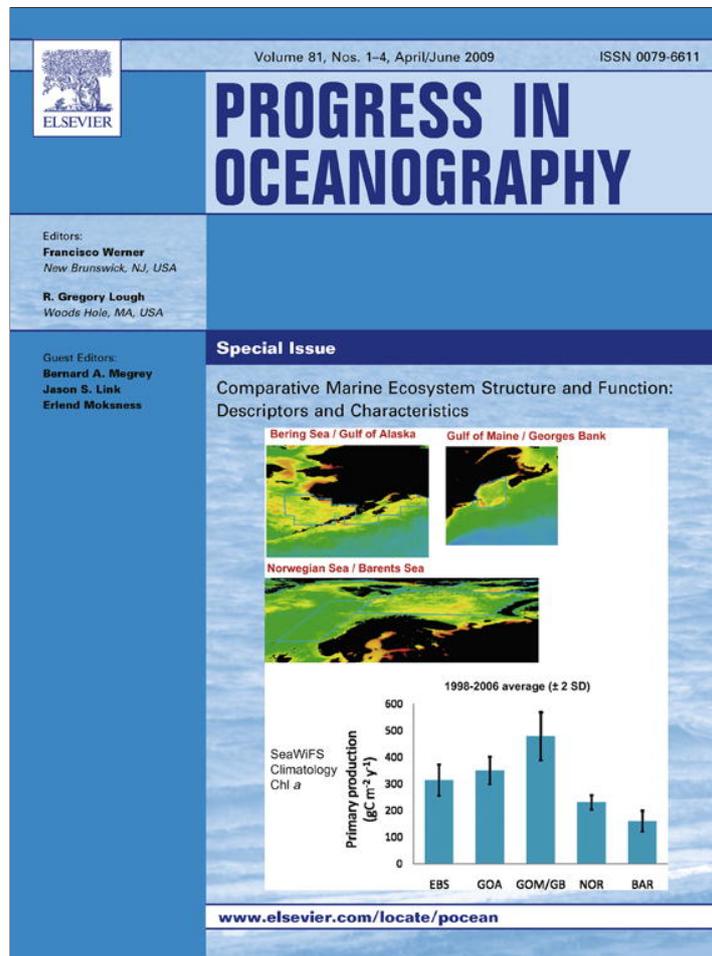


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## Environmental forcing on life history strategies: Evidence for multi-trophic level responses at ocean basin scales

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## ABSTRACT

Variation in life history traits of organisms is thought to reflect adaptations to environmental forcing occurring from bottom-up and top-down processes. Such variation occurs not only among, but also within species, indicating demographic plasticity in response to environmental conditions. From a broad literature review, we present evidence for ocean basin- and large marine ecosystem-scale variation in intra-specific life history traits, with similar responses occurring among trophic levels from relatively short-lived secondary producers to very long-lived apex predators. Between North Atlantic and North Pacific Ocean basins, for example, species in the Eastern Pacific exhibited either later maturation, lower fecundity, and/or greater annual survival than conspecifics in the Western Atlantic. Parallel variations in life histories among trophic levels also occur in adjacent seas and between eastern vs. western ocean boundaries. For example, zooplankton and seabird species in cooler Barents Sea waters exhibit lower fecundity or greater annual survival than conspecifics in the Northeast Atlantic. Sea turtles exhibit a larger size and a greater reproductive output in the Western Pacific vs. Eastern Pacific. These examples provide evidence for food-web-wide modifications in life history strategies in response to environmental forcing. We hypothesize that such dichotomies result from frequency and amplitude shifts in resource availability over varying temporal and spatial scales. We review data that supports three primary mechanisms by which environmental forcing affects life history strategies: (1) food-web structure; (2) climate variability affecting the quantity and seasonality of primary productivity; (3) bottom-up vs. top-down forcing. These proposed mechanisms provide a framework for comparisons of ecosystem function among oceanic regions (or regimes) and are essential in modeling ecosystem response to climate change, as well as for creating dynamic ecosystem-based marine conservation strategies.

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### 1. Introduction

Trade-offs are central to life-history theory, the most prominent of which being the interplay between investment in current reproduction and its two major costs: (1) reduced adult survival, and (2) reduced future reproduction (Stearns, 1989; Esposito et al., 1999; Melov et al., 1999). Evaluation of these reproductive trade-offs – experimentally, empirically, and theoretically – has generated considerable attention in the literature (e.g., Pyle et al., 1997; Nur, 1988; Golet et al., 2004; Charnov et al., 2007). Many investigations, however, have either focused on single-species comparisons within a narrow geographic range or, when comparing two or more

species over a broader spatial scale, have restricted comparisons to particular trophic levels or foraging guilds, often with reference to diversification and avoidance of competition (e.g., Levins and Culver, 1971; Bonsall and Mangel, 2004). Only rarely have comparisons been made between conspecifics inhabiting in different ecosystems (Hatch et al., 1993b; Weimerskirch, 2002; Frederiksen et al., 2005; Grosbois et al., 2006), although such comparisons provide critical insight into the range of demographic plasticity and environmental conditions that influence life history trade-offs. No investigators, to our knowledge, have conducted system-wide analyses from a food-web perspective, while also evaluating environmental forcing.

