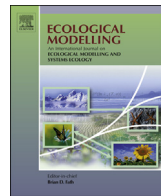




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Modeling climate change impacts on phenology and population dynamics of migratory marine species

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ABSTRACT

We review literature concerning the impacts of climate change on the migration of marine species, with an emphasis on the adaptation of migration phenology through genetic tracking and phenotypic plasticity. We then develop an individual-based modeling framework characterizing the effects of climate change on phenology and population dynamics. In the framework, an animal's ability to match its environmental preferences, its bioclimate envelope, to the environmental conditions by adjusting its migration timing between foraging and breeding habitats determines its condition, survival, and fecundity. Climate-induced changes in the envelope produce timing mismatches that result in a population adapting its phenology through both genetic and plastic processes. Model results suggest: (1) the temporal size of the bioclimate envelope is an important determinant of a population's sensitivity to climate change and susceptibility to extinction, (2) population extinction can occur if the rate of change in the timing of the envelope exceeds the rate its phenology changes or if the variability in the envelope exceeds the population's inherent capacity for variability, (3) a population with migration timing cued by photoperiod is expected to exhibit weaker phenotypic plasticity than one cued by temperature, and (4) population extinction in response to climate change follows a threshold pattern such that population size may not be a reliable indicator of extinction threat, although variability in average individual condition across years may be an extinction threat indicator. Finally, while the model is intentionally simplistic, we discuss how it can be extended to cover more complex interactions.

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1. Introduction

Global ecological responses to climate change are occurring widely in both terrestrial and marine environments (Walther et al., 2002). As temperatures increase, species ranges are expanding poleward and ranges of cold-habitat species are contracting. In the marine system, rapid impacts of climate change are predicted for pelagic species, because the seasonal abundances of predators and prey are differentially sensitive to climate change (FAO, 2010). The responses of migratory marine species (MMS) are especially important because the group includes commercial fish species, which make up nearly 16% of world protein consumed (FAO, 2010). Furthermore, this category includes apex marine predators, such as tuna, sharks, seabirds, and marine mammals that have top-down

influence on marine ecosystems and occupy irreplaceable niches in the biodiversity of the world oceans (Block et al., 2011).

Direct human impacts and climate change have already had significant impacts on the ocean environment. Marine biodiversity has changed because of multiple human influences, including commercial exploitation and harvest as well as other anthropogenic development and disturbance. Commercially exploited fisheries, including many MMS, have experienced a long history of overexploitation. While the rate of exploitation has recently declined, over 60% of the assessed marine fish stocks require rebuilding (Worm et al., 2009) and the range of many large highly mobile pelagic predators has declined (Worm and Tittensor, 2011). Furthermore 80% of the global catch lacks formal fish assessments (Costello et al., 2012). Changes in abundance have cascading impacts on ecosystem productivity and resilience, and the future of many marine populations is further expected to be significantly affected by the rate of ocean warming and the rate of exploitation (VanDerWal et al., 2013; Worm et al., 2010).

Understanding effects of climate change on the marine food web is a tremendous challenge because it involves not only the

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immediate response of species interactions with climate change (acclimation of the species through phenotypic plasticity), but also adaptation through genetic responses (Rose et al., 2010). For ecological modelers, the challenge is to develop conceptual frameworks that include the important ecological processes, but avoid “unsupportable and deleterious model complexity” (Rose et al., 2010). Because climate change has wide-ranging effects and models must provide information on the potential effects of actions made by public and governmental entities, a single modeling approach or framework will not suffice to guide decisions and consensus. While both simple intuitive models and complex models encompassing many ecological interactions are necessary, in between a heuristic framework is needed that can link the two ends of the spectrum. Our goal here is to demonstrate a framework for this middle ground that illustrates important pathways of climate effects in a heuristic way and that can be expanded to include more ecological complexity.

We focus our framework on the response of MMS to climate change. Indeed, species migration is a classic response to predictable seasonal or annual changes in the environment. It is implicitly tied to reproduction and is often driven by physiological and behavioral mechanisms (Ramenofsky and Wingfield, 2007). The overriding principle in developing our framework is that climate change, by reshaping the location, timing and size of habitats, alters species behavior, survival and ultimately genetic makeups. We apply the general idea of a closed migratory life cycle, described first by Harden-Jones (1968) and later examined by Secor (2002), as a series of seasonal and ontogenetic migrations between distinct habitats that result in homing and reproduction at localized spawning grounds and the dispersion of juveniles and adults to feeding habitats. Although highly abstracted, the closed migration cycle establishes the concept of natal philopatry in which a population returns to its place of birth to breed, in the sense that migratory species exhibit fidelity to specific breeding habitats. This is important because a trending change in the breeding habitat explicitly affects the trend in future populations' reproductive potential, though equally important is the timing of population movement through the migratory path.

Phenology is the study of how seasonal and interannual variations in the environment affect the timing of critical stages and events in a species' life cycle. Thus, a framework for exploring the effects of climate change on MMS requires defining the effects of climate on the shape and length of the migratory path, i.e. the philopatry, and the effects of climate on the timing of the population's movement over the path and the timing of its interactions with prey and predators, i.e. the phenology. Understanding migratory connections over a species' life cycle is an essential step in developing efficient conservation strategies and the general principles are applicable to migratory taxa worldwide including insects, birds, mammals and marine organisms (Martin et al., 2007). We first consider the climate effects on the phenology and philopatry underlying the MMS life history of a range of species, several of which (e.g., whales, turtles, salmon) have been proposed as possible indicators of the impact of climate change (Newson et al., 2009). Second, we review studies describing how species alter their phenology and philopatry through phenotypic plasticity and genetic mechanisms. Finally, we illustrate a framework for investigating how MMS may respond to climate change using a simplified model.

2. Review of literature

Climate can affect migratory marine species in a large number of ways because their life history strategies involve coordinating movement through a variety of climate zones. Thus, to develop a comprehensive perspective of these impacts, we need to consider

how the spatial-temporal aspects of climate change affect the philopatry and phenology of a species and then build on concepts unique to each field. A central concept is the bioclimate envelope, which correlates climate variables with observed species distributions to indirectly describe environmental preferences or limits, and how that might affect any match-mismatch in the optimality of the timing of a life cycle stage for survival, growth and reproduction.

We begin with a brief characterization of the physical aspects of climate change (Section 2.1), develop a general picture of philopatry in terms spatial properties of MMS (Section 2.2), and then consider phenology (Section 2.3). In the final section of the literature review, we address how species adapt to climate change in terms of genetic selection and phenotypic plasticity (Section 2.4). Throughout the paper, we seek to identify the essential processes needed in a modeling framework.

2.1. Spatial-temporal change of physical habitat

In the marine ecosystem, the most important physical factors affecting philopatry and phenology are water temperature and light, with the response to and importance of each factor being species dependent (Edwards and Richardson, 2004). Importantly, climate change affects temperature but not photoperiod or light. This becomes important when considering the environmental cues that trigger migrations.

The most obvious change is in global temperature, which in the ocean has already increased by 0.1 °C over the last 40 years (Bindoff et al., 2007). In response, oceanic surface isotherms are moving poleward on the order of 2 km/year and correspondingly the onset of springtime ocean temperatures are advancing at 2–3 days/decade; 30–40% faster than on land; by mid-century, sea surface temperature is projected to be 1–1.5 °C warmer in the North Pacific (Burrows et al., 2011). Corresponding to increases in ocean temperature, annual sea ice in polar regions is decreasing rapidly, and models project that by mid-century ice coverage in the circumpolar Arctic may be free of annual summertime sea ice (Wang et al., 2010).

In addition to large-scale changes, regional effects of climate change on marine environments are expected. Perhaps one of the most important changes for many marine species is the expected strengthening of coastal upwelling dynamics. Through a combination of altered flow regimes via increased intensity and frequency of El Niño and other large-scale ocean events (Yeh et al., 2009) and increases in the pressure gradient between land and ocean temperatures, coastal upwelling is expected to increase in intensity and duration (Bakun et al., 2010). This will have subsequent and frequently positive effects on regional temperature and productivity because upwelling brings cold, nutrient-rich water to the surface where it facilitates plankton growth. For species that migrate through coastal environments, altered upwelling dynamics could influence multiple navigational cues, such as temperature gradients and ocean currents (Booker et al., 2008) and prey distributions (Keister et al., 2011).

