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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.

Key words: anchovy, cod, connectivity, eco-physiology, habitat, herring, plaice

INTRODUCTION

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

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

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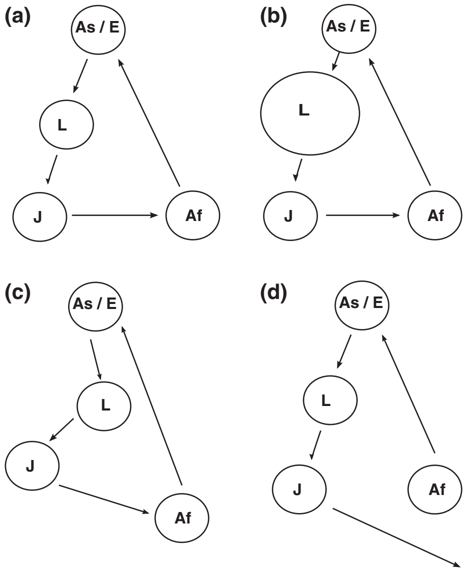
and change. Thus, it is critical to characterize the life cycle of species in terms of specific habitat requirements, habitat availability, and connectivity.

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

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

Figure 1. Schematics of a life cycle (a) and different impacts of climate change on its organization (b–d). Impacts may concern habitat availability (b, the larger the bubble the greater the availability), a shift in the location of available habitats (c, the available habitat is spatially shifted from its position in comparison to scheme a) or disruption of connectivity (d, the life cycle cannot be closed). Af, feeding adults; As/E, spawning adults and eggs; L, larvae; J, juveniles. The bubble represents the size of the multidimensional available habitat. Each arrow represents connectivity to the next stage.



ANALYSIS FRAMEWORK AND SPECIES CONSIDERED

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

Each case study was reviewed using a similar template. For each life stage, (i) physiological habitat requirements, (ii) habitat availability, and (iii) connectivity to the next life stage were examined, followed by (iv) an assessment of the likely impact of climate variability and climate change on each of these factors. *Habitat requirements* were defined by physiological requirements, critical habitat features such as specific topographic or sediment features, or other requirements that were based on first principles. Habitat requirements were ranked qualitatively in terms of importance within categories of 'narrow' (restrictive), 'medium' or 'broad' (less restrictive). *Habitat availability* considered how accessible the required conditions were to the species in the studied region, i.e., the geographical location of habitats, vertical distribution, timing in the season, etc. Habitat availability was summarized with a glossary made of three terms: 'ok' (no significant problem of availability expected), 'small' (reduced availability) or 'var' (high interannual variability). *Connectivity* considered how the habitat of one life stage was linked to that of the next life stage, such as through drift and dispersal (e.g., egg to larval phase) including the importance of behaviour (e.g., vertical movements) and 'active' migration (e.g., feeding to spawning adults). Connectivity was summarized within each of the studied regions using the following terms: 'ok' (slightly sensitive to environmental variability: connectivity assured), 'crucial' (precise connectivity needed for life cycle closure), and 'var' (high interannual variability).

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 (yrs)	4	17	25	17
Lmax (cm)	20	35	60	200
Maturation age (yrs)	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
Preys of larvae	Microzooplankton	Microzooplankton	Appendicularian	Nauplii C. *finmarchicus*
Preys of juveniles	Small mesozooplankton	Small mesozooplankton	Regenerating parts of polychaetes, bivalves	Capelin, fish, invertebrates
Preys of adults	Copepods and other mesozooplankton	Copepods and other mesozooplankton	Polychaetes,bivalves	Capelin, fish, invertebrates
Domain of eggs then larvae	Pelagic	Benthic then pelagic	Pelagic	Pelagic
Jdomain of uveniles and 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), Vikebø *et al.* (2005)

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

To evaluate the potential impact of climate change on life cycles, we focused the analyses of impacts on the availability of suitable habitats for the different life stages and on the connectivity between habitats and life stages. Again, a qualitative categorization was used to characterize the expected impacts. The following categories were used: ‘larger’ or ‘smaller’ (spatio-temporal extension or contraction of suitable habitats), ‘shift’ (spatio-temporal displacement of suitable habitats), ‘ok’ (no particular impact expected), and ‘?’ (unknown consequences).

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

European anchovy

European anchovy: habitat requirements. European anchovy is a fecund, indeterminate multiple batch spawner. The start of the spawning season coincides with the initiation of seasonal stratification and a

Table 3. Atlantic herring in the North Sea. 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 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 ?

