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Contribution to the Theme Section 'Marine ecosystems, climate and phenology: impacts on top predators'

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Marine ecosystems, climate and phenology: introduction

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ABSTRACT: Mid to high-latitude marine ecosystems are characterized by strong intra-seasonal variability in productivity across multiple trophic levels. It is understood that climate variability, as well as projected climate change, is likely to cause substantial changes in the timing of key seasonal events, such as the spring phytoplankton bloom, dates of diapause for zooplankton, or nesting dates in seabirds. However, it is not well known how changes in timing across multiple trophic levels will impact predator-prey relationships. Several mechanistic hypotheses have been put forth to explain changes in fish production in relation to phenological variability of prey, including Cushing's (1990; Adv Mar Biol 26:249–293) 'match-mismatch' hypothesis, yet there have been few tests of these ideas relative to ongoing oceanographic change. In this Theme Section, we present 9 papers that relate ocean climate variability and climate change to timing of key events for zooplankton, fish, and seabirds from northern hemisphere marine ecosystems. They cover phenological variability and consequences of timing changes for species of the California Current, Gulf of Alaska, NE Atlantic Ocean, Arctic Ocean and northern Japan Sea, all cold-water ecosystems, and highlight the importance of phenology as a key response variable, as well as the complexity of ecological relationships to be impacted by marine climate change. Multi-trophic level changes in phenology of species abundance and productivity are likely to have important consequences to marine ecosystem structure and function.

KEY WORDS: Abundance · Match-mismatch · Ocean warming · Plankton · Prey · Seabirds · Timing

Anthropogenic warming of the world's oceans is evident for most of the globe (Levitus et al. 2000, 2005), but until recently reports of impacts of climate change in marine ecosystems have lagged behind those of terrestrial counterparts. Despite the role of the oceans in driving and modulating earth's climate system, and the substantial importance of marine organisms to providing numerous ecosystem services to humanity (Cheung et al. 2009), marine climate impacts received scant attention in the latest International Panel on Climate Change (IPCC) assessment report (Richardson & Poloczanska 2008). This is surprising given that interannual and lower frequency climate variability are known to have dramatic and sometimes devastating effects on marine biota, from plankton to fish, marine birds and mammals (Hurrell et al. 2003). Therefore, it seems likely that anthropogenic warming (AW) would strongly impact marine environments and ecosystems.

In terrestrial systems, diverse studies have shown that plants and animals have shifted their ranges towards higher latitudes or altitudes in response to AW (Walther et al. 2002, Parmesan & Yohe 2003, Parmesan 2006). In marine ecosystems, range shifts have been observed for groundfish in the North Sea (Perry et al. 2005) and Bering Sea (Mueter & Litzow 2008). Moreover, in many terrestrial systems, changes in phenology, i.e. the study of 'timing' of seasonal activities (such as reproduction, migration, bud-burst) within a given year have been documented. In most cases, and in accordance with AW, timing has become earlier (Parmesan 2006). In marine systems, changes in timing have been documented, but less frequently than in terrestrial systems (Mackas et al. 2007, Richardson 2008)

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and both climate variability and climate change have been related to phenological variation.

Observed responses of individual species, however, are just a starting point in understanding change in complex marine ecological systems that may result from climate variability, ocean warming and other forms of anthropogenic climate change (e.g. change in wind strength and circulation). While organisms may respond to ocean warming by advancing — or delaying, both situations have been observed, even in the same locality (Byrd et al. 2008) — seasonal timing, there are physiological, evolutionary, and ecological reasons to expect that different species will change at varying rates (Visser et al. 2004, Visser & Both 2005, Parmesan 2006). Indeed, some studies of warming impacts in disparate communities worldwide have found that previously tight trophic coupling (i.e. feeding or mutualistic interactions) between predator and prey, herbivore and food plant, parasite and host, have been disrupted because the resource (prey or host) is not available at the right time or place, i.e. climate change has caused a 'mismatch' in phenology (Stenseth & Mysterud 2002, Gremillet et al. 2008). Changes in important ecological interactions such as predator–prey relationships could have fitness consequences, thereby ultimately affecting populations and communities. For example, a reduction in foraging efficiency could cause a decline in key demographic attributes (e.g. annual reproductive success) leading to poor recruitment and population decreases in future years. If persistent, decoupling of trophic linkages could have severe impacts on marine ecosystem organization and functions. Cushing (1990) suggested that the degree of 'match–mismatch' between predator and prey in time or space is a key influence on fisheries recruitment, affecting fish biomass and fisheries yield, and a number of studies have related the loss of groundfish in the North Atlantic (cod) to trophic mismatches with their prey (large calanoid copepods) (Beaugrand et al. 2003).