Environmental constraints often influence life history trade-offs. There are, however, conflicting conclusions as to whether or not environmental instability favors greater reproductive

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investment in the current reproductive effort at the expense of survival (Pianka, 1974; Weimerskirch, 2002). An important factor to be considered is the degree to which environmental forcing drives age-specific mortality patterns, especially whether it disproportionately affects juvenile or adult mortality (Cohen, 1966, 1968; Schaffer, 1974). Stearns (1989), however, noted that inter-generational trade-offs are arguably just as important as individual trade-offs, yet are relatively ignored. Such considerations may be particularly important in understanding how environmental forcing has shaped current life history traits.

In the marine environment, variation in life span and annual fecundity is commonly reported for short-lived species, such as invertebrates (Mackas and Tsuda, 1999). Indeed, studies of zooplankton provide some of the best examples of demographic plasticity in relation to water temperature, timing of the spring bloom, or length of the growing season (Halsband-Lenk et al., 2004; Mackas et al., 2007). Variation in growth and mortality in relation to water temperature are also evident for a variety of fishes (Pauly, 1980; Brander, 1995). Comparable patterns are little known and rarely reported, however, for long-lived species such as upper trophic-level consumers and, in general, this seems to be a neglected topic capable of providing valuable insight into ecosystem function (Frederiksen et al., 2005).

A thorough understanding of mechanisms controlling life history traits, plasticity within species, and of time-scales of adaptation has broad-reaching implications. For example, such understanding is critical to predicting how a given species or food-web structure will respond to climate change, which has significant implications for conservation strategies in an ecosystem-based management framework. Life history and physiological constraints limit the rate and degree to which a given species can adapt, resulting in temporal mismatches of predators and prey, with population increases and range expansion for some species and contraction of others, depending on survival and reproduction under changing environmental conditions (Halsband-Lenk et al., 2004; Winder and Schindler, 2004; Bonnet et al., 2005; Mackas et al., 2007). This is true for not only basal trophic-level organisms, but also for upper trophic-level species (e.g., Gaston et al., 2005; Greenwood, 2007). Mackas and Tsuda (1999) noted that biological oceanographers are challenged to understand changes large in amplitude but widely and unevenly spaced across decades. Geographic comparisons of both present ecosystem state and historical precursors where species occupy different positions within the food-web will be essential for predicting future climate change scenarios (Trathan et al., 2007).

The interplay of ecological and evolutionary processes structure ecological communities, and life-history trade-offs are of fundamental importance to this process (Bonsall et al., 2004; Conover et al., 2006). Furthermore, these processes can be relatively “rapid”, with ecologically significant evolutionary change occurring within tens of generations (ecological evolution) or even on humanly observable timescales (contemporary evolution) and are likely more prevalent than previously recognized (Carroll et al., 2007).

Examining environmental controls influencing “contemporary evolution” is easiest for species with short generation times relative to the human observer and where the organism’s environment can be experimentally manipulated. Similar examination of long-lived, slowly reproducing species is considerably more challenging. An alternative is to compare life histories of conspecifics inhabiting diverse environments that could theoretically affect life history strategies. Furthermore, the novel approach of examining life histories of conspecifics under naturally varying environments can also be applied cross sectionally, examining multiple species throughout the food-web, the approach taken herein. We conducted a literature review and present examples of life history variation in conspecifics exposed to varying environmental forcing regimes. This review is

not exhaustive, but an attempt to represent a broad range of trophic levels and life history strategies; and, most importantly, to generate interest and discussion of this topic and the hypothetical mechanisms proposed. In this review, we address four main questions – the first three documenting the conceptual approach and the fourth presenting potential mechanisms: (1) How broadly do life history trade-offs vary in concert across trophic levels when comparing one ocean basin to another? (2) Do dichotomies in trade-offs occur within ocean basins? (3) What experimental and molecular evidence supports phenotypic plasticity in life history traits vs. genetic control? and (4) What are potential driving forces and mechanisms behind geographic variation in life histories?

## 2. Environmental forcing and life history variation

### 2.1. Life history variation between ocean basins at various trophic levels

Dichotomies in life history traits between ocean basins are evident in parallel responses among trophic levels ranging from secondary producers to apex predators (Table 1). One well-documented example is the black-legged kittiwake (*Rissa tridactyla*), a high latitude, circumpolar, colonial nesting seabird that is considered to be long-lived, despite exhibiting considerable variation in demographic traits. Northeast Pacific populations have consistently higher adult survival rates (mean [range of colony means] = 0.924 [0.922–0.926]) and lower annual fecundity (0.23 [0.05–0.42] chicks per breeding pair) than the same species in the Northeast Atlantic (0.840 [0.801–0.896] and 0.81 [0.55–1.19], respectively; Hatch et al., 1993a, 1993b; Golet et al., 1998; Frederiksen et al., 2005). Indeed, of the seven species examined ranging from krill (*Thysanoessa inermis*) to leatherback sea turtles, all but one species in the North Pacific exhibited lower annual fecundity, later maturation, and/or higher annual adult survival than conspecifics in the similar geographic region of the North Atlantic. The one species, spiny dogfish (*Squalus acanthias*), where fecundity is greater in the Northeast Pacific than Atlantic, in contrast to others, has been exposed to greater top-down fishing pressure in the Atlantic vs. Pacific. If fishing removes a greater proportion of older age classes, reproduction could be shifted to younger age/smaller size classes, thereby reducing annual reproductive output (at least initially), but providing equal or greater life-time reproduction (see Section 2.4.3 below). For zooplankton, Parsons and Lalli (1988) suggested that these differences may be attributed to the dominance of a longer flagellate-microzooplankton food chain in the North Pacific compared to a diatom-macrozooplankton food chain in the North Atlantic. The difference in food-webs possibly stems from the longer time-span of evolutionary development in the older Pacific ecosystem. In contrast, the Atlantic is more similar to coastal ecosystems that evolved since the appearance of diatoms (about 100 million years ago). There are, however, other potential drivers of food-web dynamics as described below.

