

**LINKING PHYSIOLOGICAL RATES AND COMMUNITY ECOLOGY:
EFFECTS OF OCEAN TEMPERATURE ON DISPERSAL AND SPECIES
INTERACTIONS**

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A dissertation submitted to the faculty of the University of North Carolina at Chapel Hill in
partial fulfillment of the requirements for the degree of Doctor of Philosophy in the
Curriculum in Ecology.

Chapel Hill
2008

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Abstract

MARY ISABEL O’CONNOR: Linking Physiological Rates and Community Ecology: Effects of Ocean Temperature on Dispersal and Species Interactions (Under the direction of John Bruno)

Our ability to predict and manage ecological change in the face of climate warming requires an understanding of the influence of climate on critical demographic and community-level processes. In spite of a rich history of research on ecological processes and the patterns they create, responses to climate change have been interpreted as species-specific, such as shifts in geographic ranges and the timing of seasonal life cycle events. However, recently described general and predictable responses of organisms to non-lethal changes in temperature may provide an important mechanistic link between local climate conditions and ecological processes. I have applied the metabolic theory of ecology to dispersal and food web dynamics to test the effect of temperature on complex, community-structuring processes. I used statistical and theoretical models to determine the generality of the effect of temperature on larval development and dispersal, and to consider consequences for biogeographic patterns, population connectivity and conservation. Using experiments, I tested the effect of temperature on herbivore-plant interaction strength, food web structure and production. Results show that general effects of temperature on fundamental metabolic components are consistent with community level responses to changing temperature, and these effects may provide a mechanistic explanation for broad biogeographic patterns and marine ecosystem response to climate change.

To Will and Caroline,
you deserve my best

Acknowledgements

This work would not have been possible without the support of John Bruno, who provided me with exceptional opportunities to succeed and who taught me to think big. My research and writing skills improved tremendously due to the examples, advice and moral support provided by my labmates Elizabeth Selig and Sarah Lee. My work and life have been enriched by countless creative and stimulating discussions with Drew Steen, Karen Lloyd, Christy Violin, Ken Fortino, Patrick Gibson, Catherine Edwards, and the members of the Bruno Lab and Aquaeco discussion groups.

My research philosophy and my perspective on my career have been heavily influenced by several people. Jack Weiss implanted in my brain a constant reminder to maintain standards of high quality and logic. Mike Piehler showed me that good, basic and applied science can be done together, with good humor and while maintaining a balance of personal and professional life. Steve Gaines has shown me that logic, creativity and a relaxed yet energetic approach to research problems can make for a fun and successful career. And from John Bruno I have learned to push myself one step farther than I think I can go, and that the rewards of tackling big problems are well worth the challenge.

Three of these chapters are or will be published with coauthors, reflecting the contributions of my colleagues Andrea Anton, John Bruno, Steve Gaines, Ben Halpern, Brian Kinlan, Dina Leech, Sarah Lester, Michael O'Donnell, Mike Piehler, and Jack Weiss.

I am grateful for administrative support provided by the Department of Marine Sciences, the Curriculum in Ecology, the Institute of Marine Sciences and the Graduate School. Specifically, Naadii Saalam, Mary Campbell, Laura White and Claude Lewis helped to solve problems and make ambitious research ideas come true.

I was able to devote my full attention to research and professional opportunities thanks to funding generously provided by the Thomas S. and Caroline H. Royster Fellowship, a National Science Foundation Graduate Research Fellowship, a National Fish and Wildlife Federation Budweiser Conservation Scholarship, a UNC Smith Research Grant, a UNC travel grant, the Sigma Xi Scientific Research Society, and National Science Foundation research grants to John Bruno.

I am always grateful for the support of Mark Bertness, Bob Paine, Chris Harley and Marjorie Wonham early on, who showed me that learning about nature first hand could be a career, and who encouraged me to pursue this wonderful and enjoyable path.

And most importantly, I am grateful to my family for their unconditional love and support.

Preface

Hungry herbivores,
It's warm; feel your tummies growl?
Graze down hot seaweed.

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INTRODUCTION

Predicting the ecological responses to global climate change is a critical issue facing ecologists today. Although research interest and resources have been increasingly devoted to this problem, comprehensive answers that could enhance predictions or mitigation efforts are lacking (Richardson and Poloczanska 2008). Accurate prediction of impacts in space and time requires general, mechanistic models of how ecological systems respond to changing climate conditions (Davis et al. 1998b, Helmuth et al. 2006), but such models have so far seemed impossibly complex.

Documented effects of climate change on species' attributes and distribution are numerous, yet a mechanistic, general model for understanding or predicting aggregate ecological changes has not emerged. For nearly two decades, ecologists have accumulated observations of species-specific responses to changing climate conditions, such as geographic range shifts or changes in the seasonal timing (phenology) of life history events such as reproduction or growth (Walther et al. 2002, Parmesan and Yohe 2003, Parmesan 2006). The strategy to identify putative generalities has been to 'scale-up' from these unique species' responses to higher levels of ecological organization, such as communities or ecosystems (Root and Schneider 1995, Beaugrand et al. 2008). This approach has not been successful, and has led to the impression that climate change causes idiosyncratic or species-specific effects (Davis et al. 1998a, Davis et al. 1998b). The 'scale-up' from species responses is unsatisfactory because it requires knowledge of how each species in each local

community is responding to climate change before predictions of change in that community may be made. Such detailed knowledge of local communities is impossible.

The 'scale-up' from species approach is also not consistent with the way community ecologists understand the structure and function of communities to be determined. Decades of experimental and theoretical research have shown that processes, not just species composition, determine community structure in general ways (Paine 1980, Menge and Sutherland 1987, Bruno et al. 2003). For example, Paine's (1966) finding that predation can increase species diversity has been demonstrated repeatedly in many ecosystems with many different kinds of species (Paine 1969, Navarrete and Menge 1996, Zacharias and Roff 2001). Similarly, studies in terrestrial and aquatic communities have shown that movement of individuals among spatially discrete populations (dispersal and recruitment) influences the genetic and demographic population structure, as well as species composition and ecosystem function (Gaines and Bertness 1992, Cadotte et al. 2006, France and Duffy 2006). Processes such as predation and dispersal, together with species composition, determine the structure and function of local communities and in turn influence broader scale evolutionary and ecosystem-level processes. By applying this process-based view of ecological systems to the problem of climate change, a more general understanding of impacts of change might be achieved.

Recent advances in basic ecological theory make possible the application of process-based community ecology to climate change impacts. The Metabolic Theory of Ecology (MTE) describes how general effects of temperature on fundamental metabolic processes generate universal constraints on individual metabolism (Brown et al. 2004). This universal temperature dependence of metabolism suggests a potentially general link between

environmental temperature and ecological processes (Gillooly et al. 2001). Rates of many ecological processes are indirectly related to individual metabolic rate, such as rates of population growth and resource use. A general effect of temperature on metabolism therefore could explain variation in population- and community-level processes known to determine community structure and function.

For my dissertation, I tested the effects of temperature on two critical ecological processes, dispersal and food web interactions, based on the universal temperature dependence of MTE. This research simultaneously advances our understanding of metabolic theory and effects of climate change (Duarte 2007). MTE has been developed and validated using macroecological methods, typically through comparisons of the effect of temperature across broad groups of species from different thermal environments (Gillooly et al. 2002, Kerkhoff et al. 2005). However, to improve our understanding of community change with climate conditions, MTE needs to be applied to how individuals of a single species at one location change with temperature change. That is, models need to address how small, non-lethal changes in environmental temperature as predicted with climate change (IPCC 2007) affect rates of critical ecological processes operating at the individual or population level. By determining how rates of processes change with small changes in temperature, we may understand how community structure and function respond to temperature regardless of species composition, and therefore improve our ability to understand existing and future ecological change.

Chapter 1: Temperature control of larval dispersal and implications for marine ecology, evolution and conservation.

Many marine animals have a life cycle in which offspring are released from their parents and disperse passively with currents away from parental populations while they develop to a juvenile stage that can settle and maintain a more sedentary existence (Levin and Bridges 1995). This period of planktonic development is a time when offspring, or larvae, are subject to a high risk of mortality and consequently very low survival rates (Morgan 1995). Therefore, the duration of the planktonic larval period determines the potential distance larvae may travel (Shanks et al. 2003, Siegel et al. 2003), and is critical to demographic processes such as survival and population connectivity. According to tests of MTE, development rates of nearly all organisms are constrained by temperature in almost exactly the same way (Gillooly et al. 2002). I applied the universal temperature dependence of metabolism model to the effect of temperature on larval development, and explored the consequences of this constraint for dispersal related processes (O'Connor et al. 2007).

I assembled a database of laboratory studies testing the effect of different temperatures on larval development duration. Together with my colleagues, I identified a single quantitative model that described the temperature dependence of larval duration for 69 of the 72 species in my database. Although the effects of temperature on larval development have been known for a century (Hjort 1914), the recognition that this effect is highly conserved across very broad taxonomic divisions is entirely new.

I applied this temperature-dependent larval duration model to other models to explore the potential effects for demographic processes. The model suggests that at colder temperatures dispersal distances may be much longer for individuals compared to their relatives in warmer water. I also found that survival may be dramatically decreased in colder water, simply due to the extended duration of exposure to environmental sources of

mortality. General links between environmental temperature and larval dispersal and survival allowed my colleagues and I to consider how population connectivity, evolution and conservation may be influenced by climate change. At colder temperatures, populations may be more connected due to greater dispersal distances, species may experience natural selection for traits related to their larval development period, and conservation methods need to consider these responses in order to be effective in the future.

Chapter 2: Universal temperature constraints on the biogeography of marine life histories.

The universal temperature dependence of marine larval duration implies extremely low survival rates at very low temperatures. These survival rates are projected to be unsustainable, even if extremely large numbers of offspring were released from parents to compensate for high juvenile mortality. However, the existence of species with a planktonic larval duration in very cold environments implies compensation is possible for this temperature constraint on survival. Because it has been shown that metabolic rate is not able to compensate for temperature effects (Gillooly et al. 2002), such compensation must be the indirect effect of variation in life history traits related to the planktonic larval duration. If true, selection on these traits should manifest in temperature-driven biogeographic patterns.

In fact, biogeographic trends in offspring life history traits have been observed in marine systems for nearly a century (Orton 1920, Thorson 1950). These patterns have defied a single mechanistic explanation, largely due to the many exceptions to each proposed rule. Together with several colleagues, I explored the possibility that water temperature indirectly influences parental investment in individual offspring by altering larval development times, with large impacts on cumulative larval mortality. I drew upon MTE to modify a traditional

life history model of offspring size-dependent fitness. The modified model illustrates how the trade-off between offspring size and number could drive a shift to fewer, larger offspring at very low temperatures given a constant daily mortality rate. In contrast, at warmer temperatures, releasing more numerous and smaller offspring as optimal.

Environmental temperature may therefore provide a single explanation for long-observed geographic gradients in parental investment in life history traits. This temperature-based optimality model supports a framework for understanding latitudinal trends in egg size, and related traits of larval feeding and the proportion of species with no planktonic larval stage. A systematic effect of temperature on larval traits suggests that larval dispersal and related ecological and evolutionary processes likely change predictably with latitude, which has important implications for forecasting the ecological effects of climate change.

Chapter 3: Warming strengthens an herbivore-plant interaction.

General effects of temperature on individual metabolism influence rates of resource use or food consumption, as well as individual and population growth rates. Growth and resource use rates are key processes governing food web dynamics, and their vulnerability to environmental variation has been perceived as highly species-specific. However, metabolic theory suggests that consumers and primary producers may systematically differ in their response to temperature (Allen et al. 2005, Lopez-Urrutia et al. 2006). Consumer metabolic rates are driven by cellular respiration, while metabolic rates of primary producers are limited by photosynthesis (Farquhar et al. 1980, Taylor et al. 1982, Dewar et al. 1999). Respiration is approximately twice as sensitive to temperature changes as photosynthesis (Lopez-Urrutia et al. 2006, Padilla-Gamino and Carpenter 2007). Therefore, I predicted that small amounts

of warming should increase herbivore consumption relative to algal production, and thus herbivore effects should strengthen with warming. This prediction is consistent with observed effects of warming in prairie, forest and rocky intertidal communities (Ritchie 2000, Logan et al. 2003, Thompson et al. 2004), and biogeographical and temporal patterns of ocean plankton food web structure (Behrenfeld et al. 2006, Lopez-Urrutia et al. 2006), though the mechanism outlined here has not been widely invoked.

Nearly all food webs include herbivore-plant interactions, and the strength of these interactions determines the abundance of primary producers in a community (Lubchenco and Gaines 1981, Hawkins and Hartnoll 1983, Paine 1992, Duffy and Hay 2000). To test the effect of temperature on an herbivore-plant interaction, I experimentally investigated the effects of temperature on plant and animal growth rates and whether these effects translate to a temperature dependence of interaction strength at a local scale. At UNC's Institute of Marine Sciences, I manipulated temperature and measured the effects of amphipod herbivores on seaweed growth, and found that at higher temperatures herbivores had a stronger effect on seaweed, reducing seaweed stocks below levels observed at lower temperatures.

Chapter 4: Effects of metabolic temperature scaling and nutrients on marine food webs.

Physical and biological causes of variation in marine food web productivity have long been a focus of scientific research (Harvey et al. 1935, Schaefer 1965, Ryther 1969). Factors such as nutrient availability, light and temperature drive variation in primary productivity (Platt and Jassby 1976, Keller 1989, Behrenfeld et al. 2006), yet direct causes of variation in secondary productivity at higher trophic levels are less clear (Iverson 1990, Finney et al.

2002). The problem of understanding how food web structure and production responds to environmental change has seemed overwhelmingly complex due to the lack of a general, quantitative and testable mechanism that links food web processes to environmental conditions such as temperature or nutrient availability (McGowan et al. 1998, Brander 2007). This gap hinders a predictive understanding of ecological effects of variation in ocean conditions associated with geography and climate change.

Together with several colleagues, I tested the hypothesis that differential temperature scaling of consumer and primary producer metabolism can explain variation in food web structure and production with climate change. Mesocosm experiments using a pelagic marine food web demonstrated that temperature alone can shift food web structure towards greater consumer biomass relative to producer biomass. Temperature increased food web biomass production only when nutrients were abundant. These results support a general model of temperature scaling of food web structure and production based on metabolic theory, and inform our understanding of how major pelagic ecosystems vary with geographic change as well as climate change.

References

- Allen, A. P., J. F. Gillooly, and J. H. Brown. 2005. Linking the global carbon cycle to individual metabolism. *Functional Ecology* **19**:202-213.
- Beaugrand, G., M. Edwards, K. M. Brander, C. Luczak, and F. Ibanez. 2008. Causes and projections of abrupt climate-driven ecosystem shifts in the North Atlantic. *Ecology Letters* **11**:1157-1168.
- Behrenfeld, M. J., R. T. O'Malley, D. A. Siegel, C. R. McClain, J. L. Sarmiento, G. C. Feldman, A. J. Milligan, P. G. Falkowski, R. M. Letelier, and E. S. Boss. 2006. Climate-driven trends in contemporary ocean productivity. *Nature* **444**:752-755.
- Brander, K. M. 2007. Global fish production and climate change. *Proceedings of the National Academy of Sciences of the United States of America* **104**:19709-19714.
- Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage, and G. B. West. 2004. Toward a metabolic theory of ecology. *Ecology* **85**:1771-1789.
- Bruno, J. F., J. J. Stachowicz, and D. Bertness Mark. 2003. Inclusion of facilitation into ecological theory. *Trends in Ecology and Evolution* **18**:119-125.
- Cadotte, M. W., A. M. Fortner, and T. Fukami. 2006. The effects of resource enrichment, dispersal, and predation on local and metacommunity structure. *Oecologia* **149**:150-157.
- Davis, A. J., L. S. Jenkinson, J. H. Lawton, B. Shorrocks, and S. Wood. 1998a. Making mistakes when predicting species range shifts in response to global warming. *Nature* **391**:783-786.
- Davis, A. J., J. H. Lawton, B. Shorrocks, and L. S. Jenkinson. 1998b. Individualistic species responses invalidate simple models of community dynamics under global environmental change. *Journal of Animal Ecology* **67**:600-612.
- Dewar, R. C., B. E. Bedlyn, and R. E. McMurtrie. 1999. Acclimation of the respiration / photosynthesis ratio to temperature: insights from a model. *Global Change Biology* **5**:615-622.
- Duarte, C. M. 2007. Marine ecology warms up to theory. *Trends in Ecology and Evolution* **22**:331-333.
- Duffy, J. E., and M. E. Hay. 2000. Strong impacts of grazing amphipods on the organization of a benthic community. *Ecological Monographs* **70**:237-263.
- Farquhar, G. D., S. von Caemerrer, and J. A. Berry. 1980. A biochemical model of photosynthetic CO₂ assimilation in leaves of C₃ plants. *Planta* **149**:78-90.

- Finney, B. P., I. Gregory-Eaves, M. S. V. Douglas, and J. P. Smol. 2002. Fisheries productivity in the northeastern Pacific Ocean over the past 2,200 years. *Nature* **416**:729-733.
- France, K. E., and J. E. Duffy. 2006. Diversity and dispersal interactively affect predictability of ecosystem function. *Nature* **441**:1139-1143.
- Gaines, S. D., and M. D. Bertness. 1992. Dispersal of juveniles and variable recruitment in sessile marine species. *Nature* **360**:579-580.
- Gillooly, J. F., J. H. Brown, G. B. West, V. M. Savage, and E. L. Charnov. 2001. Effects of size and temperature on metabolic rate. *Science* **293**:2248-2251.
- Gillooly, J. F., E. L. Charnov, G. B. West, V. M. Savage, and J. H. Brown. 2002. Effects of size and temperature on developmental time. *Nature* **417**:70-73.
- Harvey, H. W., H. N. Cooper, M. V. Lebour, and F. S. Russell. 1935. Plankton production and its control. *Journal of the Marine Biological Association of the U.K.* **20**:407-440.
- Hawkins, S. J., and R. G. Hartnoll. 1983. Grazing of intertidal algae by marine-invertebrates. *Oceanography and Marine Biology* **21**:195-282.
- Helmuth, B., N. Mieszkowska, P. Moore, and S. J. Hawkins. 2006. Living on the edge of two changing worlds: Forecasting the responses of rocky intertidal ecosystems to climate change. *Annual Review of Ecology, Evolution and Systematics* **37**:373-404.
- Hjort, J. 1914. Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. . *Rapports et Proces-Verbaux des Reunions du conseil International pour l'Exploration de la Mer* **20**:1-228.
- IPCC. 2007. *Climate Change 2007: The Physical Science Basis*. Intergovernmental Panel on Climate Change.
- Iverson, R. L. 1990. Control of marine fish production. *Limnology and Oceanography* **35**:1593-1604.
- Keller, A. A. 1989. Modeling the effects of temperature, light and nutrients on primary productivity: An empirical and a mechanistic approach compared. *Limnology and Oceanography* **34**:82-95.
- Kerckhoff, A. J., B. J. Enquist, J. J. Elser, and W. F. Fagan. 2005. Plant allometry, stoichiometry and the temperature-dependence of primary productivity. *Global Ecology And Biogeography* **14**:585-598.
- Levin, L. A., and T. S. Bridges. 1995. Pattern and diversity in reproduction and development. Pages 1-48 *in* L. R. McEdward, editor. *Ecology of marine invertebrate larvae*. CRC Press, Inc, Boca Raton, Fl.

- Lopez-Urrutia, A., E. San Martin, R. P. Harris, and X. Irigoien. 2006. Scaling the metabolic balance of the oceans. *Proceedings of the National Academy of Sciences USA* **103**:8739-8744.
- Lubchenco, J., and S. D. Gaines. 1981. A Unified Approach to Marine Plant-Herbivore Interactions. I. Populations and Communities. *Annual Review of Ecology and Systematics* **12**:405-437.
- McGowan, J. A., D. R. Cayan, and L. M. Dorman. 1998. Climate-ocean variability and ecosystem response in the Northeast Pacific. *Science* **281**:210-216.
- Menge, B. A., and J. P. Sutherland. 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *The American Naturalist* **130**:730-757.
- Morgan, S. G. 1995. Life and Death in the Plankton: Larval mortality and adaptation. Pages 279-322 *in* L. R. McEdward, editor. *Ecology of Marine Invertebrate Larvae*. CRC Press, Inc., Boca Raton, FL.
- Navarrete, S. A., and B. A. Menge. 1996. Keystone predation and interaction strength: Interactive effects of predators on their main prey. *Ecological Monographs* **66**:409-429.
- O'Connor, M. I., J. F. Bruno, S. D. Gaines, S. E. Lester, B. S. Halpern, B. P. Kinlan, and J. M. Weiss. 2007. Temperature control of larval dispersal and implications for marine ecology, evolution, and conservation. *Proceedings of the National Academy of Sciences* **104**:1266-1271.
- Orton, J. H. 1920. Sea temperatures, breeding and the distribution of marine animals. *Journal of the Marine Biological Association of the U.K.* **12**:339-366.
- Padilla-Gamino, J. L., and R. C. Carpenter. 2007. Seasonal acclimatization of *Asparagopsis taxiformis* (Rhodophyta) from different biogeographic regions. *Limnology and Oceanography* **52**:833-842.
- Paine, R. T. 1966. Food web complexity and species diversity. *The American Naturalist* **100**:65-75.
- Paine, R. T. 1969. A note on trophic complexity and community stability. *The American Naturalist* **103**:91-93.
- Paine, R. T. 1980. Food webs: Linkage, interaction strength and community infrastructure. *Journal of Animal Ecology* **49**:667-685.
- Paine, R. T. 1992. Food-web analysis through field measurement of per capita interaction strength. *Nature* **355**:73-75.

- Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution and Systematics* **37**:637-639.
- Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**:37-42.
- Platt, T., and A. D. Jassby. 1976. Relationship between Photosynthesis and Light for Natural Assemblages of Coastal Marine-Phytoplankton. *Journal Of Phycology* **12**:421-430.
- Richardson, A. J., and E. S. Poloczanska. 2008. Under-resourced, under threat. *Science* **320**:1294-1295.
- Root, T. L., and S. H. Schneider. 1995. Ecology and Climate: Research Strategies and Implications. *Science* **269**:334-341.
- Ryther, J. H. 1969. Photosynthesis and fish production in the sea. *Science* **166**:72-76.
- Schaefer, M. B. 1965. The potential harvest of the sea. *Transactions of the American Fisheries Society* **94**:123-128.
- Shanks, A. L., B. A. Grantham, and M. H. Carr. 2003. Propagule dispersal distance and the size and spacing of marine reserves. *Ecological Applications* **13**:S159-S169.
- Siegel, D. A., B. P. Kinlan, B. Gaylord, and S. D. Gaines. 2003. Lagrangian descriptions of marine larval dispersal. *Marine Ecology-Progress Series* **260**:83-96.
- Taylor, C. R., N. C. Heglund, and G. M. O. Maloiy. 1982. Energetics and mechanics of terrestrial locomotion. I. Metabolic energy consumption as a function of speed and body size in birds and mammals. *Journal of Experimental Biology* **97**:1-27.
- Thorson, G. 1950. Reproductive and larval ecology of marine bottom invertebrates. *Biological Review* **25**:1-45.
- Walther, G. R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J. M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. *Nature* **416**:389-395.
- Zacharias, M. A., and J. C. Roff. 2001. Use of focal species in marine conservation and management: a review and critique. *Aquatic Conservation-Marine and Freshwater Ecosystems* **11**:59-76.

CHAPTER 1: TEMPERATURE CONTROL OF LARVAL DISPERSAL AND IMPLICATIONS FOR MARINE ECOLOGY, EVOLUTION, AND CONSERVATION

Abstract

Temperature controls the rate of fundamental biochemical processes and thereby regulates organismal attributes including development and mortality rates. The increase in metabolic rate with temperature explains substantial among-species variation in life-history traits, population dynamics, and ecosystem processes. Temperature can also cause variability in metabolic rate within species. Here we compare the effect of temperature on a key component of marine life cycles – the development of larvae – among a geographically and taxonomically diverse group of marine fish and invertebrates. Although innumerable lab studies document the positive effect of temperature on larval development time, little is known about the generality versus taxon-dependence of this relationship. We present a unified, parameterized model for the temperature dependence of larval development in marine species. Because the duration of the larval period is known to influence larval dispersal distance and survival, changes in ocean temperature could have a direct and predictable influence on population connectivity, community structure, and regional to global scale patterns of biodiversity.

Introduction

Through a general effect on metabolic rate, variation in environmental temperature can influence population, species, and community level processes (Enquist et al. 2003, Brown et al. 2004, Allen et al. 2006). Recently, evidence for a universal temperature dependence has linked individual metabolism to community-wide productivity, which in turn leads to predictable rates of population growth, carbon flux and patterns of regional diversity (Gillooly et al. 2001, Allen et al. 2002, Savage et al. 2004, Allen et al. 2005). Though less appreciated in this context, the universal temperature dependence of metabolism implies an inverse relationship between temperature and life stage duration (Gillooly et al. 2002). For marine animals whose offspring develop in the water column, the duration of the larval life stage determines the length of time that larvae are subject to movement by currents and exposed to sources of mortality. Therefore, a general and quantitative influence of temperature on larval duration potentially implies a mechanistic link between ocean temperature and the biogeographic patterns mediated by the ecological processes of larval dispersal and survival.

Two aspects of the influence of temperature on larval duration are well documented. First, Thorson's rule describes the latitudinal gradient of a decreasing proportion of marine species with planktonic larval development toward the poles (Pechenik 1987, Houde 1989). Second, temperature is known to cause among-species variation in larval development and duration (Houde 1989, Houde and Zastrow 1993). Previous studies in this vein have emphasized between-species comparisons without accounting for within-species relationships between temperature and PLD; therefore these studies report strong relationships only within narrower taxonomic groupings. Numerous other studies have

documented the temperature dependence of the larval development period *within* species. Typically this relationship is described as exponential (e.g., de Severeyn et al. 2000) with species-specific parameter values. Therefore, the generality of the temperature dependence of larval duration remains untested. If general for a wide variety of animals, a quantitative model of the effect of temperature on planktonic larval duration (PLD) could enhance hypotheses and existing models to evaluate the ecological and evolutionary consequences of temperature change in the ocean.

Here we test the generality of the temperature dependence of planktonic larval duration for 72 species of marine animals (Tables A1.3, A1.4). We synthesize the effect of temperature on planktonic larval duration by comparing results from 62 laboratory experiments in which vertebrate and invertebrate larvae were reared at multiple, non-lethal temperatures (Appendix A, Table A1.4). We then use a multilevel model to estimate parameter values that describe the influence of temperature on development of marine larvae (Supplementary Information 2 of O'Connor et al. 2007, Singer and Willett 2003). We use our results to formulate models of the effect of temperature on dispersal and survival and we discuss the implications of these findings.

Methods

Data transformation

The temperature dependence of larval development time typically follows a power law (Pechenik 1987, Pepin 1991). To linearize this relationship and satisfy statistical assumptions, both *PLD* and temperature were ln-transformed (Supplementary Information 2 of O'Connor et al. 2007, Section II). To aid interpretation and improve numerical stability of

the model, we express temperature as $\ln(T/T_c)$, where T is temperature ($^{\circ}\text{C}$) and $T_c = 15^{\circ}\text{C}$.

This is equivalent to subtracting $\ln(T_c)$ from each temperature observation on a log scale and thus is a form of centering (Supplementary Information 2 of O'Connor et al. 2007).

Statistical results from centered and uncentered models are identical (Supplementary Information 2 of O'Connor et al. 2007). All statistical analyses were performed in R 2.4.0 (R Development Core Team (2006). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org>).

Statistical analyses

To estimate the relationship between planktonic larval duration and temperature and to compare that effect among species we used a random effects (multilevel) model (also called a hierarchical model (Singer and Willett 2003)). Because observations are nested within species we treat this as a two-stage sample and fit a random effects model in which parameters are allowed to vary across species. A multilevel model allowed us to explore intra- and inter-specific patterns while respecting the inherent structure of the data. Different models were possible depending on which parameters were allowed to vary across species. We treated model parameters for each species as random effects at the species level, treating these species as random representatives of all species. Because the analysis fits the model to all species at once, we were able to include in the analysis even those species that provided only two datapoints. See Supplementary Information 2 of O'Connor et al. 2007 for a more detailed description of statistical methods.

Model selection

We compared ln-transformed versions of three theoretical models of temperature effects on *PLD*. In each model, β_0 is the intercept and β_1 and β_2 are linear and quadratic scaling parameters, respectively. T = temperature ($^{\circ}\text{C}$) and $T_c = 15$ $^{\circ}\text{C}$.

1) A linearized power law model that has traditionally been used to approximate the effect of temperature on *PLD* (Belehradek 1930):

$$\ln(PLD) = \beta_0 + \beta_1 * \ln(T/T_c) \quad \text{Eqn 1.1}$$

2) A linearized power law model that is quadratic in temperature (McKinney 1984). We are calling this the exponential-quadratic model:

$$\ln(PLD) = \beta_0 + \beta_1 * \ln(T/T_c) + \beta_2 * (\ln(T/T_c))^2 \quad \text{Eqn 1.2}$$

3) The universal temperature dependence (UTD) equation (Gillooly et al. 2001), where k is the Boltzmann constant (8.62×10^{-5} eV K^{-1}) and $(T$ ($^{\circ}\text{C}$) + 273) is absolute temperature (K):

$$\ln(PLD) = \beta_0 + \beta_1 / (k*(T+273)) \quad \text{Eqn 1.3}$$

We assumed individual observations were realizations from a normal distribution with constant variance σ^2 and conditional mean given by the respective theoretical models.

Within each model type (Eqns 1.1–1.3), we first investigated the need for including random effects that allow the intercepts, slopes, and/or quadratic coefficients to vary among species. We used modified likelihood ratio tests, adjusted for boundary conditions, to compare nested models that differed in the number of random effects they contained (Table A1.8; Supplementary Information 2 of O’Connor et al. 2007). Having chosen the best random effects model of each type (e.g., Eqn 1.1, 1.2 or 1.3), the winners were then compared using Akaike’s Information Criterion (AIC, Burnham and Anderson 2002, Table A1.5). We conclude that a multilevel linearized power law model with a quadratic temperature term (Eqn 1.2) best approximates the relationship between temperature and PLD. Based on model diagnostics (Supplementary Information 2 of O’Connor et al. 2007) we identified those species not well described by our chosen model (Figures 1.1A, 1.2A). With these outliers removed, the model requires random effects only for the intercept (β_{0i}) (Eqn 1.4). Our final model written in statistical form, where i indexes species and j indexes observations, is the following:

$$\begin{aligned} \text{Level 1: } \ln(PLD_{ij}) &= \beta_{0i} + \beta_1 * (\ln(T_{ij} / T_c)) + \beta_2 * (\ln(T_{ij} / T_c))^2 + \varepsilon_{ij} \\ \text{Level 2: } \beta_{0i} &= \beta_0 + u_{0i} ; \quad u_{0i} \sim N(0, \tau^2), \quad \varepsilon_{ij} \sim N(0, \sigma^2) \end{aligned} \quad \text{Eqn 1.4}$$

β_1 and β_2 are fixed for all species (Figure 1.2B). u_{0i} is a random effect that allows β_{0i} to vary across species.

Variation in PLD with climate

We estimated species' normal temperature range by calculating the mean of the $\ln(\text{temperatures})$ tested for each species, and considered this value to be a proxy for the average temperature in the species' normal geographic range. In the majority of studies, test temperatures spanned the range of temperatures experienced by the organism during most of the year.

Projection of temperature scaling of dispersal distance and survival

We used a model linking nearshore current velocity and flow patterns to average passive larval dispersal distance. The model projects larval movement in coastal surface currents and accounts for serial correlation in larval trajectories introduced by large turbulent eddies. See Kinlan et al. 2005 for further discussion of this use of the Siegel et al. 2003 model. The model presented in Figure 1.5A is:

$$DD = 0.695 (PLD) * U + 0.234 * (PLD) * s \quad \text{Eqn 1.5}$$

Terms are the current velocity (U in km/d), its standard deviation (s in km/day), and the temperature dependent larval duration model presented in Figure 1.1B (PLD in days).

Numeric constants in Eqn 1.5 are fit parameters for dispersal kernels as functions of the flow parameters for nearshore coastal environments (Siegel et al. 2003).

To calculate the survival of a cohort based on temperature effects on PLD , we used the exponential decay model:

$$S_c = S_d^{PLD} \quad \text{Eqn 1.6}$$

Terms are the percent of a cohort surviving through metamorphosis (S_c), daily survival rate ($S_d = 1 - M_d$, where M_d is the daily mortality rate), and the temperature dependent larval duration model presented in Figure 1.2B (PLD in days).

Results

The quantitative relationship between PLD and temperature is highly predictable across taxa, latitudes and oceans (Figures 1.1, 1.2). Using Akaike Information Criteria (AIC) for model selection, we determined that an exponential model quadratic in temperature on a log-log scale, hereafter called the exponential-quadratic model (methods: Eqn 1.2), best describes the general temperature dependence of planktonic larval duration within species (Table A1.5; Supplementary Information 2 of O'Connor et al. 2007).

An analysis of species-level (level-2) residuals using caterpillar plots (Rasbash et al. 2004) suggests that a species-specific model with random intercepts but constant linear and quadratic coefficients fits nearly all species under consideration (Figure 1.1, Supplementary Information 2 of O'Connor et al. 2007). However, a few species deviate significantly from this overall pattern (Figure 1.1A, Supplementary Information 2 of O'Connor et al. 2007). We identified these species by constructing 95% confidence intervals for species-level residuals of the model parameters (Figure 1.1). Sequential removal of the most deviant species reveals that only three species (*Limulus polyphemus*, *Laqueus californianus*, and *Callinassa tyrrhena*, Figure 1.2A) are driving the need for random linear and quadratic terms in the log-linear formulation of the model. When these three species are removed from

the analysis, a multilevel model with only random intercepts fits the remaining 69 species. Therefore, we present a population-averaged model for a dataset that excludes the three outliers (Figure 1.2B).

We find that PLD shows essentially the same relationship with temperature across species (Figure 1.1A) and differs only in how the curve is scaled (as determined by the factor β_0 in Eqn 1.2, Figure 1.1B). Individual intercept values (β_{0i}) are highly species specific and most are not well represented by the population-averaged estimate (Figures 1.1B, 1.2B). Thus, most of the variation among species is with respect to the magnitude of the larval duration at a given temperature, but not its relationship to changing temperature.

The nearly uniform temperature sensitivity of larval development rate is consistent with a model derived from first principles of physics and biology (Gillooly et al. 2001, Brown et al. 2004) (Figures 1.3, A1.2). Gillooly et al. (2001) described the universal temperature dependence of biological processes (UTD), a mechanistic theory that links whole-organism metabolic rates to the effects of temperature on biochemical processes. Although the UTD model was not the best fit of the models we tested (Table A1.5), the functional forms of the mechanistic UTD model (Eqn 1.3) and the purely descriptive exponential-quadratic model (Eqn 1.2) are similar over most of the temperature range (Figure A1.3). The primary difference is that the exponential model predicts a steeper slope to the temperature dependence below approximately 7 °C. This similarity suggests that the mechanistic basis of the UTD model may be relevant to the temperature dependence of PLD. Another important difference between the two models is their treatment of larval mass: the UTD model assumes mass-normalized development durations (Gillooly et al. 2002), while the exponential-quadratic model (Eqn 1.2) does not. Although sufficient larval mass data

were not available for this analysis, the omission of mass could explain why Eqn 1.2 is a better fit for these data.

The within-species temperature dependence of PLD matches the predicted effect of temperature based on among-species analyses (Gillooly et al. 2001, Gillooly et al. 2002). Gillooly *et al.* (2001) predicted that the average activation energy (i.e., temperature scaling) for metabolic processes in ectotherms is approximately 0.62 eV, which matches our estimate for developing larvae using the UTD model (95% CI: 0.59-0.69, Figures 1.3, A1.2). To date, the UTD hypothesis has generally been tested by making among-species comparisons of mass-normalized resting metabolic rates (Gillooly et al. 2001, Clarke 2004). In contrast, our estimate of the temperature sensitivity of planktonic larval duration focuses on within-species temperature dependence. This similarity between the within- and among- species patterns (Figures 1.3, A1.2) suggests that the effect of temperature on larval development is universal and not species-specific. Our result is consistent with the only other test of this question (Gillooly et al. 2006).

In colder water, increased temperature dependence and generally longer development times (Figure 1.2) may affect the evolution of molecular processes and life history traits. Because high cumulative mortality rates are associated with very long larval duration, there may be selection to reduce PLD in animals that evolve in cold climates (Pearse et al. 1991). We tested whether home range temperature could explain variation in PLD among species by adding a species-level regional temperature variable to the multilevel model (Figure 1.4, Eqn A1.1). The addition of this variable significantly improved the ability of the model to predict species-specific PLDs (Table A1.6), and explains 17% of the variation in intercepts among species (Appendix A). Species from colder climates tend to have shorter PLDs (lower values

of β_{0i}) compared to species from warmer regions (Figure 1.4). Adding a variable for developmental mode (lecithotrophic vs planktotrophic) to the model increases the explained variance in intercepts to 27%; planktotrophs tend to have longer PLDs than lecithotrophs (Figure 1.4).

Discussion

Our results demonstrate a strong effect of temperature on planktonic larval duration that is quantitatively constant across nearly all species tested. A single, parameterized model describes the temperature dependence of the planktonic larval period for a diverse group of species from six phyla over a range of body sizes and habitats. A general temperature dependence of larval duration implies common and predictable effects of ocean temperature on larval dispersal distance and survival.

The universal form of the temperature dependence emerges in spite of enormous differences in larval size and other life history traits among species. Conceptually, the remaining variation in planktonic larval duration among species can be thought of as partitioning into three categories: 1) variation in PLD among species at any particular temperature (the intercept parameter β_{0i} in Eqn 1.4, Figures 1.1B, 1.4), 2) variation among species in the scaling effect of temperature (parameters β_{1i} and β_{2i} in Eqn 1.4, Supplementary Information 2 of O'Connor et al. 2007), and 3) scatter of measured PLDs around the individual regression lines due to measurement error or other unmeasured variation (Appendix A). Variation among species in PLD at any given temperature (variation type 1), as observed in Figures 1.1 and 1.2, could be due to life history traits such as development

mode, larval size at hatching or competency, or assimilation efficiency. For example, lecithotrophic (nonfeeding) larvae tend to be larger and generally have shorter planktonic larval durations than planktotrophic (feeding) larvae (Strathmann 1985, Figure 1.4). There are contrasting predictions for how larval size affects planktonic duration. Large eggs and larvae can result from increased parental investment before release, allowing for shorter planktonic periods (Strathmann 1977, Emlet 1995, Levitan 2000). Alternatively, metabolic ecological theory predicts that development time and body size should be positively correlated such that species with larger larvae require longer larval durations (Gillooly et al. 2002, Brown et al. 2004). Metabolic theory might accommodate this apparent contradiction. Part of the solution may lie in appropriately separating the disparate effects of variation in larval size at hatching from larval size at competency. In addition, lecithotrophs may have higher food quality than planktotrophs, or may be more efficient at assimilating energy. Food quality and assimilation efficiency are held constant in the general metabolic scaling model (Gillooly et al. 2002) but may in fact vary systematically among lecithotrophs and planktotrophs.

We observed very little variation among species in the scaling effect of temperature (type 2 variance above). Residual analysis suggests that a single model fits 69 of 72 species (Figure 1.2A, Supplementary Information 2 of O'Connor et al. 2007). We suggest three hypotheses for the species with unique temperature dependence: a) unique evolutionary history, b) unique selective environments, or c) metabolic cold adaptation. Regarding hypothesis (a), two of the species are the sole representatives of their taxonomic order in this dataset (the brachiopod *L. californianus* and the horseshoe crab *L. polyphemus*). Because the deviations in temperature dependence of these species are outliers in different directions,

their selective environment may have driven their unique temperature dependence (hypothesis b). These hypotheses do not appear to explain the third outlier, the ghost shrimp *C. tyrrhena*. A common species in the warm temperate eastern Atlantic, adult *C. tyrrhena* are widely distributed among shallow sand flat environments and larvae are commonly found in the plankton (Thessalou-Legaki 1990).

Common and predictable temperature control of larval duration may have important implications for many ecological processes and applied issues, including larval dispersal, larval mortality, population connectivity and recruitment dynamics. For many marine species, the planktonic larval phase is the only life stage in which individuals disperse away from the parental population. Unless oceanographic retention processes or larval behaviors change radically in concert with water temperature (Kinlan and Gaines 2003), an increased development rate effectively shortens the duration of the planktonic larval phase (Pepin 1991). Syntheses of marine dispersal data show that planktonic larval duration is, in turn, positively correlated with larval dispersal distance (Shanks et al. 2003, Siegel et al. 2003). Although a variety of other factors may also influence realized dispersal distances, including active larval behavior and complex oceanography (Sponaugle et al. 2002), on average, the more time larvae spend in the planktonic phase, the farther they tend to travel before they settle (Siegel et al. 2003).