2.2. Philopatry

A distinguishing characteristic of MMS is their fidelity to foraging and breeding habitats, or philopatry. Here we briefly characterize the nature of the habitats and significance of this fidelity to the life history strategy. As examples, we focus on species such as salmon and steelhead, tuna, and sharks, which are high in the trophic food web and targeted in commercial or subsistence fisheries. We note that characterizing changes in the distribution of MMS species in response to climate change is a particular challenge because the locations of the habitats and the migratory routes between them may be associated with topographical properties,

such as semi-enclosed seas and gulfs, as is the case with bluefin tuna (Rooker et al., 2008), or be defined by oceanic properties (Perry et al., 2005; Ravier and Fromentin, 2004), or by the current distribution during their juvenile life stage, as has been proposed for sea turtles (Hays et al., 2010). Thus, there is often not a static geographic location representing a particular habitat, but rather a dynamic and ephemeral set of conditions that define the habitat.

2.2.1. Breeding habitat

Breeding habitats are typically well defined with a population returning to the same location to breed from generation to generation. Often, the population occupies the breeding habitat in the spring and summer. Both semelparous and iteroparous species can exhibit high fidelity to breeding habitats, i.e. “natal philopatry” (Weatherhead and Forbes, 1994), and this site fidelity is particularly high in migratory species. A number of specific examples include adult Pacific salmon, which roam the North Pacific for 1–5 years before returning to spawn in their natal stream reach (Groot and Margolis, 1991). Separate Atlantic bluefin tuna (*Thunnus thynnus*) stocks that are comingled in the Atlantic Ocean return to spawn in distinct locations in the Gulf of Mexico and Mediterranean Sea (Block et al., 2001, 2011; Muhling et al., 2011; Rooker et al., 2008). North Sea plaice (*Pleuronectes platessa*) exhibit spawning site fidelity, traveling 250 km from foraging habitats to within 20 km of the breeding habitat from previous years (Hunter et al., 2003). Halibut (*Hippoglossus stenolepis*) in the Gulf of Alaska migrate to deep water in the winter and return to within 20 km of their tagging sites the following summer (Loher, 2008). Many shark species exhibit site fidelity to natal and nursery areas including hammerhead sharks in Kaneohe Bay Hawaii and lemon sharks at Bimini Islands (Hansson et al., 2013). Marine mammals also exhibit site fidelity. For example, elephant seals (*Mirounga angustirostris*) return to their home colony after being translocated (Matsumura et al., 2011).

2.2.2. Foraging habitat and migration corridors

Unlike the often-specific requirements of breeding habitats, adult foraging habitats may not be well defined, and in many highly migratory species, the habitat instead consists of a migratory route (or corridor) through which the animal travels. In such situations, the foraging habitat may involve specific winter and summer habitats as well as the migration route between them, as species often show high fidelity to the migration corridors.

Salmon generally follow regular migration routes. For example, eastern North Pacific salmon follow coastal migration routes northward during the first year in the ocean (Melnichuk et al., 2010; Trudel et al., 2009; Welch et al., 2011), while salmon in the western North Pacific also appear to migrate northward against the prevailing current to remain in that ocean basin (Azumaya and Ishida, 2004; Beamish et al., 2005; Hinke et al., 2005). Although the details of salmon distributions after the first few months at sea are largely unknown (Chittenden et al., 2009; Drenner et al., 2012), the homeward migration of many salmon is well established because they are captured in coastal fisheries during their return migration (Sharma and Quinn, 2012). Modeling studies suggest that salmon populations beginning their homeward migration offshore can move along geomagnetic isolines to the river mouth (Bracis and Anderson, 2012, 2013; Putman et al., 2013).

Pacific white sharks (*Carcharodon carcharias*) exhibit distinct annual cycles, migrating between central California coastal habitats to subtropical and tropical pelagic habitats. These sharks exhibit high fidelity to foraging habitats, annually traveling thousands of km to a common pelagic environment and returning to within a few km of their initial coastal location (Jorgensen et al., 2010). Broad-nose sevengill sharks (*Notorynchus cepedianus*) exhibit site fidelity

to the coastal area of Tasmania after making winter northerly migrations of a 1000 km or more (Barnett et al., 2011).

Migratory routes and feeding habitats of many pelagic MMS are associated with large-scale oceanic or bathymetric features; for example, running north south is the California Current Large Marine Ecosystem (CCLME) and running east west at about 40° N is the North Pacific transition zone (NPTZ) between the low chlorophyll subtropical gyre and the high chlorophyll subarctic gyre. Both bluefin tuna and loggerhead turtles travel along the NPTZ (Polovina et al., 2001), and limited catch and tracking studies indicate salmon move from summer (high latitude) habitats to winter habitats near the NPTZ (Abdul-Aziz et al., 2011; Myers et al., 2007; Welch et al., 1995). Bluefin tuna foraging migrations and vertical distributions are affected by the spatial and seasonal changes in the vertical profile of water temperature (Kitagawa et al., 2000). A hypothesis that Bluefin tuna migrations are affected by prey abundance patterns (Polovina, 1996) was supported in a computer model of a wider range of migratory predatory fishes (Dagorn et al., 2000). Leatherback sea turtles, bluefin tuna, and salmon sharks undergo long annual migrations (>2000 km) from the western, central and south Pacific basins to the CCLME. A number of species follow seasonally reoccurring north–south migrations in the North Pacific and the CCLME including: bluefin and yellowfin tunas, mako, white and salmon sharks, blue whales, elephant seals and leatherback sea turtles (Block et al., 2011). Other species move from near-shore to offshore waters of the NPTZ, the subtropical gyre and the north equatorial current (Block et al., 2001, 2011). In migrating between spawning and foraging habitats, marine turtles disperse across ocean basins (Lohmann et al., 2008). At the end of the breeding season sea turtles disperse to distant foraging sites. One study suggests that the pattern of adult dispersal reflects the passive dispersion they experienced as hatchlings; consequently, the restructuring of ocean current patterns by climate change may allow for rapid evolution of new migration destinations (Hays et al., 2010).

Prey of apex predators also exhibit migrations. For example, the capelin (*Mallotus villosus*), a short-lived osmerid pelagic species, displays long-distance movements (200–1200 km) between its overwinter feeding in the cold margins of the Arctic Ocean and variable spawning habitats including the deep waters and beaches of the North Pacific and North Atlantic oceans (Rose, 2005a).

2.2.3. Bioclimate envelope

Bioclimate envelopes are associations between a multivariate space of climate variables and the observed distribution of a species. Envelopes have been used to identify the potential geographic ranges of invasive species and forecast the effects of climate change on species distributions (Araújo and Peterson, 2012). In essence, bioclimate envelope models provide a measure of the habitat range of a species under the assumption that the distributions are determined largely by the climate and the population is in equilibrium with the climate. These assumptions limit the interpretation of the impact of climate on a species, life history strategy, and in particular, the models say little about the effect of climate change on the dynamics of a species. However, the wide range of studies using bioclimate modeling techniques make it a useful tool for examining the whole-range geography and ecology of species (Araújo and Peterson, 2012).

Many species distributions are shifting as they track the changing thermal environment (Chen et al., 2011; Pearson and Dawson, 2003; Watling et al., 2012). In both terrestrial and marine systems, the patterns of change are heterogeneous, and animals are expected to move according to the changes in their local environment (Burrows et al., 2011). For many terrestrial species, the effects have been mapped by changes in the latitude and elevation of their thermal envelopes define by thermal tolerance or presence–absence distributions (Schloss et al., 2012). These

bioclimate envelope models are relatively coarse but useful in predicting the range shifts of species under climate change (Hijmans and Graham, 2006). Similarly, marine species bioclimate envelopes have been defined by the temperature, salinity and sometimes chlorophyll values in which the species are observed. For example, future ranges of over 1000 marine species were projected using bioclimate envelopes and information on species growth, larval dispersal and adult migration (Cheung et al., 2008, 2009). The study hypothesized strong biodiversity changes in Arctic and southern Oceans with some extinction of species in the tropics and semi-enclosed seas. In temperate regions, sea surface temperature appears to be a key factor in determining the habitat of striped dolphin (*Stenella coeruleoalba*), fin whale (*Balaenoptera physalus*) and sperm whale (*Physeter macrocephalus*) (Azzellino et al., 2008). Cold-water species such as winter flounder (*Pseudopleuronectes americanus*) and Arctic cod are vulnerable to changes throughout much of their range while boreal species may benefit from warmer conditions. For migratory species that utilize the subarctic for feeding, but spawn further south, such as tunas and mackerel (*Scomber scombrus*), climate change may influence their migration patterns and phenology through changes in temperature and feeding opportunities (Cheung et al., 2008, 2009). Changes in sea surface temperature and chlorophyll will have mixed effects on core Pacific Ocean habitats by 2100: shark habitat is projected to decrease about 20%, marine mammal and turtle habitats are projected to decrease about 5% and tuna habitat will expand about 10% (Hazen et al., 2013). Deep water species, such as Greenland halibut (*Reinhardtius hippoglossoides*), live in more stable conditions and so their bioclimate envelopes may experience little change, although their prey may be impacted (Rose, 2005b). In general, deep-sea ecosystems will be indirectly affected by climate change because their food webs depend on surface productivity and vertical mixing (Smith et al., 2009).

