habitat requirements*
102 were defined by physiological requirements, critical habitat features such as specific
103 topographic or sediment features, or other requirements that were based on first
104 principles. Habitat requirements were ranked qualitatively in terms of importance within
105 categories of “narrow” (restrictive), “medium” or “broad” (less restrictive). *Habitat*
106 *availability* considered how accessible the required conditions were to the species in the
107 studied region, i.e., the geographical location of habitats, vertical distribution, timing in
108 the season, etc. Habitat availability was summarized with a glossary made of three
109 terms: “ok” (no significant problem of availability expected), “small” (reduced
110 availability), or “var” (high inter-annual variability). *Connectivity* considered how the
111 habitat of one life stage was linked to that of the next life stage, such as through drift
112 and dispersal (e.g. egg to larval phase) including the importance of behaviour (e.g.

113 vertical movements) and ‘active’ migration (e.g. feeding to spawning adults).
114 Connectivity was summarized within each of the studied regions using the following
115 terms: “ok” (little sensitive to environmental variability: connectivity assured), “crucial”
116 (precise connectivity needed for life cycle closure), and “var” (high inter-annual
117 variability). To evaluate the potential impact of climate change on life cycles, we
118 focussed the analyses of impacts on the availability of suitable habitats for the different
119 life stages and on the connectivity between habitats and life stages. Again, a qualitative
120 categorisation was used to characterize the expected impacts. The following categories
121 were used: “larger” or “smaller” (spatio-temporal extension or contraction of suitable
122 habitats), “shift” (spatio-temporal displacement of suitable habitats), “ok” (no particular
123 impact expected) and “?” (unknown consequences).

124 The categorizations were based on a critical review of the literature for each
125 species and populations and compiled in Tables 2 to 5. The following sections justify
126 the categorization presented in these tables.

127

128 **European anchovy**

129 *European anchovy: habitat requirements*

130 European anchovy is a fecund, indeterminate multiple batch spawner. The start of
131 the spawning season coincides with the initiation of seasonal stratification and a
132 concomitant increase in surface water temperature above 14 °C occurring in April or
133 May and eggs are generally found in the surface layer (<15 m) (Motos *et al.*, 1996;
134 Planque *et al.*, 2007). Adult European anchovy shows a versatile feeding ecology
135 (Tudela and Palomera, 1997; Plounevez and Champalbert, 1999; Raab *et al.*, 2011). The
136 species feeds mainly on medium-sized copepods (0.5 to 1.5 mm) and cladocerans but
137 also ingests mysids and phytoplankton. The average daily ration of adults during
138 spawning is ~20% wet body weight (Bulgakova, 1992). The consumption rates of
139 zooplankton by anchovy in the western Mediterranean Sea can represent 20% of the
140 mesozooplankton spring production (Tudela and Palomera, 1997). Despite this, no food
141 limitation has been reported during this period (Marquis *et al.*, 2006). Feeding continues
142 during spawning allowing fish to extend the spawning season in years when prey
143 resources are abundant (Dubreuil and Petitgas, 2009). Therefore the requirements for
144 spawning adults seem moderately restrictive, the major constraints being that minimum
145 temperature thresholds are reached and that spawning is initiated during the onset of
146 zooplankton production.

147 The larvae are found during the summer within stratified waters (Allain *et al.*,
148 2007; Irigoien *et al.*, 2008) and growth is potentially most rapid above 16 °C
149 (Urtizberea *et al.*, 2008). The larval stage lasts approximately 1 to 2 months (La Mesa,
150 2009; Aldonando *et al.*, 2010). The larvae feed on microzooplankton and
151 mesozooplankton in the size range 50 to 500 µm (Tudela *et al.*, 2002) with prey size
152 increasing with increasing larval size. Although the nutritional condition of larvae has
153 been related to carbohydrate assimilated from feeding on mesozooplankton (Bergeron,
154 2009), food-limited growth has not been reported during the larval stage (Diaz *et al.*,
155 2008). However the vertical structure of larval habitats has been correlated with larval
156 condition and ultimately recruitment. Detrimental conditions include frequent gales
157 (Bergeron, 2004) as well as intense stratification (Allain *et al.*, 2007).

158 Early juveniles are found in late summer and autumn in stratified waters that are >
159 18°C. Depending on the direction and intensity of currents as well as dispersion, larvae
160 can be transported into many different areas, from near-shore coastal habitats to off-
161 shelf oceanic areas (e.g., Petitgas *et al.*, 2010a). There is a lack of information on
162 juvenile habitat requirements, but these seem to be broad, as suggested by the
163 distribution of juveniles in a variety of habitats. However, in the Bay of Biscay a
164 minimum length (ICES, 2009) and/or energy content (Dubreuil and Petitgas, 2009)
165 appear necessary for juveniles to survive the overwinter period. This could also be a
166 limiting factor in the southern North Sea as increased winter temperatures are associated
167 with increased survival through to age 1 (Kanstinger and Peck, 2009; Petitgas *et al.*,
168 2012)

169 Overall, habitat requirements of larvae are satisfied via a temporal match between
170 seasonal warming, river plumes, and zooplankton production and were thus considered
171 medium. Juveniles are widely distributed and their habitat requirements were classified
172 as broad (Table 2, column 1).

173

174 *European anchovy: habitat availability in the Bay of Biscay*

175 Pelagic habitats within the Bay of Biscay are dynamic and characterized by the
176 presence of a variety of meso-scale physical features such as river plumes, upwelling
177 areas, gyres, eddies and fronts with the strength of these features depending upon the
178 season and climatic conditions (Koutsikopoulos and Le Cann, 1996). The anchovy life
179 cycle in the Bay of Biscay is associated with seasonal changes in a variety of these
180 physical features and to specific biological factors. For example, water temperature is

181 one of the triggers for spawning and interannual differences in water temperature may
182 lead to interannual differences in spawning times. Moreover, clear limits to habitat
183 availability for spawning exist in the northern Bay of Biscay, where water temperatures
184 are often too cold and unsuitable for spawning until late spring. The spawning duration
185 may vary between years depending upon the feeding conditions encountered on
186 spawning grounds. In spring, the zooplankton production seems sufficient as no feeding
187 limitation has been reported (Marquis *et al.*, 2006). In summer, warmer temperatures
188 associated with lower plankton production can be unsuitable for the adults in the
189 southern Biscay (Struski *et al.*, 2009). Larval drift can vary significantly among years
190 depending on wind conditions and river discharges (Allain *et al.*, 2007; Huret *et al.*,
191 2010), with consequences for survival and ultimately recruitment. Specifically, prey
192 fields may vary with hydrographic conditions and higher predation is thought to occur
193 within on-shelf areas as opposed to off-shelf areas (Irigoien *et al.*, 2007). Autumn and
194 winter temperature and feeding conditions also affect reserve storage and juvenile
195 growth with consequences for the energy available for spawning in the subsequent
196 spring (Pecquerie *et al.*, 2009). Thus, the habitat requirements of anchovy in the Bay of
197 Biscay in the different life stages seem to be satisfied in many but not all years, as
198 evidenced by the recruitment variability observed in the region. Therefore, we
199 considered habitat availability as not limiting although variable from year to year (Table
200 2, column 2).