To illustrate the potential influence of water temperature on larval dispersal, we employed a simple, idealized model of the relationship between planktonic larval duration and passive larval dispersal distance (Siegel et al. 2003). This ‘null model’ of larval dispersal predicts the average dispersal distance of passive larvae along a linear coastline as a function of two-dimensional nearshore current velocity statistics and the larval competency

period. Despite its simplicity, predictions of this model correspond well with available empirical measures of marine larval dispersal for currents typical of coastal oceans (Siegel et al. 2003). Our results suggest that water temperature may have a striking effect on the dispersal distance of marine larvae (Figure 1.5A). Because dispersal distance scales non-linearly with planktonic larval duration, maximum predicted dispersal distances for larvae in colder water are much greater than those in warmer water. Using the temperature-PLD model (Figure 1.2B), we predict that all else being equal mean dispersal distance should vary by over an order of magnitude (20 versus 225 km) as temperature varies from warm tropical conditions (30 °C) to cold temperate waters (5 °C). More detailed numerical models tailored to the oceanography of particular regions and investigations into how larval behavior and life history traits may modulate the temperature effect on dispersal will lead to further insight on the impacts of changing temperature on connectivity in actual populations.

By controlling larval duration, temperature also mediates the duration of exposure to important sources of larval mortality (Thorson 1950, Houde 1989). Larval survival is generally very low—often less than 1% (Thorson 1950, Morgan 1995)—and decreases exponentially with time when mortality sources such as predation or the likelihood of encountering harsh environmental conditions are relatively constant over the lifespan of a larva (Thorson 1950, Morgan 1995). Assuming mortality remains constant with temperature, the exponential loss of larvae with increasing PLD (Houde 1987) should lead to much lower cumulative larval survival rates in cold water than in warmer water (Figure 1.5B). Some sources of mortality, however, such as starvation, oxygen limitation or predation, are not constant through the larval development period and may change either with larval density,

age (Strathmann 1987) or temperature (Pepin 1991). Survival of a larval cohort reflects mortality due to both these temperature sensitive factors and to constant factors.

Reduced survival over long larval periods may select for shorter planktonic larval durations in colder climates than expected based on temperature (Figure 1.4) (Pearse et al. 1991). There are two adaptive explanations for shorter than expected cold water PLDs: either organisms have adapted life history traits that reduce time spent in the plankton, or molecular processes have evolved to be faster at cold temperatures (Clarke 1991). Within some taxa, life history traits correlated with reduced PLD are more common in cold regions. There is a greater proportion of species with either lecithotrophic or nonplanktonic development in polar regions for some taxa (Thorson 1950, Houde 1987, Strathmann 1987, Pearse et al. 1991), consistent with Thorson's rule (Pearse et al. 1991, Clarke 1992). Because we observe declining PLD with home-range ocean temperature in both lecithotrophs and planktotrophs (Figure 1.4), we suggest that lecithotrophy and larval size are two distinct strategies for reducing PLD that can occur separately or together.

The general influence of temperature on marine larval dispersal has fundamental implications for the understanding and management of marine populations and ecosystems. Effective management requires knowledge of population size, genetic diversity and connectivity; these properties depend on propagule and gene flow maintained by both frequent, medium-range and rare, long-distance dispersal events. Because larval duration influences both medium- and long-range dispersal (Kinlan et al. 2005), and dispersal distances can be far greater in cold water, population connectivity and effective population size should, in general, be inversely related to ocean temperature. Consequently, the spacing among individual reserves in networks of marine protected areas (MPAs) (Gaylord et al.

2005) may need to be far closer in the tropics than in high latitude regions to ensure connectivity. The degree of connectivity and openness also affects local and landscape scale processes, including predator-prey interactions, local community composition and metacommunity dynamics (Kareiva 1987, Pepin 1991, Leibold et al. 2004).

Temperature effects on planktonic larval duration may also explain some inter-annual variation in recruitment. It has long been hypothesized that events or factors that influence vital rates during early life-history stages are linked to recruitment variation (Hjort 1914, Pepin 1991). Whether increased temperature results in increased or decreased recruitment depends on the species' ecology, the spatial arrangement of essential habitat, and how larval duration relates to recruitment. The effect of temperature on recruitment via its effect on planktonic larval duration may help explain recruitment variation in commercially important or invasive species.

Temperature is one of several factors that influence larval duration, dispersal and survival in the field. For example, changes in nutrient availability or ocean current dynamics are often associated with change in ocean temperature, and their influence on larval dispersal would ultimately need to be accounted for in a species- or system- specific model of larval dispersal and recruitment. Nonetheless, two lines of evidence suggest that the temperature-dependent dispersal model we present here will be a useful tool for dispersal models: 1) most lab studies that factorially tested the effect of temperature and another environmental variable such as salinity or food availability found temperature to have the greatest effect on development time (e.g., Hoegh-Guldberg and Pearse 1995), and 2) the quantitative model we present here is applicable to nearly all species, and so can either serve as a null model for the

effects of changing ocean temperature, or can be easily combined with other quantified effects.

This research provides a context for understanding the effect of environmental temperature on the patterns and processes that influence population dynamics and species diversity. The universal temperature dependence of metabolism previously documented extends to the development rate of ectothermic marine organisms, and hence to their planktonic larval duration. Recognition that this temperature effect is common to the most motile life stage of many marine organisms will improve our ability to predict the effects of variation in temperature on demographic and evolutionary processes and to incorporate the effects of temperature into marine species and ecosystem management. Our results suggest that the fundamental constraints of enzyme kinetics can explain a remarkable degree of variation in local, regional and global patterns and processes, and possibly even macro-evolutionary processes that take place over geological time scales.

Figures

Figure 1.1. Species-level residuals for larval duration temperature dependence parameters.

Caterpillar plots comparing ranked species-level residuals (random effects) for 72 species, along with 95% confidence intervals, for two of the three level-1 parameters. Confidence intervals that do not intersect zero identify species whose species-specific value for that parameter is significantly different from the corresponding population-averaged value. The caterpillar plot graphically identifies those species poorly represented by the population-averaged model (Supplementary Information 2 of O'Connor et al. 2007). A) Predictions and 95% confidence intervals (black triangles and grey error bars) for the random effect component (u_{1i}) of the linear scaling parameter β_{1i} for each species (Eqn A1.9). Confidence intervals do not include 0 for seven species (red points): *L. polyphemus*, *C. tyrrhena*, *H. americanus*, *G. morhua*, *S. spirorbis*, *S. balanoides*, *L. californianus*. After removing the three most deviant outliers, *L. polyphemus*, *L. californianus* and *C. tyrrhena*, there is no longer a need for random effects for the linear and quadratic scaling parameters. B) Caterpillar plot for species-level residuals u_{0i} . Since the majority (46 out of 72) of the confidence intervals fail to include 0 we conclude that the species-specific intercept parameters β_{0i} are significantly different from the population-averaged value β_0 for most species. No adjustments for multiple testing were made.

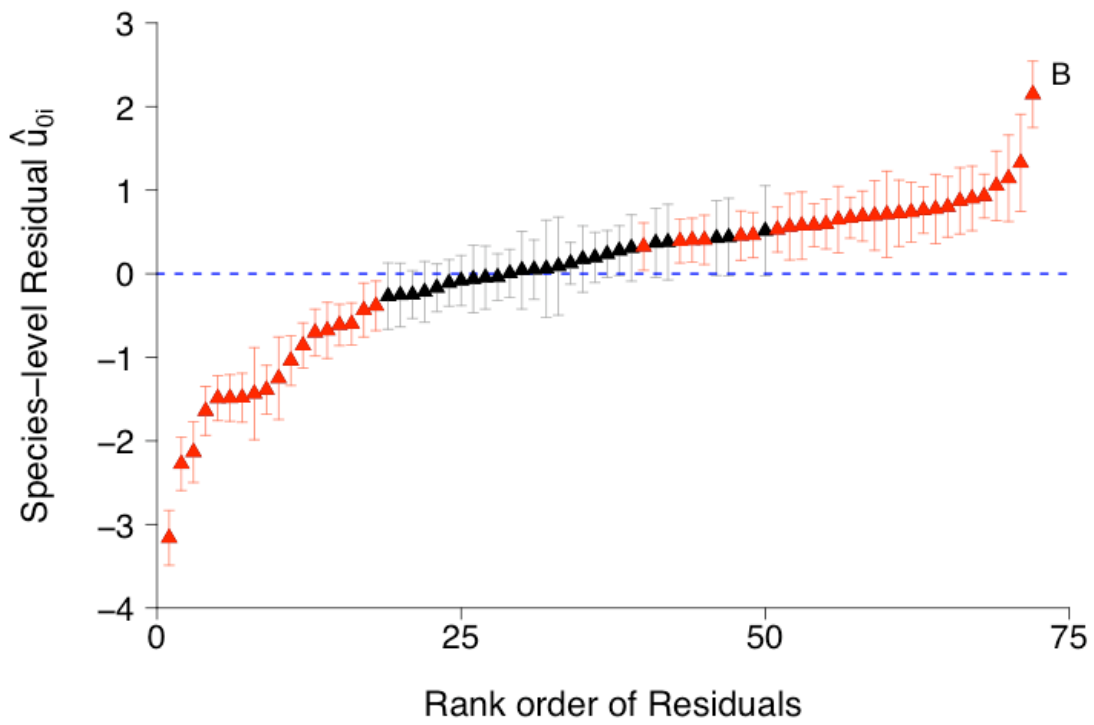
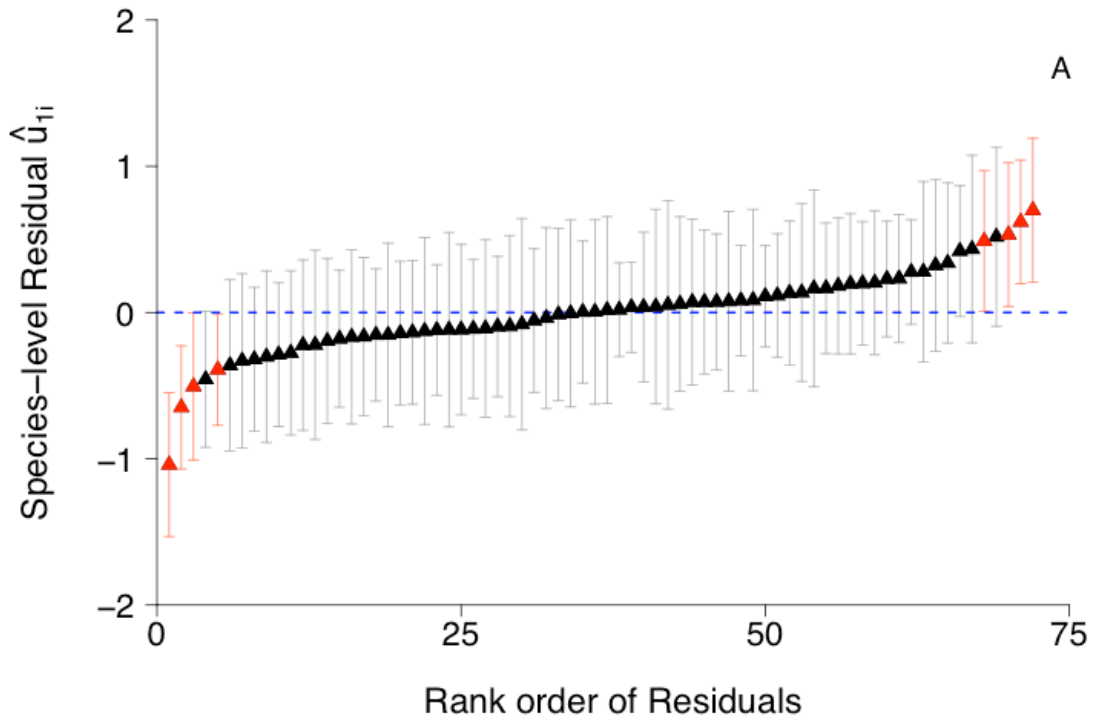


Figure 1.2. The relationship between water temperature and planktonic larval duration.

Temperature dependence of planktonic larval duration based on results from published experimental laboratory studies on the effect of temperature on larval duration for 72 species (6 phyla: 6 fish, 66 invertebrates; Tables A1.3, A1.4). (A) Mean recorded larval duration at each temperature for each species; 2 – 6 data points per species connected by grey lines. Subsequent analyses identified three outliers (black diamonds). (B) Population-averaged (black) and species-specific (grey) trajectories obtained from a multilevel exponential model quadratic in temperature on a log-log scale with random intercepts displayed here on an arithmetic scale. Estimated population-averaged curve: $\ln(PLD) = 3.17 - 1.34 \cdot \ln(T/T_c) - 0.28 \cdot (\ln(T/T_c))^2$, which yields the plotted estimated geometric mean curve: $PLD = \exp(3.17) \cdot (T/T_c)^{(-1.40 - 0.27 \cdot \ln(T/T_c))}$, $T_c = 15 \text{ }^\circ\text{C}$ (Supplementary Information 2 of O'Connor et al. 2007). The parameter estimates $\beta_1 = -1.34$ and $\beta_2 = -0.28$ accurately describe 69 species, while β_0 is highly variable among species (see Appendix A for model application). Shown here is the population-averaged trajectory for *PLD* about which individual species-level trajectories are assumed to vary randomly. $\beta_0 = 3.17$ is interpretable as the value of $\ln(PLD)$ at $15 \text{ }^\circ\text{C}$. Three outliers were excluded in estimating the model (not shown); dashed lines represent the 95% confidence band for the population-averaged trajectory.

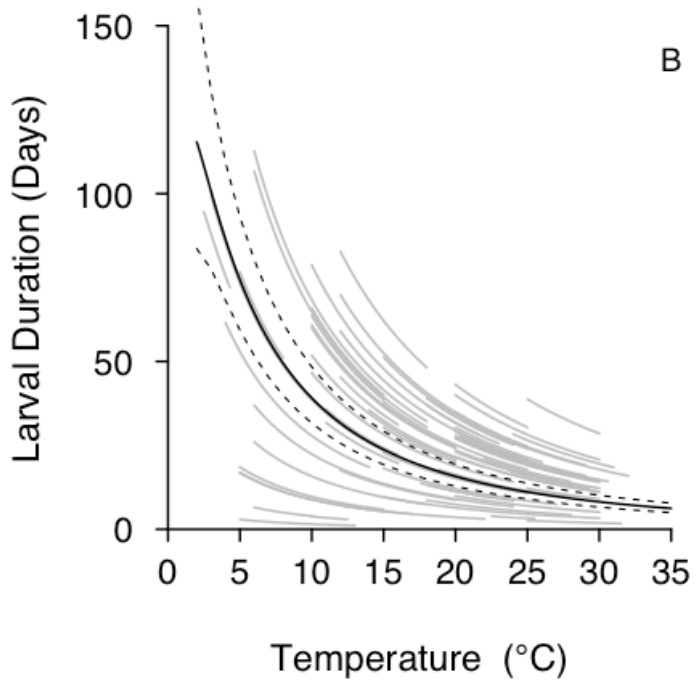
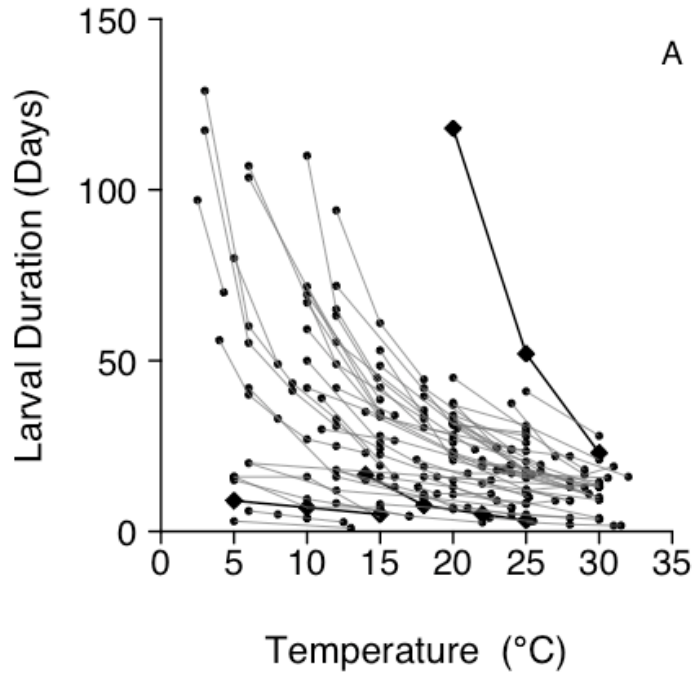


Figure 1.3. Arrhenius plot of Universal Temperature Dependence model.

Arrhenius plot of Universal Temperature Dependence model (Eqn 1.3) for within-species variation in PLD with temperature (n=72). Temperature (°C) is expressed as its reciprocal adjusted to Kelvin and multiplied by the Boltzmann constant (k). Population-averaged trajectory for the temperature effect within species as estimated from a multilevel model with random slopes and intercepts: $\ln(PLD) = -22.47 + 0.64*(1/(k*(T+273)))$ for T in °C (solid line), or $PLD \propto \exp(0.64/(k*(T+273)))$. The model-based empirical Bayes trajectories shown here differ from the ordinary least squares fitted trajectories that would be obtained from fitting individual temperature dependence models to each species one species at a time (Supplementary Information 2 of O'Connor et al. 2007). Metabolic theory predicts that on average the slope is 0.62 eV (Gillooly et al. 2001)(dotted line), and within the range 0.60 - 0.70 eV (Brown et al. 2004). As with the linearized power law model, a random slopes and intercepts UTD model is required for this dataset of 72 species (Table A1.9).

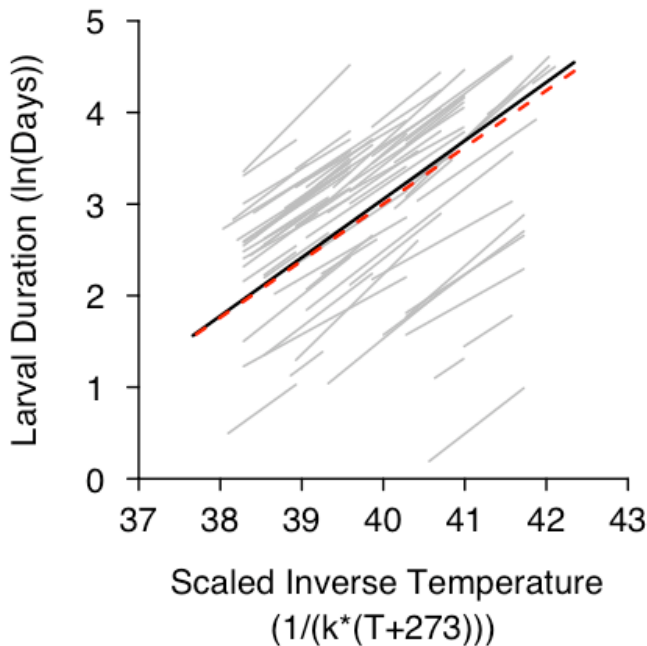


Figure 1.4. Effect of climate and developmental mode on the temperature dependence of PLD for 69 species.

We used mean $\ln(\text{test temperature})$ for each species as a proxy for the average temperature in each species' geographic range. The best model among those we examined was one in which the random intercepts model (Eqn 1.4) was extended to allow $\ln(PLD)$ to vary additively with mean $\ln(\text{test temperature})$ and developmental mode (Table A1.6). In the multilevel modeling framework these two species-level variables are considered predictors of the species-specific intercept, β_{0i} . In the centered level-1 model presented here (Table A1.7), this intercept is interpretable as $\ln(PLD)$ at 15 °C. The predicted intercepts from a random intercepts multilevel model (Eqn 1.4) are plotted here against mean $\ln(\text{test temperature})$ (left) and developmental mode (right). LEFT: The lowess (solid curve) and linear trend (dotted line) suggest that larvae tested at colder temperatures tend to have smaller predicted intercepts than do larvae tested at warmer temperatures. RIGHT: Schematic boxplots, following standard conventions for such graphs, of predicted intercepts for each developmental mode are displayed, with means indicated by asterisks. Lecithotrophs (filled circles) tend to have smaller predicted intercepts than do planktotrophs (unfilled circles).

