

Environmental forcing of life history strategies: Multi-trophic level response at ocean basin scales

Robert M. Suryan.

*Oregon State University, Hatfield Marine Science Center, 2030 S.E. Marine Science Dr.,
Newport, Oregon, 97365, USA Tel: +1.541.867.0223, Fax +1.541.867.0138, E-mail:
rob.suryan@oregonstate.edu*

Morten Frederiksen* and Sarah Wanless

*Centre for Ecology and Hydrology Banchory, Hill of Brathens, Banchory AB31 4BW, UK, Tel.:
+44.1330.826300; Fax: +44.1330.823303, E-mail: swanl@ceh.ac.uk. *Current address:
National Environmental Research Institute, Department of Arctic Environment, P.O. Box 358,
Frederiksborgvej 399 DK-4000, Roskilde, Denmark Email: mfr@dmu.dk*

Bryan P. Wallace

*Duke University Marine La, 135 Duke University Marine Lab Road, Beaufort, North Carolina
28516, USA, Tel.: +1.252.504.7653, Fax: +1.252.504.7689, E-mail: bwallace@duke.edu*

Vincent S. Saba

*Department of Fisheries Science, Virginia Institute of Marine Science, College of William and
Mary, Rt. 1208 Greate Rd., Gloucester Point, Virginia 23062, USA, Tel: +1.757.870.4056,
Fax: +1.804.684.7327, E-mail: vssaba@vims.edu*

Scott A. Hatch

*US Geological Survey, Alaska Science Center, 1011 East Tudor Road, Anchorage, Alaska
99503, USA Tel: +1.907.786.3529, Fax: +1.907.786.3636 E-mail: scott_hatch@usgs.gov*

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. Between North Atlantic and North Pacific Ocean basins, intra-specific variation in life history traits has been observed among trophic levels from zooplankton to sharks, seabirds, and sea turtles. In all cases examined, species in the Eastern Pacific exhibited later maturation and lower fecundity, but greater annual survival, than conspecifics in the Atlantic. We hypothesize that this dichotomy results from frequency and amplitude shifts in resource availability over varying temporal and spatial scales. Captive studies of fishes have shown that differences in growth and age of reproduction can indeed be a function of environmental control rather than genetic variation. Similar parallel occurrences also have been observed in adjacent seas and between eastern vs. western ocean boundaries. For example, zooplankton and seabird species in cooler North Sea waters exhibit lower fecundity and greater annual survival than conspecifics in the northeast Atlantic and leatherback sea turtles exhibit a larger size and greater reproduction frequency in the Western Pacific vs. Easter Pacific. These examples show system-wide adaptations in life history strategies resulting from environmental

forcing and provide a framework for comparisons of ecosystem function among oceanic regions (or regimes) and may prove valuable in modeling ecosystem response to environmental change.

Keywords: basin scale processes, food webs, life history strategies, population dynamics

Introduction

Trade-offs have played a central role in the development of life-history theory, the most prominent being the cost of reproduction, which has two major components: 1) costs paid in survival and 2) costs paid in future reproduction (Stearns 1989). Testing of these reproductive trade-offs, experimentally, empirically and theoretically, has garnered considerable attention in the literature (e.g., Nur 1988, Charnov 1997, Pyle et al. 1997, Charnov 2001, Golet et al. 2004). Many investigations, however, have focused on single species comparisons within a narrow geographic range or if among species in a broader spatial scale, often using broad generalizations within trophic levels or foraging guilds. Only rarely have comparisons been made between conspecifics existing in different ecosystems (Hatch et al. 1993, Weimerskirch 2002, Frederiksen et al. 2005), which provide critical insight into the range of demographic plasticity and environmental conditions influencing life history trade-offs. We further expand on this theme by considering multiple-trophic levels, food web dynamics, and environmental forcing. In doing so, we attempt to identify dominant drivers of life history variation and the range of species-specific plasticity, with the premise that current life history traits reflect a long-term ecological response of a species or food web to past environmental forcing. This, in turn, could prove valuable in modeling ecosystem response to future environmental change.