Table 4. European plaice in the North Sea. Table documenting how critical different stages are in the life cycle. Habitat requirements are at species level. Habitat availability, connectivity 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

Table 5. Atlantic cod in the Barents and Norwegian Seas (North East Artic cod stock). Habitat requirements are at species level. Habitat availability, 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

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

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

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

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

European anchovy: habitat availability in the Bay of Biscay. Pelagic habitats within the Bay of Biscay are dynamic and characterized by the presence of a variety of meso-scale physical features such as river plumes, upwelling areas, gyres, eddies, and fronts, with the strength of these features depending upon the season and climatic conditions (Koutsikopoulos and Le Cann, 1996). The anchovy life cycle in the Bay of Biscay is associated with seasonal changes in a variety of these physical features and to specific biological factors. For example, water temperature is one of the triggers for spawning and interannual differences in water temperature may lead to interannual differences in spawning times. Moreover, clear limits to habitat availability for spawning exist in the northern Bay of Biscay, where water temperatures are often too cold and unsuitable for spawning until late spring. The spawning duration may vary between years depending upon the feeding conditions encountered on spawning grounds. In spring, the zooplankton production seems sufficient, as no feeding limitation has been reported (Marquis *et al.*, 2006). In summer, warmer temperatures associated with lower plankton production can be unsuitable for the adults in the southern Biscay (Struski *et al.*, 2009). Larval drift can vary significantly among years depending on wind conditions and river discharges (Allain *et al.*, 2007; Huret *et al.*, 2010), with consequences for survival and ultimately recruitment. Specifically, prey fields may vary with hydrographic conditions and higher predation is thought to occur within on-shelf areas as opposed to off-shelf areas (Irigoien *et al.*, 2007). Autumn and winter temperature and feeding conditions also affect reserve storage and juvenile growth, with consequences for the energy available for spawning in the subsequent spring (Pecquerie *et al.*, 2009). Thus, the habitat requirements of anchovy in the Bay of Biscay in the different life stages seem to be satisfied in many but not all years, as evidenced by the recruitment variability observed in the region. Therefore, we considered habitat availability to not be limiting, but variable from year to year (Table 2, column 2).

European anchovy: habitat connectivity in the Bay of Biscay. Connectivity between habitats for the Bay of Biscay anchovy population was summarized in Petitgas *et al.* (2010a). The spring spawning habitats are mainly located in the southern regions of the Bay of Biscay, associated with river plumes, as well as offshore close to the shelf-break (Motos *et al.*, 1996). From these locations, larval drift is generally oriented along the shelf to the southwest, although large cross-shelf dispersion can also occur. Late larvae and early juvenile habitats are widely distributed, covering the shelf and off-shelf areas (Irigoien *et al.*, 2008; Petitgas *et al.*, 2010a), but they appear to be mostly confined to the south of the bay. Offshore juveniles actively migrate back to the coastal areas. The mechanism controlling this migration is unknown. When they encounter adults and recruit to the population in autumn, juveniles change their schooling behaviour (Petitgas, 2007). Adults seem, therefore, to play the role of facilitators, enhancing naive juveniles to rapidly adopt adequate, habitat-specific behaviours which, theoretically, could reduce mortality. Life cycle closure and habitat connectivity between spawning and recruitment is believed to be under the direct influence of variability in larval drift. Although larvae may drift to areas providing survival into the juvenile stage, connectivity in the life cycle may be disrupted if those juveniles do not encounter adults. As for habitat availability, the major characteristic of connectivity was the large interannual variability (Table 2, column 3).

European anchovy: climate change impact in the Bay of Biscay. For anchovy in the Bay of Biscay, different models constructed for different life stages predicted an expansion of the population to the north under scenarios of climate change (Petitgas *et al.*, 2009a). An increase in temperature throughout the year may influence the potential habitats of the adults towards a more northern distribution at spawning time. Winter unsuitability may decrease over the entire Bay of

Biscay due to warmer temperatures but warmer summer temperatures associated with lower zooplankton production may increase the unsuitability of habitats in southern Biscay (Struski *et al.*, 2009). An increase in temperature may shift peak spawning by 1 month earlier in the season (Petitgas *et al.*, 2009a). In this situation and given current seasonal circulation patterns, the larvae may disperse more towards the north (Huret *et al.*, 2009). Under such a scenario, changes in the larval dispersion patterns could disrupt the current life cycle organization in space and time. The survival probability of juveniles in novel areas is unknown, as is the potential for connectivity with new adult habitats.

