

REVIEWS AND SYNTHESIS

Plastic and evolutionary responses to climate change in fish

Lisa G. Crozier¹ and Jeffrey A. Hutchings^{2,3}¹ Northwest Fisheries Science Center, Seattle, WA, USA² Department of Biology, Dalhousie University, Halifax, NS, Canada³ Department of Biosciences, Centre for Ecological and Evolutionary Synthesis, University of Oslo, Oslo, Norway**Keywords**

adaptation, climate change, evolutionary theory, fisheries management, life-history evolution, phenotypic plasticity

Correspondence

Lisa G. Crozier, Northwest Fisheries Science Center, 2725 Montlake Blvd E., Seattle, WA 98112, USA.

Tel.: +1 206 860 3395

fax: +1 206 860 3267

e-mail: lisa.crozier@noaa.gov

Received: 10 May 2013

Accepted: 31 October 2013

doi:10.1111/eva.12135

Abstract

The physical and ecological ‘fingerprints’ of anthropogenic climate change over the past century are now well documented in many environments and taxa. We reviewed the evidence for phenotypic responses to recent climate change in fish. Changes in the timing of migration and reproduction, age at maturity, age at juvenile migration, growth, survival and fecundity were associated primarily with changes in temperature. Although these traits can evolve rapidly, only two studies attributed phenotypic changes formally to evolutionary mechanisms. The correlation-based methods most frequently employed point largely to ‘fine-grained’ population responses to environmental variability (i.e. rapid phenotypic changes relative to generation time), consistent with plastic mechanisms. Ultimately, many species will likely adapt to long-term warming trends overlaid on natural climate oscillations. Considering the strong plasticity in all traits studied, we recommend development and expanded use of methods capable of detecting evolutionary change, such as the long term study of selection coefficients and temporal shifts in reaction norms, and increased attention to forecasting adaptive change in response to the synergistic interactions of the multiple selection pressures likely to be associated with climate change.

Introduction

Anthropogenic climate change¹ is one of the most important threats to global biodiversity over the next century (Sala et al. 2000; Thomas et al. 2004; Lovejoy and Hannah 2005). Now that ‘Warming of the climate is unequivocal’ (IPCC 2013), how are biological systems reacting? A rich literature documents *potential* evolutionary and plastic responses to physical drivers in fish. However, predicting *actual* responses in natural populations remains a core challenge because observed responses typically fail to match predictions based on theory or laboratory experiments (Merilä et al. 2001). To clarify what patterns have been observed, we undertook a specific review of the literature that detected phenotypic responses to climate change in wild fish populations, with a particular interest in the

extent to which these responses could be attributed to evolutionary or plastic processes.

To anticipate the phenotypic consequences of climate change in fish, we can draw on a vast literature (for reviews, see Brett 1956; Fry 1967; Brett 1995; Wootton 1998; Walters and Martell 2004; Rijnsdorp et al. 2009). This volume of work stems from the high economic and cultural value of fisheries globally, fish farming and hatcheries, the aquarium trade, and use of fish as model systems in developmental genetics and disease research. The concept of fisheries-induced evolution, initiated primarily in the late 1970s/early 1980s (Handford et al. 1977; Ricker 1981), generated numerous analyses to evaluate the magnitude and likelihood of this form of evolutionary change (reviewed by Dieckmann and Heino 2007; Hutchings and Fraser 2008). Over roughly the same period of time, the salmon aquaculture industry and the salmonid hatchery ‘industry’ generated numerous papers pertaining to selection responses, trait heritability, temperature effects on myriad characteristics and genetic differentiation (e.g. references cited by Mousseau and Roff 1987; Purdom 1993). Armed with

¹We use the term anthropogenic climate change *sensu* the United Nations Framework Convention on Climate Change as ‘a change in climate due to human activity that alters the composition of the global atmosphere and which is in addition to natural climate variability observed over comparable time periods’.

significantly enhanced (relative to most other taxa) empirically and financially rewarding research opportunities, fish geneticists, population biologists, ecologists and evolutionary biologists have made considerable advances in our knowledge of adaptation, selection responses, and rates of evolutionary change in fishes (e.g. Carlson et al. 2004; Hendry and Stearns 2004; Barrett et al. 2011). However, the profoundly intertwined mechanisms of evolution and plasticity in most climate-sensitive traits presents a major challenge for detecting adaptation to climate change in natural populations.

Reaction norms and acclimation

Phenotypic responses (e.g. growth rate, timing of reproduction) to environmental conditions, especially temperature, are routinely plastic in nature, but genetic variability differentiates the plastic response among families within populations, among populations and between species (e.g. Haugen and Vøllestad 2000; Jensen et al. 2008; Baumann and Conover 2011; Hutchings 2011). Reaction norms, graphical representations of phenotypic change along an environmental gradient (Scheiner 1993; Schlichting and Pigliucci 1998; Hutchings et al. 2007), constitute a standard means of describing plasticity. Evidence of genetic differentiation, and possible adaptation, appear through differences in the shape, intercept and (or) slope of reaction norms (Lande 2009; Chevin et al. 2010).

Plasticity in stress tolerance usually takes the form of 'acclimation', in which a history of exposure to particular conditions changes an organism's response to a challenge (Angilletta 2009; Kassahn et al. 2009). Because climate change involves prolonged exposure to altered conditions, acclimation will presumably play a key role in effecting phenotypic changes (Stillman 2003; Hofmann and Todgham 2010). Experiments measuring stress tolerance typically expose all individuals to a common rearing environment, attempting to control for acclimation responses (Beitinger et al. 2000; Johansen and Jones 2011). Variation in the extent to which acclimation alters performance can, in some instances, reflect local adaptation, as evidenced by Antarctic fishes that experience unusually constant temperatures (Bilyk and DeVries 2011). However, the conditions necessary to trigger an acclimatory response differ among species, complicating full characterization of this response by experimental methods. For example, prolonged warm acclimation enhances high-temperature tolerance in killifish (*Fundulus heteroclitus*), but repeated heat shocks do not (Healy and Schulte 2012). In zebrafish (*Danio rerio*), developmental plasticity affects acclimation to temperature substantially later in life (Scott and Johnston 2012). Similarly, developmental conditions can affect reaction norms for growth in Atlantic cod, *Gadus morhua*

(Hurst et al. 2012). Thus, short-term exposure to acclimatory conditions during later life stages might underestimate the full acclimation potential of some species. At the extreme, a full generation might be necessary to trigger acclimation responses, as shown in the tropical damselfish *Acanthochromis polyacanthus* (Donelson et al. 2012) and sheepshead minnows *Cyprinodon variegatus* (Salinas and Munch 2012).

Are these responses adaptive?

There is some evidence that genetic changes in phenotypically plastic responses to temperature can be adaptive. One notable example in freshwater fish pertains to Norwegian populations of grayling (*Thymallus thymallus*). Although they once shared a common ancestor, the populations have been reproductively isolated from one another and exposed to different environments for more than 15 generations. Based on the results of a common-garden experimental protocol, this timeframe was sufficient to allow for population differences to emerge in plastic responses of several early-life traits to temperature (Haugen and Vøllestad 2000). Populations in colder lakes developed a more cold-adapted reaction norm for growth, including better growth at cooler temperatures and more efficient conversion from yolk to body mass compared with populations from warmer lakes (Kavanagh et al. 2010). These responses show a signature of selection as opposed to genetic drift ($Q_{st} > F_{st}$), and these patterns correlated with lake temperature rather than physical distance.

Arguments in favour of the hypothesis that population differences in thermal reaction norms represented adaptive responses to local environments were based on observations that the traits examined were closely linked to fitness and that survival was highest at the temperatures that they were most likely to experience in the wild (a similar approach was adopted by Hutchings et al. 2007 in their reaction-norm study in Atlantic cod). The hypothesis that genetic variation in plasticity represents adaptive responses to different thermal regimes in early life is also supported by the discovery of temperature-associated SNPs (single nucleotide polymorphisms) in Atlantic cod that appear to be under selection (Bradbury et al. 2010, 2013). A particularly interesting example of genomic thermal plasticity in fish was reported by Croisetière et al. (2010) in brook trout (*Salvelinus fontinalis*). They found that the way in which the expression of the MHC classII β gene changes with temperature is associated with the basepair length of an associated temperature-sensitive mini-satellite, which may suggest a genomic underpinning for thermal plasticity. Immune-relevant genes in general follow latitudinal clines that are correlated with temperature (Dionne et al. 2007; Tonteri et al. 2010).

Common-garden experiments have featured prominently in many studies of the adaptive significance of population differences in phenotypic responses to temperature (Franks et al. 2013). Particularly relevant examples in fish include those of countergradient variation, which occurs when genetic differences counteract environmental effects, reducing phenotypic variation between populations; it is expected when stabilizing selection favours similar phenotypes in different environments (Conover and Schultz 1995). In fishes, evidence that countergradient variation reflects adaptation to thermal environments exists for some species – for example, Atlantic silversides, *Menidia menidia* (Conover and Present 1990) and Atlantic cod (Marcil et al. 2006) but not necessarily others – for example, mummichog, *Fundulus heteroclitus* (Fangue et al. 2009).

Given the genetic variability in temperature responses documented in many fish species (Beitinger et al. 2000), coupled with persuasive evidence in support of the hypothesis that phenotypic responses to temperature can be adaptive, it seems highly probable that many fish possess sufficient additive genetic variability to respond adaptively to climate change, although our review reveals only limited evidence of this to date.

Primary physical impacts of climate change relevant for fishes

The two primary physical drivers of climate change in the ocean are rising ocean temperature and carbon dioxide absorption (Hoegh-Guldberg and Bruno 2010; Gruber 2011; Hale et al. 2011; Koehn et al. 2011; Doney et al. 2012; Gruber et al. 2012; Collins 2014; Reusch 2014). These drivers have clearly changed over the past century in response to rising greenhouse gas emissions (IPCC 2007; Blunden and Arndt 2013; NCADAC 2013). Effects of warming oceans cascade beyond temperature change alone to alter Arctic ice volume, sea level and hence coastal habitat quality and quantity, salinity, vertical stratification, weather (i.e. precipitation, storm intensity and wind; Francis and Vavrus 2012; Liu et al. 2012), ocean current circulation and hypoxia (i.e. low oxygen levels; IPCC 2007). Carbon dioxide absorption interacts with many of these thermally induced phenomena to increase exposure to corrosive and hypoxic water. Rates of change vary geographically and in some cases local processes reverse the global trends (e.g. more intense wind shear can increase coastal upwelling of deep water, which reduces local temperatures because deep water is much cooler than surface water). Forecasted large-scale changes in ocean circulation patterns are uncertain, as are consequences for multidecadal oscillations in climate, as reflected by indices such as the North Atlantic Oscillation (NAO), the Pacific Decadal Oscillation (PDO) and El Niño-Southern Oscillation (ENSO).

In fresh water, the primary drivers of climate change include rising water temperature, altered hydrological regimes (i.e. the timing of flows of different magnitudes), thermal stratification, decreased dissolved oxygen and increased toxicity of pollutants (Ficke et al. 2007; Stoks et al. 2014; Urban 2014). Hydrological regimes are in transition in regionally specific ways, including shifts in the magnitude and timing of floods, increasingly intense droughts and heat waves (IPCC 2012). More frequent and more intense precipitation events have numerous consequences, including added run-off of pollutants and nutrients into the water, increasing sediment load and eutrophication. These inputs can reduce the quality of fish habitat and result in harmful algal blooms and hypoxic 'dead zones' (NCADAC 2013). Loss of water, due to increased water vapour in the air and competition with humans, will affect groundwater, aquifers and wetlands. Many cold-water fish are expected to move or contract their ranges to higher elevation (Wenger and Olden 2012), while warm-water invasive species expand their ranges (Rahel and Olden 2008; Al-Chokhachy et al. 2013). Key fish habitats, such as coral reefs, mangrove and kelp forests, will likely decline (Hoegh-Guldberg and Bruno 2010).

Natural climatic fluctuations

Although many recent environmental trends are consistent with anthropogenic climate change, these trends might not continue in a linear fashion. Short-term trends easily nest within longer climate cycles, and generally ecological studies encompass only parts of these cycles. Figure 1 shows the NAO and PDO indices for 100–150 years and the portions of these time series captured by the studies listed in Table 1. The trend lines fit to the shorter time series show a range of slopes from negative to positive, depending on which phase of the larger oscillation coincided with the study. Although local temperatures do not track the larger climate indices perfectly, there are clear signals of these oscillations across continents as well as the ocean (Mantua et al. 1997; Stenseth and Mysterud 2005). For example, more streams in the western United States have cooled than warmed since 1987 (Arismendi et al. 2012). Warming trends predominate when records stretch back to 1950 (Arismendi et al. 2012), consistent with PDO cycling (Fig. 1).