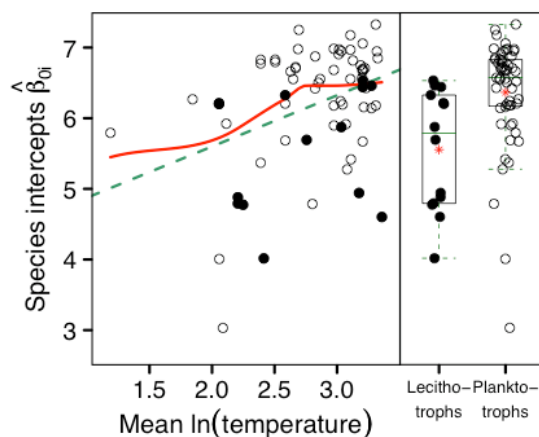
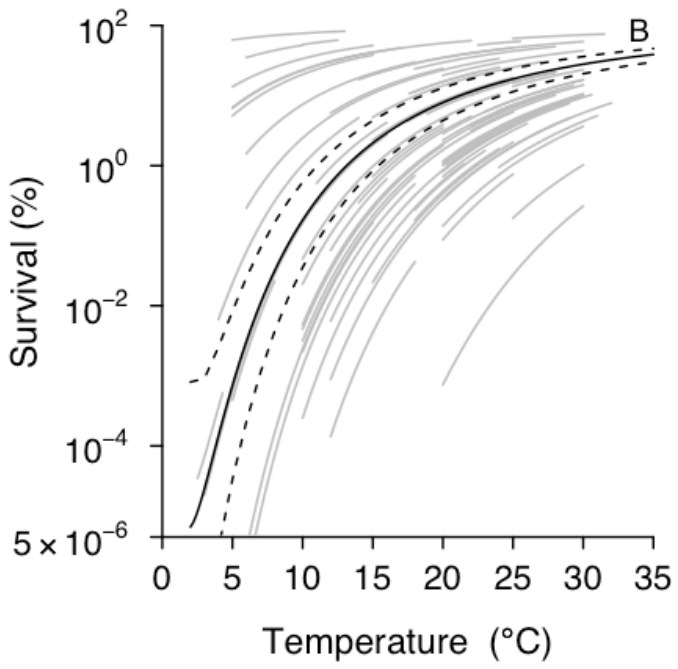
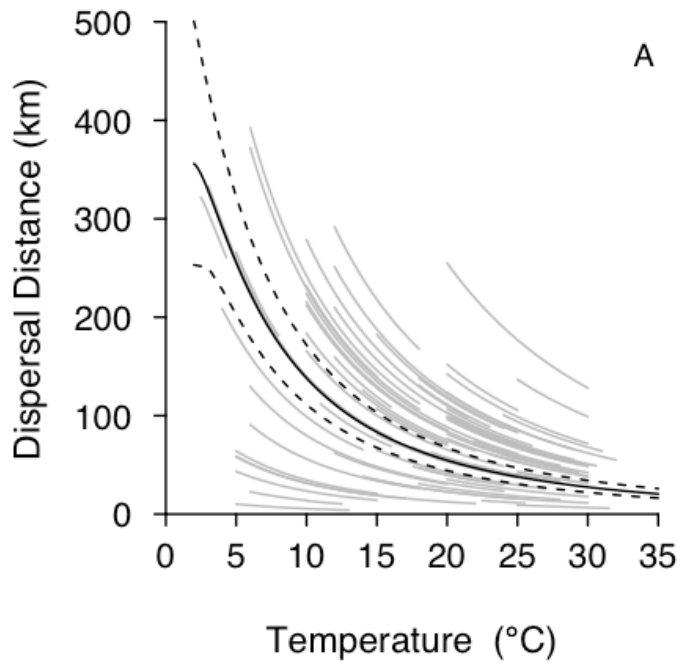


Figure 1.5. Effects of temperature on dispersal distance and survival.

The predicted effects of ocean temperature on two important ecological and evolutionary parameters. (A) larval dispersal distance and (B) larval survival. The predicted effect on dispersal distance is based on our population-averaged temperature-*PLD* model (Figure 1.1B) and on a previously published model relating *PLD* to dispersal (Siegel et al. 2003) using mean current velocity (U) = 0 km/d and with standard deviation (s) = 12.96 km/d to reflect typical near-shore coastal ocean currents. Species-specific projections are shown (grey lines) to convey the range of variability. Confidence band (95%) is for prediction of mean temperature effect on *PLD*, as in Figure 1.1B. Predicted effects on cumulative survival assume a constant density- and temperature-independent daily mortality rate of 15% (Strathmann 1985).



References

- Allen, A. P., J. H. Brown, and J. F. Gillooly. 2002. Global biodiversity, biochemical kinetics, and the energetic-equivalence rule. *Science* **297**:1545-1548.
- Allen, A. P., J. F. Gillooly, and J. H. Brown. 2005. Linking the global carbon cycle to individual metabolism. *Functional Ecology* **19**:202-213.
- Allen, A. P., J. F. Gillooly, V. M. Savage, and J. H. Brown. 2006. Kinetic effects of temperature on rates of genetic divergence and speciation. *Proceedings of the National Academy of Sciences of the United States of America* **103**:9130-9135.
- Belehradek, J. 1930. Temperature coefficients in biology. *Biological Review* **5**:30-58.
- Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage, and G. B. West. 2004. Toward a metabolic theory of ecology. *Ecology* **85**:1771-1789.
- Burnham, K. P., and D. R. Anderson. 2002. *Model selection and multimodel inference*. Springer-Verlag, New York.
- Clarke, A. 1991. What is cold adaptation and how should we measure it? *American Zoologist* **31**:81-92.
- Clarke, A. 1992. Reproduction in the cold: Thorson revisited. *Invertebrate Reproduction and Development* **22**:175-184.
- Clarke, A. 2004. Is there a Universal Temperature Dependence of metabolism? *Functional Ecology* **18**:252-256.
- de Severeyn, Y. G., H. Severeyn, W. Grant, and Y. Reverol. 2000. Effect of water temperature on larval development of the bivalve mollusk *Tivela mactroides*: Evaluation in the laboratory and via simulation. *Ecological Modelling* **129**:143-151.
- Emler, R. B. 1995. Developmental mode and species geographic range in regular sea urchins (Echinodermata: Echinoidea). *Evolution* **49**:476-489.
- Enquist, B. J., E. P. Economo, T. E. Huxman, A. P. Allen, D. D. Ignace, and J. F. Gillooly. 2003. Scaling metabolism from organisms to ecosystems. *Nature* **423**:639-642.
- Gaylord, B., S. D. Gaines, D. A. Siegel, and M. H. Carr. 2005. Marine reserves exploit population structure and life history in potentially improving fisheries yields. *Ecological Applications* **15**:2180-2191.
- Gillooly, J. F., A. P. Allen, V. M. Savage, E. L. Charnov, G. B. West, and J. H. Brown. 2006. Response to Clarke and Fraser: effects of temperature on metabolic rate. *Functional Ecology* **20**:400-404.

- Gillooly, J. F., J. H. Brown, G. B. West, V. M. Savage, and E. L. Charnov. 2001. Effects of size and temperature on metabolic rate. *Science* **293**:2248-2251.
- Gillooly, J. F., E. L. Charnov, G. B. West, V. M. Savage, and J. H. Brown. 2002. Effects of size and temperature on developmental time. *Nature* **417**:70-73.
- Hjort, J. 1914. Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. . *Rapports et Proces-Verbaux des Reunions du conseil International pour l'Exploration de la Mer* **20**:1-228.
- Hoegh-Guldberg, O., and J. S. Pearse. 1995. Temperature, food availability and the development of marine invertebrate larvae. *American Zoologist* **35**:415-425.
- Houde, E. D. 1987. Fish early life dynamics and recruitment variability. *American Fisheries Society Symposium* **2**:17-29.
- Houde, E. D. 1989. Comparative growth, mortality and energetics of marine fish larvae: temperature and implied latitudinal effects. *Fishery Bulletin (Washington D C)* **87**:471-495.
- Houde, E. D., and C. E. Zastrow. 1993. Ecosystem- and taxon-specific dynamic and energetics properties of larval fish assemblages. *Bulletin of Marine Science* **53**:290-335.
- Kareiva, P. 1987. Habitat fragmentation and the stability of predator-prey interactions. *Nature* **326**:388-390.
- Kinlan, B. P., and S. D. Gaines. 2003. Propagule Dispersal in Marine and Terrestrial Environments: A Community Perspective. *Ecology* **84**:2007-2020.
- Kinlan, B. P., S. D. Gaines, and S. E. Lester. 2005. Propagule dispersal and the scales of marine community process. *Diversity and Distributions* **11**:139-148.
- Leibold, M. A., M. Holyoak, N. Mouquet, P. Amarasekare, J. M. Chase, M. F. Hoopes, R. D. Holt, J. B. Shurin, R. Law, D. Tilman, M. Loreau, and A. Gonzalez. 2004. The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters* **7**:601-613.
- Levitan, D. R. 2000. Optimal egg size in marine invertebrates: Theory and phylogenetic analysis of the critical relationship between egg size and development time in Echinoids. *The American Naturalist* **156**:175-192.
- McKinney, M. L. 1984. Allometry and heterochrony in an Eocene Echinoid lineage: Morphological change as a by-product of size-selection. *Paleobiology* **10**:407-419.
- Morgan, S. G. 1995. Life and Death in the Plankton: Larval mortality and adaptation. Pages 279-322 *in* L. R. McEdward, editor. *Ecology of Marine Invertebrate Larvae*. CRC Press, Inc., Boca Raton, Fl.

- O'Connor, M. I., J.F. Bruno, S.D. Gaines, B.S. Halpern, S.E. Lester, B.P. Kinlan and J.M. Weiss. 2007. Temperature control of larval dispersal: implications for marine ecology, evolution and conservation. *Proceedings of the National Academy of Sciences of the United States of America* **104**: 1266-1271.
- Pearse, J. S., J. B. McClintock, and I. Bosch. 1991. Reproduction of Antarctic Benthic Marine Invertebrates: Tempos, Modes and Timing. *American Zoologist* **31**:65-80.
- Pechenik, J. A. 1987. Environmental influences on larval survival and development. Pages 551-608 *in* A. C. Giese, J. S. Pearse, and V. B. Pearse, editors. *Reproduction of marine invertebrates*, Vol. IX. Blackwell Scientific Publications, Palo Alto, California.
- Pepin, P. 1991. Effect of Temperature and Size on Development, Mortality and Survival Rates of the Pelagic Early Life History Stages of Marine Fish. *Canadian Journal of Fisheries and Aquatic Sciences* **48**:503-518.
- Rasbash, J., F. Steele, W. Browne, and B. Prosser. 2004. A user's guide to MLwiN version 2.0. Institute of Education, London.
- Savage, V. M., J. F. Gillooly, J. H. Brown, G. B. West, and E. L. Charnov. 2004. Effects of body size and temperature on population growth. *The American Naturalist* **163**:E429-E441.
- Shanks, A. L., B. A. Grantham, and M. H. Carr. 2003. Propagule dispersal distance and the size and spacing of marine reserves. *Ecological Applications* **13**:S159-S169.
- Siegel, D. A., B. P. Kinlan, B. Gaylord, and S. D. Gaines. 2003. Lagrangian descriptions of marine larval dispersal. *Marine Ecology-Progress Series* **260**:83-96.
- Singer, J. D., and J. B. Willett. 2003. *Applied longitudinal data analysis*. Oxford University Press, New York.
- Sponaugle, S., R. K. Cowen, A. Shanks, S. G. Morgan, J. M. Leis, J. Pineda, G. W. Boehlert, M. J. Kingsford, K. Lindeman, C. Grimes, and J. L. Munro. 2002. Predicting self-recruitment in marine populations: biophysical correlates and mechanisms. *Bulletin of Marine Science* **70**:341-375.
- Strathmann, R. R. 1977. Egg size, larval development, and juvenile size in benthic marine invertebrates. *The American Naturalist* **111**:373-376.
- Strathmann, R. R. 1985. Feeding and nonfeeding larval development and early life-history evolution in marine invertebrates. *Annual Review of Ecology and Systematics* **16**:339-361.
- Strathmann, R. R. 1987. Larval Feeding. Pages 465-550 *in* A. C. Giese, J. S. Pearse, and V. B. Pearse, editors. *Reproduction of Marine Invertebrates*, Vol. IX. Blackwell Scientific Publications, Palo Alto, California.

- Thessalou-Legaki, M. 1990. Advanced larval development of *Callinassa tyrrhenia* (Decapoda: Thalassinidea) and the effect of environmental factors. *Journal of Crustacean Biology* **10**:659-666.
- Thorson, G. 1950. Reproductive and larval ecology of marine bottom invertebrates. *Biological Review* **25**:1-45.

CHAPTER 2: UNIVERSAL TEMPERATURE CONSTRAINTS ON THE BIOGEOGRAPHY OF MARINE LIFE HISTORIES

Abstract

Biogeographic trends in offspring life history traits have been observed in marine systems for nearly a century. These patterns have defied a single mechanistic explanation, largely due to the many exceptions to each proposed rule. Here we explore the possibility that water temperature indirectly influences parental investment in individual offspring by altering larval development times, with large impacts on cumulative larval mortality. We draw upon the metabolic theory of ecology to modify a traditional life history model of offspring size-dependent fitness. Our model illustrates how the trade-off between offspring size and number could drive life history shifts to fewer, larger offspring at very low temperatures given a constant daily mortality rate. In contrast, at warmer temperatures, releasing more numerous and smaller offspring yields more settlers. This shift in optimal offspring size is explained by the temperature dependence of larval duration, which implies that larval duration and exposure to mortality are much greater at colder temperatures. The effect of temperature on optimal larval size depends on the relationship between temperature and larval mortality. However, if drivers of mortality vary directly and positively with temperature and size, small offspring are optimal at all temperatures. Therefore, environmental temperature provides a single explanation for long-observed geographic

gradients in parental investment in life history traits. This temperature-based optimality model supports a framework for understanding latitudinal trends in egg size, and related traits of larval feeding and the proportion of species with no planktonic larval stage. A systematic effect of temperature on larval traits suggests that larval dispersal and related ecological and evolutionary processes likely change predictably with latitude, which has important implications for forecasting the ecological effects of climate change.

Introduction

Temperature exerts a fundamental control on development rate in all organisms (Gillooly et al. 2001). Kinetic effects of temperature on basic metabolic processes drive quantitatively similar patterns of temperature dependence in development rates, life stage durations and population growth rates among diverse taxa (Gillooly et al. 2002, Savage et al. 2004). These inevitable metabolic constraints on demographic processes are likely to be evolutionarily significant, potentially leading to temperature-related patterns of selection on developmental and reproductive life history traits. For most marine animals, offspring (larval) development is a distinct life stage characterized by very small size, high risk of mortality and dispersal in a moving pelagic environment away from adult habitats (Strathmann 1977, Levin and Bridges 1995, Kinlan and Gaines 2003). The general model of metabolic temperature dependence, called the Universal Temperature Dependence or UTD (Gillooly et al. 2001), describes the influence of temperature on the duration of planktonic larval development and implies that water temperature predictably influences dispersal and larval mortality for marine animals (O'Connor et al. 2007). Therefore, the temperature dependence of planktonic larval development may drive latitude- and depth-related

biogeographic patterns in traits known to influence larval mortality rates such as larval or egg size (Thorson 1950, Mileikovsky 1971, Pearse 1994).

Biogeographic trends in larval or egg size and their putative causes have received much attention (reviews by Clarke 1992, Iverson et al. 1993, Griebeler and Bohning-Gaese 2004, Pearse and Lockhart 2004, Laptikhovsky 2006). For many species, egg or larval size reflects parental investment per offspring and increases with latitude or depth (Rass 1941, Thorson 1950, Emlet et al. 1987). However, important exceptions to these patterns have defied a general understanding of whether a single adaptive mechanism is responsible (Emlet et al. 1987, Pearse et al. 1991, Clarke 1992, Gallardo and Penchaszadeh 2001). This question is complicated by the consideration of other patterns reflecting increased parental investment in individual offspring, such as latitudinal increases in the proportion of species with non-feeding larvae or direct development (no planktonic period) (Thorson 1950, Mileikovsky 1971, Clarke 1992). Although each pattern reflects increasing parental investment in colder water with the effect of reducing the planktonic larval period, these three patterns of egg size, feeding mode and planktonic versus direct development have rarely been considered as effects of a single causative factor.

Increasing parental investment per offspring in colder water could be caused by indirect effects of temperature on cumulative mortality during the planktonic larval development period. Most larvae do not survive to metamorphosis and settlement (Rumrill 1990, Morgan 1995), and predictably longer planktonic larval durations at lower temperatures have the potentially serious fitness consequence of prolonging exposure to the elevated risk of mortality during planktonic life. One solution to this problem of high mortality rates is to reduce the time larvae spend in the plankton (Emlet et al. 1987). This could be done through physiological mechanisms that increase development rate, by

provisioning larvae with greater nutritional stores when development rate is food limited, or by altering traits such as size at hatch or size at settlement/metamorphosis. Direct reduction of development rate is constrained by extremely limited variation in the fundamental biochemical components of metabolism (Gillooly et al. 2002). Thus, the greatest scope for selection to counter the temperature effects on development rates is in the total amount of growth that must be achieved. Development time can be reduced by the production of larger offspring relative to their size at metamorphosis or settlement (Havenhand 1993, Charnov and Gillooly 2004). There is an unavoidable trade-off between parental investment per offspring and number of offspring produced if the total allocation to reproduction is not increased; larger eggs or larvae require more nutritional resources and therefore come at a predictable cost to the parent in terms of number of offspring (fecundity) (Lack 1954, Smith and Fretwell 1974, Emlen et al. 1987). In many taxa, increased offspring mortality shifts the balance of this trade-off toward increased parental investment and lower fecundity (Vance 1973, Kolding and Fenchel 1981, Clutton-Brock 1991). Therefore, producing fewer, larger offspring may be favorable at cold temperatures if longer larval durations result in higher mortality during this life stage (Pearse et al. 1991, Yampolsky and Scheiner 1996).

Here we ask whether the constraint imposed by water temperature on larval duration, and consequently on cumulative larval mortality, predictably shifts the balance of the trade-off between parental investment per offspring and fecundity toward greater per-offspring investment (Figure 2.1). To test this hypothesis, we combine a traditional, theoretical model focusing on a single life history trait – offspring release size – with the universal temperature dependence (UTD) model to explore the mechanistic relationship between the number of settling offspring and three factors that can modify the fitness of size: larval mass at hatching, environmental temperature and mortality. We predict that for comparisons within species,

larger larval size at release relative to size at metamorphosis is favored as temperatures decline. We then discuss the ability of this within-species model to explain among-species latitudinal trends in larval feeding mode, egg size and direct development, thus addressing the long-standing question of whether latitudinal trends in larval traits could arise in response to a single environmental factor (Thorson 1950, Pearse and Lockhart 2004).

Larval size optimality model

The basic fitness model

Theoretical models have balanced the risk of larval mortality against parental investment in offspring since the work of Vance (1973). These models share the same basic form (Eqn 2.1):

$$N_m = B_R / m_h * e^{-PLD * M} \quad \text{Eqn 2.1}$$

relating instantaneous mortality rate (M), development time (here, planktonic larval duration PLD), total reproductive investment (expressed as biomass B_R), and the investment per offspring, (expressed as mass at hatching m_h), to a measure of fitness, the number of offspring that reach settlement/metamorphosis (N_s) (Smith and Fretwell 1974, Emlet et al. 1987, Levitan 1996). Empirically, mass at hatch is highly correlated with egg mass (Collin 2003). In this simple model form, development time (PLD) implicitly scales with the difference between size at hatching (m_h) and size at settlement or metamorphosis, which is assumed to be fixed. There is an explicit trade-off between initial offspring size and number within each reproduction cycle. These models have generally been applied to comparisons

among groups of species, though they are relevant to our consideration of selection within species.

Size-dependent planktonic larval duration

Because *PLD* is a function of initial larval size, finding the optimal patterns of investment requires specifying the explicit form of this relationship. Early models assumed a linear relationship between *PLD* and larval size, which led to predictions of a U-shaped relationship between fitness and larval size at hatching (e.g., Vance 1973). By contrast, Levitan (2000) showed that a negative nonlinear effect of hatch size on *PLD* yields a very different outcome – fitness is maximized at an intermediate size at hatching.

None of these assumed relationships between offspring size at hatching and *PLD* have been based on likely allometric relationships between size and growth rates. The metabolic theory of ecology offers a possible solution by providing a mechanistic model based on the relationship between mass and development time, that closely mirrors empirical patterns observed in a wide range of taxa (West et al. 2001, Brown et al. 2004, Charnov and Gillooly 2004). Using this framework, we can explicitly define *PLD* as a function of hatch size. Eqn 2.2 uses an integrated form of the von Bertalanffy equation for mass-dependent growth rate with a scaling exponent of 3/4 (Gillooly et al. 2002):

$$\int_{T_h}^{T_s} dt = \int_{m_h}^{m_s} \frac{1}{am^{3/4}} dm \quad \text{Eqn 2.2}$$

or

$$PLD = \frac{4}{a} \left(m_s^{1/4} - m_h^{1/4} \right)$$

where a represents a taxon-specific normalizing constant, which is proportional to fundamental cellular energetic properties and is temperature dependent, m_h is the mass at hatch, and m_s is the mass at settlement/metamorphosis. This model allows larval hatch size to influence development time in two ways. Larger hatchlings have both less total development to accomplish while in the plankton and a higher rate of development (Strathmann 1985, Emler et al. 1987, Hart 1995, Gillooly et al. 2002). With an explicit, mechanistic trade-off between hatching size and PLD , we can ask whether the reduction in development time (and consequent reduction in cumulative mortality) associated with increasing larval size at hatching can compensate for the reduced number of larvae produced.

Temperature-dependent planktonic larval duration

To couple the above allometric scaling of PLD to the temperature dependence of development rates, we again draw upon metabolic theory. Rather than using a normalizing constant a (Eqn 2.2), we define a as a function of temperature.

$$a(T_C) = a(T_0)e^{(E/kT_0^2)(T_C/(1+T_C/T_0))} \quad \text{Eqn 2.3}$$

where E is the average energy for the reaction (0.62 eV (Gillooly et al. 2001)), k is the Boltzmann constant, and T_C and T_0 are any two temperatures greater than 0°C. This functional relationship has been shown to apply to planktonic larval durations (Gillooly et al. 2002, O'Connor et al. 2007).