Background

In many cases it is evident that environmental constraints influence these life history trade-offs. There are, however, conflicting conclusions regarding whether environmental instability favors greater reproductive investment at the expense of survival or vice versa {e.g., Pianka 1972; Weimerskirch, 2002}. An important consideration in this discussion is whether environmental forces are causing age-specific mortality, especially if disproportionately affecting juvenile or adult mortality (Cohen 1966, 1968; Schaffer 1974). Furthermore, Stearns {1989} noted that inter-generational trade-offs are arguably just as important as individual trade-offs, yet are relatively ignored. These 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, in response to changes in water temperature, or day length (Mackas and Tsuda 1999). Similar discussions are less common, however, regarding long-lived species, such as upper trophic-level consumers (Frederiksen et al. 2005). Take for example the black-legged kittiwake (*Rissa tridactyla*), a high latitude, circumpolar, colonial nesting seabird. In general, kittiwakes would be considered long-lived animals, however, there is considerable variation in their demographics. Northeast Pacific populations have consistently higher survival rates (0.924, range of colony means = 0.922-0.926) and lower annual fecundity (0.23, 0.05-0.42) than Northeast Atlantic (0.840, 0.801-0.896 and 0.81 0.55-1.19, respectively: Hatch et al. 1993, Golet et al. 1998, Frederiksen et al. 2005). These occurrences led us to consider: 1) How broadly does this apply across trophic levels; 2) Do

dichotomies occur within ocean basins; 3) Genetic control vs. phenotypic plasticity; and 4) What are the driving forces/mechanisms?

1) How broadly does this apply across trophic levels?

We found evidence for intra-specific variation in life history traits among many trophic levels ranging from zooplankton (Parsons and Lalli 1988) to fish (Haldorson and Craig 1984), sharks (Ketchen 1972), seabirds (Hatch et al. 1993), and sea turtles (Wallace et al. 2006). In most cases, species in the Pacific exhibited lower annual fecundity but, when possible to measure, slower maturation and/or greater annual survival than conspecifics in the Atlantic. There is, however, considerable variation in ecosystem structure and function within ocean basins that may affect life histories (e.g., eastern vs. western boundary currents or gyres, inshore vs. offshore systems, etc.).

2) Do dichotomies occur within ocean basins?

Yes, and at varying trophic levels. In the Pacific Ocean life history strategies of euphausiids vary spatially, ranging from annual in warmer, southern and eastern regions (*E. pacifica*, *Thysanoessa* spp.) to biennial or occasionally triennial in colder, northern and western regions (*Thysanoessa* spp.: Ponomareva 1963, Mauchline and Fisher 1969). Similarly Miller et al. (1984) noted differences in *Neocalanus plumchrus* development between coastal and oceanic habitats in the Northeast Pacific. Also in the Pacific, Saba et al. (in press) noted dichotomies in size and reproductive effort (frequency) between western and eastern Pacific populations of leatherback turtles (*Dermochelys coriacea*).

In the North Atlantic and marginal seas, black-legged kittiwakes breeding in the Northeast Atlantic (United Kingdom and France) showed lower annual survival and slightly greater fecundity than conspecifics breeding in the Barents Sea (Norway: Frederiksen et al. 2005). In concordance, *Calanus finmarchicus* in the Northeast Atlantic exhibited greater annual fecundity (two generations per year) than conspecifics in the Barents Sea (one generation per year: Parsons and Lalli 1988).

3) Genetic control vs. phenotypic plasticity?

Many experimental studies demonstrate phenotypic plasticity in the expression of life history traits, primarily in response to varying environmental conditions. For example, through laboratory experiments, Godo and Moksness (1987) showed that differences in growth and age of reproduction of Atlantic and Norwegian Cod (*Gadus* spp.) can indeed be a function of environmental control rather than genetic variation. Comfort (1963) found differential effect of feeding rate on lifespan, with intermittent feeding extending lifespan in guppies (*Lebistes reticulatus*). In a “natural experiment” involving the long-term warming of an inland lake, Wilhelm and Adrian (2007) documented an increase in length and survival of *Dreissena polymorpha* larvae in response to changes in trophic level. Additionally, studies have demonstrated that reproduction occurring later in life extends life span in species ranging from *Drosophila* (Rose and Charlesworth 1980, Partridge et al. 1999) to a colonial seabird (Pyle et al. 1997).