2.3. Phenology

Phenology plays a central role in ecology and evolution, and it is integral to a species' life history since it encompasses the timing of growth, reproduction and senescence (Forrest and Miller-Rushing, 2010). Climate change has profound and varied effects on the phenology of species, and a major research focus has been on understanding phenological impacts of temporal mismatches in food webs (Davis et al., 2010). While many uncertainties exist, evidence suggests that recruitment will be especially impacted and will be a major factor in altering population trajectories of many species over the next century (Rijnsdorp et al., 2009). Central to recruitment success is the seasonal coupling of the multiple trophic levels that determine the effectiveness of predator–prey transfers of marine primary productivity to the higher trophic levels (Drinkwater et al., 2010). To develop a framework to model effects of climate change on phenology of migration we focus on this mismatch.

2.3.1. Match–mismatch

The match–mismatch hypothesis, first proposed by Cushing (1975), is perhaps the dominant paradigm for envisioning the processes controlling recruitment success in higher trophic levels of the marine food web. Initially, the hypothesis considered the immediate link between a juvenile consumer and its food source. However, with climate change the perspective has to be expanded to multispecies trophic interactions (Nakazawa and Doi, 2012) and a central focus is in exploring how advancing spring phenology will affect species recruitment (Durant et al., 2007). The general mechanisms are understood; critical changes in phenology include the time-sensitive coupling between migration, breeding and predation, which in turn alter survival and reproduction (Miller-Rushing

et al., 2010). However, the changes in phenology are not uniform across a food web; some species may be sensitive while others may exhibit no response to changes in climate. For example, when species that rely on temperature cues (which will be altered by climate change) to initiate migration interact with species that use daylight (not affected by climate change), a mismatch will ensue. Additionally, the impacts of phenology on predator–prey interactions depend on the ontogeny of the different members of the food web and so the effects of climate change are likely to involve the differential impacts on the species' ontogeny, not just their individual relationships to calendar day (Yang and Rudolf, 2010).

2.3.2. Observations of climate impact on phenology

Ecological changes in the phenology of animals are occurring in most marine and freshwater ecosystems (Robinson et al., 2009; Walther et al., 2002). Observed changes generally agree with predictions based on field studies correlating climate and biological variation, on laboratory experiments, and on physiological research (Parmesan, 2006). For example, migration of juvenile salmon smolts downstream (Kennedy and Crozier, 2010) and adults salmon upstream (Crozier et al., 2011) are occurring earlier and appear to be driven by warmer river temperatures that affect survival and consequently have genetically altered migration timings. The annual migration of adult Yukon River Chinook salmon varies with the timing of sea surface and air temperatures and sea ice cover (Mundy and Evenson, 2011). The homeward migration timing of sockeye salmon is closely related to ocean temperatures (Martins et al., 2012). However, less information is available on the impact of climate change on the phenology of salmon during their ocean residence. For example, 85% of literature on the effect of climate change on phenology in sockeye salmon has focused on the freshwater stages. Excluding the immediate homing migration, only a few percent has focused on the marine phase (Martins et al., 2012).

The few examples available other than salmon also indicate that seasonal temperature patterns are important. The spawning date of North Sea mackerel (*Scomber scombrus*) is correlated with sea surface temperature (Jansen and Gislason, 2011). The arrival date of North Atlantic albacore and Atlantic bluefin tunas to their feeding locations in the Bay of Biscay are increasing at a rate of 2 and 5.6 days per decade, respectively (Dufour et al., 2010). In a study of multiple trophic levels of a North Sea food web, phenological trends were inconsistent, indicating that trophic mismatches are currently occurring (Burthe et al., 2012). Evidence for climate change induced trophic mismatch has also been found in a marine plankton community (Edwards and Richardson, 2004).

2.3.3. Mechanisms of phenology

Ultimately, phenological patterns adjust over evolutionary time scales through the differential fecundity of animals differing in phenology. However, variance in fecundity among individuals is the result of complex ecological processes that are dependent on phenology, including environmental, physiological and behavioral factors. To a first order, food abundance, an environmental factor, has been proposed as a measure of how animals should shift phenology (Visser and Both, 2005), which suggests that growth, a physiological factor, is critical in determining phenology. For example, the timing of departure of white sharks *Carcharodon carcharias* from California water coincides with the end of the seal pupping season, suggesting that prey density may initiate offshore migration (Papastamatiou and Lowe, 2012). However, phenological patterns of animals are more complex and involve seasonal cycles of food availability, predation risk, and abiotic conditions such as temperature (Jonzén et al., 2007; Varpe, 2012).

Because the timings of migration and reproduction depend on the physiology of the individual, the timing of physiological development in one life stage can affect the phenology in another

stage (Varpe, 2012), and such cross-stage changes involve complex ecosystem changes as well as ontogenetic factors (Yang and Rudolf, 2010). Because phenology patterns are complex, the case has been put forward that understanding the mechanisms of phenology requires integrating chronobiology, physiology, molecular genetics, evolutionary ecology and social behavior (Visser et al., 2010).

Secondary processes can alter phenology as well. For example, when competition for territories and pre-breeding mortality are significant, the optimal shift in migration timing in response to shifting food distributions is not obvious. Model studies have indicated that the optimal shift in arrival date should be less than the shift in peak food abundance (Jonzén et al., 2007). Nonlinear dynamics can further complicate the effect of climate change on predators, which may be mediated by prey availability (Lusseau et al., 2004). Asynchronous responses to climate change among trophic levels can exacerbate the mismatch between predators and prey availability (Pörtner and Peck, 2010).

2.3.4. Phenology cues and MMS

The effect of climate change on phenology is further complicated for MMS with long-distance migrations. Trophic mismatches are expected to be greater in migratory species than in sympatric species due to the decoupling of the cues that initiate migration from the state of the target habitat. Highly seasonal habitats can exacerbate the mismatch. This decoupling has been considered a primary reason for the decline of several long-distance migrating insectivorous passerine species (Both et al., 2010). In general, the greater the delay between the cue and the event, the less information is contained in the cue (Lof et al., 2012). Furthermore, environmental cues that shape phenology may occur in one habitat and while the genetic selection occurs in another habitat (Visser et al., 2010).

In general, the proximate cues signaling phenology are not well understood (Bauer et al., 2009). A climate-induced shift in an environmental cue relative to the actual optimal migration timing can have varied effects of population fitness depending on the predictive power of the cue and the mismatch between the old response of the cue and the new environmental conditions (McNamara et al., 2011). Also, the nature of the cue is important. Cues that are fixed to calendar date, such as photoperiod, give no direct information on climate change, while cues that change with climate, such as trophic-level phenological shifts related to prey availability or migration triggered by temperature thresholds (Fujioka et al., 2012) may adjust with climate change. Photoperiod tends to be the most important cue for events that are distant in time or space, while other ecological cues such as temperature or food may be more important when they are temporally closer to the event (Bradshaw and Holzapfel, 2008). This can set up the perfect storm for MMS: the longer a migration is, the more an animal may rely on the environmental cue that is insensitive to climate change (i.e., photoperiod). At the same time, the differential rate of change among ecosystem types suggests the temporal mismatch between migration timing and peak destination conditions will increase.

2.4. Phenological adaptation to climate change

Central questions regarding phenology and climate change are how do animals adjust to a mismatch and how well are they able to adapt to rapid climate change? Rapid change imposes strong selection pressures on life history traits; however, microevolution in response to climate-induced selection may mitigate negative consequences of the change. Phenological shifts can occur through both genetic and phenotypic mechanisms, and distinguishing the contributions of each form is difficult (Gienapp et al., 2008). Many, if not most projections of the impacts of climate change on populations,

and particularly the possibility of extinction, do not consider the individual contributions of genetic selection and phenotypic plasticity, and are therefore likely to have biased estimates of the probabilities of extinction (Reed et al., 2011a,b). In particular, bioclimate envelope models assume the historical correlation of a population with its envelope will persist in future conditions. However, populations can in principle shift to more optimal bioclimate envelopes, but understanding the details of the adaptation may be complex. In the sections below, we review literature on adaptation mechanisms and their complexity.