Varying mortality with size and temperature

Several models have shown that optimal offspring size can be modified by size- and temperature-dependent mortality rates (Levitan 2000, Kiflawi 2006), though the direction and shape of these relationships is variable. The size-dependent mortality hypothesis (Bailey and Houde 1989, Pepin 1993, Cowan et al. 1996) predicts that the two major sources of larval mortality, predation and starvation, are strongly size-dependent. Applications of the size-dependent mortality hypothesis to comparisons among species suggest larval size and mortality rate are negatively correlated (Pepin 1991, 1993, Morgan 1995, Cowan et al. 1996). Studies of other taxa suggest different functional relationships between larval size and mortality (Bailey and Houde 1989, Pepin 1991, Cowan et al. 1996). However, studies comparing larval size and mortality rate within species suggest that size variation can be correlated with reduced or increased vulnerability to predation (Litvak and Leggett 1992, Pepin et al. 1992), or no significant correlation may be apparent (Pepin 1993).

We modeled three scenarios of size-dependent mortality based on an allometric scaling model: constant mortality rate (Eqn 2.4a), increasing mortality with larval size (Eqn 4b), and decreasing mortality with larval size (Eqn 2.4c). To incorporate variable mortality rates, we modify the M term in Eqn 1 as follows:

$$M_M = C_d \quad \text{Eqn 2.4a}$$

$$M_M = C_d * m_h^{1/4} \quad \text{Eqn 2.4b}$$

$$M_M = C_d \div m_h^{1/4} \quad \text{Eqn 2.4c}$$

where C_d is a constant component of the instantaneous mortality rate and is modified by hatch mass (m_h).

Temperature can affect mortality indirectly by determining larval duration and consequent exposure, and directly by influencing ecological interactions such as predation or larval feeding. Field estimates of daily larval mortality rates reflect mortality due to physiological stress as well as ecological factors, and generally increase with temperature among temperate fish species (Houde 1989, Pepin 1991). There is no clear, single effect of temperature on mortality due to physiological stress; lab studies have demonstrated negative, positive and equivocal correlations (Johns 1981, MacKenzie 1988, Manoj Nair and Appukuttan 2003). Ecological factors such as predation pressure have also been shown to change with temperature in the lab (Elliott and Leggett 1997), though general effects of temperature on predation rates are still poorly understood. Without other information, we assume that the predominant pattern of increasing mortality risk with increasing temperature estimated for among-species comparisons applies to within species comparisons, and we therefore consider the effects of temperature on daily mortality using a standard mortality function (Pepin 1991):

$$M_T = C_d * e^{P*T} \tag{Eqn 2.5a}$$

$$M_{TxM} = C_d * e^{P*T} * m_h^{1/4} \tag{Eqn 2.5b}$$

where P is an empirically measured scaling factor that characterizes the effect of temperature (T in °C). When modeling each equation, we chose a value of C_d that allowed mean mortality rates to be approximately 0.15 / d (Rumrill 1990). Considering these size- and

temperature-dependent mortality scenarios allows us to consider the effects of the selection model under different potential field conditions.

Model assumptions

This optimality model incorporates five key assumptions that are well supported by precedent or other studies. First, we assume there is a trade-off between offspring size and offspring number within a single reproductive event. This is a common component of life history models, and is justified based on theoretical and empirical evidence derived from echinoderms as well as other taxa (Lack 1954, Smith and Fretwell 1974, Emler et al. 1987, Sinervo and McEdward 1988). Second, we assume that mortality in the plankton is generally greater than in the benthos, consistent with data reviewed by Morgan (1995) for invertebrates.

In addition, we assume that variation must exist for initial offspring size. A wide range of variation in egg size exists within populations, and even within the offspring of a single parent (Lessios 1987, McEdward and Coulter 1987, Phillips 2007), and the range of possible variation may be constrained by factors such as phylogeny, resource availability, or maternal traits (reviewed by Lessios 1990). A fourth assumption is that such variation is heritable. Heritability of initial offspring size has been demonstrated in fish and a polychaete (Levin et al. 1991, Kokita 2003). Finally, we assume that hatch size varies independently of and to a greater degree than metamorphosis size. Variability in size at metamorphosis is indeed relatively low for comparisons within species and closely related taxa (Werner and Gilliam 1984, Emler et al. 1987, Sinervo and McEdward 1988, Havenhand 1993, Benoit et al. 2000), but see (Strathmann 1974, Hart 1995), and uncorrelated with variation in hatch size (Emler et al. 1987).

Results

Our model demonstrates that the balance of the trade-off between offspring size and number can shift to favor fewer, larger offspring at very low temperatures under conditions of invariant daily mortality rates (Figure 2.2). However, this shift is not favored when mortality rates due to ecological factors are directly influenced by temperature or larval size (Figure 2.3). Therefore, the fitness of offspring size at different temperatures strongly depends on the direction and magnitude of size- and temperature-dependent variation in mortality.

When mortality is constant with respect to larval size and temperature, hatch size strongly affects larval duration. Assuming a constant metamorphosis size, increasing hatch size reduces *PLD* (Figure 2.2A, solid line) with the greatest effect at the smallest hatch sizes. If the assumption of constant metamorphosis size is violated, as is often the case for comparisons among species, the hatch size – *PLD* relationship reverses (Figure 2.2A, dashed line). While changes in hatch size reflect an internal constraint on development time, one that is subject to some parental control, environmental temperature imposes an external constraint resulting in severe declines in *PLD* with increasing temperature (Figure 2.2B). When size-dependent larval duration is incorporated into the fitness model, the number of larvae reaching metamorphic size varies with larval hatch size (Figure 2.2C, e.g., black line).

The effect of hatch size on the number of larvae reaching metamorphosis changes with temperature (Figure 2.2C). At low temperatures, larger offspring with shorter *PLDs* have increased survival rates and greater numbers of settlers (Figure 2.2C, black line). At warmer temperatures, *PLDs* are generally shorter for larvae of any size, and the higher

fecundity leads to higher numbers of settlers (Figure 2.2C, red line). For any generation, a minimum number of settlers is necessary to ensure a reasonable probability that at least one offspring will survive to reproduce. The initial offspring size necessary to achieve this minimum number increases at cold temperatures (Figure 2.2D). Thus, the model supports our prediction (Figure 2.1) that increases in larval size (e.g., parental investment per offspring) may compensate for the constraint imposed by low temperature on development time (Figure 2.2D).

When larval mortality is considered to be independent of larval size (e.g., Figure 2.2) and temperatures are not extremely cold, smaller hatch sizes will yield more settlers and greater fitness (e.g., red and green lines in Figure 2.2C). Under such conditions, organisms should produce the smallest larvae possible given physiological, phylogenetic or developmental constraints. Size-dependent mortality changes the general relationship between size, fitness and temperature (Figure 2.3). For example, a positive correlation between larval mortality and larval size (Eqn 2.4b) leads to higher survival rates of very small larvae even at colder temperatures (Figure 2.3A). In contrast, a negative relationship (Eqn 2.4c) means that larger hatchling larvae settle in greater numbers at all temperatures, but the overall pattern, in which larger sizes required to achieve a minimum settlement number at colder temperatures, is maintained (Figure 2.3B).

When risk of mortality increases with temperature, the effect of temperature on survival varies little with offspring size (Figure 2.3C versus Figure 2.2C). Instead, it is the relative temperature sensitivity of *PLD* versus ecological mortality factors that determines the magnitude and direction of the overall influence of temperature on size and survival to metamorphosis. When mortality is positively related both to size and temperature (Figure

2.3D), optimal hatch sizes are either very large or very small larvae at all temperatures, and the difference among temperatures is minimal.

Discussion

Our model provides a mechanistic ecological explanation for variation in egg size based on a quantitative link between temperature and mortality, suggesting that geographic patterns of parental investment may be driven by environmental temperature and its influence on larval mortality rate. In the absence of direct effects of temperature on mortality, environmental temperature can determine which larval hatch size yields the greatest number of survivors by indirectly altering the relative survival rates of larvae of different hatch sizes. The strength of the effect of temperature on optimal hatch size can be modified or even nullified by temperature- or size-dependent mortality. Therefore, the general effect of temperature on larval development can influence selection on larval size, but the broader implications of this effect for evolution of life history traits likely depend on the relationship between temperature and mortality.

A shift in the tradeoff between offspring size and number due to environmental conditions is consistent with previous modeling outcomes, but our model provides a new quantitative, mechanistic link between mortality and temperature. For example, a demographic model by Yampolsky and Scheiner (1996) suggests that temperature could shift the balance of optimal offspring size from small to large, but based only on an assumed qualitative relationship between mortality and temperature. The recent recognition that temperature exerts an unavoidable constraint on development time and larval duration (Gillooly et al. 2002, O'Connor et al. 2007) provides a quantitative and general mechanism

for an effect of temperature on one aspect of larval mortality. The model presented here incorporates these new findings from metabolic theory, leading to testable hypotheses and a framework for how this process might influence biogeographic trends at different taxonomic levels.

To conclude that temperature-dependent larval duration is an underlying cause of biogeographic variation in life history traits implies that an adaptive mechanism is responsible for latitudinal and depth trends. Though it has been suggested that non-adaptive physiological or maternal effects are sufficient to explain latitudinal trends in larval traits, the prevalence of these patterns in both hemispheres and among diverse taxonomic groups (Collin 2003, Laptikhovsky 2006) supports an adaptive mechanism. Possible adaptive mechanisms underlying latitudinal variation in egg size have been extensively considered (Clarke 1992, Pearse 1994, Yampolsky and Scheiner 1996, Pearse and Lockhart 2004), though specific, testable mechanisms remain poorly understood (Clarke 1992, Laptikhovsky 2006). Thorson (1950) and others have proposed that harsh polar environments with low food availability and extreme seasonality select for species with larger eggs and/or brooded larvae. However, support for this widely-held belief that food availability is the underlying cause is contradicted by numerous examples of polar and deep water species with planktotrophic development or wintertime spawning (Pearse 1994).

Our temperature-based optimality model provides a framework for understanding mechanisms behind latitudinal trends in early life history traits of marine organisms. Understanding latitudinal biogeographic trends among species requires a mechanistic connection between among- and within-species patterns. A within-species trend toward larger optimal egg or hatch sizes in cold water could lead to a trend among species of cold-water species characterized by larger eggs than warm-water species. Increasing egg size

relative to metamorphosis size is not the only life history solution to the problem of mortality associated with a long planktonic larval duration. Other larval traits reflecting increased parental investment per offspring, such as increased nutritional stores and partial brooding of offspring, are correlated with shorter larval durations than found in planktotrophic larvae (Table 2.2) (Smith and Fretwell 1974, Emler et al. 1987, McEdward and Morgan 2001, O'Connor et al. 2007) (but see McEdward and Coulter 1987). Interestingly, these traits can also be correlated with larger egg or larval hatch size (e.g., Collin 2003). Thus, latitudinal gradients among species in egg size, lecithotrophy and brooding may all be responses to high mortality rates at lower temperatures (Table 2.1).

Exceptions to the latitudinal gradient in egg size do not necessarily contradict the hypothesis underlying the temperature based optimality model, which predicts an increase in parental investment (not specifically in egg size) per offspring with decreasing temperature. One reason for this is that the link between within-species variation in optimal parental investment per offspring and among-species patterns in parental investment depends on species-specific constraints on variation in the traits in question (Collin 2003). For example, variation in egg size within a species may follow the predicted pattern of larger eggs in cold water, but phylogenetic constraints may limit the largest possible egg size relative to egg sizes in other species. If variation is constrained such that changing hatch size could not sufficiently reduce larval duration in cold temperatures, adaptation in other traits could compensate for the temperature constraint. Another factor that may complicate comparisons among species is covariation in other traits related to the larval period such as metamorphosis size. Pepin and Myers (1991) reported that the difference between hatch size and metamorphosis size ($m_s - m_h$) correlates with recruitment variation among temperate fish species, but absolute egg or hatch size do not. Thus, effects of egg or hatch size on *PLD* can

be confounded by correlated variation in metamorphosis size. Larger eggs in relation to metamorphic size (reducing $m_s - m_h$) decrease planktonic larval duration, but correlated increases in metamorphic size and hatch size increase *PLD* (Figure 2.2A) as is generally found among broader taxonomic comparisons (Emlet et al. 1987, Pepin 1991, Gillooly et al. 2002). Our model suggests that correlated increases in metamorphosis size and hatch size reflect factors other than the indirect effect of temperature on *PLD*. Therefore, the collective consideration of distinct biogeographic patterns of parental investment may be as alternative, non-exclusive solutions to the single problem of high mortality in long planktonic larval durations at low temperatures.

When considered together, it becomes clear that some apparent exceptions to one pattern actually support an alternate pattern consistent with temperature as the driving factor (Table 2.2). Evaluations of evidence for a proposed biogeographic ‘rule’ tend to focus on whether well-studied taxon supports one proposed rule. For example, Thorson’s rule is the name ascribed by various authors to latitudinal trends in egg size, planktonic versus direct development, and feeding versus nonfeeding planktonic larvae (Mileikovsky 1971, Pearse and Lockhart 2004). Most discussions of Thorson’s rule focus on the most comprehensively studied invertebrate taxa with regard to variation in reproductive traits: echinoids and gastropods. Echinoids are an exception to Thorson’s rule as originally stated, that the proportion of species with direct development increases with latitude (Pearse 1994). However, echinoids do exhibit a trend of an increasing proportion of lecithotrophic species with increasing latitude (Emlet et al. 1987). Therefore, while echinoids disprove the generality of a latitudinal gradient in brooding, they support an underlying trend of increased parental investment in individual offspring with increasing latitude. Another example can be found in calyptraeid gastropods, in which there is no geographical trend in egg size among

species, but there is a trend in the proportion of species with direct development (Collin 2003). Fish present a different case because they generally produce planktotrophic larvae and thus the predictions about gradients in lecithotrophy and brooding are not relevant. Therefore, we require additional measures of parental investment in order to test this hypothesis for fish. Nonetheless, patterns observed in well-studied invertebrate taxa suggest that the temperature based optimality model provides more comprehensive predictions for geographical variation in life history traits than previous models.

Several specific predictions can be extended from this model and framework. First, the effect of temperature on metabolic processes is generally stronger at colder temperatures (Figure 2.2B), suggesting geographic variation in the ecological effects of temperature. This leads to the prediction that species with shorter planktonic durations than expected based on temperature should be more common in very cold water. The temperature constraint on planktonic larval duration effectively disappears at warmer temperatures (above 15 – 20 °C, Figure 2.2B). Therefore the minute fitness benefit of increased larval hatch size is likely not worth the cost of increased investment in warmer climates, and small offspring sizes should be most common at all temperatures except the coldest temperatures (Figures 2.2C, 2.3D). This prediction is consistent with comprehensive reviews of invertebrate egg size distributions (Levitan 2000, Collin 2003). At warm temperatures when development is fast, larger larvae may be more likely to avoid predators and survival from this size escape may outweigh the fecundity cost of increased parental investment. Thus, the ecological factors influencing selection on larval size likely shift from temperature in high latitudes to predation or food availability in lower latitudes.

Predation is thought to be the most important source of mortality for larvae in the plankton (Morgan 1995), yet variation in predation with larval traits or environmental

conditions is difficult to study and consequently remains poorly understood. Our model suggests that a constant and predictable positive effect of temperature on an ecological mortality factor like predation pressure eliminates any effect of temperature on optimal offspring size. Predation pressure is unlikely to be constant and predictable in the field. For example, predation pressure varies substantially due to factors other than those incorporated in our model, such as predator identity and diversity (Elliott and Leggett 1997, Finke and Denno 2005), predator size (Connell and Anderson 1999), food chain length (Frank et al. 2005) and season. This unpredictable threat to larval survival may therefore not be as strong a selective pressure on larval traits as the highly predictable effect of temperature on *PLD*, which effectively integrates mortality due to all factors over the entire development period.

Ocean temperature potentially explains several broad-scale biogeographic patterns in marine life history traits, with consequences for complex ecological and evolutionary processes. Larval duration, size, and feeding mode are related to the distance larvae can disperse (Shanks et al. 2003, Siegel et al. 2003), which is a critical determinant of connectivity among populations and in turn of species' range size, range expansion, differentiation among populations, and the effectiveness of conservation measures such as marine protected areas (Hart 1995, Shanks et al. 2003, Lester and Ruttenberg 2005, Laurel and Bradbury 2006). Identifying temperature as a significant modifier of these diverse and important processes provides a key to understanding ecological processes and also evolutionary responses to them, thus potentially enhancing our understanding of existing biogeographic patterns. Such an integrated understanding will in turn aid projections of future patterns of dispersal, species distributions and species range dynamics as ocean temperatures change with small- and large-scale disturbances such as climate cycles or anthropogenic climate change.

Tables.

Table 2.1. Relationship of larval life history traits to vulnerability to mortality in the plankton.

Trait	Mechanism of reducing mortality
Hatch size	Increasing hatch size relative to metamorphosis size shortens development time and reduces vulnerability to inverse size-dependent mortality
Development mode	Lecithotrophic larvae are larger and have shorter planktonic larval periods than planktotrophic larvae. Selection may have favored a switch among feeding modes from larval types that must feed in the water column (planktotrophs) to larvae that do not need to feed (facultative planktotrophs or lecithotrophs).
Brooding	Brooding or partially brooding offspring allows larvae to be released at a more advanced state of development, thus reducing mortality due to exposure in the plankton.
Egg size	If metamorphosis size is held constant, increases in egg size will generally lead to shortened larval durations because less development is necessary in the plankton before reaching metamorphosis and settlement size. However, if metamorphosis size changes proportionally with hatch size, larger eggs would lead to longer development periods.

Table 2.2. Test of Thorson’s rule within taxonomic groups.

Several taxa for which evidence for multiple versions of Thorson’s rule have been examined. Studies reported the presence (Y) or absence (N) of significant trends in egg size, feeding mode or direct development (DD, including brooding) with either latitude or depth for large numbers of species (N column).

Biogeographic gradient	Taxon	N	Size	Feeding mode	DD	Refs
Latitude	Echinoderms	~188	N	Y	N	Pearse 1994 Emlet et al 1987
Latitude	Echinoidea - Planktotrophic	~100	Y	NA	NA	Emlet et al 1987
Latitude	Echinoidea	110	Y	Y	Y	Emlet et al 1987
Latitude	Asteroidea	88	Y	Y	Y	Emlet et al 1987
Latitude	Asteroidea - Planktotrophic		N	NA	NA	Emlet et al 1987
Depth	Echinoidea	215	Emlet 1987	Y	Y	Emlet 1995
Latitude	Calyptraeid gastropods	78	N		Y	Collin 2003

Figures.

Figure 2.1. Conceptual model of temperature effects on larval mortality and parental investment.

Effect of temperature on hypothesized trend of larval mortality (dashed line) and parental investment (PI) per offspring (solid line) in terms of temperature and latitude. The vertical line in indicates a point above which the magnitude of the effect of a temperature differential on PI and mortality decreases.

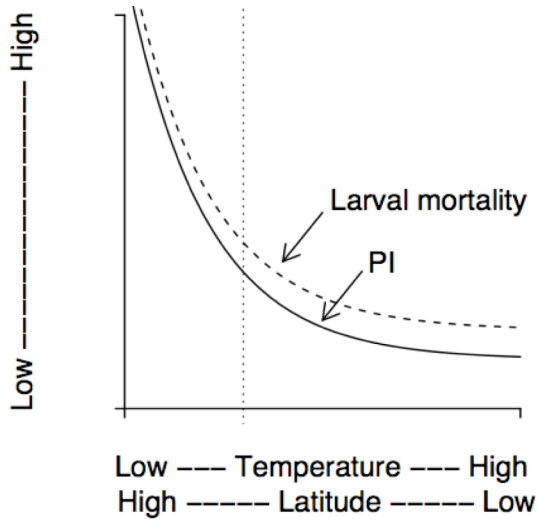


Figure 2.2. Model results for larval size optimality model.

A) *PLD* as a function of hatch mass, assuming that hatch size varies in relation to a constant settlement size (solid line), and assuming increase in hatch size correlates with increase in settlement size (dashed line). Values for parameters are chosen based on cod life histories.

B) *PLD* as a function of temperature for a typical hatch size ($m_h = 0.25$ g). C) Proceeding with the modeled solid line in panel A, the number of larvae reaching metamorphic mass at different temperatures (black to red = 5 – 25 °C in increments of 5 °C), dashed lines indicate 50 and 400 larvae surviving to metamorphosis as arbitrary minimums to ensure that at least one offspring survives to reproduce, D) minimum hatch size necessary to achieve 50 larvae reach metamorphic size at each temperature.