It is critical, therefore, that upper trophic level predators adjust energy-intensive phases of their life cycle (e.g. migration, reproduction) to periods of maximum food availability within each year. The overlap in predator activities/needs and prey availability is influenced by both the timing and abundance of the prey (Fig. 1). Mid-trophic-level forage fish, squids, and zooplankton should also time their breeding schedules to coincide with the intra-seasonal peak of their prey (including micro-zooplankton and phytoplankton) availability. With ocean warming, and the multiple food web links involved, severe trophic mismatches between supply and demand may develop if the timing of multiple trophic levels responds to climate change in different ways.

With this background in mind, we convened a symposium entitled 'Phenology and climate change in the North Pacific: implications of variability in the timing of zooplankton production to fish, seabirds, marine mammals, and fisheries (human)' on 2 November 2007 at the 16th Annual Meeting of the North Pacific Marine Science Organization (PICES) in Victoria, Canada. The contributions to this Theme Section by Batten & Mackas (2009), Schroeder et al. (2009), and Watanuki et al. (2009) were originally presented in that topic session. Additional papers were solicited to provide a broader survey of phenological impacts on top marine predators.

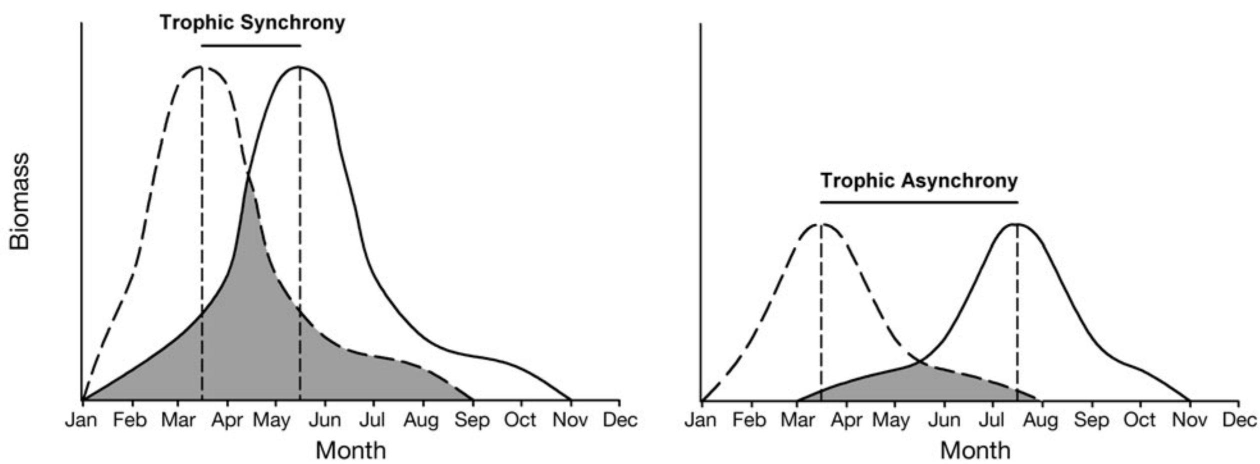

Fig. 1. Schematic of how phenology (timing) and relative abundance (biomass) affect the degree of trophic match-mismatch (after Durant et al. 2005). The key variable is the degree of trophic overlap of predator needs (continuous line) and prey availability (dashed line) in time and space. Dashed curves reflect biomass of prey (height) and seasonality of prey abundance (position of maximum). Reproductive success and other demographic traits will be high when there is great trophic overlap (grey area under curves)

Our intentions in preparing this Theme Section were 4-fold. (1) We wished to investigate the physical basis for phenological changes in marine animal populations. To demonstrate effects of AW, it is necessary to link change in populations to a physical 'state' variable; typically, this is temperature, but we also considered winds, degree of ocean stratification, currents and circulation flow rates, and date of the spring transition as potentially important links between AW and marine populations. All of the papers in this Theme Section contain data and analyses on physical-biological interactions, focused primarily on temperature and atmospheric or oceanographic drivers of temperature variation (e.g. the North Atlantic Oscillation).