201

202 *European anchovy: habitat connectivity in the Bay of Biscay*

203 Connectivity between habitats for the Bay of Biscay anchovy population was
204 summarized in Petitgas *et al.* (2010a). The spring spawning habitats are mainly located
205 in the southern regions of the Bay Biscay, associated with river plumes, as well as off-
206 shore close to the shelf-break (Motos *et al.*, 1996). From these locations, larval drift is
207 generally oriented along shelf to the southwest although large cross-shelf dispersion can
208 also occur. Late larvae and early juvenile habitats are widely distributed, covering the
209 shelf and off-shelf areas (Irigoien *et al.*, 2008; Petitgas *et al.*, 2010a), but they appear to
210 be mostly confined to the south of the bay. Off-shore juveniles actively migrate back to
211 the coastal areas. The mechanism controlling this migration is unknown. When they
212 encounter adults and recruit to the population in autumn, juveniles change their
213 schooling behaviour (Petitgas, 2007). Adults seem, therefore, to play the role of
214 facilitators, enhancing naive juveniles to rapidly adopt adequate, habitat-specific

215 behaviours which, theoretically, could reduce mortality. Life cycle closure and habitat
216 connectivity between spawning and recruitment is believed to be under the direct
217 influence of variability in larval drift. Although larvae may drift to areas providing
218 survival into the juvenile stage, connectivity in the life cycle may be disrupted if those
219 juveniles do not encounter adults. As for habitat availability, the major characteristic of
220 connectivity was the large inter-annual variability (Table 2, column 3).

221

222 *European anchovy: climate change impact in the Bay of Biscay*

223 For anchovy in the Bay of Biscay, different models constructed for different life
224 stages predicted an expansion of the population to the north under scenarios of climate
225 change (Petitgas *et al.*, 2009a). An increase in temperature throughout the year may
226 influence the potential habitats of the adults towards a more northern distribution at
227 spawning time. Winter unsuitability may decrease over the entire Bay of Biscay due to
228 warmer temperatures but warmer summer temperatures associated with lower
229 zooplankton production may increase the unsuitability of habitats in southern Biscay
230 (Struski *et al.*, 2009). An increase in temperature may shift peak spawning by one
231 month earlier in the season (Petitgas *et al.*, 2009a). In this situation and given current
232 seasonal circulation patterns, the larvae may disperse more towards the north (Huret *et*
233 *al.*, 2009). Under such a scenario, changes in the larval dispersion patterns could disrupt
234 the current life cycle organisation in space and time. The survival probability of
235 juveniles in novel areas is unknown as is the potential for connectivity with new adult
236 habitats.

237 Thus, a warming climate is expected to increase habitat availability for spawning
238 and juvenile stages, while its impact on larval and juvenile connectivity remain
239 unknown because of potential changes in currents and spawning windows (Table 2,
240 columns 4 and 5).

241

242 **Atlantic herring**

243 *Atlantic herring: habitat requirements*

244 Atlantic herring have specific habitat requirements for spawning. They are benthic
245 spawners and deposit their eggs on solid substrates, whether this be coarse sand, gravel
246 or boulders (Blaxter and Hunter, 1982; Geffen, 2009). In the Baltic, they also spawn on
247 macro-algae or mussel beds (Casini, 2010). Herring generally spawn in areas of well-
248 mixed water and it can be assumed that they require high oxygen saturation (Parrish *et*

249 *al.*, 1959; Aneer, 1985). They display great plasticity in spawning habitats across the
250 species (Geffen 2009), thus, although individual populations may utilize specific
251 habitats, overall habitat requirements for spawning are quite broad. Atlantic herring
252 populations can be found spawning in all months of the year (Dickey-Collas *et al.*,
253 2009a) and have a relatively wide temperature tolerance for spawning (4-15 °C: Pörtner
254 and Peck, 2010; Peck *et al.*, 2012). Salinity has been correlated to the genetic sub-
255 species structure of Atlantic herring but, across the species, herring can spawn from 4 to
256 35 salinity units (Gaggiotti *et al.*, 2009). They are generally thought to have predictable
257 migration routes and spawning site fidelity (Sinclair, 1988), in which learning plays an
258 important role (McQuinn, 1997; Petitgas *et al.*, 2010b). However, this is not always the
259 case as the location of spawning sites for Norwegian Spring spawning herring change as
260 the fish get older and longer (Slotte, 1999). Thus, habitat requirements for spawning
261 could be considered limiting for a herring population in a particular area.

262 Across the species, herring larvae can grow in temperatures from 2 to 21 °C
263 (Oeberst *et al.*, 2009; Pörtner and Peck, 2010) and across a wide range of salinities.
264 Specific populations may have more specific requirements. Higher prey requirements at
265 warmer temperatures may limit survival of larvae after yolk absorption in areas of
266 relatively low prey production.

267 The temperature requirements for juveniles do not appear different from those of
268 the larvae (Röckmann *et al.*, 2011). Salinity requirements seem broad. Juveniles in the
269 North Sea tend to be found in less saline water than the larvae (their nursery areas are
270 generally shallow <50m). However, nursery areas of the Norwegian spring-spawning
271 herring are offshore in deeper waters of the Barents Sea (e.g., Holst *et al.*, 2004).

272 The main factors that determine adult feeding habitats are zooplankton biomass,
273 hydrography and seabed substrate in the North, Norwegian and Baltic seas (Maravelias
274 and Reid, 2000; Nøttestad *et al.*, 2007; Peltonen *et al.*, 2007). These three factors often
275 co-vary spatially (Maravelias, 2001).

276 Thus overall, adult feeding and juvenile habitats were considered ‘broad’, but
277 those of eggs and young were classified as “narrow” (Table 3, column 1).

278

279 *Atlantic herring: habitat availability in the North Sea*

280 The availability of suitable spawning habitat for North Sea herring is limited to
281 specific areas of appropriate substrate (see above). North Sea spawning beds are limited

282 to the western areas and the English Channel (Dickey-Collas, 2010). A gradient exists
283 in the timing of spawning by North Sea herring with earlier (autumn) spawning
284 occurring in the north, and later (winter) spawning in the south. There is some evidence
285 that the timing of spawning by location is related to temperature-specific windows of
286 optimal prey requirement for the larvae. Herring larvae individual-based model (IBM)
287 simulations suggested that North Sea temperatures in summer are too high to support
288 the survival of newly-hatched larvae at current levels of prey availability and that those
289 individuals released in Orkney/Shetland do not have the opportunity to survive if
290 spawned in November or December (Hufnagl and Peck, 2011). Therefore, although the
291 physical habitat for the larvae is widely available, the availability of optimal habitats
292 would be very restricted to time periods and locations having sufficient prey to meet
293 larval metabolic requirements and ensuring the avoidance of predator hotspots. In
294 contrast, habitats required for juveniles and adults are largely non-specific and are
295 widely available in the North Sea (Dickey-Collas, 2010). Thus, habitat availability was
296 considered ‘small’ for spawning adults and eggs, ‘variable’ for larvae and ‘ok’ for
297 feeding adults and juveniles (Table 3, column 2).

298

299 *Atlantic herring: connectivity to next stage in the North Sea*

300 Beyond substrate requirements, spawning habitats are limited to areas that are
301 upstream of the juvenile nursery grounds since larval and post-larval transport is
302 primarily through drift (Heath *et al.*, 1997; Dickey-Collas *et al.*, 2009b). During these
303 early life stages, transport is governed by prevailing water currents that, in turn, can be
304 altered by atmospheric or oceanographic phenomena. This connectivity has long been
305 postulated to control recruitment success in herring (Isles and Sinclair, 1982). Transport
306 and retention interact with the degree of spatial overlap with prey and predators to
307 determine how successfully larvae are “connected” to juvenile nursery grounds (larvae
308 cannot merely be transported, they must also grow and survive).

309 In the case of the northern North Sea, larvae are occasionally entrained in
310 northward flowing currents and are transported to the central coastline of Norway
311 (Fossum and Moksness, 1993) where they mix with spring-spawned larvae of
312 Norwegian / fjordic populations. The fate of these autumn-spawned larvae is unknown
313 (i.e. whether they are adopted into the Norwegian spring spawning populations or die,
314 or return to the North Sea). There is evidence that late larvae and juveniles from the
315 stocks to the west of the British Isles utilise portions of the northern North Sea as

316 nursery areas (Heath, 1989; ICES, 1994). Again, the fate of these fish is unknown (i.e.
317 whether they return to their parent stock, die or become North Sea herring by adoption).