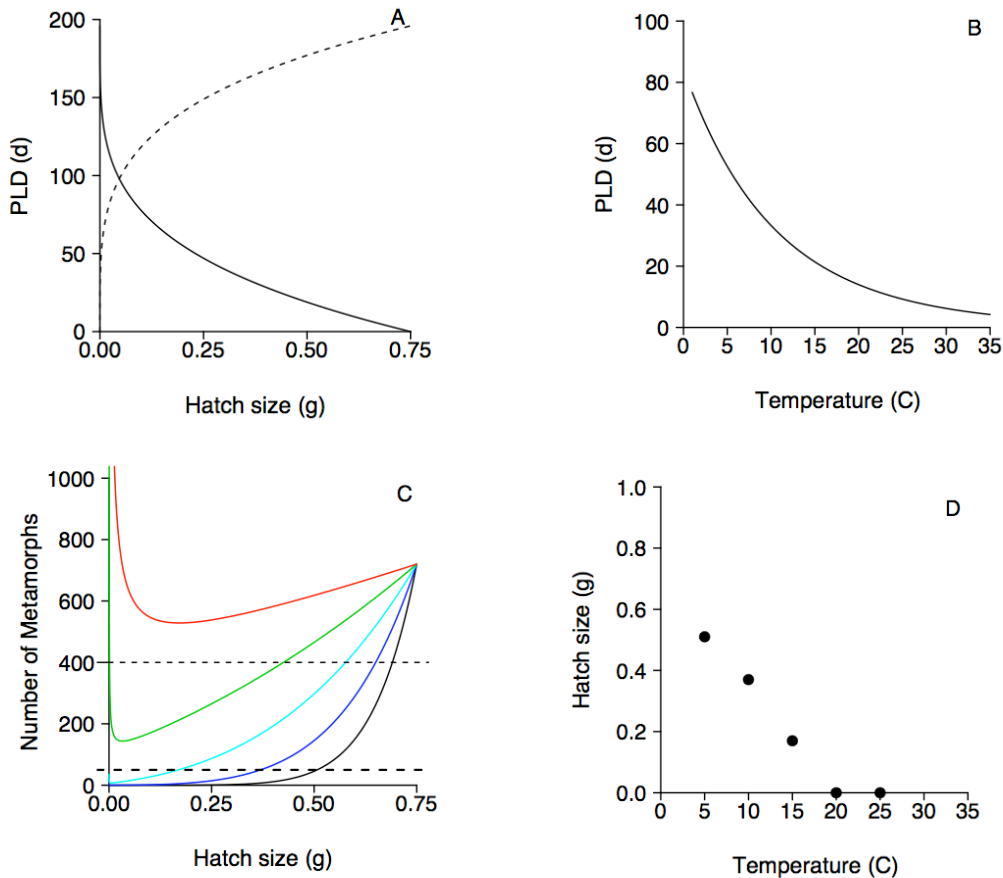
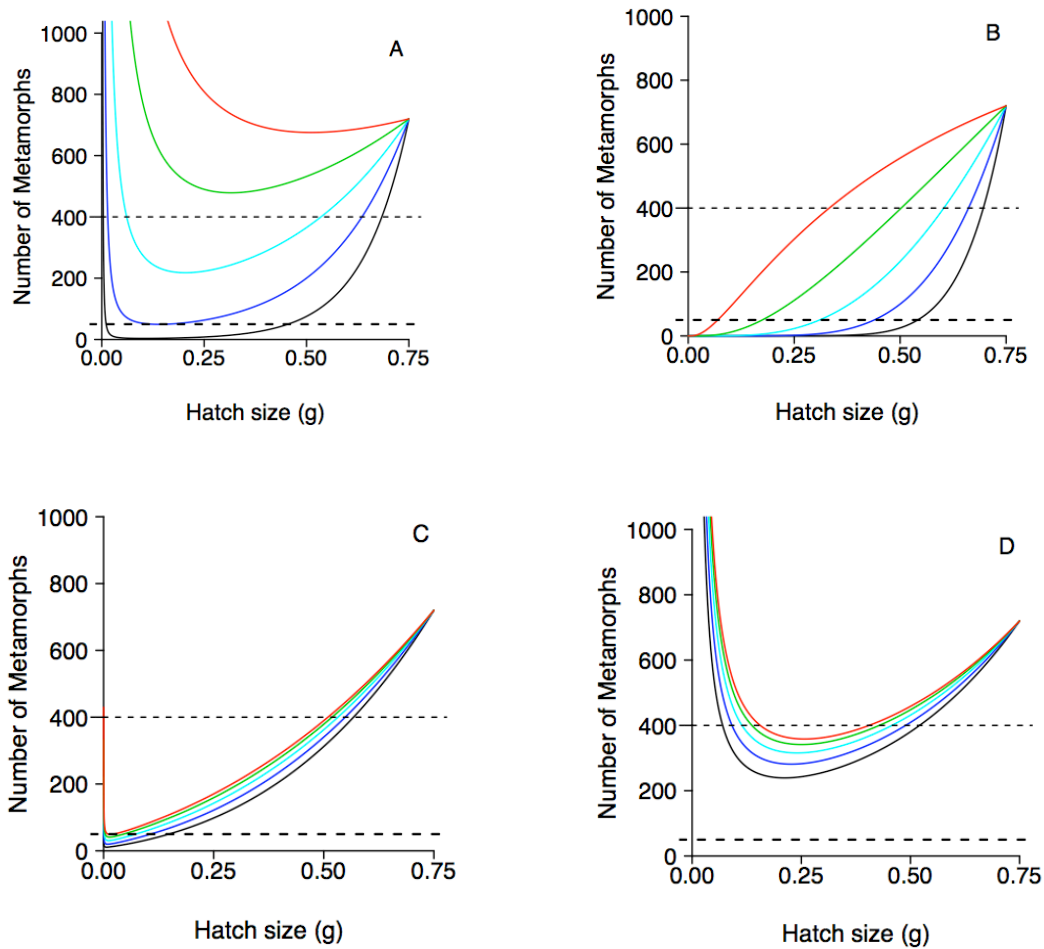


Figure 2.3. Effects of size- and temperature-dependent mortality during the planktonic phase on model predictions.

Positive (A) and negative (B) size-dependent mortality with constant component of daily mortality ($M_d = 0.15/d$), temperature dependent mortality (C) and temperature and positive size dependent mortality (D) ($M_d = .04$) as in Eqns 2.4b, 2.4c, 2.5a, and 2.5b respectively at different temperatures (black to red = 5 – 25 °C in increments of 5 °C), dashed lines indicate arbitrary levels of 50 and 400 larvae reaching metamorphosis as in Figure 2.2. Compare with scenario of constant mortality shown in Figure 2.2C.



References

- Bailey, K. M., and E. D. Houde. 1989. Predation on eggs and larvae of marine fishes and the recruitment problem. *Advances in Marine Biology* 25:1-83.
- Benoit, H. P., P. Pepin, and J. A. Brown. 2000. Patterns of metamorphic age and length in marine fishes, from individuals to taxa. *Canadian Journal of Fisheries and Aquatic Sciences* 57:856-869.
- Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage, and G. B. West. 2004. Toward a metabolic theory of ecology. *Ecology* 85:1771-1789.
- Charnov, E. L., and J. F. Gillooly. 2004. Size and temperature in the evolution of fish life histories. *Integrative And Comparative Biology* 44:494-497.
- Clarke, A. 1992. Reproduction in the cold: Thorson revisited. *Invertebrate Reproduction and Development* 22:175-184.
- Clutton-Brock, T. H. 1991. *The evolution of parental care*. Princeton University Press, Princeton.
- Collin, R. 2003. Worldwide patterns in mode of development in calyptraeid gastropods. *Marine Ecology-Progress Series* 247:103-122.
- Connell, S. D., and M. J. Anderson. 1999. Predation by fish on assemblages of intertidal epibiota: effects of predator size and patch size. *Journal of Experimental Marine Biology and Ecology* 241:15-29.
- Cowan, J. H., E. D. Houde, and K. A. Rose. 1996. Size-dependent vulnerability of marine fish larvae to predation: An individual-based numerical experiment. *Ices Journal of Marine Science* 53:23-37.
- Elliott, J. K., and W. C. Leggett. 1997. Influence of temperature on site-dependent predation by a fish (*Gasterosteus aculeatus*) and a jellyfish (*Aurelia aurita*) on larval capelin (*Mallotus villosus*). *Canadian Journal of Fisheries and Aquatic Sciences* 54:2759-2766.
- Emlet, R. B., L. R. McEdward, and R. R. Strathmann. 1987. Echinoderm larval ecology viewed from the egg. Pages 55-136 *in* M. Jangoux and J. M. Lawrence, editors. *Echinoderm Studies*. A.A. Balkema, Rotterdam.
- Finke, D. L., and R. F. Denno. 2005. Predator diversity and the functioning of ecosystems: the role of intraguild predation in dampening trophic cascades. *Ecology Letters* 8:1299-1306.
- Frank, K. T., B. Petrie, J. S. Choi, and W. C. Leggett. 2005. Trophic cascades in a formerly cod-dominated ecosystem. *Science* 308:1621-1623.

- Gallardo, C. S., and P. E. Penchaszadeh. 2001. Hatching mode and latitude in marine gastropods: revisiting Thorson's paradigm in the southern hemisphere. *Marine Biology* 138:547-552.
- Gillooly, J. F., J. H. Brown, G. B. West, V. M. Savage, and E. L. Charnov. 2001. Effects of size and temperature on metabolic rate. *Science* 293:2248-2251.
- Gillooly, J. F., E. L. Charnov, G. B. West, V. M. Savage, and J. H. Brown. 2002. Effects of size and temperature on developmental time. *Nature* 417:70-73.
- Griebeler, E. M., and K. Bohning-Gaese. 2004. Evolution of clutch size along latitudinal gradients: revisiting Ashmole's hypothesis. *Evolutionary Ecology Research* 6:679-694.
- Hart, M. W. 1995. What are the costs of small egg size for a marine invertebrate with feeding planktonic larvae? *American Naturalist* 146:415-426.
- Havenhand, J. N. 1993. Egg to Juvenile Period, Generation Time, and the Evolution of Larval Type in Marine-Invertebrates. *Marine Ecology-Progress Series* 97:247-260.
- Houde, E. D. 1989. Comparative growth, mortality and energetics of marine fish larvae: temperature and implied latitudinal effects. *Fishery Bulletin (Washington D C)* 87:471-495.
- Iverson, J. B., C. P. Balgooyen, K. K. Byrd, and K. K. Lyddan. 1993. Latitudinal variation in egg and clutch size in turtles. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* 71:2448-2461.
- Johns, D. M. 1981. Physiological studies on *Cancer irroratus* larvae. I. Effects of temperature and salinity on survival, development rate and size. *Marine Ecology-Progress Series* 5:75-83.
- Kiflawi, M. 2006. On optimal propagule size and developmental time. *Oikos* 113:168-173.
- Kinlan, B. P., and S. D. Gaines. 2003. Propagule Dispersal in Marine and Terrestrial Environments: A Community Perspective. *Ecology* 84:2007-2020.
- Kokita, T. 2003. Potential latitudinal variation in egg size and number of geographically widespread reef fish, revealed by common environment experiments. *Marine Biology* 143:593-601.
- Kolding, S., and T. M. Fenchel. 1981. Patterns of reproduction in different populations of five species of the amphipod genus *Gammarus*. *Oikos* 37:167-172.
- Lack, D. 1954. *The Natural Regulation of Animal Numbers*. Clarendon Press, Oxford.

- Laptikhovsky, V. 2006. Latitudinal and bathymetric trends in egg size variation: a new look at Thorson's and Rass's rules. *Marine Ecology-An Evolutionary Perspective* 27:7-14.
- Laurel, B. J., and I. R. Bradbury. 2006. "Big" concerns with high latitude marine protected areas (MPAs): trends in connectivity and MPA size. *Canadian Journal of Fisheries and Aquatic Sciences* 63:2603-2607.
- Lessios, H. A. 1987. Temporal and spatial variation in egg size in 13 Panamanian echinoids. *Journal of Experimental Marine Biology and Ecology* 114:217-239.
- Lessios, H. A. 1990. Adaptation and phylogeny as determinants of egg size in echinoderms from the two sides of the Isthmus of Panama. *The American Naturalist* 135:1-13.
- Lester, S. E., and B. I. Ruttenberg. 2005. The relationship between pelagic larval duration and range size in tropical reef fishes: a synthetic analysis. *Proceedings of the Royal Society, Series B* 272:585-591.
- Levin, L. A., and T. S. Bridges. 1995. Pattern and diversity in reproduction and development. Pages 1-48 *in* L. R. McEdward, editor. *Ecology of marine invertebrate larvae*. CRC Press, Inc, Boca Raton, Fl.
- Levin, L. A., J. Zhu, and E. Creed. 1991. The genetic basis of life history characters in a polychaete exhibiting planktotrophy and lecithotrophy. *Evolution* 45:380-397.
- Levitan, D. R. 1996. Predicting optimal and unique egg sizes in free-spawning marine invertebrates. *The American Naturalist* 148:174-188.
- Levitan, D. R. 2000. Optimal egg size in marine invertebrates: Theory and phylogenetic analysis of the critical relationship between egg size and development time in Echinoids. *The American Naturalist* 156:175-192.
- Litvak, M. K., and W. C. Leggett. 1992. Age and size-selective predation on larval fishes: the bigger-is-better hypothesis revisited. *Marine Ecology-Progress Series* 81:13-24.
- MacKenzie, B. R. 1988. Assessment of temperature effects on interrelationships between stage durations, mortality and growth in laboratory-reared *Homarus americanus* Milne Edwards larvae. *Journal of Experimental Marine Biology and Ecology* 116:87-98.
- Manoj Nair, R., and K. K. Appukuttan. 2003. Effect of temperature on the development, growth, survival and settlement of green mussel *Perna viridis* (Linnaeus, 1758). *Aquaculture Research* 34:1037-1045.
- McEdward, L. R., and L. K. Coulter. 1987. Egg volume and energetic content are not correlated among sibling offspring of starfish: Implications for life history theory. *Evolution* 41:914-917.

- McEdward, L. R., and K. H. Morgan. 2001. Interspecific relationships between egg size and the level of parental investment per offspring in echinoderms. *Biological Bulletin* 200:33-50.
- Mileikovsky, S. A. 1971. Types of larval development in marine bottom invertebrates, their distribution and ecological significance: a reevaluation. *Marine Biology* 10:193-213.
- Morgan, S. G. 1995. Life and Death in the Plankton: Larval mortality and adaptation. Pages 279-322 *in* L. R. McEdward, editor. *Ecology of Marine Invertebrate Larvae*. CRC Press, Inc., Boca Raton, Fl.
- O'Connor, M. I., J. F. Bruno, S. D. Gaines, S. E. Lester, B. S. Halpern, B. P. Kinlan, and J. M. Weiss. 2007. Temperature control of larval dispersal and implications for marine ecology, evolution, and conservation. *Proceedings of the National Academy of Sciences* 104:1266-1271.
- Pearse, J. S. 1994. Cold water echinoderms break 'Thorson's rule'. Pages 26-39 *in* K. J. Eckelbarger and C. M. Young, editors. *Reproduction, larval biology, and recruitment in the deep sea benthos*. Columbia University Press, New York.
- Pearse, J. S., and S. J. Lockhart. 2004. Reproduction in cold water: paradigm changes in the 20th century and a role for cidaroid sea urchins. *Deep-Sea Research Part II-Topical Studies In Oceanography* 51:1533-1549.
- Pearse, J. S., J. B. McClintock, and I. Bosch. 1991. Reproduction of Antarctic Benthic Marine Invertebrates: Tempos, Modes and Timing. *American Zoologist* 31:65-80.
- Pepin, P. 1991. Effect of Temperature and Size on Development, Mortality and Survival Rates of the Pelagic Early Life History Stages of Marine Fish. *Canadian Journal of Fisheries and Aquatic Sciences* 48:503-518.
- Pepin, P. 1993. An appraisal of the size-dependent mortality hypothesis for larval fish: comparison of a multispecies study with an empirical review. *Canadian Journal of Fisheries and Aquatic Sciences* 50:2166-2174.
- Pepin, P., and R. A. Myers. 1991. Significance of egg and larval size to recruitment variability of temperate marine fish. *Canadian Journal of Fisheries and Aquatic Sciences* 48:1820-1828.
- Pepin, P., T. H. Shears, and Y. de Lafontaine. 1992. Significance of body size to the interaction between a larval fish (*Mallotus villosus*) and a vertebrate predator (*Gasterosteus aculeatus*). *Marine Ecology-Progress Series* 81:1-12.
- Phillips, N. E. 2007. High variability in egg size and energetic content among intertidal mussels. *Biological Bulletin* 212:12-19.

- Rass, T. S. 1941. Geographic Parallelisms in Morphology and Development of Teleost Fish of Northern Seas. MOIP, Moscow.
- Rumrill, S. S. 1990. Natural mortality of marine invertebrate larvae. *Ophelia* 32:163-198.
- Savage, V. M., J. F. Gillooly, J. H. Brown, G. B. West, and E. L. Charnov. 2004. Effects of body size and temperature on population growth. *The American Naturalist* 163:E429-E441.
- Shanks, A. L., B. A. Grantham, and M. H. Carr. 2003. Propagule dispersal distance and the size and spacing of marine reserves. *Ecological Applications* 13:S159-S169.
- Siegel, D. A., B. P. Kinlan, B. Gaylord, and S. D. Gaines. 2003. Lagrangian descriptions of marine larval dispersal. *Marine Ecology-Progress Series* 260:83-96.
- Sinervo, B., and L. A. McEdward. 1988. Developmental consequences of an evolutionary change in egg size: an experimental test. *Evolution* 42:885-899.
- Smith, C. C., and S. D. Fretwell. 1974. Optimal Balance between Size and Number of Offspring. *American Naturalist* 108:499-506.
- Strathmann, R. R. 1974. Introduction to function and adaptation in echinoderm larvae. *Thalassia Jugoslav* 10:321-339.
- Strathmann, R. R. 1977. Egg size, larval development, and juvenile size in benthic marine invertebrates. *The American Naturalist* 111:373-376.
- Strathmann, R. R. 1985. Feeding and nonfeeding larval development and early life-history evolution in marine invertebrates. *Annual Review of Ecology and Systematics* 16:339-361.
- Thorson, G. 1950. Reproductive and larval ecology of marine bottom invertebrates. *Biological Review* 25:1-45.
- Vance, R. R. 1973. On reproductive strategies in marine bottom invertebrates. *The American Naturalist* 107:339-352.
- Werner, E. E., and J. F. Gilliam. 1984. The Ontogenetic Niche and Species Interactions in Size Structured Populations. *Annual Review of Ecology and Systematics* 15:393-425.
- West, G. B., J. H. Brown, and B. J. Enquist. 2001. A general model for ontogenetic growth. *Nature* 413:628-631.
- Yampolsky, L. Y., and S. M. Scheiner. 1996. Why larger offspring at lower temperatures? A demographic approach. *American Naturalist* 147:86-100.

CHAPTER 3

WARMING STRENGTHENS AN HERBIVORE-PLANT INTERACTION

Abstract:

Temperature has strong, predictable effects on metabolism. Through this mechanism, environmental temperature affects individuals and populations of poikilotherms by determining rates of resource use, growth, reproduction, and mortality. Predictable variation in metabolic processes such as growth and reproduction could affect the strength of species interactions, but the community-level consequences of metabolic temperature dependence are virtually unexplored. I experimentally tested the hypothesis that plant-herbivore interaction strength increases with temperature using a common species of marine macroalga (*Sargassum filipendula*) and the grazing amphipod *Ampithoe longimana*. Increasing temperature increased per capita interaction strength in two independent experiments, and reversed a positive effect of temperature on plant growth. Temperature did not alter palatability of plant tissue to herbivores or average herbivore feeding rate. A predictable effect of temperature on herbivore-plant interaction strength could provide key information toward understanding local food web responses to changing temperatures at different spatial and temporal scales. Efforts to extend the effects of physiological mechanisms to large scale patterns, including projections of the ecological effects of climate change, must be expanded to include the effects of changing conditions on trophic interactions.

Introduction

Understanding large-scale patterns as products of local processes involving individual organisms has been a central goal of ecological research for nearly a century (Gleason 1926, Paine 1966, Kareiva 1982, Brown et al. 2004). Individual organisms respond to their environment and to other organisms, and the integrated effects of these interactions create patterns at more complex levels of organization such as populations, communities and ecosystems (Schoener 1986, Kingsolver 1989, Helmuth et al. 2006). The complexity of variation among individuals and their responses to the environment can impede a general understanding of the link between the environment and community-level patterns and processes. However, variation in consumption, growth, and reproduction can be explained at least in part by predictable effects of environmental temperature on individual metabolic rate (Davison 1987, Sanford 1999). Indeed, many studies have shown that temperature can differentially influence species within a community, substantially affecting the outcome of competitive and trophic interactions (Park 1954, Sanford 1999, Thompson et al. 2004, Yee and Murray 2004, Morelissen and Harley 2007).