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

Atlantic herring

Atlantic herring: habitat requirements. Atlantic herring have specific habitat requirements for spawning. They are benthic spawners and deposit their eggs on solid substrates, whether these be course sand, gravel or boulders (Blaxter and Hunter, 1982; Geffen, 2009). In the Baltic, they also spawn on macro-algae or mussel beds (Casini, 2010). Herring generally spawn in areas of well mixed water and it can be assumed that they require high oxygen saturation (Parrish *et al.*, 1959; Aneer, 1985). They display great plasticity in spawning habitats across the species (Geffen, 2009), thus, although individual populations may utilize specific habitats, overall habitat requirements for spawning are quite broad. Atlantic herring populations can be found spawning in all months of the year (Dickey-Collas *et al.*, 2009a) and have a relatively wide temperature tolerance for spawning (4–15°C: Pörtner and Peck, 2010; Peck *et al.*, 2012). Salinity has been correlated to the genetic sub-species structure of Atlantic herring but, across the species, herring can spawn from 4 to 35 salinity units (Gaggiotti *et al.*, 2009). They are generally thought to have predictable migration routes and spawning site fidelity (Sinclair, 1988), in which learning plays an important role (McQuinn, 1997; Petitgas *et al.*, 2010b). However, this is not always the case, as the location of spawning sites for Norwegian Spring spawning herring change as the fish get older and longer (Slotte, 1999). Thus, habitat requirements for spawning could be considered limiting for a herring population in a particular area.

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

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

The main factors that determine adult feeding habitats are zooplankton biomass, hydrography and seabed substrate in the North, Norwegian and Baltic Seas (Maravelias and Reid, 2000; Nøttestad *et al.*, 2007; Peltonen *et al.*, 2007). These three factors often covary spatially (Maravelias, 2001).

Thus overall, adult feeding and juvenile habitats were considered 'broad', whereas those of eggs and young were classified as 'narrow' (Table 3, column 1).

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

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

In the case of the northern North Sea, larvae are occasionally entrained in northward flowing currents and are transported to the central coastline of Norway (Fossum and Moksness, 1993), where they mix with spring-spawned larvae of Norwegian/fjordic populations. The fate of these autumn-spawned larvae is unknown (i.e., whether they are adopted into the Norwegian spring spawning populations or die, or return to the North Sea). There is evidence that late larvae and juveniles from the stocks to the west of the British Isles utilize portions of the northern North Sea as nursery areas (Heath, 1989; ICES, 1994). Again, the fate of these fish is unknown (i.e., whether they return to their parent stock, die or become North Sea herring by adoption).

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

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

Atlantic herring: climate change impact in the North Sea. Although North Sea herring is close to its southern-most boundary in the Northeast Atlantic (the Bay of Biscay), little evidence exists to suggest that an increase in sea temperature of 1–2°C, will reduce the suitable habitat for the species, as the range in tolerable temperatures is broad (up to 20°C in the Baltic). However the mortality of larvae does co-vary with increasing temperature in the northern North Sea (Fässler *et al.*, 2011), suggesting that temperature may impact productivity. As herring spawn layers of benthic eggs, any reduction in dissolved oxygen, through less mixing, increased eutrophication, etc., is expected to decrease egg survival. Also, the higher prey requirements after yolk absorption associated with warmer temperatures may indirectly limit the spatial and temporal extent of habitats allowing larval survival. Temperature is also expected to affect the growth of juveniles and adults, with cohorts experiencing warmer temperature growing faster and reaching a smaller asymptotic size than individuals within cohorts growing at colder temperatures (Brunel and Dickey-Collas, 2010). How this would affect overall population productivity remains unclear. In relation to a changing growth pattern the spawning strategy could be impacted: it has been suggested that an increase in temperature favours the autumn spawning strategy in western Atlantic herring stocks (Melvin *et al.*, 2009), and Hufnagl and Peck (2011) show a physiological link between larval survival at seasonal temperature and the zooplankton production cycle. Whether life history closure is possible given a different spawning strategy and a changed zooplankton production cycle is unknown. Furthermore, an increase in biodiversity in the North Sea (e.g., increase in anchovy and sardine) may also introduce competition for pelagic habitats due to overlap in zooplankton diet (Raab *et al.*, in press). Overall, habitat availability in a changed climate is not expected to be limiting but habitats utilized may possibly shift towards higher latitudes (Table 3, column 4).