318 Connectivity of the adults (multiple and first spawners) to the spawning grounds is
319 crucial as herring show conservatism in migration and are thought to “learn” migration
320 routes (Corten, 2001; Huse *et al.*, 2010). Even when spawning beds are physically
321 damaged or eradicated (e.g. by gravel extraction or closing the Zuiderzee) herring keep
322 returning to the location of these beds, until the spawning groups die off (de Groot,
323 1980). Likewise, when herring are removed from historic spawning grounds (e.g. by
324 over fishing), it can take many decades to re-establish spawning in those areas (Corten,
325 1999; Schmidt *et al.*, 2009; Dickey-Collas *et al.*, 2010). This is a core part of the life
326 cycle closure in herring (Petitgas *et al.*, 2010b) and appears most sensitive to disruption.

327 Therefore the migration to the spawning grounds was considered crucial while
328 larval connectivity from egg to juvenile habitats was considered ‘ok’ or ‘variable’
329 (Table 3, column 3).

330

331 *Atlantic herring: climate change impact in the North Sea*

332 Although North Sea herring is close to its southern-most boundary in the
333 Northeast Atlantic (the Bay of Biscay), little evidence exists to suggest that an increase
334 in sea temperature of 1 to 2 °C, will reduce the suitable habitat for the species, since the
335 range in tolerable temperatures is broad (up to 20 °C in the Baltic). However the
336 mortality of larvae does co-vary with increasing temperature in the northern North Sea
337 (Fässler *et al.* 2011) suggesting that temperature may impact on productivity. As herring
338 spawn layers of benthic eggs, any reduction in dissolved oxygen, through less mixing,
339 increased eutrophication, etc., is expected to decrease egg survival. Also, the higher
340 prey requirements after yolk absorption associated with warmer temperatures may
341 indirectly limit the spatial and temporal extent of habitats allowing larval survival.
342 Temperature is also expected to affect the growth of juveniles and adults with cohorts
343 experiencing warmer temperature growing faster and reaching a smaller asymptotic size
344 than individuals within cohorts growing at colder temperatures (Brunel and Dickey-
345 Collas, 2010). How this would affect overall population productivity remains unclear.
346 In relation to a changing growth pattern the spawning strategy could be impacted: it has
347 been suggested that an increase in temperature favours the autumn spawning strategy in
348 western Atlantic herring stocks (Melvin *et al.*, 2009) and Hufnagl and Peck (2011) show
349 a physiological link between larval survival at seasonal temperature and the

350 zooplankton production cycle. Whether life history closure is possible given a different
351 spawning strategy and a changed zooplankton production cycle is unknown.
352 Furthermore, an increase in biodiversity in the North Sea (e.g., increase in anchovy and
353 sardine) may also introduce competition for pelagic habitats due to overlap in
354 zooplankton diet (Raab *et al.*, 2012). Overall, habitat availability in a changed climate is
355 not expected to be limiting but habitats utilized may possibly shift towards higher
356 latitudes (Table 3, column 4).

357 For most of the herring life stages, the impact of climate change on connectivity
358 is unclear. Regional models are currently unable to predict the likely impact(s) of global
359 climate change on the oceanography of the North Sea (see discussion). Thus, it is
360 difficult to project the future influence of climate change on the transport of larvae or
361 the location of adult feeding grounds with any confidence. Therefore, the impact of
362 climate change on connectivity is difficult to predict and remains largely unknown
363 (Table 3, column 5).

364

365 **European plaice**

366 *European plaice: habitat requirements*

367 Plaice is a broadcast spawner that exhibits spawning site fidelity (Rijnsdorp and
368 Pastoors, 1995; Hunter *et al.*, 2003; Solmundsson *et al.*, 2005). Spawning occurs at
369 depths of 20 to 50 m from the Bay of Biscay in the south to Iceland and the Barents Sea
370 in the north (Wimpenny, 1953). Spawning shifts from December and January in the
371 southern areas to April and May in more northerly ones (Harding *et al.*, 1978;
372 Gunnarsson *et al.*, 2010) and is affected by water temperatures experienced during
373 gonad development and the spawning period (Nash and Geffen, 1999; Teal *et al.*, 2008).
374 Eggs and larvae are pelagic for about 2 to 3 months (Ryland and Nichols, 1975; Fox *et*
375 *al.*, 2003). The range in average conditions experienced and the range in tolerable
376 temperatures and salinities change with successive life stages. Juveniles are collected at
377 warmer temperatures (from 3 to 18°C) than eggs (5 to 7 °C), larvae (4 to 6 °C) or settlers
378 (3 to 6 °C) and can tolerate warmer temperatures (2 to 22 °C) compared to eggs (2 to
379 12°C: Ryland *et al.*, 1975; Fonds *et al.*, 1992). Adults, eggs and larvae occur in
380 seawater, whereas settlers and juveniles can occur in estuarine waters (20-32 psu) (Jager
381 *et al.*, 1993). Successful spawning only occurs in waters >15 psu (Nissling *et al.*, 2002).

382 Mortality rates of eggs and larvae tend to increase with increasing temperature
383 (Rijnsdorp and Vingerhoed, 1994; Dickey-Collas *et al.*, 2003), possibly due to an

384 associated increase in predation mortality (e.g., Harding *et al.*, 1978; van der Veer,
385 1985; Seegers *et al.*, 2007).

386 Plaice larvae feed on prey items abundant in the winter such as the
387 appendicularian *Oikopleura dioica* (Shelbourne, 1953; Last, 1978). There are no studies
388 reporting the importance of a match-mismatch between the timing of plaice spawning
389 and food availability nor on the presence of potential predators on eggs and larvae (e.g.
390 herring and sprat). Around metamorphosis, larvae become demersal and settle onto
391 nursery grounds which are generally inshore, shallow (<10 m deep), sandy or muddy
392 areas (e.g. Able *et al.*, 2005; Gunnarsson *et al.*, 2010). During settlement, the temporal
393 and spatial overlap with predators is a key, temperature-dependent match-mismatch
394 process affecting the survival of plaice settlers (post-larvae) in shallow nursery habitats
395 (van der Veer and Bergman, 1987). Juvenile plaice feeds on a variety of macrobenthic
396 species (de Vlas, 1979) while larger demersal stages mainly feed on polychaetes and
397 molluscs (Rijnsdorp and Vingerhoed, 2001). As they grow, plaice gradually disperse
398 from shallow coastal nurseries into deeper water. After maturation they seasonally
399 migrate between spawning and feeding grounds. Demersal stages of plaice have a clear
400 preference for soft sediments with a grain size of coarse to very fine sand (e.g. Gibson
401 and Robb, 2000).

402 Thus overall, habitat requirements at the juvenile stage seem more restricted than
403 for other life stages, for which requirements are “medium” (Table 4, column 1). Yet,
404 populations living in areas such as the Baltic Sea where the ratio of adult to juvenile
405 habitat is much lower may also experience density-dependent regulation of survival in
406 other life history stages (Rijnsdorp, 1994).