The metabolic theory of ecology describes the potential for fundamental biochemical constraints of temperature on enzyme kinetics to determine not only whole organism metabolic rate, but also broad ecological patterns of species diversity, population dynamics and carbon cycling (Brown et al. 2004, Allen et al. 2005). This theory therefore provides a testable hypothesis that there is a general and predictable, mechanistic link between individual-environment interactions and larger scale ecological patterns. Although this hypothesis has been tested at large scales using statistical methods and theoretical models (Allen et al. 2005, Vasseur and McCann 2005), the role of such simple and general metabolic

constraints on local species interactions involving the simultaneous responses of species at different trophic levels to environmental temperature remains poorly understood. A predictable effect of temperature on individual-level food web interactions over relatively short scales of space and time would suggest that metabolic theory is relevant not only to very broad spatial scales, but also to local responses to environmental changes such as those expected with seasons, land use change, or climate change.

Nearly all food webs include herbivore-plant interactions, and the strength of these interactions determines the abundance of primary producers in a community (Lubchenco and Gaines 1981, Hawkins and Hartnoll 1983, Paine 1992, Duffy and Hay 2000). Understanding processes that drive variation in interaction strength will enhance a broader understanding of the distribution of plant biomass and food web dynamics. ‘Interaction strength’ is an estimate of the magnitude of effect of one species on another (Laska and Wootton 1998), and has been quantified using a variety of metrics that differ in their scope and assumptions (Berlow *et al.* 2004). Generally, interaction strength metrics quantify either the per capita or species level effect of one species on another’s abundance or population dynamics (May 1973, Wootton 1997). A negative interaction strength indicates that one species reduces the abundance (or parameter of interest) of another species, and the absolute value indicates the strength of this effect. Per capita interaction strength metrics typically describe the abundance or density of a target species (e.g., the plant) in the presence and absence of a known density of another species (e.g., the herbivore), while species level effects describe all the direct and indirect effects of a population of one species on some property of the other (MacArthur 1972, Wootton 1997, Laska and Wootton 1998). Quantitative interaction strength metrics for a given species pair can vary with environmental context or internal

factors such as population density (Paine 1992, Wootton 1997, Ruesink 1998). Whether through shifts in per capita or species level effects, stronger interactions result in greater effects of herbivores on plant biomass (Lubchenco and Gaines 1981, Hawkins and Hartnoll 1983, Paine 1992).

Herbivore-plant interaction strength integrates the effects of two distinct metabolic processes: consumption by herbivores and primary production by plants. Numerous studies have shown that these processes are differentially influenced by environmental factors such as temperature and light, and their relative sensitivity can alter the strength and outcome of trophic interactions (i.e., Gaines and Lubchenco 1982, Cubit 1984, Sanford 1999, Thompson et al. 2004). Although plant metabolism consists of both photosynthetic and respiratory processes, the rate of primary production is limited by the rate of carbon fixation during photosynthesis (Farquhar et al. 1980, Dewar et al. 1999). Herbivore consumption rates are linked to herbivore metabolism and therefore are limited by rates of cellular respiration (Taylor *et al.* 1982), which are generally more sensitive to temperature than rates of photosynthesis (Allen et al. 2005, Padilla-Gamino and Carpenter 2007). With increasing temperature and adequate light and nutrient supplies, increasing primary production should lead to greater plant growth rates and biomass accumulation (Padilla-Gamino and Carpenter 2007), while consumption by herbivores should also increase to an even greater degree. Although this differential temperature dependence of respiration and photosynthesis has generally been considered in the context of within-plant metabolism (Davison et al. 1991) or net metabolism of large ecosystems (del Giorgio *et al.* 1997), this difference should also apply to the net metabolism of local food webs. All else being equal, at higher temperatures consumption rates should match or exceed elevated rates of primary production. In other

words, assuming no correlated variation in light or nutrient levels, at higher temperatures herbivore-plant interactions should be stronger and plant biomass should be more limited by consumption than at lower temperatures (Figure 3.1). This prediction is consistent with observed effects of warming in prairie, forest and rocky intertidal communities (Ritchie 2000, Logan et al. 2003, Thompson et al. 2004), and biogeographical and temporal patterns of ocean plankton food web structure (Behrenfeld et al. 2006, Lopez-Urrutia et al. 2006), though the mechanism outlined here has not been widely invoked.

The simple prediction of how temperature should influence trophic interactions could be complicated by several aspects of plant and herbivore ecology. Temperature-driven increases in metabolic rate often lead to increased demand for resources and therefore increased feeding (Sanford 2002). However, if increased resource use is balanced by less efficient metabolic processing rather than channeled to growth or reproduction, or if increased production becomes limited by other resources, the net temperature effect could be reduced ecological performance (Sanford 2002, Somero 2002). Another possible effect of increased temperature is altered chemistry of certain metabolic pathways (Hochachka and Somero 2002). For example, plants may alter the production of certain compounds and become more or less palatable to their consumers as an ancillary effect of elevated temperature. Finally, individuals can acclimate to changes in temperature so that after a short acclimation period (hours to days), metabolic rates return to a base level (Davison *et al.* 1991). Any of these changes would reduce the predicted effect of temperature on interaction strength.

I investigated the effects of temperature on plant and animal growth rates and whether these effects translate to a temperature dependence of interaction strength at a local scale.

Specifically, I tested the hypothesis that the negative effect of herbivores on plant biomass strengthens with increasing environmental temperature (Figure 3.1). I predicted that such an effect of temperature could be explained by differential temperature dependence of plant and herbivore instantaneous metabolic rates and subsequent effects on plant growth and herbivore consumption rates. These experiments testing the temperature dependence of interaction strength between two species explore a possible link between temperature dependence of metabolism and community structure.

Methods

Study organisms and collection

I tested the effect of temperature on the interaction between the common subtidal herbivorous amphipod *Ampithoe longimana* and the benthic brown macroalga *Sargassum filipendula* (hereafter, *Sargassum*). *Sargassum* commonly dominates subtidal macroalgal canopies on coastal hard substrates throughout the tropical and temperate Atlantic Ocean (Schneider and Searles 1991). *A. longimana* is an important consumer of macro- and microalgae on the U.S. East coast, and its strong grazing effect on *Sargassum* and other algae is seasonally controlled through predation (Duffy and Hay 2000). In addition to the temperature variation over their wide geographic ranges, these species persist year-round in temperate regions with wide annual variation in temperature. For example, temperatures range from approximately 6 – 30 °C between January and August in Bogue Sound, NC, where both *Sargassum* and *A. longimana* thrive (Figure 4.3). Responses to changing temperature of those species that persist year-round through local temperature variations

provide an interesting case study for understanding the effects of temperature on ecological interactions.

Amphipods and seaweeds were collected from Radio Island Jetty (RIJ) near Morehead City, North Carolina (34° 42' W, 76° 46' N). Average (\pm s.d.) *Sargassum* cover was 361 (\pm 156) g wet weight *Sargassum* / 0.06 m². Amphipods were removed from algae by hand, and maintained in culture indoors at 24-28°C (ambient incoming seawater) for 1-4 weeks prior to experiments. Algae were collected and immediately transported to the laboratory in a cooler filled with seawater within 6 hours of starting the experiments. All experiments were conducted in a temperature-controlled, indoor facility at the University of North Carolina's Institute of Marine Science.

Measuring the effect of temperature on interaction strength

Temperatures normally experienced by an individual have non-lethal effects on individual metabolism, also called physiological rate effects, while extreme temperatures have stressful or lethal effects (Hochachka and Somero 2002, Sanford 2002). In general, physiological stress reduces the performance of individuals and shifts the importance of species interactions in a community from predation and competition to facilitation (Menge and Sutherland 1987, Bruno et al. 2003). Like stress responses, non-stressful responses to temperature can moderate the role of a species in a community, although generally the stress responses have received the most attention. One important difference between physiological stress effects and physiological rate effects is that stress effects reduce performance (Menge and Sutherland 1987), while physiological rate effects can increase or decrease the

performance of an individual without long-term effects (Sanford 2002, Thompson et al. 2004).

I conducted two independent growth experiments to test the effects of non-lethal temperatures on amphipod-algae interaction strength. Both experiments were designed to test the effect of a range of non-lethal temperatures on algal growth in the presence and absence of herbivores. The two experiments differed in design, specifically in the number of experimental factors, the range and levels of manipulated temperatures, and pairing of replicates. The first experiment (*Experiment I*) was a three-way factorial design testing the effects of temperature (4 levels), herbivory and experimental duration on algal growth. All replicates were set up on June 14th, 2007, and half were chosen randomly to run for 11 days (*Experiment I_s*) and the other half for 17 days (*Experiment I_l*). The two durations tested whether the effect of temperature changed over time, due to processes such as acclimation of organisms, herbivore population dynamics or carrying capacity of the mesocosms. Replicates in +/-0 herbivore treatments were paired by position in the table. The second experiment (*Experiment II*) tested the effect of 5 temperature levels over 14 days beginning on July 2nd, 2007. In this experiment, replicates of + and 0 herbivore treatments were paired according to algal plants (clones), controlling for within-plant variation in palatability and growth rate by including basal and mid stipe or tip portions of each clone in each mesocosm of the paired replicates (Taylor *et al.* 2002).

Paired replicates were used to calculate the per capita effect of herbivores by comparing the final biomass of algae in the presence and absence of herbivores according to Eqn 3.1:

$$DI = \ln \left[\frac{S_{t,A>0}}{S_{t,A=0}} \right] = -c_{S,A} At \quad \text{Eqn 3.1}$$

where interaction strength is the daily per capita effect ($-c_{S,A}$) of a known density of *A. longimana* (*A*) on *Sargassum* (*S*) biomass over a known period of time (*t* in days), as estimated by the natural log of the ratio of final *Sargassum* biomass in the presence ($S_{t,A>0}$) and absence ($S_{t,A=0}$) of herbivores (Wootton 1997). This metric, called the dynamic index (DI) by Berlow et al. (1999), is ideal for short term experiments because it does not assume equilibrium dynamics and when applied to a pair of species under controlled conditions is not confounded by unidentified indirect interactions (Wootton 1997, Laska and Wootton 1998). The species level effect ($-c_{S,A}At$) takes into account both density and per capita effects over the duration of the experiment. The DI is related to theoretical metrics of interaction strength in food web models (Wootton 1997).

In both experiments, measurements were made of initial and final algal biomass and final herbivore density (see Appendix B for detailed methods). Algae and amphipods were placed in 6-L plastic mesocosms and received a fresh supply of temperature conditioned, gravel filtered seawater. Mesocosms were grouped in water tables equipped with a full-spectrum aquarium light (10 K Ushio bulbs and T-5 fluorescent lighting with true actinic bulbs set on a 15L:9D timer cycle) that maintained light levels between 250 – 300 $\mu\text{mol photons} / \text{m}^2 / \text{s}$. These light levels are less than summertime full sun levels at 1 m depth in the field ($\sim 1000\text{-}1500 \mu\text{mol photons} / \text{m}^2 / \text{s}$), but are well within the range of light conditions experienced throughout the tidal cycle in turbid water at RIJ (i.e., $\sim 200 \mu\text{mol photons} / \text{m}^2 / \text{s}$ at 1 m depth on cloudy days in June and July 2007, M. Piehler, unpublished data) and well

above typical compensation irradiances for shallow subtidal algae ($\sim 2\text{-}11 \mu\text{mol photons} / \text{m}^2 / \text{s}$ (Lobban and Harrison 1997)). Nutrient levels (NO_x , NH_4 and PO_4) in flow-through seawater were consistent with ambient levels in Bogue Sound.

Starting conditions for each mesocosm were 20 g wet weight *Sargassum* and 10 adult *A. longimana*, including at least 2 males and 2 females. These grazer densities are consistent with field observations from June 2007 of 10 ± 1.1 amphipods or isopods (including 2 ± 1.3 *A. longimana*) per 20 g *Sargassum*. Final amphipods were grouped into two size classes: $> 3\text{mm}$ long (juveniles and adults) and $< 3\text{ mm}$ (newborns); densities of amphipods $> 3\text{ mm}$ at the end of the experiment were used to calculate interaction strengths because these individuals would have been born early enough in the experiment to have had a grazing impact by the end. Interaction strengths, final herbivore density and daily average *Sargassum* growth rates were analyzed with ANOVA.

Herbivore feeding preference

Increasing temperature could alter plant tissue chemistry and thus palatability to herbivores. To explore this possibility, I conducted a set of feeding assays in which adult *A. longimana* were exposed to live *Sargassum* tissue sampled from temperature treatments near the end of *Experiment II*. Two $30 (\pm 2)$ mg pieces of *Sargassum* leaf were offered to one fresh adult *A. longimana* in a small cup for 48 hours. I tested four hypotheses using four concurrent assays ($n = 32$). Herbivores were given a choice of algal tissue from + and 0 herbivore treatments at 24.5°C (Assay 1) and 28.9°C (Assay 2). Comparison of effect sizes between these two independent assays would determine whether prior exposure to herbivores affected leaf palatability, and whether this effect varies with temperature. In a second set of

assays, herbivores were presented with a choice of algal tissue from 24.5°C and 28.9°C treatments from 0 (Assay 3) and + herbivore treatments (Assay 4). An additional assay (Assay 5) with no *A. longimana* was used to control for autogenic tissue loss. Replicates were discarded prior to analysis if *A. longimana* died during the assay or if the total amount consumed did not exceed 3 mg (weighing error) (Taylor *et al.* 2002). Assays were analyzed with a paired t-test.

Herbivore feeding rate

I conducted feeding rate assays in August 2007 to test the effect of temperature on per capita *A. longimana* feeding rates. For these, *Sargassum* and *A. longimana* were cultured at two temperatures (25 and 29°C) for 7 days prior to assays. Adult *A. longimana* were given one 30 (\pm 1) mg piece of *Sargassum* leaf tissue from the same temperature treatment, and final algal biomass was measured after approximately 48 hours (n = 32). *Sargassum* tissue was also tested for autogenic loss (n = 32) at each temperature. Feeding rate assays were analyzed with a two-way ANOVA.

Respiration and Photosynthesis measurements

To estimate the performance of metabolic pathways (net photosynthesis and respiration) under experimental conditions, I measured oxygen production and consumption rates for *Sargassum* and *A. longimana* under identical light and nutrient conditions as the growth experiments. As for the feeding rate assays, algal tissue and amphipods were incubated for 7 days at 25 and 29°C to approximate experience of organisms in the lowest and highest treatments in *Experiment II* and allow time for acclimation to the experimental

temperatures (Davison 1991). To measure oxygen production or consumption, initial and final oxygen concentrations were measured for *Sargassum* ($0.8 \pm .02$ g of leaf tissue), *A. longimana* (4 adults) and paired blanks (seawater only) (n=7) using a YSI-85 oxygen sensor. After the initial measurement, cups were covered with plastic to minimize exchange of oxygen with the air and left undisturbed for approximately 80 minutes for *Sargassum* assays and 18 hours for amphipod assays. Net photosynthesis rates were estimated by subtracting measurements of dark oxygen consumption from light oxygen production. Oxygen evolution tests were analyzed with a t-test on calculated change in $[O_2]$ with temperature. All statistical analyses were performed in R (v. 2.4.0).

Results

Growth experiments

Temperatures fluctuated diurnally and over the course of both experiments due to natural fluctuation in the incoming water temperature, but differences among temperature treatments were maintained (ANOVA with post hoc Tukey tests between all pairs, $p < 0.001$ for both experiments). Mean \pm s.d. temperatures for *Experiment I* were 23.4 ± 1.6 , 25.3 ± 1.4 , 25.8 ± 1.4 , and 27.7 ± 1.4 °C (n = 4, 2, 2, and 4, respectively, for each level of herbivory (0, 1) at each temperature). In *Experiment II*, temperatures were 24.5 ± 1.3 , 25.7 ± 1.5 , 26.3 ± 1.4 , 28.4 ± 1.2 and 28.9 ± 0.9 °C (n = 4 for each level of herbivory (0, 1) at each temperature).

The absolute value of daily per capita interaction strength ($-c_{S,A}$) increased with temperature in both experiments from zero (no net measurable interaction) at low

temperatures to a negative interaction strength at higher temperatures (Table 3.1, Figure 3.2 A-C). Species level interaction strength ($-c_{S,A}t$) was not affected by temperature in *Experiment I*, but increased with experimental duration (mean: -0.02 in *Experiment I_s* and -0.14 in *Experiment I_l*). In *Experiment II*, species-level interaction strength increased with temperature (Table 3.1). There was no effect of temperature on final herbivore density, although densities increased with experimental duration in *Experiment I_l* due to the greater time allowed for reproduction (Table 3.1, Figure 3.2D-E). One replicate in *Experiment I_l* (at 25.3 °C) and two replicates in *Experiment II* (one each at 25.7 and 28.9 °C) were excluded from analyses because algae had severely senesced by the end of the experiments. Senescence occurs naturally in the field and can affect just part of the plant, so these replicates likely reflected natural aging of the plant and not treatment effects.

The stronger effect of herbivores at warmer temperatures reduced or reversed the positive effect of temperature on *Sargassum* growth in the absence of herbivores in both experiments (Figure 3.3). The effect of temperature on algal growth varied with experimental duration (Table 3.1), shifting from no effect in the shorter replicates of *Experiment I* to a weak, positive effect in the longer replicates.

Herbivore Feeding Assays

Assays to determine whether herbivore-plant interactions vary with temperature due to responses of plant defenses to growing temperature also revealed no significant trend (Table 3.2). There were also no significant differences among mean per capita feeding rate of *A. longimana* on *Sargassum* leaves between 25 and 29 °C (two way ANOVA: temperature $p = 0.19$, herbivore $p < 0.01$, interaction $p = 0.15$). There was, however, a trend toward higher

consumption rates and greater variation among replicates (CVs: +H_{25°C} = 11.8% and +H_{29°C} = 16.7%) at the higher temperature (Figure 3.4).

Photosynthesis and Respiration

Oxygen consumption did not vary with temperature for *A. longimana* (mean \pm s.e. at 25 °C = -0.012 ± 0.002 $\mu\text{g O}_2 / \text{L} / \text{amphipod} / \text{hr}$; 29 °C = -0.006 ± 0.003 $\mu\text{g O}_2 / \text{L} / \text{amphipod} / \text{hr}$, t-test $p = 0.14$) or *Sargassum* (mean \pm s.e. at 25 °C = -0.7 ± 0.2 $\mu\text{g O}_2 / \text{L} / \text{g tissue} / \text{hr}$, 29 °C = -0.4 ± 0.2 $\mu\text{g O}_2 / \text{L} / \text{g tissue} / \text{hr}$, t-test $p = 0.38$). *Sargassum* produced more oxygen at the cooler temperature (mean \pm s.e. at 25 °C = 4.2 ± 0.2 $\mu\text{g O}_2 / \text{L} / \text{g tissue} / \text{hr}$, 29 °C = 2.9 ± 0.2 $\mu\text{g O}_2 / \text{L} / \text{g tissue} / \text{hr}$, t-test $p < 0.05$). Net photosynthesis rates were approximately $3.5 \mu\text{g O}_2 / \text{L} / \text{g tissue} / \text{hr}$ at 25 °C and $2.5 \mu\text{g O}_2 / \text{L} / \text{g tissue} / \text{hr}$ at 29 °C.

Discussion

The strength of species interactions is one of the most important metrics of community dynamics. Systematic variation in interaction strength with temperature could be a key to understanding changes in community structure associated with seasonal, geographic or climate variation. Consistent with the hypothesis based on metabolic theory (Figure 3.1), these experiments show that increasing temperature can strengthen an herbivore-plant interaction. Increasing temperature lead to a nearly 100% reduction in algal average daily growth by herbivores at high temperatures relative to growth at lower temperatures with or without herbivores (Figure 3.3C). Temperature explained more than 20% of the variation in

per capita interaction strength (Figure 3.2 A-C), leaving less unexplained variation than in other studies (Paine 1992, Berlow 1999).

Stronger species interactions can be caused by increased abundance or increased per capita effects. In these experiments, increased herbivore per capita effects were not accompanied by clear changes in herbivore density (Table 3.1, Figure 3.2 D-F). Final amphipod densities were highly variable among replicates, possibly due to variable population growth rates resulting from loosely constrained initial amphipod sex ratios, and this variation may have obscured a more subtle temperature effect. In any case, the relatively constant final herbivore densities across temperature treatments lead to the expectation that the stronger per capita effects should increase the total effect of the herbivore assemblage with temperature. Species-level interaction strength ($-c_{S,A}At$) increased with temperature in *Experiment II* as expected, but not in *Experiment I*. The lack of a temperature effect on species level interaction strength in *Experiment I* is unexpected given the significant increase in per capita interaction strength and algal daily growth with temperature, and the absence of an increase in herbivore density. A probable explanation is the difference in pairing method used for replicates across herbivory treatments in *Experiment I* (position in the water table) relative to *Experiment II* (algal clone and position). The less precise method used in *Experiment I* likely contributed more error to the interaction strength estimates. Another difference between experiments is the range of temperature levels tested. Temperatures in *Experiment II* are shifted about one degree Celsius warmer relative to *Experiment I*, reflecting a seasonal warming that occurred during the two weeks between the start of the first and second experiments. The similarity of the overall patterns of per capita, density and algal growth responses between the two experiments suggests that

the slightly different temperature range does not explain the species-level interaction strength results. A temperature-dependent herbivore effect is apparent in both experiments, and is further illustrated by the additional analysis of algal biomass accumulation (Figure 3.3), which does not require pairing of replicates across treatments.