If the variability of the NAO or PDO increases, subperiod trends will be steeper and persist longer. Although the impact of anthropogenic climate change on the variability in these oscillations is uncertain (NCADAC 2013), some authors have argued that changes are already apparent. First, a long-term linear trend in global temperature overlies the oscillations (Fig. 1 in Klyashtorin et al. 2009). When this trend is removed, the ~60-year cycle is quite

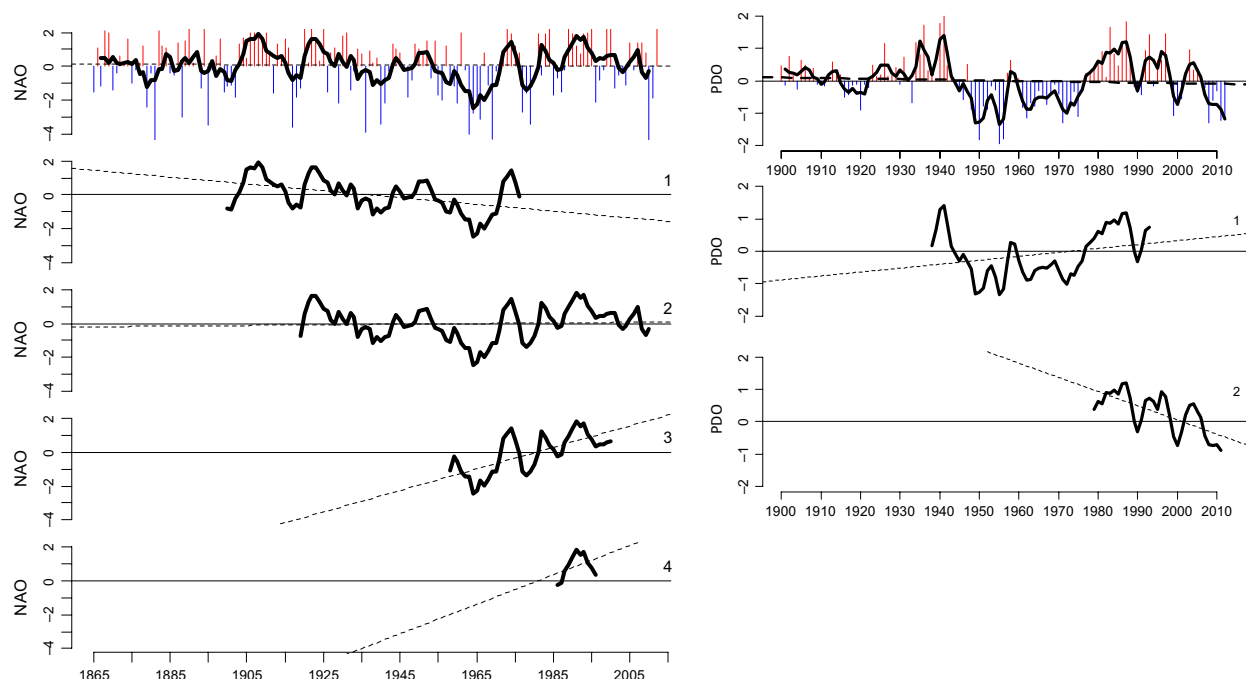


Figure 1 a Left: The North Atlantic Oscillation (NAO) station-based seasonal index for winter (includes December – February) since 1865 (Hurrell 1995): annual index (vertical lines) are shown in the top panel, and 5 year running mean (black line) is shown in all panels. The portion of the NAO time series in each lower panel show the years included in a selection of studies in Table 1: (i) Sundby and Nakken (2008); (ii) Rogers et al. (2011); (iii) Beaugrand et al. (2003); (iv) Kjesbu et al. (1998). Dotted lines are linear regression lines fit to the period of data shown. Right: The PDO index since 1900: annual index (vertical lines) are shown in the top panel, and 3 year running mean (black line) is shown in all panels. The portion of the PDO time series in each lower panel show the years included in selected studies from Table 1: (i) Quinn and Adams (1996); (ii) Kovach et al. (2012). Dotted lines are linear regression lines fit to the period of data shown. Note that local temperatures do not necessarily follow the PDO, but may have additional trend upon them, as in the Kovach study.

apparent (Fig. 2 in Klyashtorin et al. 2009). The impact of the trend is most pronounced at the peaks of the oscillation but could be detected at any point if the natural cycle is accounted for. Second, the intensity of the periodicity has increased during the last millennium, reaching a peak at the end of the twentieth century (Klyashtorin et al. 2009). Climate change might be affecting the range (peak to trough) of these cycles (Goodkin et al. 2008).

Proximate drivers and traits likely to respond to climate change

Ecological impacts of these physical changes will vary by species and location. Physiologically, rising temperatures have some nearly universal effects in fish, such as increasing metabolic rates (Fry 1967). However, the ecological and evolutionary consequences of rising temperature depend on many factors, including population-specific proximity to lethal limits or growth optima (Pörtner and Peck 2010; Somero 2010), interspecific dynamics (Finstad et al. 2011) and disease impacts (Marcos-Lopez et al. 2010). Behavioural responses can reduce expression of physiological

responses through thermoregulation (Angilletta 2009), or increase them because of competing pressures such as disease infection (Landis et al. 2012). Multiple stressors might act additively or synergistically (e.g. with compounding effects) and thus need to be considered in any examination of phenotypic shifts. Nonetheless, most research has focused on single factors.

Direct stress (temperature, hypoxia, pCO₂, diseases)

The most straightforward proximate driver of global change in fish is direct physiological stress due to various factors – such as lowered pH, lowered oxygen levels, rising temperature – which leads secondarily to increased disease prevalence and morbidity in many cases (Rijnsdorp et al. 2009). Organisms integrate multiple stressors physiologically, accumulating factors that limit oxygen metabolism and aerobic scope (Pörtner et al. 2001; Pörtner and Farrell 2008; Anttila et al. 2013). Tolerance of these conditions has a strong genetic basis and shows high levels of local adaptation (Côté et al. 2012; Donelson and Munday 2012;

Table 1. Environmental drivers and temporal coverage of the studies of phenotypic change.

Species	Location	Years	# Years	Reference	Trait	Driver
Atlantic salmon (<i>S. salar</i>)	Norway	1991–2005	14	Otero et al. (2012)	Age at maturity	SST
Atlantic salmon (<i>S. salar</i>)	Scotland	1975–2010	35	Todd et al. (2012)	Age at maturity	Stream T
Atlantic salmon (<i>S. salar</i>)	River Imsa, Norway	1976–2001	25	Juanes et al. (2004)	Age at maturity	NAO
Cod (<i>G. morhua</i>)	North Atlantic	1943–1999	56	Ottersen et al. (2006)	Age at maturity	SST
Sockeye salmon (<i>O. nerka</i>)	Fraser River, Canada	1952–1993	42	Cox & Hinch, (1997)	Age at maturity	SST
Atlantic salmon (<i>S. salar</i>)	Scotland	1975–2010	35	Todd et al. (2012)	Age at smolting	Stream T
Atlantic salmon (<i>S. salar</i>)	31 stocks N. Am & Eur	1989–2009	20	Russell et al. (2012)	Age at smolting	
Eurasian ruffe (<i>G. cernuus</i>)	Estonia	1951–1998	47	Ahas and Aasa (2006)	Appearance	Air T, NAO
European perch (<i>Perca fluviatilis</i>)	Estonia	1951–1998	47	Ahas and Aasa (2006)	Appearance	Air T, NAO
Cod (<i>G. morhua</i>)	Arcto-Norwegian region	1900–1976	76	Sundby and Nakken (2008)	Fecundity	SST
Cod (<i>G. morhua</i>)	Barents Sea	1986–1996	10	Kjesbu et al. (1998)	Fecundity	SST-capelin
Atlantic salmon (<i>S. salar</i>)	Scotland & Canada	1964–1993	29	Friedland et al. (2005)	Growth	SST
Atlantic salmon (<i>S. salar</i>)	NE Atlantic	1992–2006	14	Todd et al. (2008)	Growth	SST
Cod (<i>G. morhua</i>)	Gulf of Alaska	2006–2008	3	Hurst et al. (2012)	Growth	SST
Herring (<i>Clupea harengus</i>)	Thames estuary, UK	1977–1992	16	Attrill and Power (2002)	Growth	NAO
Plaice (<i>Pleuronectes platessa</i>)	North Sea	1970–2004	34	Teal et al. (2008)	Growth	SST
Smelt (<i>Osmerus eperlanus</i>)	Thames estuary, UK	1977–1992	16	Attrill and Power (2002)	Growth	NAO
Sole (<i>Solea solea</i>)	North Sea	1970–2004	34	Teal et al. (2008)	Growth	SST
Sprat (<i>Sprattus sprattus</i>)	Thames estuary, UK	1977–1992	16	Attrill and Power (2002)	Growth	NAO
Whiting (<i>Merlangius merlangus</i>)	Thames estuary, UK	1977–1992	16	Attrill and Power (2002)	Growth	NAO
Cod (<i>G. morhua</i>)	Barents Sea	1958–2000	42	Beaugrand et al. (2003)	Juvenile survival	SST–copepods
American shad (<i>Alosa sapidissima</i>)	Columbia River, US	1938–1993	55	Quinn and Adams (1996)	Migration timing (A)	Stream T
Atlantic salmon (<i>S. salar</i>)	NE US & SE Canada	1978–1999	21	Juanes et al. (2004)	Migration timing (A)	Stream T
Atlantic salmon (<i>S. salar</i>)	Dalälven River	1960–2002	42	Dahl et al. (2004)	Migration timing (A)	SST & stream T
Atlantic salmon (<i>S. salar</i>)	Asturian Rivers, Spain	1956–2006	50	Valiente et al. (2011)	Migration timing (A)	Air T & NAO
Brown Trout (<i>S. trutta</i>)	Dalälven River	1960–2002	42	Dahl et al. (2004)	Migration timing (A)	SST & stream T
Cutthroat trout (<i>O. clarkii clarkii</i>)	Auke Creek, Alaska	1970–2010	40	Kovach et al. (2013)	Migration timing (A)	Stream T
Dolly Varden char (<i>S. malma</i>)	Auke Creek, Alaska	1970–2010	40	Kovach et al. (2013)	Migration timing (A)	Stream T
Flounder (<i>Platichthys flesus</i>)	UK	1953–1965	13	Sims et al. (2004)	Migration timing (A)	SST, NAO
Pink salmon (<i>O. gorbuscha</i>)	Auke Creek, Alaska	1979–2011	32	Kovach et al. (2012)	Migration timing (A)	Stream T
Pink salmon (<i>O. gorbuscha</i>)	Auke Creek, Alaska	1972–2005	33	Taylor (2008)	Migration timing (A)	Stream T
Sockeye salmon (<i>O. nerka</i>)	Columbia River, US	1949–1993	44	Quinn and Adams (1996)	Migration timing (A)	Stream T
Sockeye salmon (<i>O. nerka</i>)	Columbia River, US	1949–2005	56	Crozier et al. (2011)	Migration timing (A)	Stream T & flow
Atlantic salmon (<i>S. salar</i>)	Northern Ireland	1978–2008	30	Kennedy and Crozier (2010)	Migration timing (J)	Stream T
Atlantic salmon (<i>S. salar</i>)	62 stocks N. Am & Eur	Variable		Russell et al. (2012)	Migration timing (J)	
Pink salmon (<i>O. gorbuscha</i>)	Auke Creek, Alaska	1972–2005	33	Taylor (2008)	Migration timing (J)	Stream T

(continued)

Table 1 (continued)

Species	Location	Years	# Years	Reference	Trait	Driver
Coho salmon (<i>O. kisutch</i>)	Auke Creek, Alaska	1970–2010	40	Kovach et al. (2013)	Migration timing (J,A)	Str T, flow & SST
Pink salmon (<i>O. gorbuscha</i>)	Auke Creek, Alaska	1970–2010	40	Kovach et al. (2013)	Migration timing (J,A)	Stream T
Sockeye salmon (<i>O. nerka</i>)	Auke Creek, Alaska	1970–2010	40	Kovach et al. (2013)	Migration timing (J,A)	Stream T & flow
Bass (<i>Dicentrarchus labrax</i>)	Thames estuary, UK	1977–1992	16	Attrill and Power (2002)	Size	NAO
Cod (<i>G. morhua</i>)	Norway	1919–2010	91	Rogers et al. (2011)	Size	SST
Dab (<i>Limanda limanda</i>)	Thames estuary, UK	1977–1992	16	Attrill and Power (2002)	Size	NAO
Flounder (<i>Platichthys flesus</i>)	Thames estuary, UK	1977–1992	16	Attrill and Power (2002)	Size	NAO
Plaice (<i>Pleuronectes platessa</i>)	Thames estuary, UK	1977–1992	16	Attrill and Power (2002)	Size	NAO
Smelt (<i>Osmerus eperlanus</i>)	Thames estuary, UK	1977–1992	16	Attrill and Power (2002)	Size	NAO
Sockeye salmon (<i>O. nerka</i>)	SW Alaska	1962–2002	40	Schindler et al. (2005)	Size	Ice out
Sole (<i>Solea solea</i>)	Thames estuary, UK	1977–1992	16	Attrill and Power (2002)	Size	NAO
Bream (<i>Abramis brama</i>)	Estonia	1951–1990	39	Noges and Jarvet (2005)	Spawn timing	Stream T
Burbot (<i>Lota lota</i>)	Estonia	1951–1998	47	Ahas and Aasa (2006)	Spawn timing	Air T, NAO
Eurasian dace (<i>Leuciscus cephalus</i>)	Estonia	1951–1998	47	Ahas and Aasa (2006)	Spawn timing	Air T, NAO
Eurasian ruffe (<i>G. cernua</i>)	Estonia	1951–1998	47	Ahas and Aasa (2006)	Spawn timing	Air T, NAO
European perch (<i>Perca fluviatilis</i>)	Estonia	1951–1998	47	Ahas and Aasa (2006)	Spawn timing	Air T, NAO
Northern pike (<i>Esox lucius</i>)	Estonia	1951–1998	47	Ahas and Aasa (2006)	Spawn timing	Air T, NAO
Roach (<i>Rutilus rutilus</i>)	Estonia	1951–1990	39	Noges and Jarvet (2005)	Spawn timing	Stream T
Roach (<i>Rutilus rutilus</i>)	Lake Geneva, France	1983–2000	18	Gillet and Quélin (2006)	Spawn timing	Lake T
Smelt (<i>Osmerus eperlanus</i>)	Estonia	1951–1998	47	Ahas and Aasa (2006)	Spawn timing	Air T, NAO
Walleye (<i>Sander vitreus</i>)	12 populations, Minnesota, US		Variable	Schneider et al. (2010)	Spawn timing	Ice out

Species genera: *S. Salmo*, *O. Oncorhynchus*, *G. cernua*: *Gymnocephalus*, *G. morhua*: *Gadus*. Trait: A, adult, J, juvenile. Driver: T, temperature, SST, sea surface temperature.