407

408 *Plaice: habitat availability in the North Sea*

409 The extent of suitable habitats for post-larvae (during settlement) is much smaller
410 than that of the earlier or later life history stages and the total population abundance of
411 plaice seems to be related to the availability of suitable settlement nursery grounds
412 (Rijnsdorp *et al.*, 1992; van der Veer *et al.*, 2000). Density-dependent processes are
413 restricted to the phase where plaice are concentrated in nearshore nursery grounds
414 (Beverton 1995; Nash and Geffen, 2000; van der Veer *et al.*, 2000). Nursery ground
415 quality will be affected by the productivity of suitable benthic food and by the
416 abundance of potential predators (see above). Except for the 0-group, no correlation
417 exists between inter-annual variability in growth rate and water temperatures (Rijnsdorp

418 and van Leeuwen, 1996; Teal *et al.*, 2008). Growth variability therefore seems to be
419 determined by variations in benthic productivity due to variations in ocean climate,
420 eutrophication and the effect of bottom trawling or habitat modification (Rijnsdorp and
421 van Leeuwen, 1996). Suitable sediment types and polychaete/ mollusc prey of larger
422 juveniles and adults are widely available throughout the North Sea. Over the last 20
423 years, juvenile and adult plaice have shifted to deeper and more northern areas likely in
424 response to warming (van Keeken *et al.*, 2007; Engelhard *et al.*, 2011b).

425 Thus habitat availability at the early juvenile (post-larval) stage appears to be a
426 critical bottleneck in the life cycle due to density-dependent processes, match-mismatch
427 with predators and benthic productivity (Table 4, column 2). Larger juveniles and adults
428 are not considered to experience restricted habitat availability in the North Sea despite
429 recent shifts.

430

431 *Plaice: connectivity to next stage in the North Sea*

432 The offshore spawning areas are clearly separated from inshore nursery grounds.
433 Closure of the life cycle through connectivity is dependent on the passive drift of eggs,
434 pelagic larval drift on residual currents, and the onshore transport of post-larvae by
435 bottom currents, which may be enhanced by selective tidal stream transport (Rijnsdorp
436 *et al.*, 1985; van der Veer *et al.*, 1998; Bolle *et al.*, 2009). For the other life stages,
437 connectivity does not seem to be a major control factor. The juveniles gradually
438 disperse into deeper water and will find a large area of suitable habitat open to them.
439 Feeding habitat for adults, which mainly occur in waters between 30-80 m, are large and
440 widely dispersed, although their suitability may be restricted by the distance to
441 spawning areas, and the possibilities of using tidal streams of sufficient speed to
442 enhance migration opportunities (Hunter *et al.*, 2003; 2004). For plaice, connectivity
443 between the spawning and the nursery grounds, therefore, is expected to be the critical
444 phase. This inference is corroborated by a number of observations. First, it has been
445 shown that the size of nursery habitat determines overall population abundance in
446 flatfish (Rijnsdorp *et al.*, 1992; van der Veer *et al.*, 2000). Second, the abundance of 0-
447 group plaice was positively correlated with the transport success as modelled with a 3D
448 hydrodynamic model using observed meteorological conditions and actual river
449 discharges (Bolle *et al.*, 2009). Thus connectivity at the larval stage from spawning to
450 nursery grounds was considered crucial for successful life cycle closure (Table 4,
451 column 3).

452

453 *Plaice: climate change impact in the North Sea*

454 With an increase in temperature under climate change scenarios and because
455 plaice in the North Sea is at the southern-most end of its latitudinal range, the suitable
456 habitat for egg production (spawning locations) is expected to become smaller.
457 Similarly, with increased temperatures the available habitat for juveniles (nursery
458 grounds) is also expected to decrease. The reduction in habitats will be detrimental to
459 productivity and may lead to a reduced population size in the North Sea. In contrast, the
460 connectivity between the pelagic phase and the nursery grounds (deemed as the crucial
461 part of life cycle closure) will probably not change substantially although changes in
462 currents are difficult to predict (see discussion). Moreover the production of *O. dioica*,
463 which is the main prey item of plaice larvae, depends upon picoplankton and can be
464 expected to be positively affected by temperature. Climate-driven match-mismatch of
465 plaice and their prey is unlikely to be an important factor in determining later life stages
466 (juveniles and adults). Therefore climate change is expected to reduce habitat suitability
467 and availability at early juvenile stage and for spawning (Table 4, columns 4 and 5).

468

469 **Atlantic cod**

470 *Atlantic cod: habitat requirements*

471 Cod are multiple batch spawners with most stocks spawning between February
472 and May, although some stocks spawn as early as January and some as late as August.
473 The earlier spawners tend to inhabit the warmer, more southern regions of the North
474 Atlantic (Fox *et al.*, 2008). Adults exhibit spawning site fidelity, and thus appear to
475 have specific habitat requirements for spawning (e.g. Wright *et al.*, 2006; Sundby and
476 Nakken, 2008). Depending on the stock and location, spawning sites occur at depths
477 between 20 and 300 m (Brander, 2005). Temperatures during spawning are stock
478 dependent and range from slightly below zero to 10 °C (Brander, 2005). The same
479 temperatures support embryo survival (Geffen *et al.*, 2006). The consistency in annual
480 spawning times among stocks (Ellertsen *et al.*, 1989) suggests that temperature may not
481 be a dominant factor affecting spawning times.

482 The spawned eggs are typically found in upper surface waters. Drift patterns of
483 eggs and larvae depend upon the stock. In some cases these early life stages are
484 transported >1000 km from spawning grounds (Vikebø *et al.*, 2007) while, in other
485 cases, they are often retained on specific banks (Werner *et al.*, 1996), in spawning

486 grounds (Hinrichsen *et al.*, 2002) or within tidal mixing or river plume fronts (Munk *et al.*,
487 *et al.*, 2009). Drift characteristics depend upon shelf topography, prevailing winds and
488 drift duration (affected via temperature-specific development rates) (Vikebø *et al.*,
489 2005).

490 Although the range of tolerable temperatures for cod larvae are considered broad
491 (Fahay *et al.*, 1999; Pörtner *et al.*, 2008), larval growth and survivorship are governed,
492 to a large extent, by match-mismatch dynamics occurring between larvae and their prey.
493 The prey consumed by larval cod varies among populations (Heath and Lough, 2007)
494 but larval growth rates increase with increasing temperature and photoperiod, with the
495 latter having a stronger influence in years of high prey abundance (Otterlei *et al.*, 1999;
496 Suthers and Sundby, 1996; Buckley *et al.*, 2006). Prey-limited growth has also been
497 documented for larval cod in the field (Buckley and Durbin, 2006). Also warmer
498 temperatures have a higher impact on the larvae energy requirements compared to later
499 life stages (Peck and Buckley, 2007).

500 After metamorphosis, pelagic juveniles undergo settlement and alter their diet to
501 become generalists (Dalpadado and Bogstad, 2004). Juveniles tend to prefer shallower
502 areas than adults and can be found over a wider range of temperatures than larvae and
503 adults (Fahay *et al.*, 1999). In many regions, juveniles preferentially use structured
504 habitats as refuges from predation (Gotceitas *et al.*, 1995; Cote *et al.*, 2004), but can
505 spread out to more open areas if no such structures are available (Ciannelli *et al.*, 2007;
506 Dingsør *et al.*, 2007). Younger individuals may inhabit less optimal conditions (colder
507 temperatures) to avoid predation, including cannibalism (Ciannelli *et al.*, 2007; Dingsør
508 *et al.*, 2007).

509 Large juveniles and adult cod have broad habitat requirements and are generalist
510 predators feeding on benthic and demersal prey. Adult cod have very broad diets that
511 can include smaller conspecifics but generally reflect availability of local resources
512 (Daan, 1974). Even for the more northern cod stocks that rely more heavily on single
513 forage species such as capelin (*Mallotus villosus*), when those prey are scarce, adult cod
514 will switch to other species including crustaceans. Overall, this implies broad habitat
515 requirements for adults during the feeding season. They also have a broad thermal
516 tolerance (Righton *et al.*, 2010) although adult NEA cod historically spawned within a
517 narrow range in water temperatures (5-7 °C: Brander, 2005). Tagging studies indicate
518 that adults of many stocks disperse over wide areas to feed but make very directed
519 migrations to specific spawning grounds (Righton *et al.*, 2007; Hobson *et al.*, 2009).