2.4.1. Genetic adaptation

Population responses to changes in seasonal timing are expected to be primarily under genetic selection (Bradshaw and Holzapfel, 2008) and involve a migratory gene package that includes genes controlling physiology for migration, including timing of migration, body fat and migratory route (Liedvogel et al., 2011). Among Pacific salmonids, the Clock gene, a central component of an endogenous circadian clock, is involved with sensing changes in photoperiod which in turn influences migration and breeding timing (O'Malley and Banks, 2008; O'Malley et al., 2010). Evidence suggests that many aspects of fish migration are genetically determined and can evolve within a few generations (Crozier et al., 2008; Kovach et al., 2012; Liedvogel et al., 2011; Quinn et al., 2000, 2001). In semelparous species, phenotypic life history traits such as salmon migratory routes in the ocean, philopatric spawning and coordinated timing of homing migrations are primarily under genetic control (Kallio-Nyberg et al., 2000). In particular, migration timing can be considered "innate behavior", which is in part genetically predetermined (Sznajder et al., 2011). In fact, migration has been called a "magic trait" as selection (directly or indirectly) on migratory timing alone might result in allochrony, reproductive isolation, and eventually speciation (Servodio et al., 2011).

The prevailing ecological theory is that species will initially adapt their phenology to climate change by altering the timing of the vital life stages through genetic selection. Differential phenological shifts among trophic levels can cause a mismatch, reducing overall fitness. This leads to selection of phenotypes more adapted to current conditions, which can decrease the mismatch and ultimately recover fitness. However, this concept of adaptive tracking in which the optimal trait values change continually with natural selection may be too simple to explain the effect of continuous and strong climate change acting over time scales faster than the rate of genetic adaptation or with increased environmental variability (Simons, 2011). For example, consumers that are asynchronous with their resources prior to climate change may be especially vulnerable to further asynchrony (Singer and Parmesan, 2010). Game theoretical models illustrate that evolutionarily stable asynchronous predator-prey phenology can produce different adaptive responses to climate change and thus complicate the ability to predict effects of the change on populations. For example, if early arriving individuals occupy the available habitat then an evolutionarily stable strategy may induce a mismatch between the observed arrival and the optimal arrival time based on the seasonally varying habitat quality and resource competition. Climate change in this system can either reduce the temporal mismatch, leading to temporarily increased fitness, or increase the mismatch and further reduce fitness (Johansson and Jonzén, 2012). While a breeding population that is temporally matched to its food source has an optimal phenology, a mismatching does not mean that the phenology is suboptimal (Miller-Rushing et al., 2010). Asymmetric fitness curves combined with temporal environmental fluctuations can produce apparent suboptimal strategies. The optimal timing shifts away from the side of the fitness curve with the steepest decline (Lof et al., 2012). Fitness tradeoffs of traits that favor fecundity or survival but maximize neither can result in a

historically stable asynchrony. Asynchrony between predators and prey may also indicate a co-evolutionary arms race and by the same reasoning greater synchrony is expected between trophic levels connected by mutualism (Singer and Parmesan, 2010). In habitats with limited carrying capacity, arrival and breeding prior to the peak in food availability may lead to an apparent, but evolutionary stable, mismatch in phenology. Thus, under stochastically stable conditions, asynchrony resulting in apparent suboptimal strategies can exist for several reasons (Johansson and Jonzén, 2012).

Variability in the environment affects fitness in complex ways and is important because increased variability is expected with climate change. Environmental variability can reduce the effectiveness of adaptive tracking through the interplay of environmental variance and additive genetic variance which then reduces effective heritability (Simons, 2011). Bet hedging is a form of genetic adaption that may evolve under high environmental variability that impedes adaptive tracking and phenotypic plasticity. Bet hedging traits are maximized across multiple generations but not within any single generation, so the strategy may appear detrimental when considered over a limited range of generations. However, it is not clear how bet hedging plays into climate change (Simons, 2011). Such complexities do not offer simple interpretations, but they do illustrate that when considering the response of species to climate change, the processes of natural selection, density dependence and multispecies interactions need to be taken into account in addition to the degree of mismatch between a population and its seasonally varying resource.

2.4.2. Phenotypic plasticity

Phenotypic plasticity is the phenomenon of a single genotype producing different phenotypes in response to different environmental conditions. The relationship between a phenotype and the environment is referred to as the reaction norm (Scheiner, 1993). Phenotypic properties of migration include when to begin migration, how fast to migrate, when and where to stop migrating, and when to breed. Plasticity is advantageous when the environment is heterogeneous and different phenotypes are favored in different environments (Reed et al., 2011b). However, plasticity is not always adaptive, and because of the variety of phenotypic responses within a species' repertoire, there is no single consistent framework with which we can predict the role of plasticity in adapting to new environments (Ghalambor et al., 2007). Recent models have focused on the effect of plasticity on facilitating or hindering the adaptation to climate change. For example, a plastic response can delay adaptation to a rapid change in the environment through two stages (Chevin et al., 2010). In the first generation, fitness drops and the mean phenotype jumps toward the new optimum through a plastic response. In subsequent generations, the population slowly assimilates the genetic traits for the optimal environment. A plastic response to a temporally fluctuating cue can reduce fitness when the response is strong and the correlation between the cue and the optimum trait is weak (Reed et al., 2010). In general, whether or not a plastic response is adaptive depends on the correlation between the cue's optimal trait and the strength of the response to the cue (Visser et al., 2010). The issue is especially critical to species with long distance migrations because the cue signaling the optimum conditions occurs in one environment while the condition itself occurs in the preceding environment. Thus, the cue–phenotypic response and the resulting selection processes occur in separate environments, and climate change may alter the relationship between the two. The effect of plasticity on adaption is further complicated if climate change exceeds the capacity of the plasticity. In this case, it is suggested that the microevolution of the reaction norms governing plasticity will come under selection (Visser, 2008). The physiological capacities of species will also

affect their ability to adapt to rapid change (Chown et al., 2010). However, many of these issues of adaption are likely to be less critical with highly migratory species that select their habitat through bioclimate envelopes.

3. Model description

We now develop a simple modeling framework to explore the effects of climate change on migrating marine organisms with a special focus on adaptive mechanisms. Our purpose is not to construct a comprehensive modeling structure but rather to illustrate an approach suitable across species and scenarios. Our focus on mechanisms of adaption to climate change compliments a growing library of models considering the immediate mechanisms of migration (e.g. Chapman et al., 2011; Dueri et al., 2012; Muhling et al., 2011; Piou and Prévost, 2012). A limited number of papers have addressed the adaptation of MMS to climate change (Crozier et al., 2011; Mangel and Satterthwaite, 2008; Reed et al., 2011a,b), although studies on the adaptation of terrestrial species to climate change are more abundant (e.g., Coulson et al., 2011; Hellmann and Pineda-Krch, 2007).

The literature review (Section 2) illustrates that responses of MMS to climate change can be complex, interactive and occasionally counter-intuitive. Because the risk of developing an overly complex model that is incorrect and unsupportable is high (Rose et al., 2010), our goal is to develop a simple but reasonably realistic and flexible framework. We therefore consider an individual-based approach that includes the philopatry and phenology of the individual.

Considering first an individual's philopatry, we note one challenge for MMS species is that locations of both the juvenile and adult habitats and the migratory routes between them may be associated with fixed topographical properties or defined by oceanic properties, i.e. bioclimate envelopes, and thus shift spatially with changes in climate. In either case, a model of the response of MMS requires the essential elements of the species philopatry, i.e. its migratory path. Fig. 1 illustrates the simplest example involving an adult foraging habitat and a breeding habitat where the population seasonally migrates between the two areas. This structure is flexible and can be expanded with additional components, e.g. separate breeding and juvenile habitats, or with additional habitat properties such as separation distance and size. However, after assuming population philopatry and simplifying the spatial components of the system, we consider the response to climate change in terms of the population's phenology.

Similarly, a species' phenology can reduce to elementary parts. Here the issue is linking the phenology to the individual's condition, which here we consider as the individuals mass, but other measures are possible. Fig. 2 illustrates a simple example in which an individual's relative change in condition from the previous year depends on the phenology mismatch (Section 2.3.1) between the individual's realized migration timing and the optimal migration timing. The optimum timing may shift because of climate change (Section 2.1), and the individual's realized migration timing depends on its genetically determined timing (Section 2.4.1) and any phenotypic responses (Section 2.4.2). The actual effect of the mismatch on the individual's condition depends on the temporal width of the bioclimate envelope δ and a scaling factor characterizing the annual change in its relative condition. If an individual's migration occurs outside the bioclimate envelope, its condition will decline and correspondingly its condition increases fastest when the timing mismatch is zero.