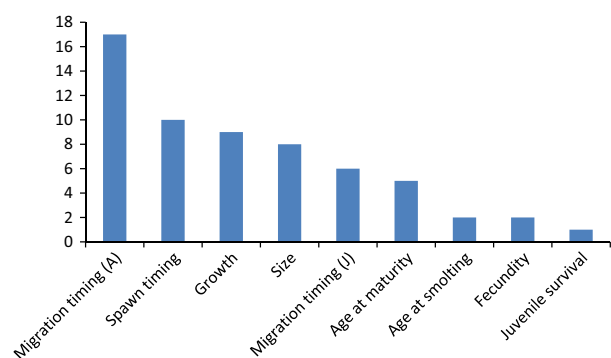


Figure 2 Frequency distribution of traits showing shifts that correlate with environmental drivers in recent decades. Migration timing is broken into adult migrations (A), which are usually spawning migrations (includes “appearance” in Table 1) or seawater to freshwater migrations, and juvenile (J) or freshwater to saltwater migrations.

Madeira et al. 2012; Munday et al. 2012), and thus, these traits clearly evolve by natural selection. Although most studies have focused on heat tolerance, because many fish

communities face prolonged winter periods in temperate and high latitude areas, specialized adaptations for tolerating winter will also face a changing selection regime (Pörtner and Peck 2010; Shuter et al. 2012). Many other traits show temperature sensitivity and might threaten population viability, such as sex determination, sexual abnormalities and fertility (Strussmann et al. 2010; Pankhurst and Munday 2011). However, the use of latent genetic variation in local adaptations, such as development time in rainbow trout (*Oncorhynchus mykiss*), suggests evolution in key traits could occur quickly (Miller et al. 2012).

Selection for disease tolerance will likely intensify because warmer environments exhibit a general increase in the diversity of diseases, increased population growth rates of most microorganisms (Macnab and Barber 2012) and increased vulnerability of coldwater fishes. Furthermore, ongoing human activity tends to spread pathogens (Harvell et al. 1999; Marcos-Lopez et al. 2010). Historically, fish have adapted to high disease loads in warmer environments by enhancing the diversity of Major Histocompatibility

Complex (MHC) genes (Dionne et al. 2007; Bowden 2008; Marcos-Lopez et al. 2010) and local adaptation to specific diseases (Beacham and Evelyn 1992; Bartholomew 1998).

Impacts of ocean acidification on fish are less well understood than those associated with temperature (Kroeker et al. 2010; Denman et al. 2011; but see examples of phytoplankton evolution in Reusch 2014). High pCO₂ affects fish physiology directly, through developmental exposure (Franke and Clemmesen 2011; Frommel et al. 2012), olfaction (Munday et al. 2009; Dixon et al. 2010), and a variety of behaviours such as settlement and the avoidance of predators (Munday et al. 2012). Fish sensitivity also includes vulnerability to habitat loss (Gruber 2011; Gruber et al. 2012) and prey availability because of difficulties for skeleton- or shell-forming organisms under lower calcium-carbonate saturation states (Orr et al. 2005; Heath et al. 2012). Marine viruses interact with ocean biogeochemical cycles and fish dynamics in ways that are currently unpredictable but may profoundly influence ocean ecosystems (Danovaro et al. 2011).

Food-web dynamics affect behaviour, growth and survival

Although direct physical stressors are clearly limiting on some level, the primary mechanism cited in the literature by which climate impacts fish population dynamics involves the food web. Physical oceanographic, hydrological and limnological drivers determine the geographical distribution, total abundance, species composition and physiological condition of phytoplankton, zooplankton and plants (Collins 2014; Reusch 2014), which then alter fish growth and survival through trophic interactions (e.g. Schindler et al. 2005). Traits in fishes influenced by individual growth are wide ranging, including (but not limited to) age at maturity, size at maturity, brood number (fecundity), offspring (egg) size, timing of developmental stage (e.g. migration, metamorphosis), habitat type, choice of prey, vulnerability to predators and many more (Roff 1986, 2002; Jobling 1994; Wootton 1998; Hutchings 2002). Differences between species or populations in thermal reaction norms for growth can lead to competitive exclusion by other species with a better adapted reaction norm for a given environment. For example, Arctic char (*Salvelinus alpinus*) are more energetically efficient under cold temperatures or under ice but can be competitively excluded by brown trout (*Salmo trutta*) under warmer or more nutrient-rich conditions (Finstad et al. 2011; Helland et al. 2011). Fish can respond to changes in prey availability and energetic quality by modifying their distribution at broad spatial scales in the ocean (Perry et al. 2005; Sorte et al. 2010; Pinsky et al. 2013), vertically in the water column in

lakes or the ocean (Dulvy et al. 2008; Pinsky et al. 2013), within stream networks (Comte and Grenouillet 2013), or by selecting different prey (Volkov 2012).

Other drivers of selection

Importantly, the effects of climate change on organisms will rarely act in isolation of other selection pressures. Many anthropogenic impacts drive contemporary evolution (Kinnison and Hendry 2001; Reznick and Ghalambor 2001; Stockwell et al. 2003; Hendry et al. 2008) and affect many of the same traits as climate change. Changes in age at maturity, demography and density (abundance), caused by fisheries, for example, feed back into the rate of response to climate change that we might expect because of the influence that factors such as effective population size, genetic variance and generation time have on rates of evolution (Hutchings and Fraser 2008). Changes in species composition can also generate rapid evolution (e.g. Reznick and Bryga 1987; Reznick et al. 1990; Walsh and Reznick 2011), and climate change is causing large-scale redistribution of fish communities simultaneously with human-mediated species movements (Perry et al. 2005; Dulvy et al. 2008; Comte and Grenouillet 2013).

Evidence for potential evolutionary responses in key traits

The most compelling evidence for the potential of evolutionary responses to anthropogenic climate change originates from cases of contemporary evolution in particularly relevant traits, especially through allochronic adaptation (i.e. changes over time) in introduced species. For example, sockeye salmon (*Oncorhynchus nerka*) introduced into Lake Washington in the 1930s and 1940s have diverged in developmental rates and survival at different temperatures (Hendry et al. 1998). Recent evolution in thermal tolerance has occurred in fish exposed to thermal effluents, such as mosquitofish tested after 30 years of exposure to abnormally warm water (Meffe et al. 1995). Artificial selection can induce much faster evolution, such as enhanced cold tolerance in three-spined sticklebacks (*Gasterosteus aculeatus*) within just three generations (Barrett et al. 2011), and improved heat tolerance in rainbow trout within 15 generations (Ineno et al. 2005). Spawn timing can also respond quickly to hatchery selection: a 2-week advance followed just four generations of selection in coho salmon (*Oncorhynchus kisutch*) (Neira et al. 2006).

Numerous other relevant traits have also evolved rapidly when exposed to a new environment (Reznick and Ghalambor 2001). For example, Chinook salmon (*Oncorhynchus tshawytscha*) from a single-source population in the Sacramento Valley in California, US, introduced to New

Zealand, diverged quickly from their ancestral phenotypes in many traits: size at age and age at maturity (Kinnison et al. 2011), freshwater growth rates and migration timing (Quinn et al. 2001), egg size and number (Kinnison et al. 1998).

Evidence for climate-induced phenotypic change in fish

For this special issue, we undertook a specific literature review of phenotypic responses to climate change in wild fish populations to clarify whether impacts of climate change are evident and what is known about the mechanisms behind these responses. We assessed the methods of inference for genetic or plastic mechanisms in each paper, using the categories identified by Merilä and Hendry (this volume). They identified six methods for inferring genetic change (quantitative genetic animal models, common-garden studies, model predictions, experimental evolution, space-for-time substitution, and molecular genetics) and five methods for inferring plastic change (quantitative genetic animal models, common-garden studies, experimental evolution, fine-grained population responses and individual plasticity in nature). They further asked whether the response was adaptive and how the causal driver was inferred.

To identify papers that described a phenotypic change in a natural population and provided evidence that climate drove the phenotypic change, we searched for literature in the Web of Science in which the words 'climate' or 'climatic change' ('climat* change'), and 'adaptation', 'plasticity' or 'phenotypic change', appeared in the publication title or topic area. Because these searches primarily identified papers addressing human adaptation to climate change or existing variation among populations, we refined our search by combining ('climat* change') with phenotypic traits we expected to be sensitive to climate ('spawning' or 'spawn timing', 'migration timing' or 'migrat*', 'emergence timing', 'age at maturity', 'egg size', 'development time' or 'development rate'). Finally, we combined 'adaptation' with common names of fishes that have been well studied (stickleback, perch, bass, char, smelt, herring, pollock, cod and salmon). Although this is not an exhaustive list of all possible search combinations, it encompasses a broad cross section of the available literature.

Most of the papers that initially appeared relevant instead described (i) existing heterogeneity among populations (e.g. along spatial climatic gradients) that presumably reflects adaptation to different environments, (ii) experimental exposure to conditions predicted with climate change, such as elevated temperature or lower pH or (iii) changes in abundance or recruitment and thus did not satisfy our criteria. Because our results might appear to be

biased towards salmonids, we made a concerted effort to obtain evidence of phenotypic change in other fish taxa by thoroughly checking major reviews of fish responses to climate change in both freshwater and marine environments (e.g. Roessig et al. 2004; Ficke et al. 2007; Graham and Harrod 2009; Staudinger et al. 2012; Griffiths 2013), and taxonomically broader reviews of evolutionary responses to climate change (e.g. Hendry and Kinnison 1999; Kinnison and Hendry 2001; Stockwell et al. 2003; Parmesan 2006; Carroll et al. 2007; IPCC 2007). In sum, we believe that our results reflect broader patterns in the literature on observed, natural fish responses to climate change.

We found 30 papers that generally fit our criteria. These papers examined 11 traits (Fig. 2) in 26 species (Table 1). Attrill and Power (2002) examined six additional species (*Trisopterus luscus*, *Trisopterus minutus*, *Pomatoschistus* spp., *Anguilla anguilla*, *Agonus cataphractus*, and *Syngnathus rostellatus*) in which they found significant correlations between the NAO and abundance but not growth. Most reports of phenotypic change described shifts in reproductive phenology ($N = 17$ adult migration timing and $N = 10$ spawn timing; Table 1). Changes in growth and juvenile size ($N = 17$), age at maturity ($N = 5$), age at seaward migration/smolting ($N = 2$) and fecundity ($N = 2$) were also reported. The distribution of studied taxa was biased towards salmon (especially Atlantic salmon [*Salmo salar*], but also Pacific salmon [*Oncorhynchus* spp.]) and Atlantic cod. All studies attributed phenotypic change to temperature variation, either through water temperature measurements directly, or air temperature and the NAO, ice break-up dates, temperature-driven changes in prey abundance or stream flow (Fig. 3). Geographically, the studies included North America and Europe, with most marine reports being from the North Atlantic (Table 1).

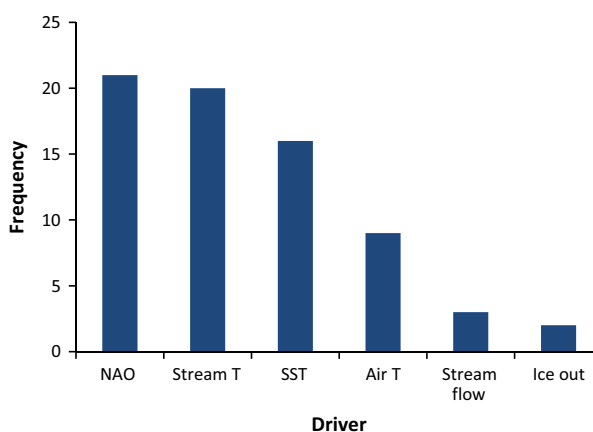


Figure 3 Frequency distribution of environmental drivers correlated with phenotypic change. NAO, North Atlantic Oscillation, T , temperature, SST, sea surface temperature; ice out is the day when a lake is free of all ice. We grouped counts by the species within a reference.

Table 2. List of studies of phenotypic trends in response to climate.