520 Thus overall, habitat requirements seem broad at adult and juvenile stage, while
521 they are smaller at larval stage and for spawning (Table 5, column 1).

522

523 *Atlantic cod: habitat availability in the Norwegian/Barents seas*

524 Important aspects of habitat availability for cod are the presence of key prey for
525 larvae, specific thermal windows allowing growth (Pörtner *et al.*, 2008), and the ability
526 of juveniles to escape predation pressure during and shortly after settlement (Juanes,
527 2007).

528 Habitat availability is likely restricted during larval stage, owing to the specific
529 zooplanktonic prey requirements, which for the Northeast Arctic (NEA) cod is *Calanus*
530 *finmarchicus* (Sundby, 2000). Correlations between the abundances of sequential life
531 stages are generally high until the larval period, indicating that critical processes operate
532 during that stage (Sundby *et al.*, 1989; Helle *et al.*, 2000). Predation pressure on
533 aggregations of juvenile cod can be very intense and localised and be critical to
534 recruitment (Temming *et al.*, 2007). Thus, availability of structured (protective) habitat
535 may act as a density-dependent bottleneck that potentially limits the survival of
536 juveniles (pre-recruits).

537 Although large juveniles and adult cod have broad habitat requirements, their
538 habitats in the Barents Sea may be restricted due to the importance of capelin in their
539 diets. Although NEA cod adjust their diets and take what is available, the production of
540 cod and abundance of capelin are strongly correlated. However, habitat requirements of
541 earlier life stages (eggs to small juveniles) are potentially more limiting.

542 Thus, we considered habitat availability variable or occasionally limiting at the
543 larval stage (Table 5, column 2) and not limiting for the other life stages.

544

545 *Atlantic cod: connectivity to next stage in the Norwegian/Barents Sea*

546 The transport of eggs and larvae from the spawning sites to the nursery grounds
547 over a 2 to 3 month period is of primary importance and the stock shows structure based
548 on that constraint. Cod in the eastern Barents Sea generally spawn in the coastal areas
549 from Lofoten northwards, while the western Barents Sea and West Spitzbergen
550 component spawn farther offshore and in the areas south of Lofoten (Randa, 1984;
551 Godø, 1986; Vikebø *et al.*, 2007). Later on, during the demersal phase, juveniles and
552 feeding adults are capable of active migrations, with adults known to range over many
553 hundreds of kilometres (Godø and Michalsen, 2000). Hence the connectivity between

554 these later life stages is not considered as problematic. However long-distance
555 migrations are energetically costly, imposing trade-offs between reproductive output
556 and the distance that can be covered to reach profitable feeding sites (Jørgensen and
557 Fiksen, 2006). From the above, we considered that variability in larval connectivity was
558 a major characteristic in cod life cycle closure (Table 5, column 3).

559

560 *Atlantic cod: climate change impacts in the Norwegian/Barents Sea*

561 Given the projected increases in water temperature, suitable habitats for cod are
562 expected to increase in the Barents and Norwegian Seas (Drinkwater, 2005). Climate-
563 driven changes in the dispersion and survival of cod eggs and larvae appear to be most
564 critical for population-level impacts. Further, climate change may influence the match-
565 mismatch dynamics between larvae and key prey including *C. finmarchicus* (Heath and
566 Lough, 2007).

567 Habitat availability may be less limiting during the juvenile to adult stages, and
568 there is evidence that growth and condition are positively affected by warmer
569 temperatures across most of the species' range (Brander 1995; Dutil and Brander,
570 2003). Climate warming may therefore improve individual juvenile and adult growth
571 conditions, although this could be offset if prey abundance decreases. On the population
572 level, improved growth conditions could be offset by declines in recruitment or
573 increased predation on early life-stages. Climate change and increased water
574 temperatures are expected to cause increase productivity in NEA cod as conditions for
575 the population will improve (Drinkwater, 2005; Cheung *et al.*, 2008).

576 For the NEA cod, changes in the dispersion of cod larvae and juveniles northward
577 to nursery grounds in the Barents Sea and West Spitzbergen may be critical. Climate-
578 driven changes in advective transport and mixing will affect dispersion and ultimately
579 the distribution of the cod, but also the temperatures they are exposed to *en route*, which
580 in turn will affect their growth rates (Vikebø *et al.*, 2005). Changes in the larval
581 dispersal pattern may result from changes in the location and time of spawning, water
582 currents and vertical and horizontal mixing. Whether the impact of altered transport
583 processes will be positive or negative cannot be determined at this time. Furthermore, it
584 is unclear whether cod can 'adapt' to changing hydrological conditions by shifting their
585 spawning sites. However, the relative importance of northerly compared to southerly
586 spawning areas of NEA cod has increased considerably during earlier and current warm
587 periods, although some spawning still occurs at southerly grounds (Sundby and Nakken,

588 2008). We consider connectivity between the demersal life stages of cod to be less
589 sensitive to climate change because these stages have higher mobility and broader
590 habitat requirements (i.e., diets, thermal range: Righton *et al.*, 2010) than eggs and
591 larvae. However, patterns of connectivity between habitats of later life stages could be
592 altered by climate-driven physiological impacts.

593 Overall, we considered climate-driven changes at the egg and larval stages to be
594 critical for NEA cod (Table 5) but, climate-driven changes in the connectivity patterns
595 at the larval stage remain uncertain.

596

597 **TOWARDS A QUANTIFICATION OF THE ANALYSIS**

598 Because of the variety of the case studies and literature sources the qualitative
599 categorizations can be difficult to assign or similar codes assigned for different reasons.
600 To identify more precisely the sensitive features of the life cycle on which climate
601 change may be impacting and thus confirm the qualitative coding performed, we
602 attempted a more quantitative characterisation of the life cycles.. For that, we
603 concentrated on temperature and food for characterizing habitat requirements, spatial
604 extend for habitat availability and distance travelled for connectivity. Ranges of
605 physiological tolerance to temperature were compared to that of conditions in their
606 natural environment at the time when the particular life history stage occurs in the
607 system. Food diversity was estimated as the Shannon-Wiener index (standardized to
608 unity) based on literature and stomach sampling data. The rationale for including food
609 diversity was that a high specificity in food requirements may be considered to enhance
610 the sensitivity of a particular life stage to changes in the environment. The availability
611 of suitable habitats for each life history stage was estimated by their spatial extent from
612 observed distribution maps. The surface area of each stage was estimated as that at
613 which 90% of the population of the stage occurred. Surface areas were standardized by
614 dividing by the largest area across the stages. Connectivity was estimated based on
615 geographical distance travelled using the distance between the gravity centres of the
616 habitats of successive life history stages. Distances were standardised to the typical
617 body size of each life history stage, and the connectivity was expressed as the
618 $\log_{10}(1/\text{distance})$. Geographical displacement is the resultant of many interactions
619 including the behavioural use of currents, temperature mediated duration of the drift or
620 migration, and energy expenditure of individuals. We considered that, whatever the
621 underlying mechanisms, precise connectivity was less probable when travelling over

622 long distances and therefore made a direct link between distance travelled and
623 connectivity. The methodology was applied to North Sea plaice and Bay of Biscay
624 anchovy as these species populations had the most contrasting life histories (Figs. 2 and
625 3).

626 For North Sea plaice (Fig. 2) habitat requirements (temperature range and food
627 diversity) are more restrictive for the early life stages than for juveniles and adults, in
628 particular because of the restrictive food regime of the larvae in winter. The juveniles
629 show the smallest spatial availability for habitats because of the specific requirements
630 for shallow coastal muddy sediments hosting particular invertebrates as food. The
631 connectivity during the larval stage between spawning grounds and nursery grounds is
632 the lowest across the life cycle and appears to be a weak point. This more quantitative
633 analysis agrees with the qualitative categorization made previously (Table 4). The life
634 cycle shows narrow habitat availability at larval and early juvenile stage as well as strict
635 connectivity at larval stage between spawning and nursery grounds. These
636 characteristics of the life cycle could be the sensitive features by which climate change
637 may impact North Sea plaice. Also, the minimum and maximum temperatures
638 experienced are slightly under and over the limits of the physiological tolerance range,
639 meaning that variability between years can also be the means by which climate change
640 is impacting.