An individual's survival and fecundity are determined by its condition, which in turn is determined by the timing mismatch. Thus, a population responds to climate change by each individual

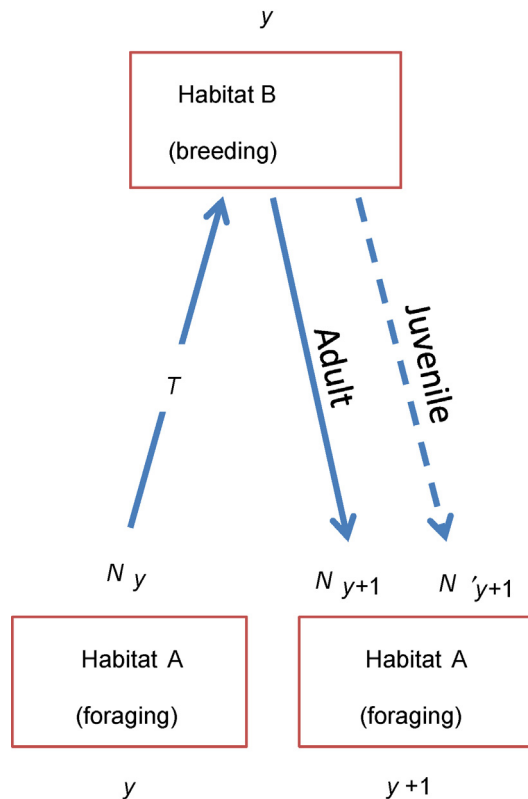


Fig. 1. Heuristic population migration and life cycle for iteroparous life history. N_y individuals comprising the population in the foraging habitat A in year y migrate to the breeding habitat B at time T . After survival and reproduction based on each individual's condition, the N_{y+1} adults and N'_{y+1} juveniles migrate back to the foraging habitat in year $y+1$. For a semelparous life history, no adults would migrate back to the foraging habitat from the breeding habitat.

plastically adjusting its migration timing and by offspring inheriting genetic component of the parents' phenology. We assume that with climate change the bioclimate envelope changes causing a timing mismatch with an individual's phenology. Thus, the essential dynamics of the model involve climate shifting the bioclimate envelope and the population attempting to stay within the envelope through genetic and plastic mechanisms.

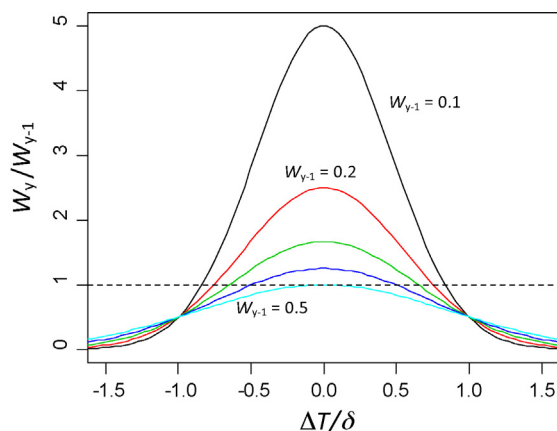


Fig. 2. Change in condition, e.g. weight, for increments of condition W_{y-1} between 0.1 and 0.5 as a function of the timing mismatch normalized by the bioclimate envelope according to Eq. (6) with $\omega = 0.5$. The relative change in condition is higher for low condition individuals, which corresponds to the asymptotic nature of the growth function.

We do not identify a specific set of biological measures for condition, other than both survival and fecundity increase as condition increases. Typically, for fish these measures increase with weight, length and growth rate (Arendt, 1997). We capture both genetic and phenotypic heterogeneity within the population and express the population's response to climate change in terms of phenology-mediated growth, survival and reproduction. We outline the basic framework, present an example model and note that many of the processes in the framework (i.e. bioenergetics, vital rates, and genetics) can be parameterized from known studies. We also discuss possibilities of expanding the model to multiple trophic levels.

3.1. Model structure

As our intent is to present a framework for modeling response of MMS to climate change and not to develop a specific model, we consider a simple generic MMS migrating between a winter foraging habitat A and a summer breeding habitat B (Fig. 1). For an iteroparous species, the surviving adults and offspring return to habitat A to complete the annual cycle. For a semelparous species, adults die after breeding and only the offspring enter habitat A.

Fig. 3 illustrates the framework by which climate change affects an individual's conditions and the population. The number of adults N_y leaving habitat A to reproduce in habitat B in year y characterizes the population state. The population returning to habitat A in year $y+1$ consists of the surviving adults N_{y+1} , and the number of offspring, N'_{y+1} , produced in habitat B in year y . Processes determining condition, survival and reproduction of individual i in year y are contained in the individual's sub-process sheet (Fig. 3). The realized migration timing depends on the individual's response to climate cues, i.e. its phenotypic plasticity, genetically determined migration timing and environmental (or "unexplained") variation. The mismatch of the realized timing and the climate-determined optimum timing determines the individual's condition $W_{i,y}$. In turn, the condition determines the migration survival and probability of reproduction. Adult survival to the next year characterizes an iteroparous life history strategy and total mortality characterizes a semelparous strategy. An offspring's genetic migration timing depends on the parent's genetic timing and genetic variability. Thus, the population tracks climate-induced changes in phenology by behavioral plasticity keyed from environmental cues (Section 2.3.4) and genetic migration timing (Section 2.4.1) that varies through mortality of individuals with mismatched timing and their replacement with better matched individuals through reproduction and genetic variability. Population size and the mean and variation in the condition and phenology of individuals summarize the population state. We present a simple form of this model in the subsequent sections, summarizing the equations and parameters in Table 1. The model coded in the R programming language and a brief user's guide is given in the online Supplementary Material.

3.2. Modeling phenology

Climate change drives the year-specific optimal time to migrate T_y^* , which can have both trend and variability (Table 1, Eq. (1)). Each individual's genetically determined time to migrate T_i^g is selected from a normal distribution with the mean defined by parent's genetic timing T_k^g and the standard deviation (sd) by genetic variability σ_g (Eq. (2)). A reaction norm b_y (Eq. (3)) defines the maximum possible phenotypic plasticity for the current timing mismatch and here is taken as the difference ΔT between the optimal and the genetic migration timing of the individual (Section 2.4.2). The realized migration time $T_{i,y}$ of individual i in year

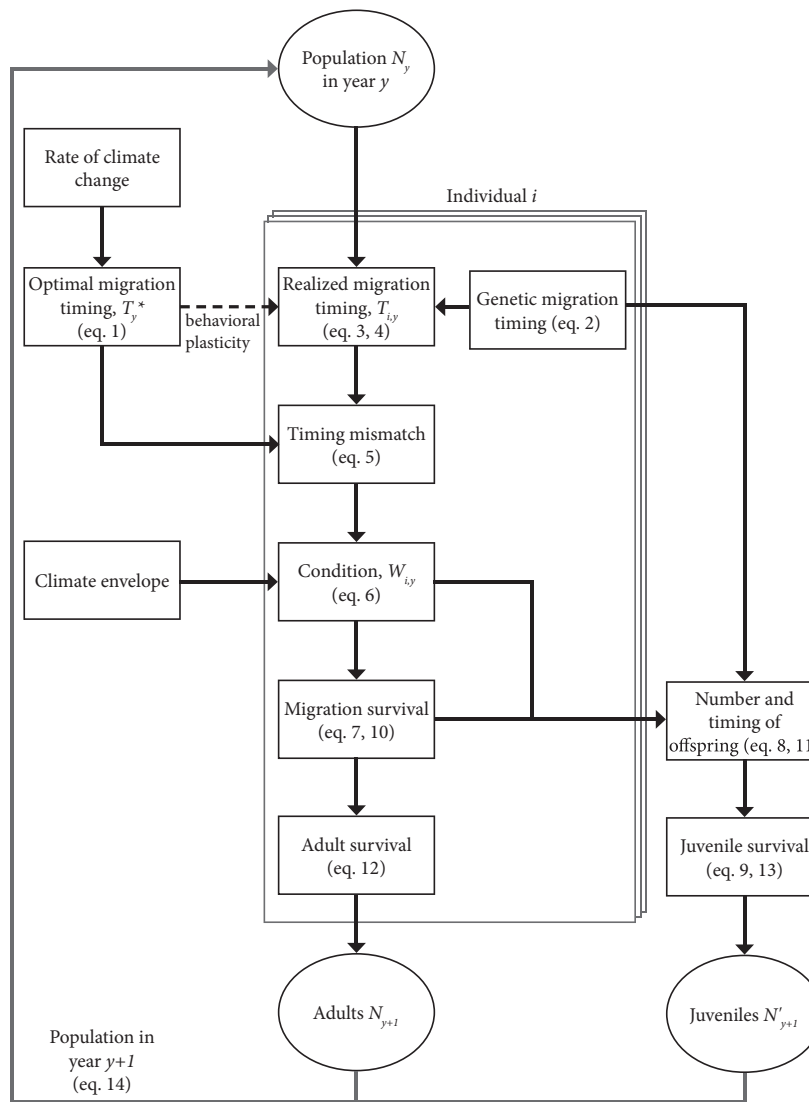


Fig. 3. Model flow diagram illustrating the effect of climate change on the optimal migration timing through the individual and population. Population parameters depicted by ovals, individual level processes contained within sheets for each individual and climate forcing and environmental processes illustrated outside the sheets.

y is drawn from a normal distribution with mean defined with genetic and phenotypic contributions and sd by environmental noise σ_g (Eq. (4)). The phenotypic contribution depends on the reaction norm scaled by the environmental cue strength μ_y in year y , which in principle depends on the lag between the migration cue received in habitat A and the realized fitness benefit in habitat B (Section 2.3.4). A value $\mu_y = 0$ indicates no plastic response in timing, whereas $\mu_y = 1$ means perfectly optimized timing for every individual. If, for example, the environmental cue is photoperiod, and therefore independent of climate, then we may assume $\mu_y = 0$. However, if the cue in habitat A is perfectly correlated with conditions in habitat B and the organism has the ability to adjust its migration behavior, then $\mu_y = 1$, such that the plastic response exactly tracks climate change. Eq. (5) describes the mismatch $\Delta T_{i,y}$ between the optimal migration time and the realized migration time.