Species	Location	Trait	Genetic	Plastic	Adaptive	Causality	Reference
American shad (<i>Alosa sapidissima</i>)	Columbia River, US	Migration timing (A)	–	Yes (1)	–	Yes (1, 2)	Quinn and Adams (1996)
Atlantic salmon (<i>S. salar</i>)	Norway	Age at maturity	–	Yes (1)	–	Yes (1, 2)	Otero et al. (2012)
Atlantic salmon (<i>S. salar</i>)	Norway	Age at maturity	–	Yes (1)	–	Yes (1, 2)	Jonsson & Jonsson (2004)
Atlantic salmon (<i>S. salar</i>)	Scotland	Age at maturity	–	Yes (1)	–	Yes (1, 2)	Todd et al. (2012)
Atlantic salmon (<i>S. salar</i>)	31 stocks N. Am & Eur	Age at smolting	–	–	–	Yes (1, 2)	Russell et al. (2012)
Atlantic salmon (<i>S. alar</i>)	Scotland	Age at smolting	–	Yes (1)	–	Yes (1, 2)	Todd et al. (2012);
Atlantic salmon (<i>S. salar</i>)	Scotland & Canada	Growth	–	Yes (1)	–	Yes (1, 2)	Friedland et al. (2005)
Atlantic salmon (<i>S. salar</i>)	NE Atlantic	Growth	–	Yes (1)	–	Yes (1, 2)	Todd et al. (2008)
Atlantic salmon (<i>S. salar</i>)	Dalälven River	Migration timing (A)	–	Yes (1)	–	Yes (1, 2)	Dahl et al. (2004)
Atlantic salmon (<i>S. salar</i>)	Asturian Rivers, Spain	Migration timing (A)	–	Yes (1)	–	Yes (1, 2)	Valiente et al. (2011)
Atlantic salmon (<i>S. salar</i>)	NE US & SE Canada	Migration timing (A)	–	Yes (1)	–	Yes (1, 2)	Juanes et al. (2004)
Atlantic salmon (<i>S. salar</i>)	Northern Ireland	Migration timing (J)	–	Yes (1)	–	Yes (1, 2)	Kennedy and Crozier (2010)
Atlantic salmon (<i>S. salar</i>)	62 stocks N. Am & Eur	Migration timing (J)	–	–	–	Yes (1, 2)	Russell et al. (2012)
Bass (<i>Dicentrarchus labrax</i>)	Thames estuary, UK	Size	–	Yes (1)	–	Yes (1, 2)	Attrill and Power (2002)
Bream (<i>Abramis brama</i>)	Estonia	Spawn timing	–	–	–	Yes (1, 2)	Ahas and Aasa (2006)
Bream (<i>Abramis brama</i>)	Estonia	Spawn timing	–	–	–	Yes (1, 2)	Noges and Jarvet (2005)
Brown Trout (<i>S. trutta</i>)	Dalalven River	Migration timing (A)	–	Yes (1)	–	Yes (1, 2)	Dahl et al. (2004)
Cod (<i>G. morhua</i>)	North Atlantic	Age at maturity	–	Yes (1)	–	Yes (1, 2)	Ottersen et al. (2006)
Cod (<i>G. morhua</i>)	Barents Sea	Fecundity	–	Yes (1)	–	Yes (1, 2)	Kjesbu et al. (1998)
Cod (<i>G. morhua</i>)	Arcto- Norwegian region	Fecundity	–	Yes (1)	–	Yes (1, 2)	Sundby and Nakken (2008)
Cod (<i>G. morhua</i>)	Gulf of Alaska	Growth	–	Yes (1)	–	Yes (1, 2)	Hurst et al. (2012)
Cod (<i>G. morhua</i>)	Barents Sea	Juvenile survival	–	Yes (1)	–	Yes (1, 2)	Beaugrand et al. (2003)
Cod (<i>G. morhua</i>)	Norway	Size	–	Yes (1)	–	Yes (1, 2)	Rogers et al. (2011)
Coho salmon (<i>O. kisutch</i>)	Auke Creek, Alaska	Migration timing (J,A)	–	Yes (1)	–	Yes (1, 2)	Kovach et al. (2013)
Cutthroat trout (<i>O. clarkii clarkii</i>)	Auke Creek, Alaska	Migration timing (FW to S)	–	Yes (1)	–	Yes (1, 2)	Kovach et al. (2013)
Dab (<i>Limanda limanda</i>)	Thames estuary, UK	Size	–	Yes (1)	–	Yes (1, 2)	Attrill and Power (2002)
Dolly Varden char (<i>S. malma</i>)	Auke Creek, Alaska	Migration timing (FW to S)	–	Yes (1)	–	Yes (1, 2)	Kovach et al. (2013)
Eurasian dace (<i>Leuciscus cephalus</i>)	Estonia	Spawn timing	–	–	–	Yes (1, 2)	Ahas and Aasa (2006)
Eurasian ruffe (<i>G. cernua</i>)	Estonia	Appearance	–	No (1)	–	Yes (1, 2)	Ahas and Aasa (2006)
Eurasian ruffe (<i>G. cernua</i>)	Estonia	Spawn timing	–	–	–	Yes (1, 2)	Ahas and Aasa (2006)
European perch (<i>Perca fluviatilis</i>)	Estonia	Appearance	–	No (1)	–	Yes (1, 2)	Ahas and Aasa (2006)
European perch (<i>Perca fluviatilis</i>)	Estonia	Spawn timing	–	–	–	Yes (1, 2)	Ahas and Aasa (2006)
Flounder (<i>Platichthys flesus</i>)	UK	Migration timing (A)	–	Yes (1)	–	Yes (1, 2)	Sims et al. (2004)
Flounder (<i>Platichthys flesus</i>)	Thames estuary, UK	Size	–	Yes (1)	–	Yes (1, 2)	Attrill and Power (2002)

(continued)

Table 2 (continued)

Species	Location	Trait	Genetic	Plastic	Adaptive	Causality	Reference
Herring (<i>Clupea harengus</i>)	Thames estuary, UK	Growth	–	Yes (1)	–	Yes (1, 2)	Attrill and Power (2002)
Northern pike (<i>Esox lucius</i>)	Estonia	Spawn timing	–	–	–	Yes (1, 2)	Ahas and Aasa (2006)
Pink salmon (<i>O. gorbuscha</i>)	Auke Creek, Alaska	Migration timing (A)	Yes (1)	–	–	Yes (1, 2)	Kovach et al. (2012)
Pink salmon (<i>O. gorbuscha</i>)	Auke Creek, Alaska	Migration timing (A)	–	Yes (1)	–	Yes (1, 2)	Taylor (2008)
Pink salmon (<i>O. gorbuscha</i>)	Auke Creek, Alaska	Migration timing (J)	–	Yes (1)	–	Yes (1, 2)	Taylor (2008)
Pink salmon (<i>O. gorbuscha</i>)	Auke Creek, Alaska	Migration timing (J,A)	–	Yes (1)	–	Yes (1, 2)	Kovach et al. (2013)
Plaice (<i>Pleuronectes platessa</i>)	North Sea	Growth	–	Yes (1,2)	–	Yes (1, 2)	Teal et al. (2008)
Plaice (<i>Pleuronectes platessa</i>)	Thames estuary, UK	Size	–	Yes (1)	–	Yes (1, 2)	Attrill and Power (2002)
Roach (<i>Rutilus rutilus</i>)	Lake Geneva, France	Ovary devpmt, spawn timing	–	Yes (1)	–	Yes (1, 2)	Gillet and Quélin (2006)
Roach (<i>Rutilus rutilus</i>)	Estonia	Spawn timing	–	–	–	Yes (1, 2)	Noges and Jarvet (2005)
Smelt (<i>Osmerus eperlanus</i>)	Thames estuary, UK	Growth	–	Yes (1)	–	Yes (1, 2)	Attrill and Power (2002)
Smelt (<i>Osmerus eperlanus</i>)	Thames estuary, UK	Size	–	Yes (1)	–	Yes (1, 2)	Attrill and Power (2002)
Smelt (<i>Osmerus eperlanus</i>)	Estonia	Spawn timing	–	–	–	Yes (1, 2)	Ahas and Aasa (2006)
Sockeye salmon (<i>O. nerka</i>)	Fraser River, Canada	Age at maturity	–	Yes (1)	–	Yes (1, 2)	Cox & Hinch (1997)
Sockeye salmon (<i>O. nerka</i>)	Columbia River, US	Migration timing (A)	Yes (2)	Yes (1)	Yes (1)	Yes (1, 2)	Crozier et al. (2011)
Sockeye salmon (<i>O. nerka</i>)	Columbia River, US	Migration timing (A)	–	No (1)	–	Yes (1, 2)	Quinn and Adams (1996)
Sockeye salmon (<i>O. nerka</i>)	Auke Creek, Alaska	Migration timing (J,A)	–	Yes (1)	–	Yes (1, 2)	Kovach et al. (2013)
Sockeye salmon (<i>O. nerka</i>)	SW Alaska	Size	–	Yes (1)	–	Yes (1, 2)	Schindler et al. (2005)
Sole (<i>Solea solea</i>)	North Sea	Growth	–	Yes (1,2)	–	Yes (1, 2)	Teal et al. (2008)
Sole (<i>Solea solea</i>)	Thames estuary, UK	Size	–	Yes (1)	–	Yes (1, 2)	Attrill and Power (2002)
Sprat (<i>Sprattus sprattus</i>)	Thames estuary, UK	Growth	–	Yes (1)	–	Yes (1, 2)	Attrill and Power (2002)
Walleye (<i>Sander vitreus</i>)	Minnesota, US	Spawn timing	–	Yes (1)	–	Yes (1, 2)	Schneider et al. (2010)
Whiting (<i>Merlangius merlangus</i>)	Thames estuary, UK	Growth	–	Yes (1)	–	Yes (1, 2)	Attrill and Power (2002)

The columns identify whether a genetic or plastic basis for the trait was identified (Yes, No, or – = not tested explicitly), and by what method (Genetic: 1 = Molecular genetic methods, 2 = Comparison to model predictions; Plastic: 1 = Fine-grained population response, 2 = Experimental studies). If the study tested whether the response was adaptive, it is indicated in the next column (1 = phenotypic selection estimates). All studies attributed causality to environmental factors through regression analysis and reference to other work (Causality = Yes, 1 = Common sense or existing knowledge, 2 = phenotype-environment correlations). Species genera: *S. Salmo*, *O. Oncorhynchus*, *G. cernua*: *Gymnocephalus*, *G. morhua*: *Gadus*. Trait: A, adult, J, juvenile, FW to S, freshwater to saltwater migration.

Evolutionary mechanisms postulated or demonstrated

Only one paper (Kovach et al. 2012) utilized molecular genetic data to document a shift in genotype frequencies associated with a shift in phenotypes (Table 2). Pink salmon (*O. gorbuscha*) in Auke Creek, Alaska, historically

maintained a bimodal distribution in migration timing, with the early and late migrants about 3 weeks apart. A putatively neutral genetic marker was experimentally inserted into late-migrants in 1979; marker frequencies were stable from 1981 to 1989 and clearly differentiated early and late migrants. The two segments of the run had distinct morphological traits and maturation schedules,

and genetic data showed little gene flow between them. Kovach et al. (2012) tracked the frequency of this late-migrant marker compared with other markers from 1983 to 2011. The late-migrant marker decreased rapidly in the late 1980s or early 1990s, and the proportion of the run exhibiting the late-migration phenotype has remained very low since then. Incidentally, this was near the peak of a PDO cycle (Fig. 1).

Rapid changes occurred in the late-migrant locus, but not numerous microsatellite loci, indicating that natural selection caused the shift rather than genetic drift. However, the phenotypic target of selection is not entirely clear. High temperatures occurred during the years of rapid allele frequency change, and the early-migrating phenotype appears to have adaptations to warm temperature at multiple life stages (Fukushima and Smoker 1997; Smoker et al. 1998). Kovach et al. (2012) noted that the loss of the late-migrating phenotype was sudden and apparently due to selection against them, but that the more gradual trend in the median migration timing was consistent with other plastic drivers of migration date. Historically, marine survival was lower in the early-migrating fish, suggesting that the shift in adult migration timing might have negative consequences at other life stages. However, the adaptiveness of ongoing phenotypic change requires further testing.

Several other studies have explored climatic drivers of selection on sockeye salmon, which appears to be more likely to respond evolutionarily to certain pressures than other species. Quinn and Adams (1996) contrasted the responses of sockeye salmon with American shad (*Alosa sapidissima*) migration timing through a shared river basin, the Columbia River. They predicted shad would employ plasticity to respond to river conditions because of the high predictability and short-time interval between adult migration timing and larval emergence, which is presumably the target of selection. Consistent with this hypothesis, they documented a very fast shift in migration timing in shad and high interannual correlation with temperature (a fine-grained population response). However, this response was faster than the cue they had postulated as the driver (river temperature), suggesting they might not have identified the full cue for the response. Quinn and Adams (1996) postulated that, unlike shad, sockeye would rely more on a genetically determined migration date because of their relatively long larval incubation time and, hence, a lack of correlation between adult and juvenile environmental conditions. Consistent with this hypothesis, they found that sockeye lagged behind the rate of temperature change and responded much more slowly than shad. Thus, the mode of inference was through phenotypic-environment correlations, and no genetic analyses or direct tests of the adaptive nature of the response were conducted. Nonethe-

less, extensive corollary evidence (Naughton et al. 2005; Keefer et al. 2008) that high migration temperatures reduce survival in Columbia River sockeye salmon supports the hypothesis that elevated river temperature is the primary driver of the response.

Crozier et al. (2011) followed up Quinn and Adams' (1996) paper with a more specific model of selection pressure on sockeye salmon. Crozier et al. (2011) used a functional relationship between river temperature and survival, based on individually-tracked migrating cohorts, to estimate the annual selection pressure experienced by the population. They calculated a selection differential for each year since 1949 by reconstructing fish exposure using daily migration counts and temperature measurements at dams. Building on a method pioneered by Swain et al. (2007) study of fisheries-induced evolution in cod, they then used this annual selection differential to predict the shift in mean return migration timing of offspring. They allowed plastic drivers of migration timing, including river flow, a direct (within-year) effect of temperature, and oceanic factors such as the PDO and the North Pacific Gyre Oscillation (NPGO, Di Lorenzo et al. 2008) to modify the mean expected migration timing as plastic effects. Through model selection in a state-space modelling framework, they found very strong support for including the selection differential as a predictor of migration timing; none of the alternative plastic drivers tested could explain the observed shift in migration timing nearly as well.

The model results indicated that plasticity for migration timing in this sockeye population is largely a function of river flow and that the intercept for the norm of reaction has shifted by 3–6 days over 60 years (15 generations). Thus, this approach utilized both inferential evidence for genetic change (i.e. comparing model predictions with observed phenotypic change) and inferential evidence for plastic change (i.e. a fine-grained population response). The analysis of phenotypic selection estimates supports the hypothesis that the change was adaptive, and phenotype-environment correlations and comparison of alternative drivers point specifically to climate as the selective force. The advantage of this approach over strictly genetic methods is the strong link between the purported driver and target of selection, and response of the population.

One final sockeye study (Carlson and Quinn 2007) empirically estimated selection differentials over a decade and linked the selection directly to environmental conditions (lake level). They demonstrated strong links between climate and selection on a phenotypic trait (body size). Although the environmental trends during that study were too short to demonstrate a persistent response to climate change, Carlson and Quinn (2007) presented a compelling argument that evolution in this trait is likely to occur under

climate scenarios of declining July precipitation and warming lake temperature. Other methods, such as the Price equation (Boutin and Lane, this special issue, and Price 1970, 1972; Coulson et al. 2010), cannot be applied to fish populations at this point. Although animal models are beginning to be used in fish populations (Neira et al. 2006; Serbezov et al. 2010; Debes et al. 2013), they are typically only practical under hatchery conditions or in highly constricted populations where nearly all the fish can be handled.