4) What are the driving forces/mechanisms?

We propose three mechanisms by which environmental conditions shape life history strategies – outlined here and discussed in more detail below.

- i. Food web structure and nutrient sources:* Systems with more complex trophic structure and potentially having large regions of high denitrification tend to promote greater adult survival and lower reproductive investment. For example, the Pacific Ocean is an older system and the oceanic northeast Pacific has evolved a more complex trophic structure than the northeast Atlantic.
- ii. Seasonality of productivity:* In systems favoring greater adult survival and lower reproductive investment, there is less difference between summer and winter productivity and there are greater overwinter resources on average, but during reproductive periods there are greater and more frequent resource limitations.
- iii. Frequency and amplitude of climate fluctuations:* Systems with higher frequency and amplitude shifts in resource availability during the reproductive period tend to favor greater adult survival and lower reproductive investment. For example, the Pacific Ocean has more frequent and greater amplitude climate variation (centennial or penta-decadal [unnamed], Pacific Decadal Oscillation [PDO] and El Niño Southern Oscillation [ENSO]) compared to the Atlantic (Atlantic Multi-decadal Oscillation [AMO] and North Atlantic Oscillation [NAO]).

Hypothetical Mechanisms

i. Food web structure and nutrient sources

Parsons and Lalli (1988) noted alternative pathways in marine food chains, suggesting that the flagellate-microzooplankton path is more common in North Pacific, whereas the diatom-copepod path is favored in the North Atlantic (Fig. 1). Indeed, upper trophic-level organisms in the North Pacific have greater $\delta^{15}\text{N}$ values vs. conspecifics in the Atlantic (Fig. 1), indicating that they occupy a higher trophic position or that baseline $\delta^{15}\text{N}$ values differ. This leaves one to consider whether systems with less complex food webs (e.g., oceanic North Atlantic) allow a more direct (rapid) bottom-up response to sudden increases and declines in food supply or changes in phenology. Furthermore, demographic effects may be realized with an increase in trophic position, as observed by Wilhelm and Adrian (2007), noting an increase in survival when occupying a higher trophic position.

ii. Seasonality of productivity

Large variation exists in the amount and seasonality of primary production within and between ocean basins, and, therefore, much remains to fully evaluate this hypothesis. Recent investigations by Saba et al. (in press), however, do show that greater primary production within the at-sea range of western North Atlantic leatherback turtles is consistent with their greater reproductive effort compared to populations in the eastern Pacific (Fig. 2). Saba et al. (in press) further report that a similar dichotomy appears to exist between western and eastern Pacific populations, in that western Pacific populations migrate to more productive waters and are larger in size with greater reproductive output (i.e., more similar to western Atlantic) than eastern Pacific populations.

iii. Frequency and amplitude of climate fluctuations

The dominant climate indices in the North Atlantic indeed show lower frequency variation (decadal and multi-decadal) in contrast to North Pacific indices (inter-annual and decadal; Fig. 3). Recent analyses by Saba et al. (2007) support the hypothesis that greater

frequency and amplitude of environmental variability in the eastern Pacific (primarily caused by El Niño and La Niña events) is responsible for the episodic and comparatively low reproductive success (including less frequent reproductive attempts) of leatherback turtles compared to western Atlantic populations.

Conclusions

We found concordance across trophic levels in life history variation that appear to indicate system-wide adaptations. We found the low survival/high fecundity vs. high survival/low fecundity dichotomy to occur between and within ocean basins. There is substantial experimental evidence that phenotypic plasticity will permit adaptation, but it is unknown how widespread and to what extent adaptation can occur among species. We found evidence to support all three proposed mechanisms: 1) Food web structure; 2) Seasonality of productivity; and 3) Climate variation. The latter two appear particularly compelling based on recent studies, however, it is likely that some combination of all three may ultimately contribute to a general theory.

Implications

A thorough understanding of mechanisms affecting life history traits, the degree of species-specific plasticity, and potential time-scales of adaptation have broad-reaching implications. For example, can a given food web structure adapt more rapidly to climate change (e.g., Winder and Schindler 2004)? Understanding the cause and extent of plasticity in life history traits is critical to understanding ecosystem response to climate change. Furthermore, recent documentation of “Ecological Evolution” (ecologically significant evolutionary change, occurring over tens of generations or fewer) counters the long-standing assumption that ecological and evolutionary processes occur on different time scales and, therefore, permit integrative studies of their interactions (Carroll et al. 2007).