3.3. Modeling condition

The change in an individual's condition within a year (Eq. (6)) depends on the timing mismatch, a bioclimate envelope δ characterizing the temporal limits for migration timing within which

the animal can improve its condition and a condition parameter ω characterizing the growth potential, i.e., the maximum possible condition. By restricting the maximum condition to less than one, $\omega < 1$, we effectively restrict an individual's condition to the interval $0 < W < 1$. Fig. 2 illustrates condition in year y relative to the condition in year $y - 1$ as a function of the degree of timing mismatch normalized by the bioclimate envelope, $\Delta T/\delta$. The normalized mismatch is a critical parameter in determining the response of an individual. For an individual to improve condition from one year to the next, i.e. $W_y/W_{y-1} > 1$, the timing mismatch must be $\Delta T/\delta < 1$ by an amount dependent on the condition in year $y - 1$. That is, as an individual's condition increases, its timing must become closer to the optimum for it to improve condition across years (Fig. 2). Thus, δ is a measure of the species sensitivity to migration timing containing the complex mechanisms of timing mismatch outlined in Section 2.3.3.

3.4. Modeling vital rates

The probability $A_{i,y}$ of adult survival and the expected fecundity $B_{i,y}$ over a year are both monotonically increasing functions of adult condition W_i (Eqs. (7) and (8), respectively). Juvenile survival probability D_y is a function of the total population size in year y (Eq.

Table 1Variables, functions and parameters of the model. The model tracks the life cycle of individual i descendant from individual k in year y .

	Process variables	Functions	Parameters (dimensions)
Phenology	Optimal migration time	$T_y^* = \text{Normal}(T_0^* + \varphi y, \sigma_e)$ (1)	$T_0^* = \text{base timing (d)}$ $\varphi = \text{rate of change (d/year)}$ $\sigma_e = \text{variability in timing (d)}$
	Genetic time of offspring i inherited from parent k	$T_i^g = \text{Normal}(T_k^g, \sigma_g)$ (2)	$\sigma_g = \text{genetic variability (d)}$
	Reaction norm slope in year y	$b_{i,y} = T_y^* - T_i^g$ (3)	
	Realized migration time of individual i in year y	$T_{i,y} = \text{Normal}(T_i^g + \mu_y b_{i,y}, \sigma_b)$ (4)	$\mu = \text{strength of plastic response to timing cue (none)}$ $\sigma_b = \text{phenotypic variability (d)}$
	Migration time mismatch	$\Delta T_{i,y} = T_y^* - T_{i,y}$ (5)	
Condition	Condition of individual i in year y	$W_{i,y} = \begin{cases} W_0 & \text{age} = 0 \\ \omega W_{i,y-1}^{\Delta T_{i,y}^2 / \delta^2} & \text{else} \end{cases}$ (6)	$W_0 = \text{condition at birth (none)}$ $\delta = \text{bioclimate envelope (d)}$ $\omega = \text{maximum condition (none)}$
Individual vital rates	Adult migration survival probability	$A_{i,y} = W_{i,y}^\alpha$ (7)	$\alpha = \text{condition/survival coefficient (none)}$
	Expected fecundity of individual	$B_{i,y} = \phi W_{i,y}^\beta$ (8)	$\beta = \text{condition/reproduction coefficient (none)}$ $\phi = \text{maximum expected fecundity (number)}$
	Juvenile survival probability	$D_y = \begin{cases} 1; & N_y < \kappa \\ \kappa / N_y; & N_y \geq \kappa \end{cases}$ (9)	$\kappa = \text{carrying capacity of breeding habitat (number)}$
Population vital rates	Migration survival	$J_{i,y} = \text{Bernoulli}(A_{i,y})$ (10)	
	Number of offspring	$K_{i,y} = \text{Poisson}(B_{i,y})$ (11)	For iteroparous $C_y = 1$
	Post-breeding survival	$L_{i,y} = \text{Bernoulli}(C_y)$ (12)	For semelparous $C_y = 0$
	Juvenile survival	$M_{i,y} = \text{Bernoulli}(D_y)$ (13)	
Population	Population size in year $y + 1$	$N_{y+1} = \sum_{i=1}^{N_y} J_{i,y}(L_{i,y} + K_{i,y}M_{i,y})$ (14)	

(9)), such that when the population exceeds the carrying capacity κ , the probability of juvenile survival declines inversely with population size. For simplicity, we do not distinguish carrying capacities of breeding and foraging habitats.

3.5. Modeling population process

The individual-based framework tracks each adult's condition, survival and reproduction for each year. The realized adult survival in habitat A (Eq. (10)), the post-breeding survival of adults (Eq. (12)) and the survival of offspring in habitat B (Eq. (13)) in year y are Bernoulli random variables with the probabilities of survival given by $A_{i,y}$, C_y and D_y , respectively. Semelparous and iteroparous life history strategies are characterized by post-breeding survival $C_y = 0$ and 1, respectively (Eq. (12)). The number of offspring $K_{i,y}$ individual i produces in year y is given by a Poisson random variable (Eq. (11)) where the expected number of offspring is $B_{i,y}$. Eq. (14) gives population size in year $y + 1$ resulting from survival and reproduction in year y .

3.6. Specific simulations for the paper

The model predicts population abundance, individual size/condition, and migration timing under any pattern of climate change for many kinds of biological and ecological processes, including various patterns of growth, survival, reproduction, inheritance, behavioral plasticity, life history strategies and changes in the bioclimate envelope. Because an exhaustive analysis is prohibitive, we only illustrate a few properties of the model under different climate change scenarios and then explore in more detail effects of the bioclimate envelope, genetic variability and phenotypic plasticity on population size and persistence. All model runs were initialized with a 50-year burn-in period in which

population size, individual condition and genetic composition reached approximate stationarity. We simulated four scenarios where ranges of model parameters for each scenario are given in Table 2.

Scenario I characterizes the response of a population to differing rates of change in optimal migration timing (Fig. 4A and B). Scenario II explores the population response to increasing variability in the optimal timing (Fig. 4C and D). Independently these analyses characterize the essential properties of a shift in phenology. In both scenarios climate conditions are stable for the first for 50 years, exhibit moderate increases in the trend (Scenario I) and variance (Scenario II) for the next 50 years and then exhibit rapid increases in the trend (Scenario I) and variance (Scenario II) after year 100. Scenarios III (Fig. 5) and IV (Fig. 6) explore the sensitivity of population size to ranges of genetic inheritance, phenotypic plasticity and the bioclimate envelope under a moderate rate of climate change, an approximate two day per decade shift in phenology which is consistent with a variety of environmental processes (Burrows et al., 2011).

4. Model results

4.1. Model response to climate trend and variability

Fig. 4 shows the response of an iteroparous population with intermediate plasticity for Scenario I, a stepwise increasing rate of change in the bioclimate envelope (Fig. 4A and B), and Scenario II, a stepwise increasing variance in the bioclimate envelope about a fixed mean envelope (Fig. 4C and D). The upper panels (Fig. 4A and C) show the scenarios' population levels (green line) and properties of the migration timing including the mean genetic migration timing (red dots), realized migration timings (blue dots) and the optimal migration timing (dashed line). In addition, the

Table 2
Parameters used in the simulations. Y0 is the year beginning simulation interval and Y1 is the year ending simulation interval. N_{sim} is the number of simulations preformed to generate statistics. Other terms are defined in Table 1. All simulations begin with 500 individuals.