Plastic responses to recent climate variability or change

The remaining papers documented correlations between phenological change and environmental drivers. A strong statistical relationship at an annual time step is consistent with a plastic response rather than an evolutionary response (Merilä and Hendry 2014, this volume). Of course, correlations alone do not establish a causal link with the driver because many environmental and other factors are correlated with each other. However, independent studies demonstrating plasticity in the trait as a function of temperature, or very high resolution responsiveness, are compelling in some cases.

Migration/spawn timing

Several papers found that migration timing in juvenile salmon has advanced at a rate similar to that of water temperature (Kennedy and Crozier 2010; Russell et al. 2012; Todd et al. 2012). The relatively short time frame (<35 years), combined with independent evidence that temperature is a strong proximate cue for smolt migration, suggests that these responses are mostly plastic. Each of these papers expressed concern that the response was maladaptive. Kennedy and Crozier (2010) showed a correlation between migration timing and marine mortality and concluded that the trend towards earlier migration has increased marine mortality because of a mismatch between river and ocean temperatures. Russell et al. (2012) and Todd et al. (2012) argued that the smaller size of younger smolts lowered their marine survival and hence could be maladaptive. However, they did not formally test for adaptiveness. Juanes et al. (2004) found that long-term trends in migration timing of Atlantic salmon are consistent with a temperature response. Most of this shift occurred almost immediately upon transplantation from a more northern stock, and thus probably represents a plastic response. They argued that the change is adaptive based on a space-for-time comparison of trends in migration timing across a latitudinal gradient associated with temperature in many populations. Ongoing changes in many populations could have an evolutionary compo-

nent, although this has not been explicitly tested. Schneider et al. (2010) examined time series of ice-out and walleye (*Sander vitreus*) spawning across numerous lakes in Minnesota, USA. They found a strong correlation between ice-out and spawn timing independent from the long-term trend, indicating a probable plastic cause.

Age at maturation

Recent work indicates that over recent decades, some Norwegian Atlantic salmon have bred at progressively older ages (1991–2005; Otero et al. 2012). The authors presented a thorough discussion of the possible mechanisms of this shift, although there is no direct evidence of a causal link between driving factors and the phenotypic change. Nonetheless, age at maturation is known to have both genetic and plastic components (Hutchings 2002). The prevailing mechanism is thought to be a threshold body size or growth rate at particular times of year, such that individuals mature only if they exceed the threshold. This threshold is genetically determined and varies among populations (Piché et al. 2008), but whether the threshold is reached in a given year depends on environmentally determined growth conditions. Thus, the immediate trend appears to be a plastic response to growth conditions.

Growth/survival

The majority of papers in our review documented annual variation in growth or survival that correlated with temperature variation, which indicates a plastic response. Attrill and Power (2002) documented strong interannual correlations between juvenile growth rates across a wide spectrum of marine fishes that use the Thames River estuary as a nursery. This appears to be a plastic response because detrended data showed even stronger statistical relationships, indicating annual response times, which is much too short to reflect evolutionary processes. Furthermore, they suggested use of the estuary is a facultative response to growing conditions, and found similar relationships between population abundance and individual body sizes. This is inconsistent with a rapid evolutionary response, which would entail strong selection and depress population sizes, at least temporarily. Thus, the primary basis for inference is the fine-grained population response and mechanistic reasoning. Similarly, sole (*Solea solea*) and plaice (*Pleuronectes platessa*) growth rates (Teal et al. 2008), sockeye juvenile growth (Schindler et al. 2005), cod size (Rogers et al. 2011) and survival (Beaugrand et al. 2003) and fecundity (Kjesbu and Witthames 2007) are well explained by plastic, reaction-norm responses to prey quality and quantity and seasonal timing. There is no indication that these represent evolutionary responses to climate change.

Plastic or evolutionary mechanisms

The remaining papers in our review documented coarser-grained correlations between temperature and phenotypic change, or no phenotypic change at all despite environmental change. Weak correlations could reflect either a plastic or an evolutionary response, or be coincidental. They might also reflect difficulty in identifying or procuring data on the most direct environmental driver (e.g., Pinsky et al. 2013). Nonetheless, Ahas and Aasa (2006) found that spring spawning periods have advanced significantly in three freshwater fish species (pike, *Esox lucius*, ruffe, *Gymnocephalus cernua* and bream, *Abramis brama*) and that migration timing has advanced in one species (smelt, *Osmerus eperlanus*) from 1951 to 1999, concurrently with a trend towards warmer springs. However, most of the monitored fish species exhibited no significant trends. They postulated that earlier snow melt and reduced spring flooding might have driven the observed shifts, partly because March and April weather showed the strongest correlations. One of the papers included in our review (Noges and Jarvet 2005) reported changes in spawning date over 40 years in two Estonian fish (bream and roach, *Rutilus rutilus*). They found that the former species had advanced its breeding date by 10 days, apparently tracking water temperature, but that roach spawn timing had remained constant. Roach now encounter water that is 3°C warmer during spawning than in the 1950s. This apparent lack of thermal plasticity might expose this species to selection and present opportunities for an evolutionary response over a longer time frame.

In summary, the majority of papers in our review documented relatively fine-grained population responses to temperature or snowmelt/ice-out over relatively short time frames. Although a very quick response was also documented from a single strong selection event in an extreme year (Kovach et al. 2012), as a general pattern, it provides strongest support for plastic responses to metrics of climate change. Most of these studies detrended time series prior to analysis, or otherwise removed the raw trend to isolate stochastic variation in the environmental factor as a driver of phenotypic variation. However, statistical sophistication varied. In two species (pink and sockeye salmon), the authors reported either genetic data (Kovach et al. 2012) or a pattern of phenotypic change consistent with an evolutionary response, based on a model of selection pressure (Crozier et al. 2011) or direct estimates of selection (Carlson and Quinn 2007). Most of these trends were considered adaptive for some life history stages, but all authors expressed concern that the responses might be maladaptive for subsequent life stages. None of these hypotheses regarding adaptiveness was explicitly tested. All studies linked the observed phenotypic changes to the environmental driver

by phenotype-environment correlation, with or without detrending.

Discussion

We found that despite significant long-term trends in influential environmental factors, such as ocean and freshwater temperature, and despite abundant evidence that rapid evolution in climate-sensitive traits is possible, studies of natural adaptation to climate change in fishes are rare. Most studies reported correlations between temperature and population responses at annual time steps, which are consistent with plastic responses to environmental conditions: growth, fecundity, survival, migration and reproductive phenology are all changing in concert with environmental change. Given the high level of plasticity in these traits, detecting shifts in reaction norms would require additional methods.

Whether these changes are adaptive in the context of a warming climate remains an open question. The adaptive significance of observed shifts is complicated by the existence of multiple selective pressures acting on multiple life stages. The general use of stage-specific measurements and proxies for fitness rather than lifetime fitness make detecting adaptiveness difficult. For example, although a shift in gene frequencies might reflect adaptation, the trait being measured might not be the target of selection and thus not in itself appear adaptive. For example, Kovach et al. (2012) suggested that earlier migrants had more warm-adapted phenotypes in other life stages, which increased their fitness over late migrants. If this is the case, we might expect a reversal of the trend towards earlier migration in this population because the trend towards earlier migration timing itself exposed the fish to higher temperatures. In fact, changes in emigration and spawn timing often appeared to produce a phenological mismatch. For example, in Scotland, advanced smolt emigration from rivers in response to rising stream temperature correlated with reduced marine survival (Kennedy and Crozier 2010). But the lifetime costs and benefits of these shifts are not known.

It is clear that sufficiently high selection intensities can yield measurable selection responses in few generations in fishes. Crucial traits such as heat tolerance (Ineno et al. 2008), thermal reaction norms for growth (Kavanagh et al. 2010) and spawn timing (Neira et al. 2006) can evolve rapidly. Thus, evolution in response to climate change is certainly possible, and indeed likely, in fish. Furthermore, many studies spanned multiple generations, with the median study duration at 34 years, and the maximum at 91 years (Fig. 4). So why did so few studies document it? We propose three possible explanations.

First, the correlation-based methods generally employed are incapable of detecting the subtle shifts in

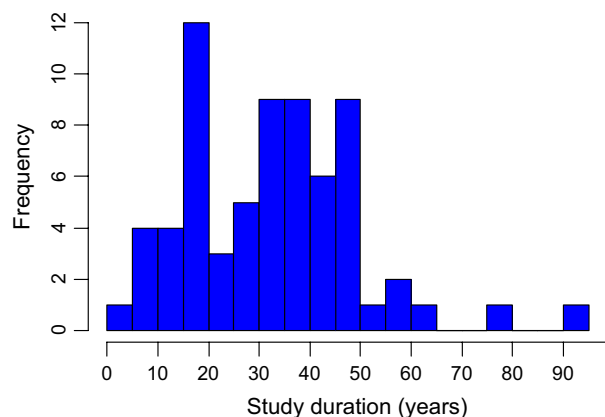


Figure 4 Frequency distribution of the number of years analyzed in each study.

reaction norms that are expected over the few generations spanned in most studies. One approach that might hold promise as a means of detecting evolutionary responses to climate change is the estimation of selection differentials over long time series (Swain et al. 2007; Crozier et al. 2011). Another might involve within-population studies of temporal shifts in the shapes of univariate or bivariate norms of reaction (Hutchings 2011). One means of detecting the latter has involved the use of probabilistic maturation reaction norms (PMRNs), albeit primarily for studies of fisheries-induced evolution (Dieckmann and Heino 2007). However, experimental studies have cautioned that temporal shifts in PMRNs can be influenced by nongenetic factors and might not always be indicative of evolution (Uusi-Heikkilä et al. 2011; Hurst et al. 2012; Díaz Pauli and Heino 2013). Research on genetic change in reaction norms could be usefully accompanied by experimental studies of selection responses by reaction norms induced by key metrics of climate change, such as temperature.

Second, natural climate variability and 'regime shifts' often dominated the temperature signals during study periods, rather than directional climate change (e.g. Kjesbu et al. 1998; Sundby and Nakken 2008; Rogers et al. 2011; Hurst et al. 2012). In addition to simple annual variation in climate, reversals in temperature and hence selection from decadal climate cycles might slow evolutionary responses to long-term warming and cause phenotypic trends in the opposite direction from that expected due to anthropogenic climate change (Fig. 1; Chevin 2013). These cycles can also amplify temperature trends in short-term records, but these trends do not necessarily reflect anthropogenic climate change alone. Decadal climate oscillations, such as the PDO and the NAO, cycle at 50–70 year periods. To capture evolution over these time frames is beyond the scope of most studies. In an oscillat-

ing climate, directional warming trends might impose strong selection primarily during extreme years, which will occur most often near peaks of natural decadal cycles. Kovach et al. (2012) demonstrated the potential long-term consequences of such a strong selection event quite eloquently. However, few studies will catch these exceptional events. The full evolutionary implications of natural climate cycles were not considered in any of the studies in our review.

Third, multiple selection pressures (e.g. fishing, competition from stocked fish) have the potential to overwhelm our ability to detect responses of fish to climate change. In the future, compounding threats from multiple stressors, such as hypoxia (Moran et al. 2010; Healy and Schulte 2012), high concentrations of $p\text{CO}_2$ (Enzor et al. 2013) or contaminants (Terzi and Verep 2012) can lower thermal tolerance, thus increasing the likelihood that many more populations will surpass critical thermal thresholds. However, the correlation between hypoxia and temperature tolerance in a more general stress response (Anttila et al. 2013) suggests that evolution might also proceed faster than independent selection on uncorrelated traits (Etterson and Shaw 2001).

In general, the strongest evolutionary responses to climate change will likely occur in species with short generation times, subject to high or consistent selection pressure, especially near peaks of natural cycles, and in traits controlled relatively simply or with genetic variation present in existing populations. Of course adaptation, while allowing genotypes to fare better than they would have otherwise, need not translate into increased probability of persistence (Kopp and Matuszewski 2014). Many species in highly variable environments, such as the intertidal zone (Somero 2010; Tomanek 2010; Madeira et al. 2012), and many coral reef fishes are currently at or very near their thermal maxima, such that a slight increase in temperature can potentially impose strong selection (Munday et al. 2008, 2012), which might then drive populations extinct before they can adapt. However, if individual fitness tends to be higher at warm temperatures (i.e. 'hotter is better'), then quantitative genetic models show that species in warmer environments might face lower extinction rates than those in cooler environments (Walters et al. 2012). Evolution is expected to be slower in Antarctic fishes, because they have lost functionality in relevant gene and gene regulatory areas, compared with simpler, single amino acid replacements, that would be necessary for other fish (Somero 2010; Tomanek 2010). Nonetheless, given abundant evidence that many traits in fish can respond rapidly to changes in environmentally driven selection pressures and that these traits are strongly plastic, we recommend exploration of more methods suitable for detecting temporal changes in reaction norms in fish.

Acknowledgements

We thank Andrew Hendry and Juha Merilä for initiating this project and providing very helpful editorial guidance, as well as two anonymous reviewers. JAH was supported by funding awarded by the Natural Sciences and Engineering Research Council (Canada).