Future Directions

We propose three steps for continued investigations: 1) a thorough literature review; 2) retrospective analyses (biological and physical); and 3) comparative ecosystem studies: multi-disciplinary investigations of representative systems

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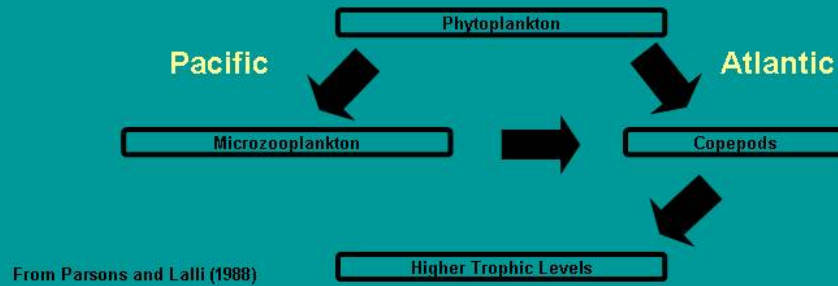
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i. Food web structure



Trophic Position ($\delta^{15}\text{N}$)	
Leatherback turtle	
15.4‰	9.8‰
Sperm whale	
19.6‰	11.1‰

Ostrom et al. (1993), Ruiz-Cooley et al. (2004), Wallace et al. (2006)

Intra-basin differences:

Minami and Ogi (1997) reported differences in $\delta^{15}\text{N}$ signatures of sooty shearwaters (*Puffinus griseus*) from E and W Pacific – due to differences in baseline $\delta^{15}\text{N}$

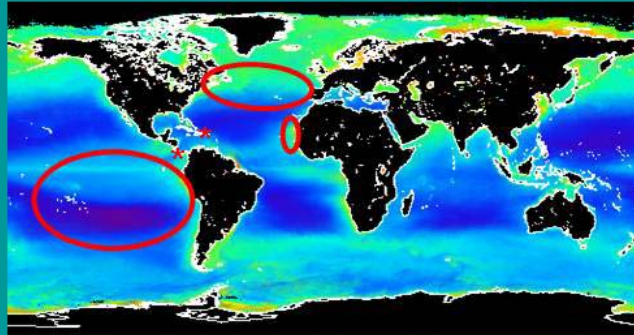
Figure 1. Generalized lower trophic structure of oceanic northeast Pacific vs. North Atlantic and differing nitrogen isotope values from conspecifics in Pacific and Atlantic Oceans.