### 2.2. Life history variation within ocean basins and between their adjacent seas

Variation in ecosystem structure and function within ocean basins may affect life histories (e.g., eastern vs. western boundary currents vs. central gyres, inshore vs. offshore systems, latitudinal variation in day length and temperature effects on growing season). In the Pacific Ocean, the life cycles of euphausiids (*Euphausia pacifica*, *Thysanoessa* spp.) vary spatially, ranging from 1 year in warmer, southern and eastern regions to 2 years or occasionally 3 years in colder, northern and western regions (Ponomareva, 1963; Mauchline and Fisher, 1969). Latitudinal variation in life

**Table 1**  
Comparison of life history demographic traits of conspecifics in the Pacific and Atlantic Oceans.

Species	Atlantic		Pacific		Source
	Fecundity	Survival <sup>a</sup>	Fecundity	Survival	
krill <sup>b</sup> ( <i>Thysanoessa inermis</i> )	1+ yr <sup>c</sup>	2+ yr <sup>d</sup>	2–3+ yr <sup>c</sup>	2–3+ yr <sup>d</sup>	Siegel (2000) and Refs. therein.
rainbow smelt <sup>e</sup> ( <i>Osmerus mordax</i> )	–	0.28	–	0.40	Haldorson and Craig (1984) and Refs. therein. Age at maturity was 2–3 yrs and 6–7 yrs, respectively
capelin <sup>f</sup> ( <i>Mallotus villosus</i> )	16.6–61.5 <sup>g</sup> 0.97–1.17 <sup>h</sup>		5.4–53.2 <sup>g</sup> 0.65–0.86 <sup>h</sup>		Stergiou (1989) and Refs. therein
black-legged kittiwake ( <i>Rissa tridactyla</i> )	0.76 <sup>i</sup> (0.55–1.19)	0.834 (0.801–0.896)	0.23 <sup>i</sup> (0.05–0.42)	0.926 (0.920–0.926)	Golet et al. (1998), Frederiksen et al. (2005) and Refs. therein
spiny dogfish ( <i>Squalus acanthias</i> )	4.7 <sup>j</sup> (1–15)		9.4 <sup>j</sup> (2–25)		Ketchen (1972) and Refs. therein
green sea turtle <sup>k</sup> ( <i>Chelonia mydas</i> )	109 <sup>l</sup>		76 <sup>l</sup>		Broderick et al. (2003), Reyes and Troëng (2002) www.euroturtle.org
leatherback turtle <sup>m</sup> ( <i>Dermodochelys coriacea</i> )	83 <sup>l</sup>		63 <sup>l</sup>		Saba et al. (2008a)

<sup>a</sup> Adult survival.

<sup>b</sup> North Pacific Aleutian Islands/Bering Sea vs. North Atlantic, boreal.

<sup>c</sup> Age at first spawning.

<sup>d</sup> Maximum age.

<sup>e</sup> Pacific Arctic vs. Northwest Atlantic.

<sup>f</sup> Thousands of eggs.

<sup>g</sup> Pacific data are from Western Pacific – Sea of Japan, Sea of Okhotsk.

<sup>h</sup> Egg diameter.

<sup>i</sup> Offspring per pair.

<sup>j</sup> Number of offspring (range).

<sup>k</sup> Pacific data are from Hawaiian Islands.

<sup>l</sup> Eggs per clutch.

<sup>m</sup> Eastern Pacific vs. Western Atlantic.

histories of American shad (*Alosa sapidissima*) and cod (*Gadus* sp.) exist and, like zooplankton, typically have greater fecundity and shorter life span in the south vs. north (Table 2). American shad in the Northwest Atlantic is smaller bodied and semelparous in southern rivers and larger bodied and iteroparous in northern rivers (Limburg et al., 2003 and references therein); additionally, fecundity tends to be higher in southern latitudes, although some variation in this latitudinal gradient does exist (Olney and McBride, 2003). Latitudinal variation in age at maturity is also observed in Pacific cod (*Gadus macrocephalus*), with fish reaching maturity at younger ages off British Columbia (2–4 years; Westrheim, 1977) vs. populations further north in the Gulf of Alaska and Bering Sea (4–5 years; Stark, 2007). Similarly, Atlantic cod (*Gadus morhua*) in coastal Norway, including northern fjords, mature at a younger age (50% maturity at 5.7 years) than cod in the Northeast Arctic and Barents Sea (6–9 years; Berg and Albert, 2003 and references therein). Temporal variation in Atlantic cod life histories have also been documented along the west coast of Scotland and North Sea, with decreasing size and age at maturity and increasing fecundity over time (1969–1970 to 2002–2003). This temporal variation coincided with large reduction in population size and occurred synoptically in the Northwest Atlantic (Fudge and Rose, 2008).