Literature cited

- Ahas, R., and A. Aasa 2006. The effects of climate change on the phenology of selected Estonian plant, bird and fish populations. *International Journal of Biometeorology* **51**:17–26.
- Al-Chokhachy, R., J. Alder, S. Hostettler, R. Gresswell, and B. Shepard. 2013. Thermal controls of yellowstone cutthroat trout and invasive fishes under climate change. *Global Change Biology* **19**:3069–3081.
- Angilletta, M. J. 2009. *Thermal Adaptation: A Theoretical and Empirical Synthesis*. Oxford University Press, Oxford.
- Anttila, K., R. S. Dhillon, E. G. Boulding, A. P. Farrell, B. D. Glebe, J. A. K. Elliott, W. R. Wolters et al. 2013. Variation in temperature tolerance among families of Atlantic salmon (*Salmo salar*) is associated with hypoxia tolerance, ventricle size and myoglobin level. *Journal of Experimental Biology* **216**:1183–1190.
- Arismendi, I., S. L. Johnson, J. B. Dunham, R. Haggerty, and D. Hockman-Wert 2012. The paradox of cooling streams in a warming world: regional climate trends do not parallel variable local trends in stream temperature in the Pacific continental United States. *Geophysical Research Letters* **39**:L10401.
- Attrill, M. J., and M. Power 2002. Climatic influence on a marine fish assemblage. *Nature* **417**:275–278.
- Barrett, R. D. H., A. Paccard, T. M. Healy, S. Bergek, P. M. Schulte, D. Schluter, and S. M. Rogers 2011. Rapid evolution of cold tolerance in stickleback. *Proceedings of the Royal Society B-Biological Sciences* **278**:233–238.
- Bartholomew, J. L. 1998. Host resistance to infection by the myxosporean parasite *Ceratomyxa shasta*: a review. *Journal of Aquatic Animal Health* **10**:112–120.
- Baumann, H., and D. O. Conover 2011. Adaptation to climate change: contrasting patterns of thermal-reaction-norm evolution in Pacific versus Atlantic silversides. *Proceedings of the Royal Society B-Biological Sciences* **278**:2265–2273.
- Beacham, T. D., and T. P. T. Evelyn 1992. Population and genetic variation in resistance of Chinook salmon to vibriosis, furunculosis, and bacterial kidney disease. *Journal of Aquatic Animal Health* **4**:153–167.
- Beaugrand, G., K. M. Brander, J. A. Lindley, S. Souissi, and P. C. Reid 2003. Plankton effect on cod recruitment in the North Sea. *Nature* **426**:661–664.
- Beitinger, T. L., W. A. Bennett, and R. W. McCauley 2000. Temperature tolerances of North American freshwater fishes exposed to dynamic changes in temperature. *Environmental Biology of Fishes* **58**:237–275.
- Bilyk, K. T., and A. L. DeVries 2011. Heat tolerance and its plasticity in Antarctic fishes. *Comparative Biochemistry and Physiology a-Molecular & Integrative Physiology* **158**:382–390.
- Blunden, J., and D. S. Arndt 2013. State of the climate in 2012. *Bulletin of the American Meteorological Society* **94**:S1–S238.
- Bowden, T. J. 2008. Modulation of the immune system of fish by their environment. *Fish & Shellfish Immunology* **25**:373–383.
- Bradbury, I., S. Hubert, B. Higgins, T. Borza, S. Bowman, I. Paterson, P. Snelgrove et al. 2010. Parallel adaptive evolution of Atlantic cod on both sides of the Atlantic Ocean in response to temperature. *Proceedings of the Royal Society B-Biological Sciences* **277**:3725–3734.
- Bradbury, I., S. Hubert, B. Higgins, S. Bowman, T. Borza, I. Paterson, P. Snelgrove et al. 2013. Genomic islands of divergence and their consequences for the resolution of spatial structure in an exploited marine fish. *Evolutionary Applications* **6**:450–461.
- Brett, J. R. 1956. Some principles of the thermal requirements of fishes. *Quarterly Review of Biology* **31**:75–87.
- Brett, J. R. 1995. Energetics. In: C. Groot, L. Margolis, and W. C. Clarke, eds. *Physiological Ecology of Pacific Salmon*. pp. 4–68, UBC Press, Vancouver.
- Carlson, S. M., and T. P. Quinn 2007. Ten years of varying lake level and selection on size-at-maturity in sockeye salmon. *Ecology* **88**:2620–2629.
- Carlson, S. M., A. P. Hendry, and B. H. Letcher 2004. Natural selection acting on body size, growth rate and compensatory growth: an empirical test in a wild trout population. *Evolutionary Ecology Research* **6**:955–973.
- Carroll, S. P., A. P. Hendry, D. N. Reznick, and C. W. Fox 2007. Evolution on ecological time-scales. *Functional Ecology* **21**:387–393.
- Chevin, L. M. 2013. Genetic constraints on adaptation to a changing environment. *Evolution* **67**:708–721.
- Chevin, L. M., R. Lande, and G. M. Mace 2010. Adaptation, plasticity, and extinction in a changing environment: towards a predictive theory. *PLoS Biology* **8**:e1000357.
- Collins, S., B. Rost, and T. A. Ryneerson. 2014. Evolutionary potential of marine phytoplankton under ocean acidification. *Evolutionary Applications* **7**:140–155.
- Comte, L., and G. Grenouillet. 2013. Do stream fish track climate change? Assessing distribution shifts in recent decades *Ecography* **36**:1236–1246.
- Conover, D. O., and T. M. C. Present 1990. Countergradient variation in growth rate: compensation for length of the growing season among Atlantic silversides from different latitudes. *Oecologia* **83**:316–324.
- Conover, D. O., and E. T. Schultz 1995. Phenotypic similarity and the evolutionary significance of countergradient variation. *Trends in Ecology & Evolution* **10**:248–252.
- Côté, J., J. M. Roussel, S. Cam, G. Bal, and G. Evanno 2012. Population differences in response to hypoxic stress in Atlantic salmon. *Journal of Evolutionary Biology* **25**:2596–2606.
- Coulson, T., S. Tuljapourkar, and D. Z. Childs 2010. Using evolutionary demography to link life history theory, quantitative genetics and population ecology. *Journal of Animal Ecology* **79**:1226–1240.
- Cox, S. P., and S. G. Hinch 1997. Changes in size at maturity of Fraser River sockeye salmon (*Oncorhynchus nerka*) (1952–1993) and associations with temperature. *Canadian Journal of Fisheries and Aquatic Sciences* **54**:1159–1165.
- Croisatière, S., L. Bernatchez, and P. Belhumeur 2010. Temperature and length-dependent modulation of the MH class II β gene expression in brook charr (*Salvelinus fontinalis*) by a cis-acting minisatellite. *Molecular Immunology* **47**:1817–1829.
- Crozier, L. G., M. D. Scheuerell, and R. W. Zabel 2011. Using time series analysis to characterize evolutionary and plastic responses to environmental change: a case study of a shift toward earlier migration date in sockeye salmon. *American Naturalist* **178**:755–773.
- Dahl, J., J. Dannewitz, L. Karlsson, E. Petersson, A. Lof, and B. Ragnarsen 2004. The timing of spawning migration: implications of environmental variation, life history, and sex. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* **82**:1864–1870.
- Danovaro, R., C. Corinaldesi, A. Dell'Anno, J. A. Fuhrman, J. J. Middelburg, R. T. Noble, and C. A. Suttle 2011. Marine viruses and global climate change. *Fems Microbiology Reviews* **35**:993–1034.

- Debes, P. V., M. C. McBride, D. J. Fraser, and J. A. Hutchings 2013. Multigenerational hybridisation and its consequences for maternal effects in Atlantic salmon. *Heredity* **111**:238–247.
- Denman, K., J. R. Christian, N. Steiner, H. O. Portner, and Y. Nojiri 2011. Potential impacts of future ocean acidification on marine ecosystems and fisheries: current knowledge and recommendations for future research. *Ices Journal of Marine Science* **68**:1019–1029.
- Di Lorenzo, E., N. Schneider, K. M. Cobb, K. Chhak, P. J. S. Franks, A. J. Miller, J. C. McWilliams et al. 2008. North Pacific Gyre Oscillation links ocean climate and ecosystem change. *Geophysical Research Letters* **35**:L08607. NPGO Index available at <http://eros.eas.gatech.edu/nngo/>.
- Díaz Pauli, B., and M. Heino 2013. The importance of social dimension and maturation stage for the probabilistic maturation reaction norm in *Poecilia reticulata*. *Journal of Evolutionary Biology* **26**:2184–2196.
- Dieckmann, U., and M. Heino 2007. Probabilistic maturation reaction norms: their history, strengths, and limitations. *Marine Ecology-Progress Series* **335**:253–269.
- Dionne, M., K. M. Miller, J. J. Dodson, F. Caron, and L. Bernatchez 2007. Clinal variation in mhc diversity with temperature: evidence for the role of host-pathogen interaction on local adaptation in Atlantic salmon. *Evolution* **61**:2154–2164.
- Dixon, D. L., P. L. Munday, and G. P. Jones 2010. Ocean acidification disrupts the innate ability of fish to detect predator olfactory cues. *Ecology Letters* **13**:68–75.
- Donelson, J. M., and P. L. Munday 2012. Thermal sensitivity does not determine acclimation capacity for a tropical reef fish. *Journal of Animal Ecology* **81**:1126–1131.
- Donelson, J. M., P. L. Munday, M. I. McCormick, and C. R. Pitcher 2012. Rapid transgenerational acclimation of a tropical reef fish to climate change. *Nature Climate Change* **2**:30–32.
- Doney, S. C., M. Ruckelshaus, J. E. Duffy, J. P. Barry, F. Chan, C. A. English, H. M. Galindo et al. 2012. Climate change impacts on marine ecosystems. *Annual Review of Marine Science* **4**, 11–37.
- Dulvy, N. K., S. I. Rogers, S. Jennings, V. Stelzenmuller, S. R. Dye, and H. R. Skjoldal 2008. Climate change and deepening of the North Sea fish assemblage: a biotic indicator of warming seas. *Journal of Applied Ecology* **45**:1029–1039.
- Enzor, L. A., M. L. Zippay, and S. P. Place 2013. High latitude fish in a high CO₂ world: synergistic effects of elevated temperature and carbon dioxide on the metabolic rates of Antarctic notothenioids. *Comparative Biochemistry and Physiology A-Molecular & Integrative Physiology* **164**:154–161.
- Etterson, J. R., and R. G. Shaw 2001. Constraint to adaptive evolution in response to global warming. *Science* **294**:151–154.
- Fangue, N. A., J. E. Podrabsky, L. I. Crawshaw, and P. M. Schulte 2009. Countergradient variation in temperature preference in populations of killifish *Fundulus heteroclitus*. *Physiological and Biochemical Zoology* **82**:776–786.
- Ficke, A. D., C. A. Myrick, and L. J. Hansen 2007. Potential impacts of global climate change on freshwater fisheries. *Reviews in Fish Biology and Fisheries* **17**:581–613.
- Finstad, A. G., T. Forseth, B. Jonsson, E. Bellier, T. Hesthagen, A. J. Jensen, D. O. Hessen et al. 2011. Competitive exclusion along climate gradients: energy efficiency influences the distribution of two salmonid fishes. *Global Change Biology* **17**:1703–1711.
- Francis, J. A., and S. J. Vavrus. 2012. Evidence linking Arctic amplification to extreme weather in mid-latitudes. *Geophysical Research Letters* **39**:L06801.
- Franke, A., and C. Clemmesen 2011. Effect of ocean acidification on early life stages of Atlantic herring (*Clupea harengus* L.). *Biogeosciences* **8**:3697–3707.
- Franks, S. J., J. J. Weber, and S. N. Aitken. 2013. Evolutionary and plastic responses to climate change in terrestrial plant populations. *Evolutionary Applications* **7**:123–139.
- Friedland, K. D., G. Chaput, and J. C. MacLean 2005. The emerging role of climate in post-smolt growth of Atlantic salmon. *Ices Journal of Marine Science* **62**:1338–1349.
- Frommel, A. Y., R. Maneja, D. Lowe, A. M. Malzahn, A. J. Geffen, A. Folkvord, U. Piatkowski et al. 2012. Severe tissue damage in Atlantic cod larvae under increasing ocean acidification. *Nature Climate Change* **2**:42–46.
- Fry, R. E. J. 1967. Responses of vertebrate poikilotherms to temperature. In: A. H. Rose, ed. *Thermobiology*, pp. 375–409. Academic Press, New York.
- Fukushima, M., and W. W. Smoker 1997. Determinants of stream life, spawning efficiency, and spawning habitat in pink salmon in the Auke Lake system, Alaska. *Canadian Journal of Fisheries and Aquatic Sciences* **54**:96–104.
- Goodkin, N. F., K. A. Huguen, S. C. Doney, and W. B. Curry 2008. Increased multidecadal variability of the North Atlantic Oscillation since 1781. *Nature Geoscience* **1**:844–848.
- Gillet, C., and P. Quélin 2006. Effect of temperature changes on the reproductive cycle of roach in Lake Geneva from 1983 to 2001. *Journal of Fish Biology* **69**:518–534.
- Graham, C. T., and C. Harrod 2009. Implications of climate change for the fishes of the British Isles. *Journal of Fish Biology* **74**: 1143–1205.
- Griffiths, R. B. 2013. Oceans and Marine Resources in a Changing Climate. Technical Input to the 2013 National Climate Assessment U.S. Global Change Research Program.
- Gruber, N. 2011. Warming up, turning sour, losing breath: ocean biogeochemistry under global change. *Philosophical Transactions of the Royal Society A-Mathematical Physical and Engineering Sciences* **369**:1980–1996.
- Gruber, N., C. Hauri, Z. Lachkar, D. Loher, T. L. Frolicher, and G. K. Plattner 2012. Rapid progression of ocean acidification in the California Current System. *Science* **337**:220–223.
- Hale, R., P. Calosi, L. McNeill, N. Mieszkowska, and S. Widdicombe 2011. Predicted levels of future ocean acidification and temperature rise could alter community structure and biodiversity in marine benthic communities. *Oikos* **120**:661–674.
- Handford, P., G. Bell, and T. Reimchen 1977. A gillnet fishery considered as an experiment in artificial selection. *Journal of the Fisheries Research Board of Canada* **34**:954–961.
- Harvell, C. D., K. Kim, J. M. Burkholder, R. R. Colwell, P. R. Epstein, D. J. Grimes, E. E. Hofmann et al. 1999. Review: marine ecology - emerging marine diseases - climate links and anthropogenic factors. *Science* **285**:1505–1510.
- Haugen, T. O., and L. A. Vøllestad 2000. Population differences in early life-history traits in grayling. *Journal of Evolutionary Biology* **13**:897–905.
- Healy, T. M., and P. M. Schulte 2012. Factors affecting plasticity in whole-organism thermal tolerance in common killifish (*Fundulus heteroclitus*). *Journal of Comparative Physiology B-Biochemical Systemic and Environmental Physiology* **182**:49–62.
- Heath, M. R., F. C. Neat, J. K. Pinnegar, D. G. Reid, D. W. Sims, and P. J. Wright 2012. Review of climate change impacts on marine fish and