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

European plaice

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

Mortality rates of eggs and larvae tend to increase with increasing temperature (Rijnsdorp and Vingerhoed, 1994; Dickey-Collas *et al.*, 2003), possibly due to an associated increase in predation mortality (e.g., Harding *et al.*, 1978; van der Veer, 1985; Seegers *et al.*, 2007).

Plaice larvae feed on prey items abundant in the winter, such as the appendicularian *Oikopleura dioica* (Shelbourne, 1953; Last, 1978). There are no studies reporting the importance of a match–mismatch between the timing of plaice spawning and food availability or on the presence of potential predators on eggs and larvae (e.g., herring and sprat). Around metamorphosis, larvae become demersal and settle onto nursery grounds which are generally inshore, shallow (<10 m deep), sandy or muddy areas (e.g., Able *et al.*, 2005; Gunnarsson *et al.*, 2010). During settlement, the temporal and spatial overlap with predators is a key, temperature-dependent match–mismatch process affecting the survival of plaice settlers (post-larvae) in shallow nursery habitats (van der Veer and Bergman, 1987). Juvenile plaice feeds on a variety of macrobenthic species (de Vlas, 1979), whereas larger demersal stages mainly feed on polychaetes and molluscs (Rijnsdorp and Vingerhoed, 2001). As they grow, plaice gradually disperse from shallow coastal nurseries into deeper water. After maturation they seasonally migrate between spawning and feeding grounds. Demersal stages of plaice have a clear preference for soft sediments with a grain size of coarse to very fine sand (e.g., Gibson and Robb, 2000).

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

Plaice: habitat availability in the North Sea. The extent of suitable habitats for post-larvae (during settlement) is much smaller than that of the earlier or later life history stages and the total population abundance of plaice seems to be related to the availability of suitable settlement nursery grounds (Rijnsdorp *et al.*, 1992; van der Veer *et al.*, 2000). Density-dependent processes are restricted to the phase where plaice are concentrated in nearshore nursery grounds (Beverton, 1995; Nash and Geffen, 2000; van der Veer *et al.*, 2000). Nursery ground quality will be affected by the productivity of suitable benthic food and by the abundance of potential predators (see above). Except for the 0-group, no correlation exists between interannual variability in growth rate and water temperatures (Rijnsdorp and van Leeuwen, 1996; Teal *et al.*, 2008). Growth variability therefore seems to be determined by variations in benthic productivity due to variations in ocean climate, eutrophication and the effect of bottom trawling or habitat modification (Rijnsdorp and van Leeuwen, 1996). Suitable sediment types and polychaete/mollusc prey of larger juveniles and adults are widely available throughout the North Sea. Over the last 20 yrs, juvenile and adult plaice have shifted to deeper and more northern areas, likely in response to warming (van Keeken *et al.*, 2007; Engelhard *et al.*, 2011b).

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

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

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

Atlantic cod

Atlantic cod: habitat requirements. Cod are multiple batch spawners with most stocks spawning between February and May, although some stocks spawn as early as January and some as late as August. The earlier spawners tend to inhabit the warmer, more southern regions of the North Atlantic (Fox *et al.*, 2008). Adults exhibit spawning site fidelity, and thus appear to have specific habitat requirements for spawning (e.g., Wright *et al.*, 2006; Sundby and Nakken, 2008). Depending on the stock and location, spawning sites occur at depths between 20 and 300 m (Brander, 2005). Temperatures during spawning are stock-dependent and range from slightly below 0 to 10°C (Brander, 2005). The same temperatures support embryo survival (Geffen *et al.*, 2006). The consistency in annual spawning times among stocks (Ellertsen *et al.*, 1989) suggests that temperature may not be a dominant factor affecting spawning times.

The spawned eggs are typically found in upper surface waters. Drift patterns of eggs and larvae depend upon the stock. In some cases these early life stages are transported >1000 km from spawning grounds (Vikebø *et al.*, 2007); in other cases, they are often retained on specific banks (Werner *et al.*, 1996), in spawning grounds (Hinrichsen *et al.*, 2002) or within tidal mixing or river plume fronts (Munk *et al.*, 2009). Drift characteristics depend upon shelf topography, prevailing winds and drift duration (affected via temperature-specific development rates) (Vikebø *et al.*, 2005).

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

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

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

Thus overall, habitat requirements seem broad at the adult and juvenile stages but are smaller at the larval stage and for spawning (Table 5, column 1).

Atlantic cod: habitat availability in the Norwegian/Barents Seas. Important aspects of habitat availability for cod are the presence of key prey for larvae, specific thermal windows allowing growth (Pörtner *et al.*, 2008), and the ability of juveniles to escape predation pressure during and shortly after settlement (Juanes, 2007).