ii. Seasonality of Productivity

Leatherback Turtles



photo: Canadian Sea Turtle Network



Composite chlorophyll concentrations, 1997-2004

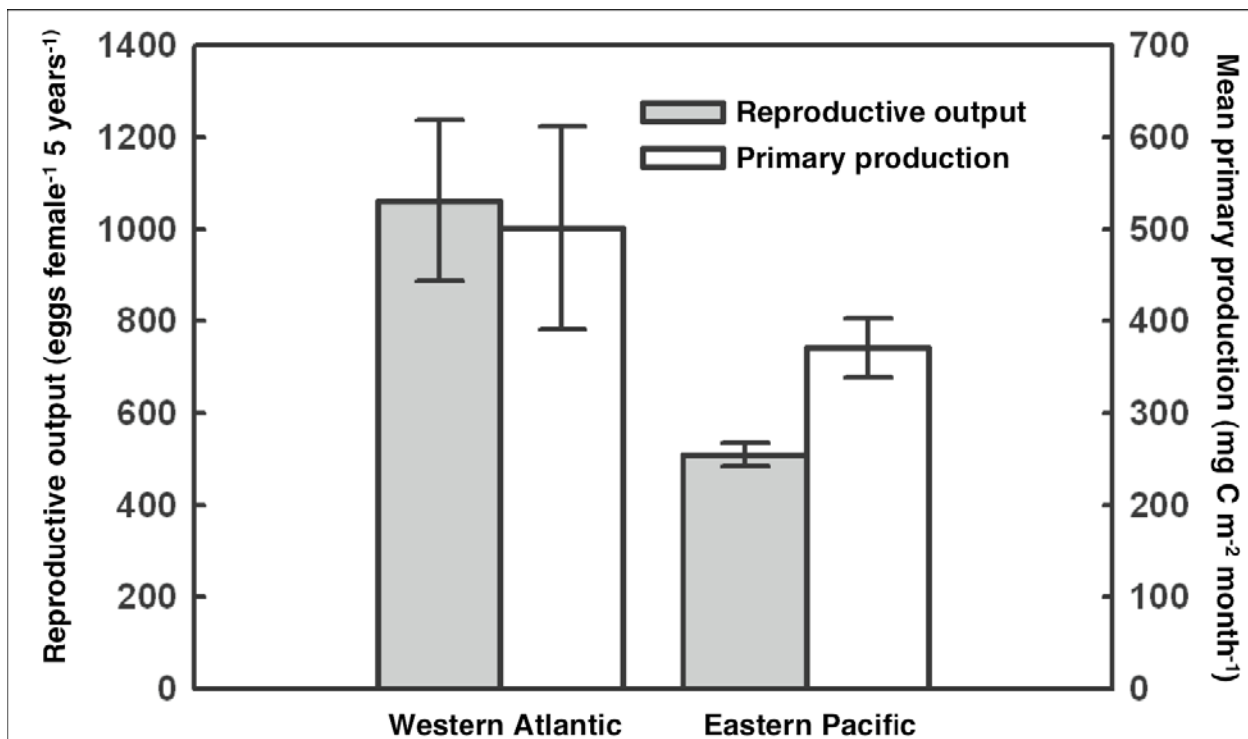


Figure 2. Studies of leatherback turtles show nesting populations (*) in the low latitude eastern Pacific, which have lower reproductive rates, occupy lower productivity waters those in the western North Atlantic (Wallace et al 2006, Saba et al. 2007, *in press*)

iii. Frequency and amplitude of climate fluctuations:

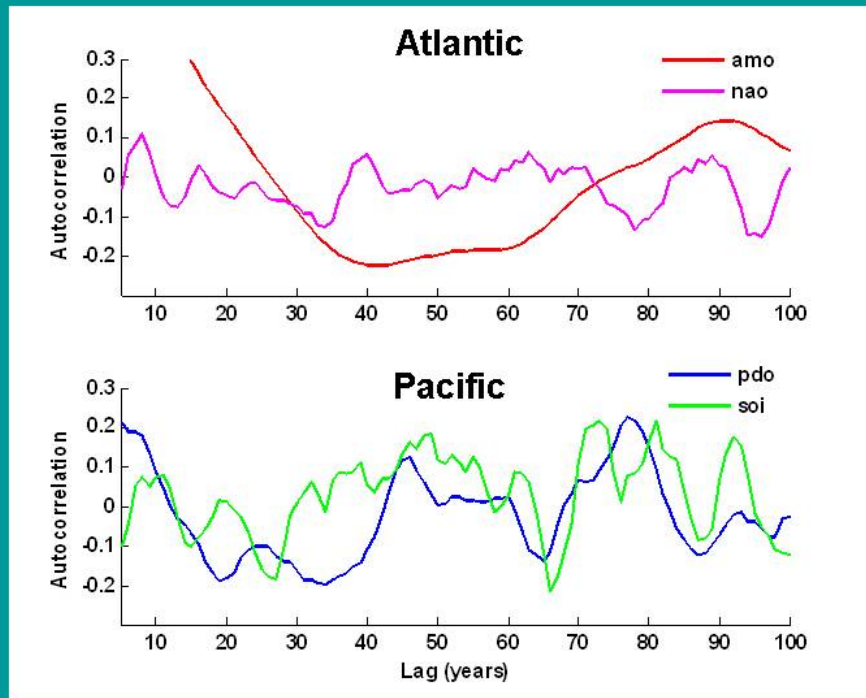


Figure 3. Time-lagged autocorrelation of primary climate indices for the North Atlantic and North Pacific Oceans. Data are annual indices from climate reconstructions based on tree-ring data.