- shellfish around the UK and Ireland. *Aquatic Conservation-Marine and Freshwater Ecosystems* **22**:337–367.
- Helland, I. P., A. G. Finstad, T. Forseth, T. Hesthagen, and O. Ugedal 2011. Ice-cover effects on competitive interactions between two fish species. *Journal of Animal Ecology* **80**:539–547.
- Hendry, A. P., and M. T. Kinnison 1999. Perspective: the pace of modern life: measuring rates of contemporary microevolution. *Evolution* **53**:1637–1653.
- Hendry, A. P., and S. C. Stearns 2004. *Evolution Illuminated: Salmon and their Relatives*. Oxford University Press, Oxford.
- Hendry, A. P., J. E. Hensleigh, and R. R. Reisenbichler 1998. Incubation temperature, developmental biology, and the divergence of sockeye salmon (*Oncorhynchus nerka*) within Lake Washington. *Canadian Journal of Fisheries and Aquatic Sciences* **55**:1387–1394.
- Hendry, A. P., T. J. Farrugia, and M. T. Kinnison 2008. Human influences on rates of phenotypic change in wild animal populations. *Molecular Ecology* **17**:20–29.
- Hoegh-Guldberg, O., and J. F. Bruno 2010. The impact of climate change on the world's marine ecosystems. *Science* **328**:1523–1528.
- Hofmann, G. E., and A. E. Todgham 2010. Living in the now: Physiological mechanisms to tolerate a rapidly changing environment. *Annual Review of Physiology* **72**:127–145.
- Hurst, T. P., S. B. Munch, and K. A. Lavelle 2012. Thermal reaction norms for growth vary among cohorts of Pacific cod (*Gadus macrocephalus*). *Marine Biology* **159**:2173–2183.
- Hutchings, J. A. 2002. Life histories of fish. In: P. J. B. Hart, and J. D. Reynolds, eds. *Handbook of Fish Biology and Fisheries*, pp. 149–174. Blackwell Science, Fish Biology. Oxford.
- Hutchings, J. A. 2011. Old wine in new bottles: reaction norms in salmonid fishes. *Heredity* **106**:421–437.
- Hutchings, J. A., and D. J. Fraser 2008. The nature of fisheries- and farming-induced evolution. *Molecular Ecology* **17**:294–313.
- Hutchings, J. A., D. P. Swain, S. Rowe, J. D. Eddington, V. Puvanendran, and J. A. Brown 2007. Genetic variation in life-history reaction norms in a marine fish. *Proceedings of the Royal Society, Series B: Biological Sciences* **274**:1693–1699.
- Hurrell, J. 1995. NAO Index Data provided by the Climate Analysis Section, NCAR, Boulder, USA. <http://climatedataguide.ucar.edu/guidance/hurrell-north-atlantic-oscillation-nao-index-station-based> (accessed on March 2013).
- Ineno, T., S. Tsuchida, M. Kanda, and S. Watabe 2005. Thermal tolerance of a rainbow trout *Oncorhynchus mykiss* strain selected by high-temperature breeding. *Fisheries Science* **71**:767–775.
- Ineno, T., M. Endo, and S. Watabe 2008. Differences in self-feeding activity between thermally selected and normal strains of rainbow trout *Oncorhynchus mykiss* at high temperatures. *Fisheries Science* **74**:372–379.
- IPCC. 2007. *Climate change 2007: the physical science basis: intergovernmental panel on climate change fourth assessment report*. <http://www.ipcc.ch/> (accessed on March 2013).
- IPCC. 2012. *Managing the risks of extreme events and disasters to advance climate change adaptation*. In C. B. Field, V. Barros, T. F. Stocker, D. Qin, D. J. Dokken, K. L. Ebi, and M. D. Mastrandrea et al., eds. *A Special Report of Working Groups I and II of the Intergovernmental Panel on Climate Change*. pp. 582. Cambridge University Press, Cambridge, UK and New York, NY, USA.
- IPCC. 2013. *Climate change 2013: the physical science basis: intergovernmental panel on climate change fourth assessment report*. <http://www.climatechange2013.org/> (accessed Sept 2013).
- Jensen, L. F., M. M. Hansen, C. Pertoldi, G. Holdensgaard, K. L. D. Mensberg, and V. Loeschcke 2008. Local adaptation in brown trout early life-history traits: implications for climate change adaptability. *Proceedings of the Royal Society B-Biological Sciences* **275**:2859–2868.
- Jobling, M. 1994. *Fish Bioenergetics*. Chapman and Hall, New York.
- Johansen, J. L., and G. P. Jones 2011. Increasing ocean temperature reduces the metabolic performance and swimming ability of coral reef damselfishes. *Global Change Biology* **17**:2971–2979.
- Jonsson, N., and B. Jonsson 2004. Size and age of maturity of Atlantic salmon correlate with the North Atlantic Oscillation Index (NAOI). *Journal of Fish Biology* **64**:241–247.
- Juanes, F., S. Gephard, and K. Beland 2004. Long-term changes in migration timing of adult Atlantic salmon (*Salmo salar*) at the southern edge of the species distribution. *Canadian Journal of Fisheries and Aquatic Sciences* **61**:2392–2400.
- Kassahn, K. S., R. H. Crozier, H. O. Portner, and M. J. Caley 2009. Animal performance and stress: responses and tolerance limits at different levels of biological organisation. *Biological Reviews* **84**:277–292.
- Kavanagh, K. D., T. O. Haugen, F. Gregersen, J. Jernvall, and L. A. Vollestad 2010. Contemporary temperature-driven divergence in a Nordic freshwater fish under conditions commonly thought to hinder adaptation. *Bmc Evolutionary Biology* **10**:350.
- Keefer, M. L., C. A. Peery, and M. J. Heinrich 2008. Temperature-mediated en route migration mortality and travel rates of endangered Snake River sockeye salmon. *Ecology of Freshwater Fish* **17**:136–145.
- Kennedy, R. J., and W. W. Crozier 2010. Evidence of changing migratory patterns of wild Atlantic salmon *Salmo salar* smolts in the River Bush, Northern Ireland, and possible associations with climate change. *Journal of Fish Biology* **76**:1786–1805.
- Kinnison, M. T., and A. P. Hendry 2001. The pace of modern life II: from rates of contemporary microevolution to pattern and process. *Genetica* **112–113**:145–164.
- Kinnison, M. T., M. J. Unwin, W. K. Hershberger, and T. P. Quinn 1998. Egg size, fecundity, and development rate of two introduced New Zealand Chinook salmon (*Oncorhynchus tshawytscha*) populations. *Canadian Journal of Fisheries and Aquatic Sciences* **55**:1946–1953.
- Kinnison, M. T., T. P. Quinn, and M. J. Unwin 2011. Correlated contemporary evolution of life history traits in New Zealand Chinook salmon, *Oncorhynchus tshawytscha*. *Heredity* **106**:448–459.
- Kjesbu, O. S., and P. R. Witthames 2007. Evolutionary pressure on reproductive strategies in flatfish and groundfish: relevant concepts and methodological advancements. *Journal of Sea Research* **58**:23–34.
- Kjesbu, O. S., P. R. Witthames, P. Solemdal, and M. G. Walker 1998. Temporal variations in the fecundity of Arcto-Norwegian cod (*Gadus morhua*) in response to natural changes in food and temperature. *Journal of Sea Research* **40**:303–321.
- Klyashtorin, L., V. Borisov, and A. Lyubushin 2009. Cyclic changes of climate and major commercial stocks of the Barents Sea. *Marine Biology Research* **5**:4–17.
- Koehn, J. D., A. J. Hobday, M. S. Pratchett, and B. M. Gillanders 2011. Climate change and Australian marine and freshwater environments, fishes and fisheries: synthesis and options for adaptation. *Marine and Freshwater Research* **62**:1148–1164.
- Kopp, M., and S. Matuszewski. 2014. Rapid evolution of quantitative traits: theoretical perspectives. *Evolutionary Applications* **7**:169–191.
- Kovach, R. P., A. J. Gharrett, and D. A. Tallmon 2012. Genetic change for earlier migration timing in a pink salmon population. *Proceedings of the Royal Society B-Biological Sciences* **279**:3870–3878.

- Kovach, R. P., J. E. Joyce, J. D. Echave, M. S. Lindberg, and D. A. Tallmon. 2013. Earlier migration timing, decreasing phenotypic variation, and biocomplexity in multiple salmonid species. *Plos One* **8**.
- Kroeker, K. J., R. L. Kordas, R. N. Crim, and G. G. Singh. 2010. Review and Synthesis: meta-analysis reveals negative yet variable effects of ocean acidification on marine organisms. *Ecology Letters* **14**:139–1434.
- Lande, R. 2009. Adaptation to an extraordinary environment by evolution of phenotypic plasticity and genetic assimilation. *Journal of Evolutionary Biology* **22**:1435–1446.
- Landis, S. H., J. Sundin, G. Rosenqvist, and O. Roth 2012. Behavioral adjustments of a pipefish to bacterial *Vibrio* challenge. *Behavioral Ecology and Sociobiology* **66**:1399–1405.
- Liu, J. P., J. A. Curry, H. J. Wang, M. R. Song, and R. M. Horton 2012. Impact of declining Arctic sea ice on winter snowfall (vol 109, pg 4074, 2012). *Proceedings of the National Academy of Sciences of the United States of America* **109**:6781–6783.
- Lovejoy, T. E., and L. Hannah 2005. *Climate Change and Biodiversity*. CT, Yale University Press, New Haven.
- Macnab, V., and I. Barber 2012. Some (worms) like it hot: fish parasites grow faster in warmer water, and alter host thermal preferences. *Global Change Biology* **18**:1540–1548.
- Madeira, D., L. Narciso, H. N. Cabral, and C. Vinagre 2012. Thermal tolerance and potential impacts of climate change on coastal and estuarine organisms. *Journal of Sea Research* **70**:32–41.
- Mantua, N. J., S. R. Hare, Y. Zhang, J. M. Wallace, and R. C. Francis 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. *Bulletin of the American Meteorological Society* **78**:1069–1079.
- Marcil, J., D. P. Swain, and J. A. Hutchings 2006. Countergradient variation in body shape of a widespread marine fish, the Atlantic cod (*Gadus morhua*). *Proceedings of the Royal Society of London, Series B: Biological Sciences* **273**:217–223.
- Marcos-Lopez, M., P. Gale, B. C. Oidtmann, and E. J. Peeler 2010. Assessing the impact of climate change on disease emergence in freshwater fish in the United Kingdom. *Transboundary and Emerging Diseases* **57**:293–304.
- Meffe, G. K., S. C. Weeks, M. Mulvey, and K. L. Kandl 1995. Genetic differences in thermal tolerance of eastern mosquitofish (*Gambusia holbrooki* Poeciliidae) from ambient and thermal ponds. *Canadian Journal of Fisheries and Aquatic Sciences* **52**:2704–2711.
- Merilä, J., and A. P. Hendry. 2014. this volume. Climate change, adaptation and phenotypic plasticity: the problem and the evidence. *Evolutionary Applications* **7**:1–14.
- Merilä, J., B. C. Sheldon, and L. E. B. Kruuk 2001. Explaining stasis: microevolutionary studies in natural populations. *Genetica* **112**–**113**:199–222.
- Miller, M., J. Brunelli, P. Wheeler, S. Liu, C. Rexroad, Y. Palti, C. Doe et al. 2012. A conserved haplotype controls parallel adaptation in geographically distant salmonid populations. *Molecular Ecology* **21**:237–249.
- Moran, R., I. Harvey, B. Moss, H. Feuchtmayr, K. Hatton, T. Heyes, and D. Atkinson 2010. Influence of simulated climate change and eutrophication on three-spined stickleback populations: a large scale mesocosm experiment. *Freshwater Biology* **55**:315–325.
- Mousseau, T. A., and D. A. Roff 1987. Natural selection and the heritability of fitness components. *Heredity* **59**:181–197.
- Munday, P. L., G. P. Jones, M. S. Pratchett, and A. J. Williams 2008. Climate change and the future for coral reef fishes. *Fish and Fisheries* **9**:261–285.
- Munday, P. L., D. L. Dixon, J. M. Donelson, G. P. Jones, M. S. Pratchett, G. V. Devitsina, and K. B. Doving 2009. Ocean acidification impairs olfactory discrimination and homing ability of a marine fish. *Proceedings of the National Academy of Sciences of the United States of America* **106**:1848–1852.
- Munday, P. L., M. I. McCormick, and G. E. Nilsson 2012. Impact of global warming and rising CO₂ levels on coral reef fishes: what hope for the future? *Journal of Experimental Biology* **215**:3865–3873.
- Naughton, G. P., C. C. Caudill, M. L. Keefer, T. C. Bjornn, L. C. Stuehrenberg, and C. A. Peery 2005. Late-season mortality during migration of radio-tagged adult sockeye salmon (*Oncorhynchus nerka*) in the Columbia River. *Canadian Journal of Fisheries and Aquatic Sciences* **62**:30–47.
- NCADAC. 2013. National climate assessment and development advisory committee. Third national climate assessment draft report: U.S. global change research program. <http://www.globalchange.gov/publications/reports> (accessed on Jun 2013).
- Neira, R., N. F. Diaz, G. A. E. Gall, J. A. Gallardo, J. P. Lhorente, and A. Alert 2006. Genetic improvement in coho salmon (*Oncorhynchus kisutch*). II: selection response for early spawning date. *Aquaculture* **257**:1–8.
- Noges, P., and A. Jarvet 2005. Climate driven changes in the spawning of roach (*Rutilus rutilus* (L.)) and bream (*Abramis brama* (L.)) in the Estonian part of the Narva River basin. *Boreal Environment Research* **10**:45–55.
- Orr, J. C., V. J. Fabry, O. Aumont, L. Bopp, S. C. Doney, R. A. Feely, A. Gnanadesikan et al. 2005. Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. *Nature* **437**:681–686.
- Otero, J., A. J. Jensen, J. H. L'Abée-Lund, N. C. Stenseth, G. O. Storvik, and L. A. Vollestad 2012. Contemporary ocean warming and freshwater conditions are related to later sea age at maturity in Atlantic salmon spawning in Norwegian rivers. *Ecology and Evolution* **2**:2192–2203.
- Ottersen, G., D. O. Hjermann, and N. C. Stenseth 2006. Changes in spawning stock structure strengthen the link between climate and recruitment in a heavily fished cod (*Gadus morhua*) stock. *Fisheries Oceanography* **15**:230–243.
- Pankhurst, N. W., and P. L. Munday 2011. Effects of climate change on fish reproduction and early life history stages. *Marine and Freshwater Research* **62**:1015–1026.
- Parnesan, C. 2006. Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics* **37**:637–669.
- Perry, A. L., P. J. Low, J. R. Ellis, and J. D. Reynolds 2005. Climate change and distribution shifts in marine fishes. *Science* **308**:1912–1915.
- Piché, J., J. A. Hutchings, and W. Blanchard 2008. Genetic variation in threshold reaction norms for alternative reproductive tactics in male Atlantic salmon, *Salmo salar*. *Proceedings of the Royal Society B: Biological Sciences* **275**:1571–1575.
- Pinsky, M. L., B. Worm, M. J. Fogarty, J. L. Sarmiento, and S. A. Levin 2013. Marine taxa track local climate velocities. *Science* **341**:1239–1242.
- Pörtner, H., and A. Farrell 2008. Physiology and climate change. *Science of the Total Environment* **322**:690–692.
- Pörtner, H. O., and M. A. Peck 2010. Climate change effects on fishes and fisheries: towards a cause-and-effect understanding. *Journal of Fish Biology* **77**:1745–1779.