	Scenario I Climate trend effects (Fig. 4A and B)			Scenario II Climate variability effects (Fig. 4C and D)			Scenario III Genetics vs. envelope (Fig. 5)	Scenario IV Plasticity vs. genetics (Fig. 6)
Y0	0	50	100	0	50	100	50 ^a	50 ^a
Y1	50	100	150	50	100	150	250	250
φ (d ⁻¹)	0	0.36	0.7		0		0.2	0.2
σ_e (d)		0		0	5	10	3	3
σ_g (d)		1.5			1.5		1–14	0.5–16
σ_b (d)		0			0		0	0
T_0 (d)		205			187		200	200
δ (d)		7			7		0.5–10	4
μ		0.5			0.5		0.5	0–0.75
α		1			1		1	1
β		1			1		1	1
ϕ		2			2		2	2
κ		200			200		200	200
ω		0.9			0.9		0.9	0.9
C_y		1			1		1	1
N_{sim}		1			1		30	100

^a Years 0–50 were a burn-in period without climate change.

envelopes about the timing measures designate 1 sd of the distributions of individuals in the population. The lower panels (Fig. 4B and D) show the scenarios' mean population condition (orange line) and the timing mismatch (purple line), both with envelopes of 1 sd.

4.1.1. Stable conditions

The first 50 years are equivalent in Scenarios I and II with the populations achieving a pseudo-stable equilibrium of between 500 and 600 individuals with small variability (sd ~0.04) (Fig. 4A and C). In both scenarios the mean condition, 0.88, is near the maximum $\omega=0.9$ (Fig. 4B and D). This period reflects a fully adapted species

with little genetic variability, and therefore few individuals migrate outside the bioclimate envelope.

4.1.2. Moderate and rapid trends in climate change

In Scenario I, a moderate climate trend between year 50 and 100 (Fig. 4A) leads to a gradually increasing genetic mismatch in timing, a decrease in the mean condition from 0.9 to 0.7, and an increasing variance in the condition (sd ~0.12) (Fig. 4B). The timing mismatch appears to stabilize, indicating the population adapts to the decline. However, the reduced abundance, between 200 and 300 individuals, indicates the population is stressed. With a doubling in the rate of climate change after year 100 the population's rate of genetic adaptation significantly lags the optimal migration

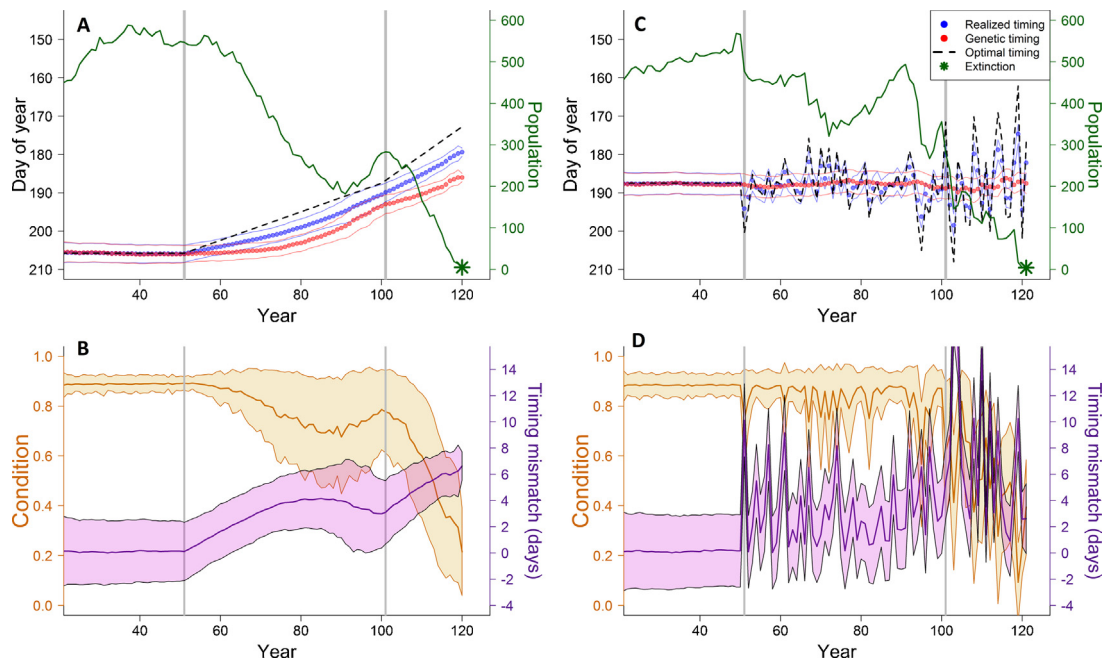


Fig. 4. Effect of climate change on population state variables for two realizations of the model. Panels A and C show changes in population numbers for patterns in optimal timing (dashed black line, Eq. (1)), genetic timing (red dots, Eq. (2)) and realized timing (blue dots, Eq. (4)), along with the total population size (solid green line) on a separate scale. The red and blue envelopes correspond to a single standard deviation around the population means for genetic and realized timing, respectively. Panels B and D show the condition (orange lines, Eq. (6)) and timing mismatch (purple lines, Eq. (5)) with shaded areas again representing one standard deviation of the population around the population mean. Vertical lines indicate three successive regimes of 50 years each: in Scenario I (panels A and B), the optimal timing shifts at a constant rate after year 50, and doubles the rate after year 100. In Scenario II (panels C and D), the mean optimal timing is constant but the variability in timing increases at 50 and 100 years. Parameter values for Scenarios I and II are given in Table 2.

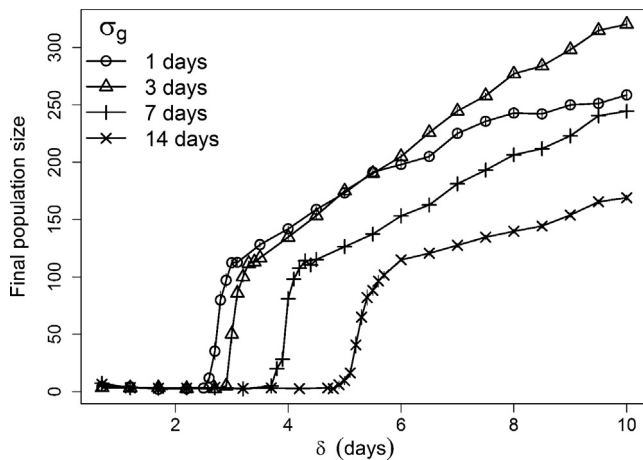


Fig. 5. Effect of climate envelope δ and genetic variability σ_g on the population size after 200 years. The final population size decreases linearly as the envelope decreases until reaching a threshold envelope size below which the population goes extinct. Parameter values for Scenario III are given in Table 2.

time (Fig. 4A) resulting in a rapid increase in the timing mismatch and decrease in condition (Fig. 4B) which together drive the population to extinction (Fig. 4A). Note that throughout Scenario I, the realized timing splits the difference between the optimal and genetic timings due to fact that we included moderate phenotypic plasticity $\mu = 0.5$. We designate this form of extinction “envelope drift” in which the ability to adapt genetically is limited by the small variability in inheritance, σ_g , relative to the rate of climate change, φ . Somewhat counter intuitively, the plasticity, which helps the population persist in the short term, may undermine the population’s ability to adapt because it diminishes the strength of genetic adaptation (see discussion in Section 2.4).

4.1.3. Moderate and large climate variability

Scenario II models stepwise increases in climate variability without a corresponding trend in the mean climate (Fig. 4C and D). Variability, which begins at year 50 and doubles at year 100, introduces, as expected, considerable interannual stochasticity in all the state variables. Because the variability is uncorrelated, there is no adaptation in the genetic timing, which stays on average close to the initial optimum since the mean climate trend is zero (red

dots, Fig. 4C). However, the plasticity in the phenologic response (blue dots, Fig. 4C) helps the individual’s realized timing follow the optimal timing (dashed line). The volatility in timing mismatch and condition are much higher after year 50, and as the average timing mismatch increases the average condition decreases (Fig. 4D). This leads to a lower population equilibrium by year 100, but not as low as in Scenario I. With a doubling of environmental stochasticity after year 100, a short series of large jumps is sufficient to drive the population to extinction. We designate this form of extinction “envelope jumping” in which the interannual variation in the optimal timing simply exceeds the bioclimate envelope width and the species’ ability to respond via plasticity. For high levels of uncorrelated environmental variation, no genetic adaptive tracking is possible and adding even a modest climate trend greatly increases the probability of extinction (see Section 2.4.1).

4.1.4. Extinction

With both climate trends and climate variance, the response of the population to climate change ultimately depends on whether the realized population timing remains within the bioclimate envelope. Extinction may result when the phenology mismatch exceeds the bioclimate envelope, i.e. when $|\Delta \bar{T}_{i,y}| > \delta$. In Scenario I (Fig. 4B), this occurs when the timing mismatch reaches $\delta = 7$ d. To avoid extinction, the rate of adaptation of the genetic component of migration timing must match the rate at which climate change shifts the optimal timing. Thus, avoiding extinction requires $dT_g/dy \geq \varphi$.