Miller et al. (1984) noted differences in *Neocalanus plumchrus* development between coastal and oceanic habitats in the Northeast Pacific, and Saba et al. (2008a) suggested that differences in size and reproductive output between Western and Eastern Pacific populations of leatherback turtles are due to differences in foraging ground productivity (Fig. 1). In the North Atlantic and its adjacent seas, black-legged kittiwakes breeding in the northeastern sector (United Kingdom and France) had lower annual survival than conspecifics breeding in the Barents Sea (Norway; Frederiksen et al.,

2005). Similarly, *Calanus finmarchicus* in the Northeast Atlantic exhibited greater annual fecundity (two generations per year) than conspecifics in the Barents Sea (1 generation per year, Parsons and Lalli, 1988; Table 2).

### 2.3. Genetic control vs. phenotypic plasticity

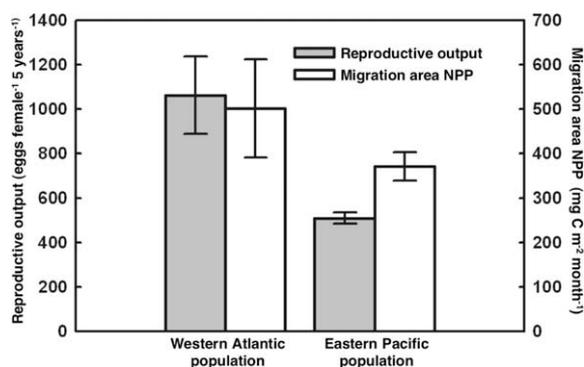
Many experimental studies demonstrate plasticity in the expression of life history traits (and subsequent life history evolution) in a large diversity of organisms. For example, introduced predators increase reproductive investment of female killifish, *Rivulus hartii*, and, importantly, the magnitude of this effect can vary with food availability for *Rivulus* (Reznick et al., 2000; Walsh and Reznick, 2008). Experimental evidence for marine vertebrate species include Godø and Moksness (1987) who verified in laboratory experiments that differences in growth and age of maturity in Atlantic and Norwegian cod (*Gadus* spp.) were a function of environmental control, independent of genetic variation. Comfort (1963) studied the effect of feeding rate on lifespan in guppies (*Lebistes reticulatus*) and found that intermittent feeding promoted longevity. Other studies have shown that delayed sexual maturity is correlated with increased life span in species ranging from *Drosophila* (Rose and Charlesworth, 1980; Partridge et al., 1999) to seabirds. For instance, western gulls (*Larus occidentalis*) that began breeding at younger ages suffered increased mortality, and females with more annual breeding attempts had lower survival rates, independent of age (Pyle et al., 1997).

Indeed, in considering phenotypic plasticity vs. genetic control, Conover et al. (2006) noted that variation in adaptive (affecting fitness) and neutral (not influencing phenotypic expression) genetic markers should be correlated if gene flow is primarily regulating

**Table 2**  
Comparison of reproductive output of conspecifics within a basin or between adjacent basins.

Species	Reproductive output		Source
copepod ( <i>Calanus finmarchicus</i> )	Northeast Atlantic 2 <sup>a</sup>	Barents Sea 1 <sup>a</sup>	Parsons and Lalli (1988) and Refs. therein
krill ( <i>Thysanoessa inermis</i> )	Barents Sea 1–2+ yr <sup>b</sup>	Greenland 3+ yr <sup>b</sup>	Siegel (2000) and Refs. therein
krill ( <i>Euphausia pacific</i> )	Southern California Current 0.3–0.6 yr <sup>b</sup>	Northern California Current 1–2 yr <sup>b</sup>	Siegel (2000) and Refs. therein.
American shad ( <i>Alosa sapidissima</i> )	Western N. Atlantic, Southern Range semelparous 4.2 yr <sup>b</sup>	Western N. Atlantic, Northern Range iteroparous 4.8 yr <sup>b</sup>	Leggett and Carscadden (1978), Limburg et al. (2003) and Refs. therein
capelin ( <i>Mallotus villosus</i> )	Newfoundland & Grand Banks 16.6–61.5 <sup>d</sup>	Barents Sea & Iceland 9.0–24.6 <sup>d</sup>	Stergiou (1989) and Refs. therein
capelin ( <i>Mallotus villosus</i> )	Barents Sea – Ocean Spawning semelparous	Norway – Inland Beach Spawning iteroparous	Christiansen et al. (2008)
cod ( <i>Gadus morhua</i> )	Northeast Atlantic <sup>c</sup> 6.2 <sup>d</sup>	North Sea Inshore 7.0 <sup>d</sup>	North Sea Offshore 5.5 <sup>d</sup> Yoneda and Wright (2004)
spiny dogfish ( <i>Squalus acanthias</i> )	Northwest Pacific 12 <sup>e</sup> (3–5)	Northeast Pacific 6.8 <sup>e</sup> (2–17)	Ketchen (1972) and Refs. therein
green sea turtles ( <i>Chelonia mydas</i> )	Mediterranean Sea 115 <sup>f</sup>	West Atlantic 109 <sup>f</sup>	Broderick et al. (2003), Reyes and Tröng (2002); www.euroturtle.org
leatherback turtle <sup>g</sup> ( <i>Dermodochelys coriacea</i> )	West Atlantic 83 <sup>f</sup>	East Atlantic 73 <sup>f</sup>	West Indian 104 <sup>f</sup> Saba et al. (2008a)