- Pörtner, H. O., B. Berdal, R. Blust, O. Brix, A. Colosimo, B. De Wachter, A. Giuliani et al. 2001. Climate induced temperature effects on growth performance, fecundity and recruitment in marine fish: developing a hypothesis for cause and effect relationships in Atlantic cod (*Gadus morhua*) and common eelpout (*Zoarces viviparus*). *Continental Shelf Research* **21**:1975–1997.
- Price, G. R. 1970. Selection and covariance. *Nature* **227**:520–521.
- Price, G. R. 1972. Extension of covariance selection mathematics. *Annals of Human Genetics* **35**:485–490.
- Purdom, C. E. 1993. *Genetics and Fish Breeding*. Chapman and Hall, New York.
- Quinn, T. P., and D. J. Adams 1996. Environmental changes affecting the migratory timing of American shad and sockeye salmon. *Ecology* **77**:1151–1162.
- Quinn, T. P., M. T. Kinnison, and M. J. Unwin 2001. Evolution of Chinook salmon (*Oncorhynchus tshawytscha*) populations in New Zealand: pattern, rate, and process. *Genetica* **112–113**:493–513.
- Rahel, F. J., and J. D. Olden 2008. Assessing the effects of climate change on aquatic invasive species. *Conservation Biology* **22**:521–533.
- Reusch, T. 2014. Climate change in the oceans: evolutionary vs. phenotypically plastic responses. *Evolutionary Applications* **7**:104–122.
- Reznick, D. N., and H. Bryga 1987. Life-history evolution in guppies (*Poecilia reticulata*). 1. Phenotypic and genetic changes in an introduction experiment. *Evolution* **41**:1370–1385.
- Reznick, D. N., and C. K. Ghalambor 2001. The population ecology of contemporary adaptations: what empirical studies reveal about the conditions that promote adaptive evolution. *Genetica* **112**:183–198.
- Reznick, D. A., H. Bryga, and J. A. Endler 1990. Experimentally induced life-history evolution in a natural population. *Nature* **346**:357–359.
- Ricker, W. E. 1981. Changes in the average size and average age of Pacific salmon. *Canadian Journal of Fisheries and Aquatic Sciences* **38**:12:1636–1656.
- Rijnsdorp, A. D., M. A. Peck, G. H. Engelhard, C. Möllmann, and J. K. Pinnegar 2009. Resolving the effect of climate change on fish populations. *ICES Journal of Marine Science* **66**:1570–1583.
- Roessig, J. M., C. M. Woodley, J. J. Cech, and L. J. Hansen 2004. Effects of global climate change on marine and estuarine fishes and fisheries. *Reviews in Fish Biology and Fisheries* **14**:251–275.
- Roff, D. A. 1986. Predicting body size with life-history models. *BioScience* **36**:316–323.
- Roff, D. 2002. Comparing G matrices: A MANOVA approach. *Evolution* **56**:1286–1291.
- Rogers, L. A., L. C. Stige, E. M. Olsen, H. Knutsen, K. S. Chan, and N. C. Stenseth 2011. Climate and population density drive changes in cod body size throughout a century on the Norwegian coast. *Proceedings of the National Academy of Sciences of the United States of America* **108**:1961–1966.
- Russell, I. C., M. W. Aprahamian, J. Barry, I. C. Davidson, P. Fiske, A. T. Ibbotson, R. J. Kennedy et al. 2012. The influence of the freshwater environment and the biological characteristics of Atlantic salmon smolts on their subsequent marine survival. *Ices Journal of Marine Science* **69**:1563–1573.
- Sala, O. E., F. S. III Chapin, J. J. Armesto, E. Berlow, J. Bloomfield, R. Dirzo, E. Huber-Sanwald et al. 2000. Global biodiversity scenarios for the year 2100. *Science* **287**:1770–1774.
- Salinas, S., and S. B. Munch 2012. Thermal legacies: transgenerational effects of temperature on growth in a vertebrate. *Ecology Letters* **15**:159–163.
- Scheiner, S. M. 1993. Genetics and evolution of phenotypic plasticity. *Annual Review of Ecology and Systematics* **24**:35–68.
- Schindler, D. E., D. E. Rogers, M. D. Scheuerell, and C. A. Abrey 2005. Effects of changing climate on zooplankton and juvenile sockeye salmon growth in southwestern Alaska. *Ecology* **86**:198–209.
- Schlichting, C. D., and M. Pigliucci 1998. *Phenotypic Evolution: A Reaction Norm Perspective*. Sunderland, MA, Sinauer Assoc.
- Schneider, K. N., R. M. Newman, V. Card, S. Weisberg, and D. L. Pereira 2010. Timing of walleye spawning as an indicator of climate change. *Transactions of the American Fisheries Society* **139**:1198–1210.
- Scott, G. R., and I. A. Johnston 2012. Temperature during embryonic development has persistent effects on thermal acclimation capacity in zebrafish. *Proceedings of the National Academy of Sciences of the United States of America* **109**:14247–14252.
- Serbezov, D., L. Bernatchez, E. M. Olsen, and L. A. Vøllestad 2010. Quantitative genetic parameters for wild stream-living brown trout: heritability and parental effects. *Journal of Evolutionary Biology* **23**:1631–1641.
- Shuter, B. J., A. G. Finstad, I. P. Helland, I. Zweimüller, and F. Holker 2012. The role of winter phenology in shaping the ecology of freshwater fish and their sensitivities to climate change. *Aquatic Sciences* **74**:637–657.
- Sims, D. W., V. J. Wearmouth, M. J. Genner, A. J. Southward, and S. J. Hawkins 2004. Low-temperature-driven early spawning migration of a temperate marine fish. *Journal of Animal Ecology* **73**:333–341.
- Smoker, W. W., A. J. Gharrett, and M. S. Stekol 1998. Genetic variation of return date in a population of pink salmon: a consequence of fluctuating environment and dispersive selection? *Alaska Fishery Research Bulletin* **5**:46–54.
- Somero, G. N. 2010. The physiology of climate change: how potentials for acclimatization and genetic adaptation will determine ‘winners’ and ‘losers’. *Journal of Experimental Biology* **213**:912–920.
- Sorte, C. J. B., S. L. Williams, and J. T. Carlton 2010. Marine range shifts and species introductions: comparative spread rates and community impacts. *Global Ecology and Biogeography* **19**:303–316.
- Staudinger, M. D., N. B. Grimm, A. Staudt, S. L. Carter, F. S. Chapin III, P. Kareiva, M. Ruckelshaus et al. 2012. Impacts of climate change on biodiversity, ecosystems, and ecosystem services: technical input to the 2013 national climate assessment, cooperative report to the 2013 national climate assessment. <http://assessment.globalchange.gov> (accessed on Jun 2013).
- Stenseth, N. C., and A. Mysterud 2005. Weather packages: finding the right scale and composition of climate in ecology. *Journal of Animal Ecology* **74**:1195–1198.
- Stillman, J. H. 2003. Acclimation capacity underlies the susceptibility to climate change. *Science* **301**:65.
- Stockwell, C. A., A. P. Hendry, and M. T. Kinnison 2003. Contemporary evolution meets conservation biology. *Trends in Ecology & Evolution* **18**:94–101.
- Stoks, R., A. Geerts, and L. De Meester 2014. Evolutionary and plastic responses of freshwater invertebrates to climate change: realized patterns and future potential. *Evolutionary Applications* **7**:42–55.
- Strussmann, C. A., D. O. Conover, G. M. Somoza, and L. A. Miranda 2010. Implications of climate change for the reproductive capacity and survival of New World silversides (family Atherinopsidae). *Journal of Fish Biology* **77**:1818–1834.
- Sundby, S., and O. Nakken 2008. Spatial shifts in spawning habitats of Arcto-Norwegian cod related to multidecadal climate oscillations and climate change. *Ices Journal of Marine Science* **65**:953–962.

- Swain, D. P., A. F. Sinclair, and J. M. Hanson 2007. Evolutionary response to size-selective mortality in an exploited fish population. *Proceedings of the Royal Society B: Biological Sciences* **274**:1015–1022.
- Taylor, S. G. 2008. Climate warming causes phenological shift in Pink Salmon, *Oncorhynchus gorbuscha*, behavior at Auke Creek, Alaska. *Global Change Biology* **14**:229–235.
- Teal, L. R., J. J. de Leeuw, H. W. van der Veer, and A. D. Rijnsdorp 2008. Effects of climate change on growth of 0-group sole and plaice. *Marine Ecology Progress Series* **358**:219–230.
- Terzi, E., and B. Verep 2012. Effects of water hardness and temperature on the acute toxicity of mercuric chloride on rainbow trout (*Oncorhynchus mykiss*). *Toxicology and Industrial Health* **28**:499–504.
- Thomas, C., A. Cameron, R. Green, M. Bakkenes, L. Beaumont, Y. Collingham, B. Erasmus et al. 2004. Extinction risk from climate change. *Nature* **427**:145–148.
- Todd, C. D., S. L. Hughes, C. T. Marshall, J. C. MacLean, M. E. Loneragan, and E. M. Biuw 2008. Detrimental effects of recent ocean surface warming on growth condition of Atlantic salmon. *Global Change Biology* **14**:958–970.
- Todd, C. D., K. D. Friedland, J. C. MacLean, B. D. Whyte, I. C. Russell, M. E. Loneragan, and M. B. Morrissey 2012. Phenological and phenotypic changes in Atlantic salmon populations in response to a changing climate. *Ices Journal of Marine Science* **69**:1686–1698.
- Tomanek, L. 2010. Variation in the heat shock response and its implication for predicting the effect of global climate change on species' biogeographical distribution ranges and metabolic costs. *Journal of Experimental Biology* **213**:971–979.
- Tonteri, A., A. Vasemagi, J. Lumme, and C. R. Primmer 2010. Beyond MHC: signals of elevated selection pressure on Atlantic salmon (*Salmo salar*) immune-relevant loci. *Molecular Ecology* **19**:1273–1282.
- Urban, J. 2014. Plasticity and genetic adaptation mediate amphibian and reptile responses to climate change. *Evolutionary Applications* **7**:88–103.
- Uusi-Heikkilä, S., A. Kuparinen, C. Wolter, T. Meinelt, A. O'Toole, and R. Arlinghaus 2011. Experimental assessment of probabilistic maturation reaction norm: condition matters. *Proceedings of the Royal Society B: Biological Sciences* **278**:709–717.
- Valiente, A. G., F. Juanes, and E. Garcia-Vazquez 2011. Increasing regional temperatures associated with delays in Atlantic salmon sea-run timing at the southern edge of the European distribution. *Transactions of the American Fisheries Society* **140**:367–373.
- Volkov, A. F. 2012. Is the mass emergence of *Themisto libellula* in the northern Bering Sea an invasion or a bloom? *Russian Journal of Marine Biology* **38**:465–473.
- Walsh, M. R., and D. N. Reznick 2011. Experimentally induced life-history evolution in a killifish in response to the introduction of guppies. *Evolution* **65**:1021–1036.
- Walters, C. J., and S. J. D. Martell 2004. *Fisheries Ecology and Management*. Princeton, New Jersey, Princeton University Press.
- Walters, R. J., W. U. Blanckenhorn, and D. Berger 2012. Forecasting extinction risk of ectotherms under climate warming: an evolutionary perspective. *Functional Ecology* **26**:1324–1338.
- Wenger, S. J., and J. D. Olden 2012. Assessing transferability of ecological models: an underappreciated aspect of statistical validation. *Methods in Ecology and Evolution* **3**:260–267.
- Wootton, R. J. 1998. *Ecology of Teleost Fishes*. Chapman & Hall, New York.