4.2. Population persistence and adaptation mechanisms

Scenarios III and IV explore the effectiveness of genetic and plastic adaption mechanisms under a moderate rate of climate change. The mean final abundance after 200 years, \bar{N}_{final} , depends on the interaction of three parameters: the bioclimate envelope size, genetic variability, and the phenotypic plastic response.

4.2.1. Climate envelope and genetic variance

Scenario III illustrates the relationship between the envelope size and the genetic variance (Fig. 5). The population always goes extinct at envelope sizes $< \delta^*$, where the threshold depends on the genetic variance σ_g . For envelope sizes greater than the threshold, \bar{N}_{final} increases approximately linearly with increasing δ (Fig. 5). We suggest that because δ^* demarks a sharp transition between population persistence and extinction it is a useful measure of a critical bioclimate envelope size. Exploring the critical envelope further, we found δ^* increases linearly with σ_g , and as μ increases δ^* decreases such that increasing plasticity buffers against extinction. At the widest bioclimate envelope modeled ($\delta = 10$ d), the largest final population size occurs at an intermediate genetic variance ($\bar{N}_{\text{final}} = 320$ at $\sigma_g = 3$ d) while the population size is significantly lower at higher variance ($\bar{N}_{\text{final}} = 169$ at $\sigma_g = 14$ d), and somewhat lower at the lowest genetic variance ($\bar{N}_{\text{final}} = 259$ at $\sigma_g = 1$ d).

4.2.2. Genetic variance and phenotypic plasticity

Scenario IV illustrates the effect of genetic and plastic adaptive processes on population size \bar{N}_{final} (Fig. 6). From Scenario III we conclude that for $\delta > \delta^*$ the effect of the climate envelope is essentially linear and so we fix δ to explore the interactions of the two forms of adaption. Results indicate that for a range of plasticity, the optimum genetic variance, i.e. that yielding the highest population abundance, occurs when σ_g is slightly smaller than the bioclimate envelope (Fig. 6). The low population size at small values of genetic variance results from the “envelope drift” effect, because offspring are too similar to their parents for the population to adapt effectively to the changing environment. Correspondingly,

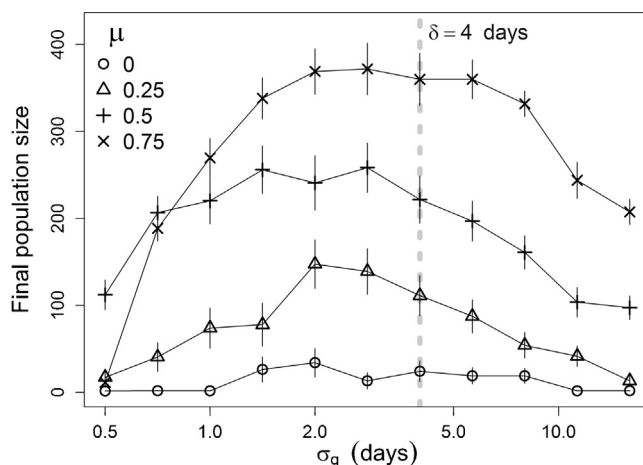


Fig. 6. The effect of genetic variability σ_g and phenotypic plasticity μ (different point characters) on the population size after 200 years for a fixed climate envelope size, $\delta = 4$ d (dashed vertical gray line). The vertical lines represent one standard error around the mean of 100 simulations for each parameter combination. Parameter values for Scenario IV are given in Table 2.

low population sizes at high genetic variances illustrate a “population jumping” effect, in which the genetic variability in the offspring is too high relative to the bioclimate envelope width. Furthermore, higher phenotypic plasticity leads to higher populations, as is largely to be expected. A noteworthy exception, at the lowest genetic variance, the population goes extinct at low ($\mu = 0$) and high ($\mu = 0.75$) levels of phenotypic plasticity. This pattern illustrates that with low genetic variability plasticity can compromise long-term adaptation by diluting the strength of the genetic process. In other words, populations optimizing phenology partially via non-inherited plasticity allow sub-optimum genotypes to persist and weaken the population as is noted in the literature (Section 2.4.2).

5. Discussion

5.1. Model summary

Our example IBM uses the biologically motivated idea that an abstract measure of the individual's condition mediates the interactions of a population's genetic, physiological and behavioral responses to climate change. The model characterizes the dynamics in terms of a moving bioclimate envelope, within which the population must maintain itself in order to survive and reproduce. A population, initially adapted to its bioclimate envelope in a stable climate regime, responds to climate change by adjusting its phenology through genetic and plastic adaptations. The model simulates the response by linking vital rates with plastic and genetic migration timing processes. While the model's spatial representation of foraging and breeding habitats is simple, additional spatial elements are readily incorporated into the framework.

5.2. Findings

Our modeling framework is largely heuristic and serves to identify and link critical concepts in simple mathematical forms. The first concept that emerges is the importance of the bioclimate envelope, δ , which expresses the width of the timing interval in which individuals must enter the breeding habitat. The impacts of all other phenological parameters depend on their magnitudes relative to δ . Species with small bioclimate envelopes are more prone to disturbance and extinction than species with wider envelopes. In essence, the envelope width is a primary measure of the sensitivity of species to environmental and ecosystem changes.

A second concept is how the mismatch occurs. The population's phenology “drifts out” of the moving envelope if the rate of climate change exceeds the rate of adaptation, and it “jumps out” if the envelope variability exceeds the capacity for phenology variability of the population. Multiple factors affect the drifting and jumping out potentials. In our example, faster genetic adaptation occurs with lower levels of genetic variance, σ_g , and phenotypic plasticity, μ . If a population does not genetically adapt its phenology, then the time to drifting-out extinction is simply proportional to δ/φ , which expresses the number of years it takes for the bioclimate envelope to drift outside the population's phenology. A critical value for jumping-out extinction is $\sigma_e/\delta > 1$, that is, when the environmental variability of the bioclimate envelope is greater than the envelope size.

A third concept is that adaptation through phenotypic plasticity requires the cue initiating migration to track the bioclimate envelope. However, some timing cues, such as photoperiod, are unaffected by climate change, and therefore adaptation via phenotypic plasticity is unlikely for populations relying on such cues, compared to timing cues correlated with a climate-driven variable such as temperature.

The fourth concept is a threshold-like nature of the extinction response to climate change. Under intermediate rates of climate change and moderate variability a population may appear robust in terms of size but be near the extinction threshold. In such conditions, increased variance in the condition of individuals may be a better indicator of stress. These results suggest that the impacts of climate change on populations should be tracked with individual measures as well as population level measures.

5.3. Challenges modeling MMS

Modeling the response of MMS to climate change is a significant challenge. Many MMS are important apex predators with both cultural and food value. They are a challenge to model because they may migrate large distances and therefore encounter a number of environments that respond in unique and unknown ways to climate change. Thus, understanding how MMS will respond to climate change involves understanding the effects on the spatial and temporal properties of their environment occurring over multiple scales (Muhling et al., 2011). MMS use both local environmental and global cues to move through their environment and information on the importance of each scale is limited (Section 2.2).

Improving models of the impact of climate change will involve identifying the migratory corridors and the productivity and size of foraging and breeding habitats, as well as the level of spatiotemporal mismatch between MMS and their forage base. Notable studies have tracked MMS movements and oceanic conditions (e.g., Chapman et al., 2011; Dufour et al., 2010; Fujioka et al., 2012; Muhling et al., 2011) but additional studies are needed. Furthermore, understanding the inheritance of phenology is critical to quantifying the capacity of MMS to adapt to climate change (Section 2.4). Characterizing the spatiotemporal characteristics of bioclimate envelopes in the context of the physiological constraints of the species and their associated prey and predators is critical to understanding and modeling the effect of climate change on MMS. We expect meeting these challenges will be slow, although perhaps ironically rapid climate may accelerate the learning.

5.4. Final thoughts

Along the spectrum of simple to complex, where should models of climate change lie? A number of studies have addressed detailed mechanism by which climate change affects populations (e.g. Dueri et al., 2012; Piou and Prévost, 2012; Reed et al., 2011a; Wiedenmann et al., 2011) and our literature review suggests that additional mechanisms of adaptation as well as multiple trophic interactions are needed to represent the effects of climate change on populations. However, as Rose et al. (2010) noted, increasingly complex models become progressively more difficult to support. Our aim in this paper is developing a simple framework to illustrate some important processes that might be hidden in models that are more complex. We gain this simplicity by probabilistically expressing vital rates in terms of the condition of individuals. From this simple framework, additional life stage, habitat, species or process can be included but at a cost of growing complexity, dimensions and computation time. Irrespective of the level of detail needed in a model, we believe that our framework is a useful tool to explore and develop an understanding of how migrating marine populations may respond to climate change.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecolmodel.2013.03.009>.

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