<sup>a</sup> Generations yr<sup>-1</sup>.  
<sup>b</sup> Age at first spawning.  
<sup>c</sup> West coast of Scotland.  
<sup>d</sup> Thousands of oocytes.  
<sup>e</sup> Offspring per female (range).  
<sup>f</sup> Eggs per clutch.  
<sup>g</sup> East Pacific data are from Costa Rica.



**Fig. 1.** Leatherback turtles nesting in the equatorial Eastern Pacific have lower reproductive rates and forage in less productive waters (presented as net primary productivity, NPP) than those in the Western Atlantic. Figure from Saba et al. (2008a).

variation in traits. Instead, however, variability was greater in adaptive vs. neutral markers for a variety of marine fishes, further highlighting the need for a new paradigm in our approach to considering the geography of phenotypic variation (phenogeography)

and the geography of lineages (phylogeography; Conover et al., 2006). Hence phenotypic plasticity permits change in life history strategies of short- and long-lived species, but limitations of the magnitude and rate of change are unknown for most species.

#### 2.4. Environmental forces driving life history variation

Schreiber and Schreiber (1989) hypothesized that environmentally driven resource limitation might have intriguing implications for life histories and population dynamics of inter-basin populations of other long-lived marine vertebrates. Weimerskirch (2007) described variation in life history trade-offs that appeared to vary with resource availability among different ocean basin populations of black-browed albatrosses (*Thalassarche melanophrys*) in the southern hemisphere. Albatrosses foraging at frontal zones (Campbell Island colony in the South Pacific) and on Antarctic krill (*Euphausia superba*; South Georgia Island colony in the South Atlantic) – relatively unpredictable resources – have lower and more variable breeding success but greater annual survival (Croxall et al., 1997; Prince et al., 1997; Waugh et al., 1999a, 1999b) than those breeding on Kerguelen Island in the Indian Ocean, where birds have access to abundant and predictable resources at the

shelf edge. Weimerskirch (2007) suggested these patterns indicate a link between marine resource predictability and the evolution of particular life history strategies. Similarly, populations of leatherback turtles (*Dermochelys coriacea*) that forage in the North Atlantic exhibit larger body size and higher reproductive output, on average, than their Eastern Pacific counterparts that are affected by El Niño Southern Oscillation (ENSO) events and forage in the South-eastern Pacific gyre where primary production is relatively low (Wallace et al., 2006a; Saba et al., 2008a,b; Shillinger et al., 2008). In addition, Wallace et al., 2006a speculated that the differences in resource availability could render Eastern Pacific leatherbacks less resilient to population perturbations than North Atlantic leatherbacks, thus resulting in current differences in population trends. Likewise, Leggett and Carscadden (1978) suggested that smaller southern populations of American shad that spawn once and die in contrast to multiple-spawning northern population appears to be an adaptation to a more benign, predictable climates in south vs. a more stochastic climates in north (lower probability of successful recruitment in a given year).

It is therefore evident that life histories of conspecifics vary with respect to different regional environmental forcing and that this variation can occur in concert among trophic levels, suggesting parallel food-web-wide response in some cases. We propose three mechanisms by which environmental conditions may shape these observed patterns: (1) food-web structure; (2) frequency and amplitude of climate variability affecting the quantity and seasonality of primary productivity, and (3) bottom-up vs. top-down forcing.

#### 2.4.1. Food-web structure and nutrient sources: systems with more complex trophic structure promote higher adult survival and lower reproductive investment

Food-chain length is a fundamental property of ecosystems (Vander Zanden and Fetzer, 2007). Comparing oceanic systems, Parsons and Lalli (1988) noted that trophic linkages in the North-east Pacific were characterized by increased complexity compared to those in the Northwest Atlantic. Indeed, many organisms in the North Pacific have greater  $\delta^{15}\text{N}$  values compared to conspecifics in the North Atlantic (Table 3), indicating a potentially higher trophic position in the former. These differences, however, may also reflect the influences of differential nutrient cycling regimes – and thus distinct oceanographic processes – on basal trophic levels being transferred through trophic systems (Minami and Ogi, 1997; Takai et al., 2000; Wallace et al., 2006b). Either way, these results reflect fundamental differences in energy flow and food-web dynamics between systems.