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

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

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

Atlantic cod: connectivity to next stage in the Norwegian/Barents Sea. The transport of eggs and larvae from the spawning sites to the nursery grounds over a 2–3 month period is of primary importance and the stock shows structure based on that constraint. Cod in the eastern Barents Sea generally spawn in the coastal areas from Lofoten northwards, while the western Barents Sea and West Spitzbergen component spawn farther offshore and in the areas south of Lofoten (Randa, 1984; God, 1986; Vikebø *et al.*, 2007). Later on, during the demersal phase, juveniles and feeding adults are capable of active migrations, with adults known to range over many hundreds of kilometres (God and Michalsen, 2000). Hence the connectivity between these later life stages is not considered problematic. However long-distance migrations are energetically costly, imposing trade-offs between reproductive output and the distance that can be covered to reach profitable feeding sites (Jørgensen and Fiksen, 2006). From the above, we considered that variability in larval connectivity was a major characteristic in cod life cycle closure (Table 5, column 3).

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

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

For the NEA cod, changes in the dispersion of cod larvae and juveniles northward to nursery grounds in the Barents Sea and West Spitzbergen may be critical. Climate-driven changes in advective transport and mixing will affect dispersion and ultimately the distribution of the cod, but the temperatures they are exposed to *en route*, will in turn affect their growth rates (Vikebø *et al.*, 2005). Changes in the larval dispersal pattern may result from changes in the location and time of spawning, water currents and vertical and horizontal mixing. Whether the impact of altered transport processes will be positive or negative cannot be determined at this time. Furthermore, it is unclear whether cod can 'adapt' to changing hydrological conditions by shifting their spawning sites. However, the relative importance of northerly compared with southerly spawning areas of NEA cod has increased considerably during earlier and current warm periods, although some spawning still occurs at southerly grounds (Sundby and Nakken, 2008). We consider connectivity between the demersal life stages of cod to be less sensitive to climate change because these stages have higher mobility and broader habitat requirements (i.e., diets, thermal range: Righton *et al.*, 2010) than eggs and larvae. However, patterns of connectivity between habitats of later life stages could be altered by climate-driven physiological impacts.

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

TOWARDS A QUANTIFICATION OF THE ANALYSIS

Because of the variety of the case studies and literature sources, the qualitative categorizations can be difficult to assign or similar codes may be assigned for different reasons. To identify more precisely the sensitive features of the life cycle on which climate change may be impacting and thus confirm the qualitative coding performed, we attempted a more quantitative characterization of the life cycles. For that, we concentrated on temperature and food for characterizing habitat requirements, spatial extent for habitat availability, and distance travelled for connectivity. The range of physiological tolerance to temperature in each life history stage was compared to the temperature range in the natural environment. Food diversity was estimated as the Shannon–Wiener index (standardized to unity) based on literature and stomach sampling data. The rationale for including food diversity was that a high specificity in food requirements may be considered to enhance the sensitivity of a particular life stage to changes in the environment. The availability of suitable habitats for each life history stage was estimated by their spatial extent from observed distribution maps. The surface area of each stage was estimated as that at which 90% of the population of the stage occurred. Surface areas were standardized by dividing by the largest area across the stages. Connectivity was estimated based on geographical distance travelled using the distance between the gravity centres of the habitats of successive life history stages. Distances were standardized to the typical body size of each life history stage, and the connectivity was expressed as the $\log_{10}$(1/distance travelled). Geographical displacement is the resultant of many interactions including the behavioural use of currents, temperature-mediated duration of the drift or migration, and energy expenditure of individuals. We considered that, whatever the underlying mechanisms, precise connectivity was less probable when travelling over long distances and therefore made a direct link between distance travelled and connectivity. The methodology was applied to North Sea plaice and Bay of Biscay anchovy, as these species populations had the most contrasting life histories (Figs 2 and 3).