641 In contrast, Biscay anchovy life cycle shows few bottlenecks (Fig. 3) as
642 temperature and food requirements are broad and available. The juvenile stage is the
643 most dispersed. The life cycle is predominantly characterized by a loose connectivity as
644 larvae, juveniles and adults drift / migrate long distances, which is compatible with a
645 large potential for dispersion over large suitable areas. Again, this quantification agrees
646 with the previous qualitative analysis (Table 2) where habitats were considered broadly
647 available and connectivity variable. In contrast to Biscay anchovy, North Sea plaice
648 shows more restrictions in habitats and a more restrictive connectivity. These two
649 contrasting examples give insight on how changes in habitat availability or connectivity
650 pathways can result in changes in the organisation of life cycles and thus population
651 dynamics.

652

653 **DISCUSSION**

654

655 *Life cycle summaries and identification of sensitive features*

656 In this study we developed a generic framework to characterize the full life cycle
657 of fish populations and identify sensitive features to evaluate how life cycles as a whole
658 could be modified by climate change. We considered all life history stages, their
659 habitats and connectivity between them. The output of the procedure was a qualitative
660 coding of habitat requirements, availability, and connectivity. We also included
661 examples of how metrics of different life history stages could be expressed
662 quantitatively. The approach allows a comparison of life cycle sensitivity to climate
663 change among populations by explicitly including the environmental characteristics
664 experienced within different systems.

665 To further identify sensitive features of specific populations from our life cycle
666 categories (Tables 2 to 5), we summed the number of “narrow” (requirements), “small”
667 (habitat availability) and “crucial” (connectivity) categories within tables; these
668 assessments corresponded to constraints in the life cycles (Table 6). Based upon these
669 sums, North Sea plaice and herring had more habitat bottlenecks (narrow requirements
670 or crucial availability) in their life cycles than did either Bay of Biscay anchovy or
671 Norwegian/Barents sea cod. Bay of Biscay anchovy and North Sea plaice were at two
672 extremes in terms of their ability to cope with environmental change. While Biscay
673 anchovy shows broad habitat requirements and flexible connectivity with high
674 dispersion, North Sea plaice has strict habitat requirements for both spawners and young
675 juveniles making connectivity a sensitive feature of its life cycle.

676

677 *Linking life cycle characteristics to potential climate change impacts*

678 The analysis of the life cycles identified two major, sensitive features: (i) whether
679 there was narrow habitat availability for a particular life stage representing a bottleneck
680 in the life cycle, and (ii) whether the life cycle closure depended upon strict connectivity
681 at larval stage that adults must strictly compensate strictly in space and time by a
682 “contranatant” migration and corresponding spawning site fidelity and phenology.
683 Changes in environmental conditions may reduce habitat availability and changes in
684 ocean circulation may disrupt connectivity pathways and life cycle closure. Thus to link
685 the sensitive features of the life cycles to the potential impacts of climate change, we
686 scored by summing across the rows of Tables 2 to 5 the categories “smaller” or “shift”
687 (impact on habitat availability) as these represented negative impacts on habitats.
688 Similarly, we scored the category “?” (impact on connectivity) as this category
689 represented uncertainty in expert judgement (Table 6).

690 North Sea plaice was assigned the most number of bottlenecks in its life cycle, the
691 most negative impacts of climate change on habitats, and least uncertainty in climate
692 impact on connectivity. This analysis, therefore, suggests that the probability is high
693 that North Sea plaice will be impacted by climate change. North Sea herring was also
694 assigned the most bottlenecks in its life cycle, but less negative impacts of climate
695 change on its habitats and more uncertainty in the influence of climate change on its
696 connectivity. Therefore, there is also an expectation of negative impacts of climate
697 change on North Sea herring. On the other hand, Bay of Biscay anchovy and NEA cod
698 were assigned none or few bottlenecks in their life cycle, less negative impacts of
699 climate change on habitats, and more uncertainty on the impact of climate change on
700 connectivity. Therefore the life cycle of these populations are not expected to be
701 impacted negatively by climate change. They may benefit from climate change with
702 increased habitat availability and stock productivity (Drinkwater, 2005; Stenevik and
703 Sundby, 2007; Petitgas et al., 2009a).

704 The response of life cycles as a whole to climate change involves many
705 interactions. The space-time matching of the schedule of key events in life cycles with
706 the seasonality in the environment (involving, e.g. flow fields and vertical stratification,
707 growth and maturation patterns, match-mismatch between predators and prey in all life
708 history stages: Dickey-Collas et al., 2009b; Peck *et al.*, 2009; Petitgas et al., 2009b; van
709 der Veer and Bergman, 1987) may be disrupted by climate change. If changes in habitat
710 availability for the various life stages under climate change can be predicted, leading to
711 maps of potential new distributions, the role of connectivity in the life cycle re-
712 organisation should not be overlooked as it may contradict these predictions.
713 Connectivity may be a limiting factor in successful adaptation of the species under
714 climate change. From our analysis, schematics of the global response based on the
715 interaction between changes in habitats and connectivity pathways (Table 7) suggest
716 that North Sea plaice could become a small, contracted population while the other
717 populations could change their distribution patterns if newly available habitats are
718 effectively colonized.

719

720 *Uncertainties in the predictions*

721 We developed a generic framework for assembling and categorizing knowledge
722 from the literature. Following the approach developed for dealing with complexity
723 when assessing risk in ecosystem management (e.g., Samhuri and Levin, 2012) we

724 attempted to convert qualitative categorizations (expert judgement) into quantitative
725 indicators (Figs. 2 and 3, Table 6) that served as a basis for conclusions. In doing so,
726 major uncertainties were identified. The impact of climate change on larval connectivity
727 was the greatest unknown. Changes in ocean currents and larval drift routes and
728 dispersion could either disrupt life cycle closure (Fig. 1d, Table 7) or lead to the
729 establishment of new life cycle patterns. The closure of the life cycle by larval
730 dispersion results from many interactions during the species life history and their
731 adequate seasonal scheduling, of which favourable patterns of ocean circulation, growth
732 pattern and predator-prey interactions are most critical.

733 Ocean circulation and seasonality. Due to the importance of larval connectivity in
734 the vast majority of marine fish species, predicting future changes will depend upon the
735 ability to adequately project climate-driven changes in water circulation at regional
736 scale. Projections of water circulation patterns arising from climate change are available
737 for areas such as the North Sea by dynamic downscaling of global climate models
738 (GCMs) to force a regional circulation model (Ådlandsvik, 2008). However, much more
739 work is required to provide robust projections (Hollowed *et al.*, 2009). Furthermore,
740 progress in quantitatively predicting regional population responses to climate-driven
741 changes will require the development of spatially-explicit full life cycle models. In
742 addition, advances in modelling bioenergetic budgets, trophic interactions and
743 behaviour will be necessary for the development of full life-cycle population models in
744 an end-to-end context to simulate the evolution of fish populations in different climate
745 change scenarios.

746 Trophic interactions. The match-mismatch dynamics between predators and their
747 prey were considered important in all species and populations (during one life history
748 stage at least) by altering survival and rates of growth and energy storage which
749 ultimately affects recruitment or fecundity and connectivity pathways. Furthermore,
750 warming will increase metabolic requirements, potentially changing the outcome of
751 match-mismatch dynamics between predators and preys, growth and maturity patterns,
752 and ultimately connectivity pathways between habitats of different life history stages.