Within a region, food-web structure can also respond to climate oscillations as demonstrated in the Eastern Pacific during ENSO events and multi-decadal regime shifts (Chavez et al., 1999, 2003). For example, Chavez et al. (1999) demonstrated that during a strong La Niña event, trophic structure in the equatorial Pacific changed from a more complex picoplankton-dominated food-web to a more simple diatom-dominated structure. During La Niña, the system became highly productive, similar to coastal envi-

ronments. This suggests systems with less complex food-webs may allow a more rapid and direct bottom-up response to sudden shifts in food supply or phenology. Furthermore, demographic effects may follow upon an increase in trophic position, as observed by Wilhelm and Adrian (2007), who noted increased survival among organisms occupying higher trophic positions.

Takai et al. (2000) noted that stable isotope analyses of conspecific populations from different ocean basins are crucial to understanding how oceanography influences the trophic ecology of high-order marine consumers. Trathan et al. (2007) further emphasized that understanding how species have adapted to past and current conditions through comparative analyses allows predictions about how they may adapt to future climate change.

#### 2.4.2. Mean levels and variability of primary production: systems with greater temporal variability in primary production and/or more frequent periods of resource limitation for early life stages favor higher adult survival and lower reproductive investment

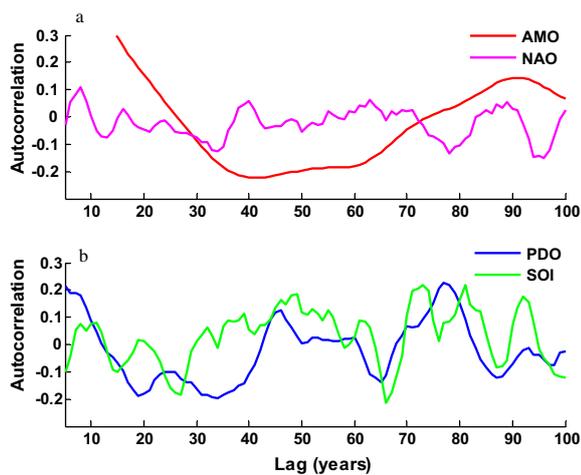
Higher variance in annual and seasonal primary productivity, which effects early life stages, leads to less predictable food resources and, in turn, lower reproductive output for consumers in general, and for long-lived species, in particular. Recent investigations by Saba et al. (2008a) showed that greater mean primary production and high seasonal variance within the foraging areas of western Atlantic leatherback turtles are consistent with their greater reproductive output and larger body size compared to populations in the eastern Pacific (Fig. 1). Saba et al. (2008a) further reported that Western Pacific populations forage in more productive waters and therefore are larger in size, and have greater reproductive output (i.e., are more similar to western Atlantic) than Eastern Pacific leatherbacks.

Large-scale climate events can directly effect primary production and the amplitude and frequency of these events vary among ocean basins. For example, the dominant modes of climate variability identified for the Pacific (Pacific Decadal Oscillation and ENSO) and Atlantic oceans (Atlantic Multi-decadal Oscillation and North Atlantic Oscillation) indicate that basin-scale climate variability occurs on shorter time scales and with higher amplitude signals in the Pacific Ocean compared to the Atlantic (Figs. 2 and 3). The dominant climate indices in the North Atlantic show multi-decadal variation, whereas both inter-annual and decadal-scale variation is prevalent in the North Pacific.

This difference in the temporal scale of climate oscillations affects the life history strategies of upper trophic level organisms. For example, recent analyses by Saba et al. (2007) supported Wallace et al.'s (2006a) hypothesis that greater frequency and amplitude of environmental variability in the Eastern Equatorial Pacific (primarily from ENSO events) is responsible for more sporadic breeding and comparatively low reproductive output of leatherback turtles in this region compared to those in the Western Atlantic. Likewise, based on a bioenergetics model, Harvey (2005) found that repeated exposure to ENSO events resulted in slower growth rates, delayed maturation, and decreased fecundity in rockfish (*Sebastes* spp.).

**Table 3**  
Comparison of nitrogen stable isotope values for conspecifics occurring in Pacific and Atlantic Oceans. means  $\pm$  SD (n). The same tissues were compared within species between regions.

Species	Pacific	Atlantic	Source
gelatinous zooplankton	14.0 $\pm$ 0.9 (2)	10.4 $\pm$ 0.4 (2)	Wallace et al. (2006b)
squid	14.0 $\pm$ 3.1 (4)	12.1 $\pm$ 1.3 (11)	Wallace et al. (2006b)
leatherback turtle ( <i>Dermochelys coriacea</i> )	15.4 $\pm$ 1.8 (37)	9.8 $\pm$ 1.4 (67)	Wallace et al. (2006b)
common murre ( <i>Uria aalge</i> )	14.7 $\pm$ 0.24 (8)	11.6 $\pm$ 0.4 (8)	Thompson and Furness (1995), Suryan unpubl. data
northern fulmar ( <i>fulmarus glacialis</i> )	15.43 $\pm$ 1.42 (19)	14.4 $\pm$ 0.09 (5)	Thompson and Furness (1995), Suryan unpubl. data
sperm whale ( <i>Physeter macrocephalus</i> )	19.6‰ $\pm$ 0.6 (34)	11.1‰ (1)	Ostrom et al. (1993), Ruiz-Cooley et al. (2004)



**Fig. 2.** Time-lagged autocorrelation showing periodicities of primary climate indices for the (a) North Atlantic and (b) North Pacific Oceans. Indices include the Atlantic Multidecadal Oscillation, AMO, North Atlantic Oscillation, NAO, Pacific Decadal Oscillation, PDO, and Southern Oscillation Index, SOI. Data are annual indices from climate reconstructions based on tree-ring data (Stahle et al., 1998; Cook et al., 2002; Gray et al., 2004; Shen et al., 2006).