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

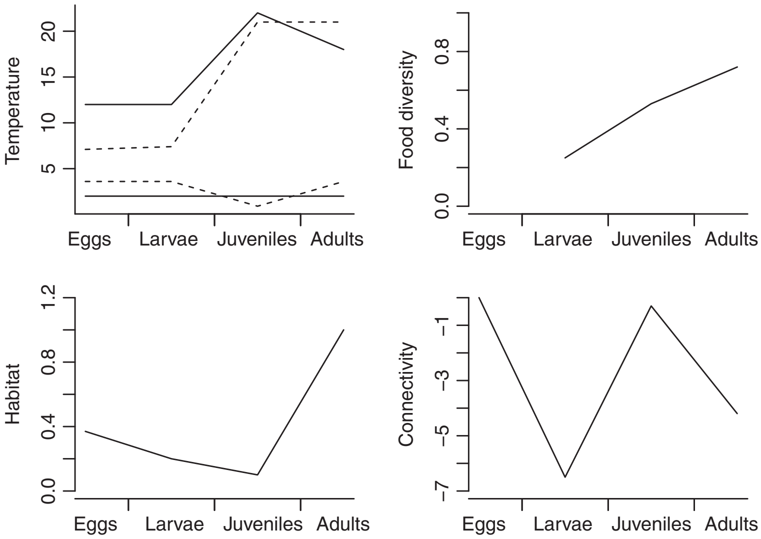


Figure 2. North Sea plaice life cycle quantified. Upper left: physiological tolerance range for temperature (full lines) and the temperature range observed (dashed lines). Upper right: food diversity (Shannon index standardized to unity). Lower left: habitat spatial availability referenced to the largest habitat across the life history stages. Lower right: connectivity between life history stages expressed as $\log_{10}(1/\text{distance travelled})$ where distance is in body length.

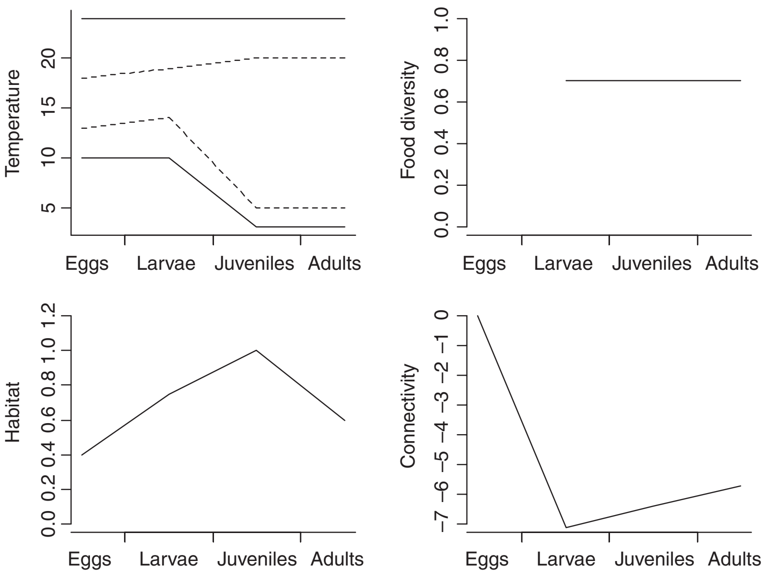


Figure 3. Bay of Biscay anchovy life cycle quantified. Upper left: physiological tolerance range for temperature (full lines) and the temperature range observed (dashed lines). Upper right: food diversity (Shannon index standardized to unity). Lower left: habitat spatial availability referenced to the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

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

DISCUSSION

Life cycle summaries and identification of sensitive features

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

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

Linking life cycle characteristics to potential climate change impacts

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

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

	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

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

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

Uncertainties in the predictions

We developed a generic framework for assembling and categorizing knowledge from the literature. Following the approach developed for dealing with complexity when assessing risk in ecosystem management (e.g., Samhouri and Levin, 2012) we attempted to convert qualitative categorizations (expert judgement) into quantitative indicators (Figs 2 and 3, Table 6) that served as a basis for conclusions. In doing so, major uncertainties were identified. The impact of climate change on larval connectivity was the greatest unknown. Changes in ocean currents and larval drift routes and dispersion could either disrupt life cycle closure (Fig. 1d, Table 7) or lead to the establishment of new life cycle patterns. The closure of the life cycle by larval dispersion results from many interactions during the species life history and their adequate seasonal scheduling, of which favourable patterns of ocean circulation, growth pattern and predator–prey interactions are most critical.

Ocean circulation and seasonality

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

Table 7. Expected population response to the interaction between changes in habitats 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

Trophic interactions

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

Regional physiological adaptations

The species considered in this analysis were examined within a single system but are distributed across a range of different systems. Their genetic diversity has undoubtedly allowed for regional adaptation. Stage-specific requirements at the level of the species could be large because of the diversity in regional adaptations. Our appreciation of changes in habitat availability for a given population in a regional sea did not account for regional adaptations, which is another factor limiting projections of regional-scale population responses to rapid climate change.

CONCLUSION

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

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