753 Regional physiological adaptations. The species considered in this analysis were
754 examined within a single system but are distributed across a range of different systems.
755 Their genetic diversity has undoubtedly allowed for regional adaptation. Stage-specific
756 requirements at the level of the species could be large because of the diversity in
757 regional adaptations. Our appreciation of changes in habitat availability for a given

758 population in a regional sea did not account for regional adaptations, which is another
759 factor limiting projections of regional-scale population responses to rapid climate
760 change.

761

762 **CONCLUSION**

763 In summary, recognising that fish populations have complex life cycles that
764 comprise different stages exploiting a variety of habitats, we analysed how climate
765 change could impact the links along the life cycle. We developed a framework to
766 understand the drivers on life cycle patterns, which considered habitat requirements in
767 the different life stages at species level, habitat availability in specific ecoregions and
768 connectivity to the next stage in these systems (Fig. 1). We reviewed the knowledge
769 available for 4 species in 3 marine ecosystems and summarized results in tables
770 structured to reflect the life cycle framework (Tables 2 to 5). The analysis is generic and
771 can be applied to any specific population to analyse changes in its life cycle pattern. The
772 present review highlighted that: i) larval connectivity represented a major unknown and
773 ii) projecting climate change impacts on fish populations while disregarding life cycle
774 organization could lead to spurious conclusions as conflicting impacts on habitats and
775 connectivity need be resolved in the different life stages. Thus, full life cycle models are
776 seen as the most adequate tools to integrate the different impacts of climate across all
777 life stages.

778

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781

782

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1259 Table 1: Summary of life history characteristics for the selected species populations

	Bay of Biscay anchovy	North Sea herring	North Sea plaice	North East Arctic cod
life span (y)	4	17	25	17
Lmax (cm)	20	35	60	200
maturation age (y)	1	3	3	6
egg and larva stage duration (days)	60	120	80	80
distance travelled from spawning to nursery (km)	220	300	250	1200
spawning period	April to July	Sept to Feb	Dec to March	Feb to April
reproductive biology	indeterminate batch spawner	determinate total spawner	determinate batch spawner	determinate batch spawner nauplii
preys of larvae	microzooplankton	microzooplankton	appendicularian regenerating parts of polychaetes, bivalves	C.finmarchicus
preys of juveniles	small mesozooplankton copepods and other	small mesozooplankton copepods and other	polychaetes, bivalve s	capelin, fish, invertebrates
preys of adults	mesozooplankton	mesozooplankton		capelin, fish, invertebrates
domain of eggs then larvae	pelagic	benthic then pelagic	pelagic	pelagic
domain of juveniles & adults	pelagic	pelagic	benthic	demersal
References	Petitgas et al. 2010a	Geffen 2009 Dickey-Collas 2010	Rijnsdorp and van der Veer 2010 Bolle et al. 2009 Last 1978 de Vlas 1979 Rijnsdorp and Vingerhoed 2001	Ottersen and Sundby 2005 Vikebo 2005

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Table 2: **European anchovy in the Bay of Biscay**. Table documenting how critical the life stages are in the life cycle. Habitat requirements are at species level. Habitat availability, connectivity and climate change impacts concern the Bay of Biscay only.

Life history stage	Habitat requirements	Habitat availability	Connectivity to next stage	Climate change Habitat availability	Climate change Connectivity
Spawning					
Adults and					
eggs	medium	ok	var	larger	ok
Larvae	medium	var	var	ok	?
Juveniles	broad	var	var	larger, shift	?
Feeding adults	medium	var	ok	ok	ok

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1270 Table 3: **Atlantic herring in the North Sea**. Table documenting how critical the life stages are
 1271 in the life cycle. Habitat requirements are at species level. Habitat availability, connectivity and
 1272 climate change impacts concern the North Sea only.

Life history stage	Habitat requirements	Habitat availability	Connectivity to next stage	Climate change Habitat availability	Climate change Connectivity
Spawning					
Adults and					
eggs	narrow	small	ok	shift	ok
Larvae	narrow	var	var		?
Juveniles	broad	ok	ok	larger, shift	ok
Feeding adults	broad	ok	crucial	ok or ?	ok or ?

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1282 Table 4: **European plaice in the North Sea**. Table documenting how critical different stages
 1283 are in the life cycle. Habitat requirements are at species level. Habitat availability, connectivity
 1284 and climate change impacts concern the North Sea only.

Life history stage	Habitat requirements	Habitat availability	Connectivity to next stage	Climate change Habitat availability	Climate change Connectivity
Spawning					
Adults and eggs	medium	ok	ok	smaller	ok
Larvae	medium	ok	crucial	ok	?
Juveniles	narrow	small	ok	smaller, shift	ok
Feeding adults	medium	ok	ok	ok	ok

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1287 Table 5: **Atlantic cod in the Barents and Norwegian Seas** (North East Artic cod stock).
 1288 Habitat requirements are at species level and thus the same as in Table 4a. Habitat availability
 1289 and connectivity and climate change impacts concern the Barents and Norwegian Seas only.

Life history stage	Habitat requirements	Habitat availability	Connectivity to next stage	Climate change Habitat availability	Climate change Connectivity
Spawning					
Adults and eggs	medium	ok	ok	ok	ok
Larvae	medium	medium	ok	larger	?
Juveniles	narrow	var	var	larger	?
Feeding adults	broad	ok	ok	ok	ok

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1300 Table 6: **Analysis of the life cycle tables for each species population** (Tables 2 to 5): the
 1301 scores correspond to the number of times a particular code was assigned over all the life history
 1302 stages: number of constraints in the life cycle (out of 12), number of negative impacts (out of 4)
 1303 and number of unknown impacts (out of 4).

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	Constraints in life cycle	Climate change negative impacts on habitats	Climate change unknown impacts on connectivity
Bay of Biscay anchovy	0	0	2
North Sea herring	4	1	2
North Sea plaice	4	2	1
NEA cod	1	0	2

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1307 Table 7: Expected population response to the interaction between changes in habitats
 1308 availability and connectivity pathways.

	No Change in connectivity	Change in connectivity
No Change in Habitats	No change	Disruption of life cycle
Expansion in Habitats	No change	Change in distribution
Reduction in Habitats	Population reduction	Disruption of life cycle

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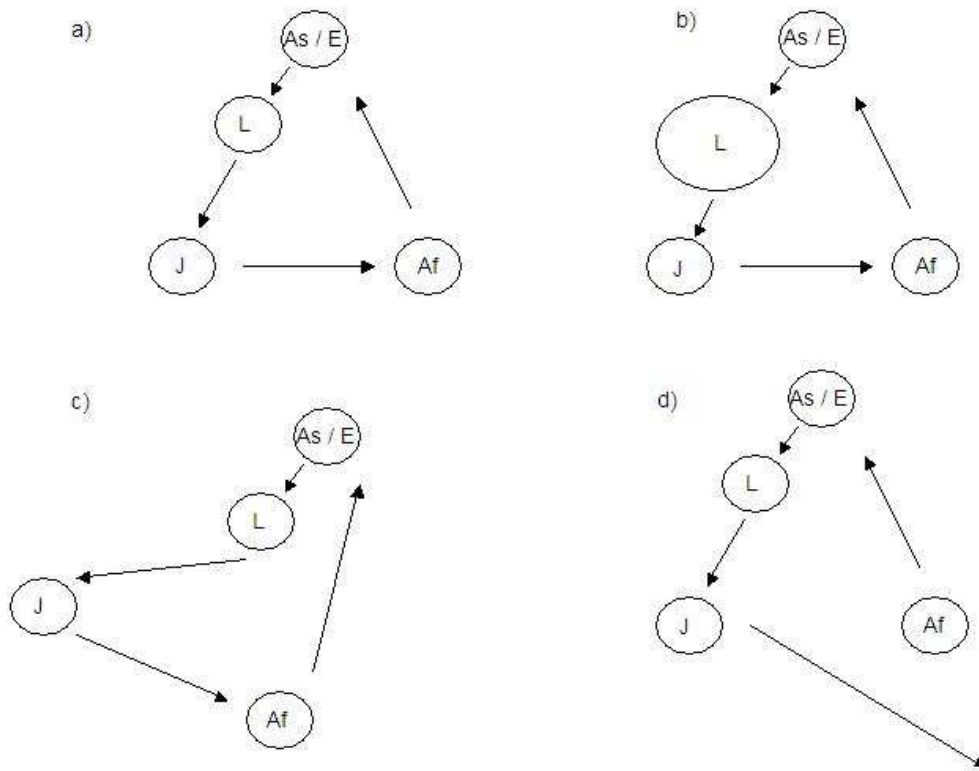
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1328 Figure 1: Schematics of a life cycle (a) and different impacts of climate change on its