Mangel et al. (2007) modeled lifespan response to environmental conditions for Pacific rockfishes (*Sebastes* spp.). They found that in a constant but low productivity environment, no value of lifespan allowed population persistence (population growth rate  $[\lambda] < 1$ ), although strategies combining longer lifespan and slower growth approached  $\lambda = 1$ . In a constant and favorable environment, short-lived species have a selective advantage because  $\lambda$  declines with maximum age. Conversely, in fluctuating environments, individuals born in an unfavorable environment are selected to extend lifespan so that some portion of reproductive life occurs under favorable environmental conditions. Physiological constraints, however, dictate whether a species is capable of sufficiently extending lifespan to correspond with favorable cycles. If not, they may be forced to invest more energy into reproduction at the expense of adult survival.

**2.4.3. Bottom-up vs. top-down control of individual species or food-webs: systems dominated by bottom-up resource limitation promote lower fecundity and higher adult survival than those dominated by top-down controls**

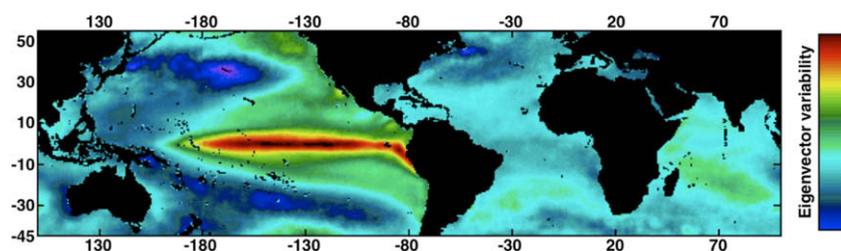
Population demographics respond differently depending on whether a species (or entire food-web) is influenced primarily by bottom-up or top-down controls. Bottom-up resource limitation often affects survival of younger life stages more so than top-down factors and thereby recruitment to the breeding population, resulting in a demographic shift toward lower fecundity and higher sur-

vival of adults and subadults. In contrast, when a species (or food-web) is regulated more by top-down forces, the demographic shift is often toward higher fecundity and lower adult survival, especially where predators (including commercial fisheries) primarily remove older life stages and age classes. Harbor seal pups (*Phoca vitulina*) born on Sable Island, Canada, provide an example of bottom-up control. The harbor seal population declined rapidly through the 1990s from 625 pups to only 32 (Bowen et al., 2003), yet indices of maternal and pup condition (maternal postpartum mass, pup birth mass, lactation duration, pup weaning mass) showed no significant trends during the decline. The mean age of parturient females increased significantly, however, indicating reduced survival and recruitment of young (Bowen et al., 2003). In contrast, following high adult mortality of a Pacific tropical seabird (masked booby, *Sula dactylatra*) during the 1982 El Niño, the proportion of first-time breeders increased (Schreiber and Schreiber, 1989). The mortality of adult birds in this case is not a result of top-down forcing per se, but it has the same effect as many commercial fisheries, for example, in removing primarily adults from the population, thereby reducing density dependent effects. Likewise for leatherback turtles, the proportion of first-time breeders in Pacific Costa Rica has increased in recent years, possibly due to the estimated high annual adult mortality (Santidrián-Tomillo et al., 2007).

Many variables besides climate affect demographics, direct harvest and density dependence being not the least among them. Regardless of the source, knowing what age classes suffer the greatest relative mortality permits testing of hypotheses regarding bottom-up vs. top-down effects and may therefore shed light on forces shaping life histories.

**3. Physiological mechanisms for life history trade-offs**

Available energy is a primary driver affecting the life history trade-off between current reproduction and survival. Short-term survival costs associated with increased reproductive investment may result from reduced adult body condition, which can magnify the negative effects of resource limitation (e.g., Golet et al., 1998). There are also, however, potential long-term survival effects of increased energy acquisition which occur at the molecular level and affect senescence and longevity. While it had been recognized for over a century that animals with higher metabolic rates often have shorter lifespans, the mechanistic link was unknown until Harman (1956) developed the “free-radical theory” of aging. The theory posits that endogenous oxygen radicals are generated in cells, resulting in a pattern of cumulative damage. Harman’s theory suggests that as metabolic rate increases, so does the production of reactive oxygen species, thereby reducing the lifespan – a “rate of living” interpretation of life-history trade-offs. Some animals, however, tend to live longer than what would be predicted by metabolic rates alone (Finkel and Holbrook, 2000). Studies of oxidant



**Fig. 3.** Variability of SST in the Pacific, Atlantic, and Indian Oceans from. First principal component (spatial mode) of sea surface temperature variation derived from an empirical orthogonal function analysis using 21 years of Pathfinder Advance Very High Resolution Radiometer (AVHRR) satellite data (1985–2005). Eigenvector variability is represented in the color scale bar and is unitless. Figure from Saba et al. (2008a).

production indicate that at a given metabolic rate, mitochondria in such species produce fewer reactive oxygen species (Ku et al., 1993). Thus, production of reactive oxygen species, rather than metabolic rate per se, provides the strongest correlation with overall longevity (Finkel and Holbrook, 2000). Other studies show that oxidative stress causes more damage in mitochondrial DNA than nuclear DNA. Compromised mitochondria, in turn, are thought to release more reactive oxygen species, thereby catalyzing a cycle of increasing damage to the DNA (Esposito et al., 1999; Melov et al., 1999; Finkel and Holbrook, 2000).