(2) We wanted to describe phenological changes in space and time, with the same species in different ecosystems and habitats if possible. For zooplankton, Batten & Mackas (2009) describe changes in developmental timing for *Neocalanus plumchrus*, a dominant mesozoplankton species in the sub-arctic North Pacific. For fish, Holt & Mantua (2009) investigate recruitment variations of sablefish *Anoplopoma fimbria* and Pacific ocean perch *Sebastes alutus* in relation to various measurements of the timing of the spring transition in the California Current. In the case of seabirds, we were able to obtain studies on a total of 5 seabird species, with 3 — Cassin's auklet *Ptychoramphus aleuticus*, common murre/muillemot *Uria aalge*, and black-legged kittiwake *Rissa tridactyla* — having data from different regions and ocean systems. Studies on murres/guillemots represent research from the California Current (Schroeder et al. 2009), NE Atlantic Ocean (Votier et al. 2009), and Gulf of Alaska (Shultz et al. 2009). The work on kittiwakes represents studies from the Gulf of Alaska (Schultz et al. 2009) and Spitsbergen, Svalbard in the high Arctic Ocean (Moe et al. 2009). The work on Cassin's auklet comes from studies in the central (Schroeder et al. 2009) and northern (Bertram et al. 2009) sectors of the California Current. Cassin's auklets are planktivorous, feeding primarily on euphausiid crustaceans and large calanoid copepods (Bertram et al. 2009). A related planktivorous species, the little auk *Alle alle*, was reported on by Moe et al. (2009). Finally, Watanuki et al. (2009) and Ito et al. (2009) provide information on another member of the seabird family Alcidae, rhinoceros auklets *Cerorhinca monocerata*, which consumes both fish and zooplankton (euphausiid crustaceans). Alcids (murres, auklets, and auks) are wing-propelled divers reliant on large and perhaps persistent prey patches for successful reproduction. Thus, they are particularly appropriate subjects for studies considering the importance of prey abundance, timing of abundance, and spatial distribution of prey.

(3) We intended to examine the hypothesis that climate change is affecting trophic interactions through changes in the degree of match-mismatch between predators and prey. To study this hypothesis, a number of steps are required, including: (a) examining relationships between climate and prey, (b) investigating the seasonality of prey abundance in the environment, (c) quantifying the use of prey by predators, and (d) determining the fitness consequences of variation in prey abundance and distribution (collectively 'prey availability') (Durant et al. 2007). The papers by Bertram et al. (2009), Schultz et al. (2009), Watanuki et al. (2009) and Ito et al. (2009) provide independent measurements of prey availability in the environment, examine relationships between prey availability and ocean climate, proxied by sea surface temperature (SST) and current flows, and relate the degree of matching and mismatching in prey availability to predator needs. Watanuki et al. (2009) take this a step further in linking indices of match-mismatch in their system to variation in large-scale atmospheric pressure cells in the northern hemisphere. This paper represents one of the most comprehensive examinations of the climate change match-mismatch hypothesis to date, including data from atmospheric science to seabird ecology.

(4) We desired to develop indices of key physical-biological interactions with which to evaluate the nexus between climate change and match-mismatch in marine ecosystems. Holt & Mantua (2009) provide a comprehensive series of indices of the 'spring transition' from winter to upwelling conditions in the California Current system. Schroeder et al. (2009) make the point that wintertime upwelling conditions are important to seabird reproductive phenology, and provide indices to key physical measurements at that time of year. Batten & Mackas (2009) provide a new index of developmental timing in zooplankton, and demonstrate that the duration of peak biomass, as well as the timing of peak biomass, has changed through time. Bertram et al. (2009) and Ito et al. (2009) provide indices to the timing of prey switching in auklets, which has consequences to reproductive performance. Schroeder et al. (2009) highlight the value of considering 'variance' in addition to measures of central tendency (mean or median) in reproductive phenology as an important indicator of change.

In tackling the issue of marine climate impacts, the complexity of ecological systems must be considered. Predator–prey interactions and changes therein are a prime example of how AW of the world's oceans could alter marine ecosystem organization, structure, and ultimately the services provided to society (food). Here we have compiled a series of papers that focus on mechanistic inter-relationships and the complexities of marine ecological systems, mainly through the lens of seabirds, but also considering important fish and zooplankton populations. Seabirds are understood to be useful indicators of marine ecosystem dynamics, though there is work to be done to resolve key relationships (Durant et al. 2009). Nonetheless, we have established in this Theme Section that climate change can have broad impacts on key trophic interactions within diverse marine ecosystems. Understanding and distinguishing the impacts of natural and anthropogenic climate impacts on marine ecosystems, within the context of other human pressures (e.g. fisheries, development), is critical for restoring and sustaining healthy ocean ecosystems.

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