1329 organization (b-d). Impacts may concern habitat availability (b, the larger the bubble the

1330 greater the availability), a shift in the location of available habitats (c, the available

1331 habitat is spatially shifted from its position in comparison to scheme a) or disruption of

1332 connectivity (d, the life cycle cannot be closed). Af: feeding adults; As/E: spawning

1333 adults and eggs; L: larvae; J: juveniles. The bubble represents the size of the

1334 multidimensional available habitat. Each arrow represents connectivity to the next stage.

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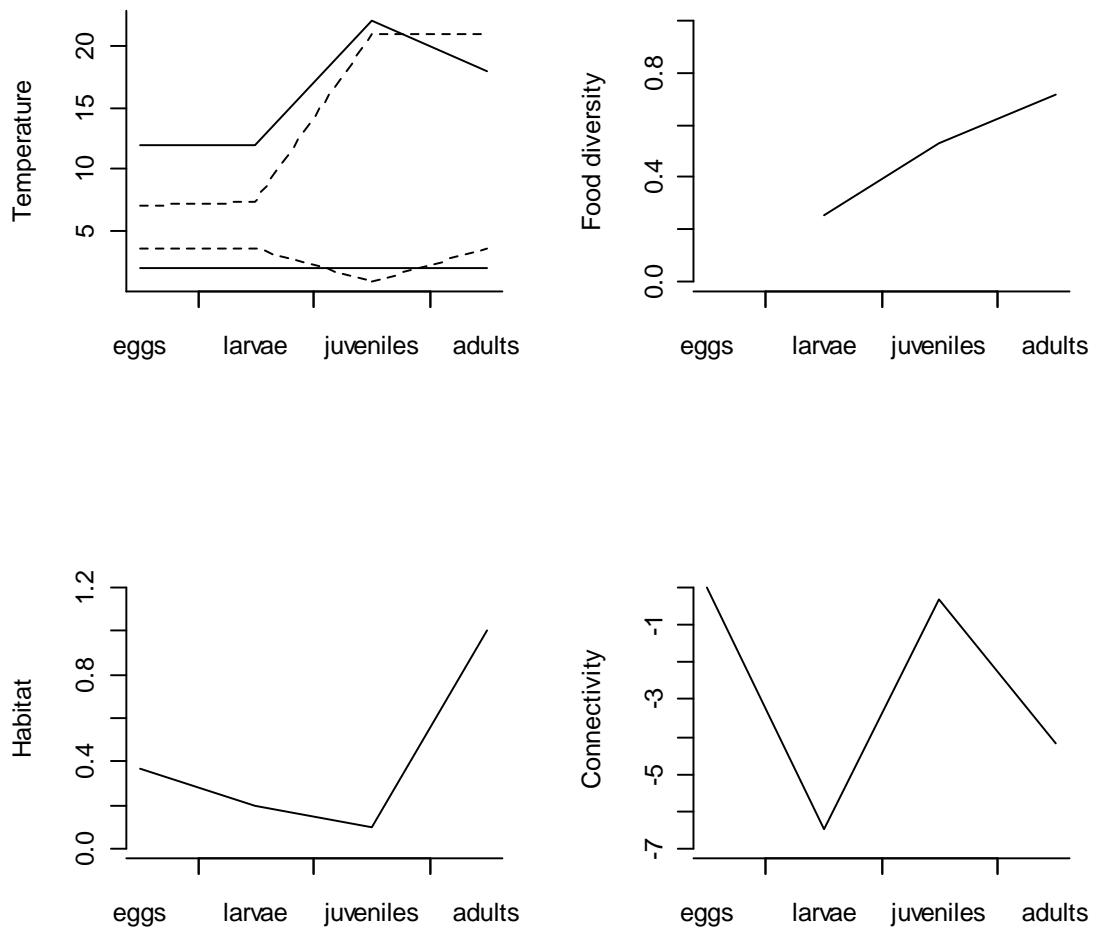
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1345 Figure 2 : North Sea plaice life cycle quantified. Upper left: physiological tolerance
 1346 range for temperature (full lines) and the temperature range observed (dashed lines).

1347 Upper right: food diversity (Shannon index standardized to unity). Lower left: habitat
 1348 spatial availability referenced to the largest habitat across the life history stages. Lower
 1349 right: connectivity between life history stages expressed as $\log_{10}(1/\text{distance travelled})$
 1350 where distance is in body length.

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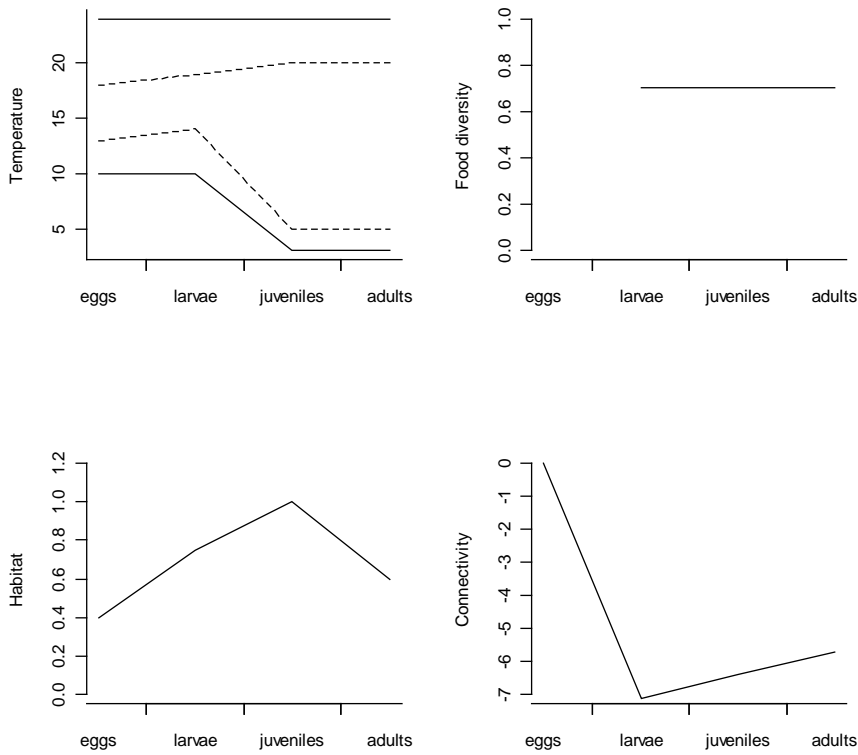
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1359 Figure 3 : Bay of Biscay anchovy. Upper left: physiological tolerance range for
 1360 temperature (full lines) and the temperature range observed (dashed lines) . Upper right:
 1361 food diversity (Shannon index standardized to unity). Lower left: habitat spatial
 1362 availability referenced to the largest habitat across the life history stages. Lower right:
 1363 connectivity between life history stages expressed as $\log_{10}(1/\text{distance travelled})$ where
 1364 distance is in body length.

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