How this relates to varying life histories in different environments is demonstrated by studies showing increased life span with increased caloric restriction (Masoro, 2000), the presumption being that caloric restriction decreases oxidative stress (Ku et al., 1993). In addition to reducing oxidative stress, caloric restriction appears to prevent many of the changes in gene expression and transcription-factor activity that normally occur with aging. Thus, the treatment increases an organism's ability to withstand a wide range of physiological stresses (Finkel and Holbrook, 2000). Support for these hypotheses in the marine environment is suggested by Cailliet et al. (2001), who noted that longevity in rockfishes increased with depth, because deeper waters are colder, have lower oxygen concentrations, and lower prey density. Evidence for a cost of increased early life reproduction was documented by Reed et al. (2008), who found that for a relatively long-lived seabird, greater reproductive investment earlier in life caused increased rates of reproductive senescence at the end of life. More generally, Pauly (1980) noted the turnover of biomass is generally correlated with warmer water temperature, which is consistent with Frank et al. (2006) who found "accelerated demographic rates" of fishes with warmer water.

#### 4. Life history adaptation and climate change

Food-web structure and the extent of species-specific plasticity in life history trade-offs will partly determine how ecosystems respond to climate change. In Lake Washington, for example, Winder and Schindler (2004) found that long-term warming caused a significant trend towards earlier timing of peak phytoplankton density. The herbivorous rotifer *Keratella* adjusted by advancing its phenology by 21 days over 40 years. Thus there was no temporal offset of the predator–prey relationship – the phenologies remained coupled. In contrast, timing of the annual spring peak of *Daphnia* exhibited no similar shift, the temporal mismatch between predator and prey increased significantly, and a long-term decline in spring/summer *Daphnia* densities occurred as a result (Winder and Schindler, 2004).

Long-term warming is projected for marine systems globally and, indeed, Belkin (in this issue) documents that since the 1980s, warming trends have existed for many of the large marine ecosystems globally. Furthermore, Mueter et al. (in this issue) noted that in the Eastern Bering Sea and Gulf of Alaska, community regime shifts accompanied increases in sea surface temperature. Little is known about how these large-scale changes in temperature and food-web structure affect life histories across trophic levels and to what extent life histories can adapt within sufficient timeframes. We argue this remains an important and currently neglected topic in marine ecosystem studies.

In the subarctic North Pacific, Mackas and Tsuda (1999) concluded that zooplankton populations have been changing to an ecologically significant extent at both interannual and inter-decadal time scales and that at least part of these changes are caused by variability of ocean climate conditions. The temporal scales over which the life histories of different organisms vary will profoundly affect their response to climate change. Species with relatively short generation times of months or years (e.g., zooplankton and

forage fishes) will be affected by finer scale processes than those with long generation times of multiple years or decades (e.g., rockfishes, sharks, seabirds). While water temperature, stratification, and the precise timing of the spring bloom on a scale of days or weeks dramatically affect zooplankton, longer-period climate events – on time scales of several years or decades – will most dramatically affect life history traits of longer-lived, middle to upper trophic level species.

#### 5. Conclusions

We found concordance across trophic levels in life history variation that appears to reflect system-wide adaptations. A low survival/high fecundity vs. high survival/low fecundity dichotomy within species occurs both between and within ocean basins. Empirical support for environmental forcing of these patterns exists and has the unifying foundation of food-web structure and function, which is primarily determined by abiotic factors such as climate, nutrient availability, and geological history. Understanding these mechanisms of environmental forcing on life history trade-offs as well as plasticity and rate of potential adaptation is important for elucidating processes on ecological and evolutionary scales, as well as for informing current and future ecosystem-based marine conservation strategies.

Patterns presented herein show food-web-wide response in life history strategy to environmental forcing with sufficiently strong evidence to warrant a larger scale review of more species and ecosystems and quantitative investigation. Future directions, therefore, should include testing proposed hypotheses using ecosystem-based, interdisciplinary studies of conspecifics from large marine ecosystems influenced by varying environmental forcing and production regimes. For example, studies such as Gaichas et al. and Link et al. (in this issue) where comparisons of energy flow and community assemblages across large marine ecosystems could be used to test hypotheses of predicted variation in life history response and to derive additional or refine mechanisms proposed herein. Ultimately, this approach may provide a unified model for understanding how environmental fluctuation and food-web alterations affect life history evolution and population response of organisms from the deep sea to terrestrial alpine systems.

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