Herbivores reproduced and density increased over time in nearly all replicates. Higher final densities led to lower estimates of per capita interaction strength values in the 17-day relative to the 14-day replicates of *Experiment I* (Figure 3.1C). The final populations were comprised of many smaller individuals with lower feeding rates relative to the initial conditions or the shorter replicates of *Experiment I*. The use of final density of herbivores larger than 3mm to calculate interaction strength deviates from convention because these densities were not constant throughout the experiment. However, this approximation is consistent for all treatments and experiments, and because there is no trend in final density with temperature, it is a reasonable approximation of per capita interaction strength while also testing population level responses. Much longer experiments that allow for equilibrium population structure could more completely reveal the effects of temperature on both per capita and species-level effects.

Although per capita interaction strength increased with temperature as predicted, the underlying mechanism appears to be more complex than a straightforward, temperature-dependent effect of metabolic rate on primary and secondary production. A simple extrapolation of metabolic theory to individual-scale processes leads to the prediction that as temperature increases, the rate of basic metabolic processes will also increase due to the kinetic effects of temperature on fundamental cellular processes (Brown et al. 2004). In the case of consumers, consumption rates should increase along with metabolic demands

(Sanford 2002). However, feeding assays revealed no effect of temperature on mean amphipod feeding rate (Figure 3.4). The assays did indicate increased variation in feeding rates at higher temperatures, and a wider range of feeding rates at warmer temperatures could explain the trend in interaction strength observed in the mesocosm experiment. For example, four grazing rates observed at 29 °C were higher than any observed at 25 °C. The population average grazing rate may not change, but if a few individuals respond strongly to temperature, they could drive the overall trend in interaction strength (Figure 3.3). Such variation in interaction strength among individuals has been observed in several other studies (reviewed by Berlow 1999), and locally can be as influential as interactions that are, on average, stronger.

When attempting to explain individual performance in terms of metabolic response to environmental factors on ecologically relevant time scales of days to weeks, it is important to consider the effects of acclimation. Short-term studies (minutes to hours) of photosynthesis and respiration rates often yield strong temperature effects, but longer studies following acclimation periods of hours to days show that these differences can change as organisms modify enzyme concentrations, pH or other factors relevant to metabolic functioning to compensate for the effects of temperature (Davison 1987, Lobban and Harrison 1997, Padilla-Gamino and Carpenter 2007). Such compensation may explain the absence of a temperature effect on *A. longimana* and *Sargassum* respiration rates following the seven-day acclimation period in the present study. The negative effect of temperature on *Sargassum* photosynthetic rate may be a combined effect of compensation and subsaturating light levels. At low light levels, warming can increase the compensation irradiance and reduce or reverse a positive effect of temperature on photosynthetic rate (Davison 1991). The subsaturating

light levels in these experiments were well above compensation irradiance, and these conditions are realistic approximations of algal performance in the field because most subtidal algae live and grow at subsaturating light levels (Davison 1991, Lobban and Harrison 1997). The effect of acclimation on the relationship between metabolic rate and growth is complicated (Lobban and Harrison 1997). These results support the expectation that *Sargassum* growth would not change or may decline with an increase in temperature over about one week, and indeed there was no clear effect of temperature on algal growth in the short, no-herbivore replicates of *Experiment I* (Figure 3.3A). Over the longer durations, however, temperature appears to have positive effect on *Sargassum* daily growth (Figure 3.3B-C), suggesting that the process of acclimation takes longer than seven days and the predicted effects of temperature on growth become apparent over longer durations.

Recently, several authors have called for physiological ecology to become incorporated into macroecological thinking, as a key to understanding the mechanistic basis of biogeographic patterns such as range boundaries, species distributions, and the intensity of carbon cycling (Chown and Gaston 1999, Allen et al. 2005, Helmuth et al. 2006, Osovitz and Hofmann 2007). Such development is indeed necessary, although when extrapolating local physiological mechanisms of temperature response to larger-scale patterns, trophic interactions need to be considered. For example, when considering plant physiology alone, one would predict increasing growth and associated increases in biomass with increasing temperature as long as variability in nutrients and light are constrained. However, when herbivores are included in the experimental system, plant growth or daily biomass accumulation can actually decline with increasing temperature (Figure 3.3C; Thompson et al. 2004). Temperature dependent trophic interaction strength could explain large-scale

observations of increasing interaction strengths between herbivores and plants with decreasing latitude (Pennings and Silliman 2005) or of open ocean ecosystems tending toward net heterotrophy in warmer regions (del Giorgio et al. 1997, Lopez-Urrutia et al. 2006).

In nature, temperature variation is not always correlated with variation in other factors that are known to influence primary production and trophic interactions, such as light intensity and nutrients. In fact, decoupled variation in these factors with climate change has caused major phenological shifts in marine pelagic communities in which some species respond to changes in temperature while others are dependent on seasonal changes in light (Edwards and Richardson 2004). Such mismatched phenological shifts can dramatically alter community structure, but the temperature conditions at any given time will influence the interactions and energy flow among species present. Therefore, phenological responses to the decoupling of temperature and light patterns and temperature effects on interaction strength are complementary processes affecting community response to climate change.

Understanding ecological processes in terms of individual organisms will be most informative if individual-level attributes vary systematically with environmental factors. Our ability to predict and manage ecological systems in the face of climate change is hampered by a limited understanding of how changing climate conditions influence important demographic and community-level processes (Davis et al. 1998a). To date, the majority of observed effects of climate change, such as pole-ward range shifts or altered phenology (Parmesan and Yohe 2003), have been species-specific resulting in a decoupling of many species interactions (Edwards and Richardson 2004, Helmuth et al. 2006). These observations have led to the suggestion that individualistic responses to climate imply no

general effects on community processes (Davis et al. 1998b). However, systematic effects of temperature on metabolism link ecological processes at the level of individuals to communities and ecosystems through processes such as rates of energy flow in food webs and interaction strength (Ryan 1991, Allen et al. 2005). Predictable phenotypic responses to non-lethal changes in environmental conditions, when considered in multi-trophic contexts, may in fact provide an important mechanistic link between local climate conditions and ecological processes.

Tables.

Table 3.1. Summary of ANOVA on the effect of temperature on daily per capita ($-c_{S,A}$) and species interaction strength ($-c_{S,A}At$) and amphipod density in two experiments.

$p < 0.05$ in bold.

Experiment	Source	df	MS	F	P
Daily Per Capita Interaction Strength					
I	Temperature	1	1.346 x 10 ⁻⁶	6.449	0.020
	Duration	1	2.931 x 10 ⁻⁷	1.404	0.251
	Temperature x Duration	1	8.128 x 10 ⁻⁷	3.894	0.063
	Error	19	2.087 x 10 ⁻⁷		
II	Temperature	1	1.683 x 10 ⁻⁷	6.590	0.021
	Error	16	2.553 x 10 ⁻⁸		
Species Interaction Strength					
I	Temperature	1	0.047	2.828	0.109
	Duration	1	0.077	4.653	0.044
	Temperature x Duration	1	0.002	0.124	0.729
	Error	19	0.017		
II	Temperature	1	0.085	7.607	0.014
	Error	16	0.011		
Final Amphipod Density					

I	Temperature	1	2858	3.949	0.062
	Duration	1	58250	80.864	<0.001
	Temperature x Duration	1	2861	3.953	0.061
	Error	19	724		
II	Temperature	1	3306	3.100	0.097
	Error	16	1066		

Table 3.2. Summary of ANOVA on the effect of temperature and herbivory on daily *Sargassum* growth.

For *Experiment I*, a three-way ANOVA on temperature, herbivory, and duration was used, and for *Experiment II*, a two-way ANOVA on temperature and herbivory was used. $p < 0.05$ in bold.

Experiment	Source	df	MS	F	p
I	Temperature	1	0.469	3.309	0.077
	Herbivory	1	1.078	7.605	0.009
	Duration	1	1.289	9.091	0.005
	Temperature * Herbivory	1	0.650	4.583	0.039
	Temperature * Duration	1	1.611	11.362	0.002
	Herbivory * Duration	1	0.398	2.807	0.102
	Temperature * Herbivory * Duration	1	0.001	0.010	0.921
	Error	39	0.142		
II	Temperature	1	0.002	0.013	0.911
	Herbivory	1	0.742	5.498	0.025
	Temperature * Herbivory	1	0.584	4.317	0.046
	Error	33	0.135		

Table 3.3. Summary of paired T-tests on the palatability of *Sargassum* tissue sampled from different temperature and herbivory treatments in *Experiment II*.

‘Clones’ indicates whether leaves for each feeding assay were drawn from algal clones, and ‘Condition’ indicates which treatment was held constant for the feeding assay. ‘Choice’ indicates the two pieces of *Sargassum* offered to each *A. longimana*. Mean \pm s.d. tissue loss in each assay is presented in the ‘Loss’ column. There was no difference among treatments in autogenic loss of tissue (two-way ANOVA: temperature $p = 0.10$, herbivore $p = 0.17$, temperature x herbivore $p = 0.24$).

Assay	Clones	Condition	Choice	Loss (mg)	t	p	n
1	Yes	28.9°C	0 / + herbivore	4.1 \pm 4.8 / 5.3 \pm 5.1	0.57	0.573	19
2	Yes	24.5°C	0 / + herbivore	4.6 \pm 2.7 / 4.3 \pm 3.4	-0.27	0.789	24
3	No	0 herbivore	28.9 / 24.5°C	4.0 \pm 3.6 / 5.2 \pm 4.6	0.71	0.486	22
4	No	+ herbivore	28.9 / 24.5°C	2.8 \pm 3.8 / 6.7 \pm 6.7	1.80	0.086	23
5			Autogenic loss	0.2 \pm 1.5			32

Figures.

Figure 3.1. Conceptual model of the effect of temperature on herbivore effects.

Effect of temperature on (A) the interaction strength between herbivores and plants (solid line), zero indicated by dashed line, and (B) standing plant biomass with (dashed lines) and without herbivores (solid line). A strong herbivore-plant interaction (dotted line) could lead to a negative effect of increasing temperature on standing plant biomass.

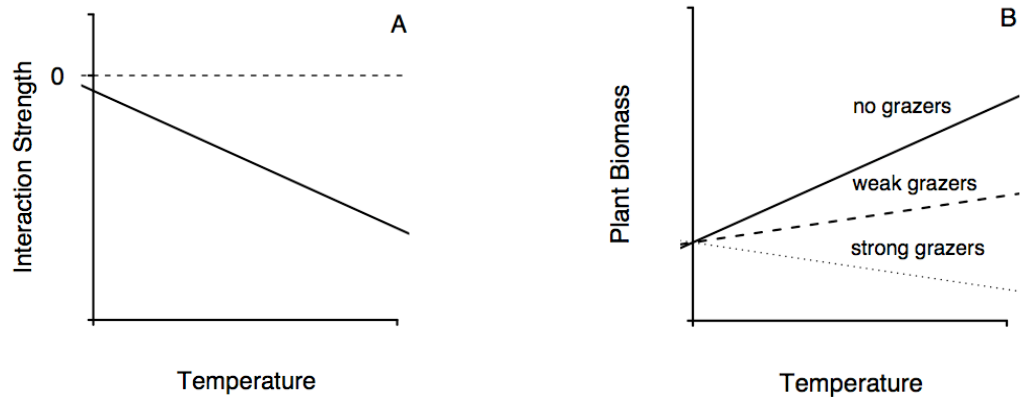


Figure 3.2. Effects of temperature on interaction strength and herbivore density.

The effect of temperature ($^{\circ}\text{C}$) on mean (\pm s.d.) daily per capita interaction strength ($\ln[\text{g}]/\text{amphipod}/\text{day}$) between *A. longimana* and *Sargassum* ($-c_{S,A}$, Eqn 3.1) in Experiments (A) I_s , (B) I_l , and (C) II , and on mean (\pm s.d.) final density of *A. longimana* $> 3\text{mm}$ (\bullet) and $< 3\text{mm}$ (\circ) in Experiments (D) I_s , (E) I_l , and (F) II . Solid lines connect observed means for statistically significant temperature effects (Table 3.1), and dashed lines indicate interaction strength = 0.

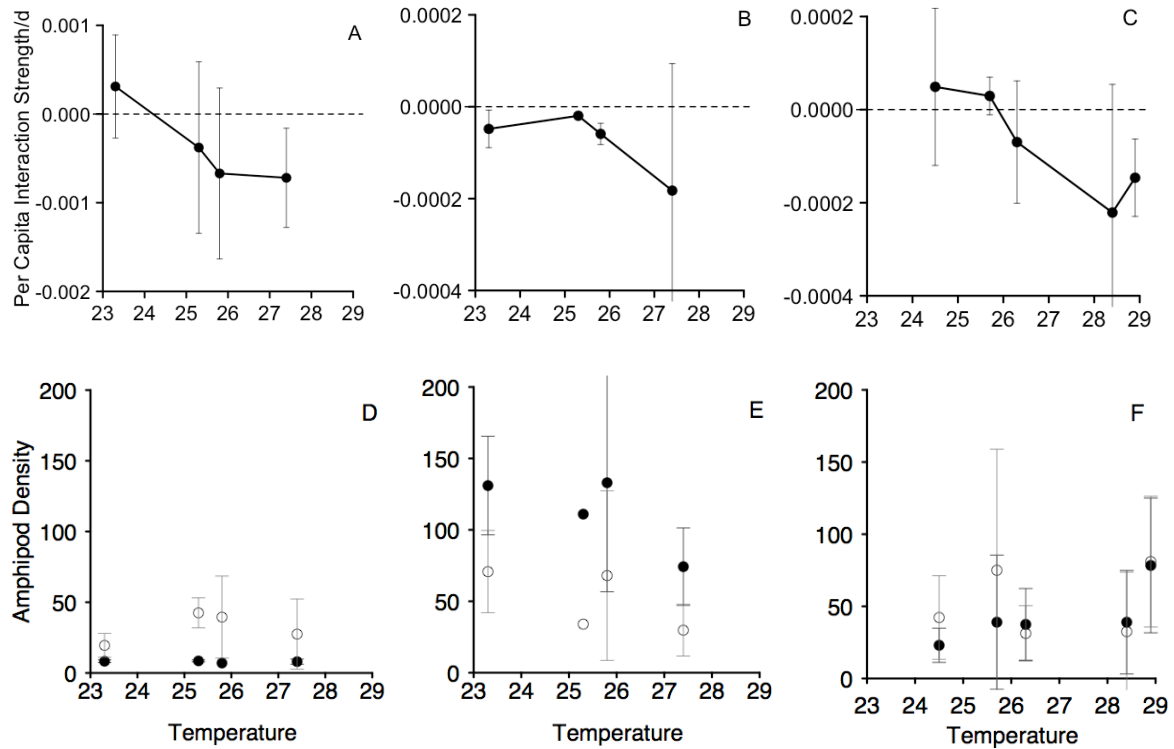


Figure 3.3. Effects of temperature and herbivory on algal growth.

The effect of temperature and herbivores on mean (\pm s.d.) daily average *Sargassum* growth rate in *Experiments* (A) I_s (11 days), (B) I_l (17 days), and (C) II (14 days). Solid lines = 0 herbivores (\bullet), dashed lines = + herbivores (\circ) and indicate significant temperature effects (Table 1).

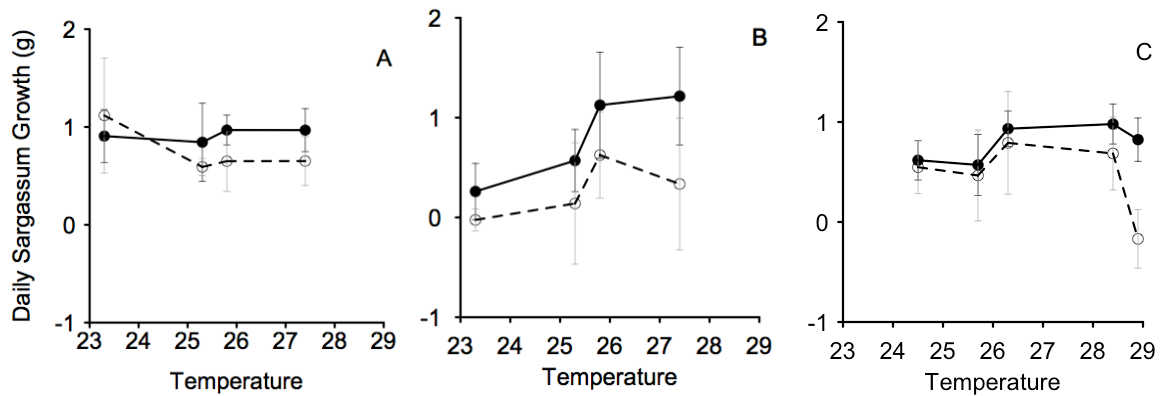
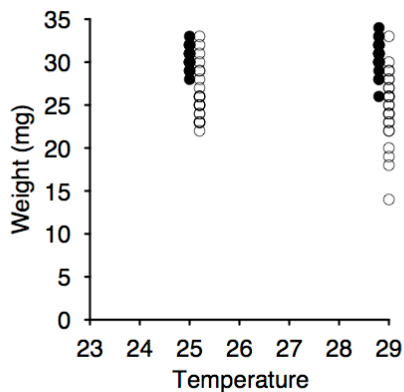


Figure 3.4. Results of feeding assays.

Final algal mass after 48-hour feeding assay at 25 and 29°C did not vary with temperature in the presence (\circ) or absence (\bullet) of *A. longimana*.



References

- Allen, A. P., J. F. Gillooly, and J. H. Brown. 2005. Linking the global carbon cycle to individual metabolism. *Functional Ecology* 19:202-213.
- Behrenfeld, M. J., R. T. O'Malley, D. A. Siegel, C. R. McClain, J. L. Sarmiento, G. C. Feldman, A. J. Milligan, P. G. Falkowski, R. M. Letelier, and E. S. Boss. 2006. Climate-driven trends in contemporary ocean productivity. *Nature* 444:752-755.
- Berlow, E. L. 1999. Strong effects of weak interactions in ecological communities. *Nature* 398:330-335.
- Berlow, E. L., S. A. Navarrete, C. J. Briggs, M. E. Power, and B. A. Menge. 1999. Quantifying variation in the strengths of species interactions. *Ecology* 80:2206-2224.
- Berlow, E. L., A. M. Neutel, J. E. Cohen, P. C. de Ruiter, B. Ebenman, M. Emmerson, J. W. Fox, V. A. A. Jansen, J. I. Jones, G. D. Kokkoris, D. O. Logofet, A. J. McKane, J. M. Montoya, and O. Petchey. 2004. Interaction strengths in food webs: issues and opportunities. *Journal of Animal Ecology* 73:585-598.
- Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage, and G. B. West. 2004. Toward a metabolic theory of ecology. *Ecology* 85:1771-1789.
- Bruno, J. F., J. J. Stachowicz, and D. Bertness Mark. 2003. Inclusion of facilitation into ecological theory. *Trends in Ecology and Evolution* 18:119-125.
- Chown, S. L., and K. J. Gaston. 1999. Exploring links between physiology and ecology at macro-scales: the role of respiratory metabolism in insects. *Biological Reviews* 74:87-120.
- Cubit, J. D. 1984. Herbivory and the seasonal abundance of algae on a high intertidal rocky shore. *Ecology* 65:1904-1917.
- Davis, A. J., L. S. Jenkinson, J. H. Lawton, B. Shorrocks, and S. Wood. 1998a. Making mistakes when predicting species range shifts in response to global warming. *Nature* 391:783-786.
- Davis, A. J., J. H. Lawton, B. Shorrocks, and L. S. Jenkinson. 1998b. Individualistic species responses invalidate simple models of community dynamics under global environmental change. *Journal of Animal Ecology* 67:600-612.
- Davison, I. R. 1987. Adaptation of photosynthesis in *Laminaria-Saccharina* (Phaeophyta) to changes in growth temperature. *Journal Of Phycology* 23:273-283.
- Davison, I. R. 1991. Environmental effects on algal photosynthesis - Temperature. *Journal Of Phycology* 27:2-8.

- Davison, I. R., R. M. Greene, and E. J. Podolak. 1991. Temperature acclimation of respiration and photosynthesis in the brown alga *Laminaria-Saccharina*. *Marine Biology* 110:449-454.
- del Giorgio, P. A., J. J. Cole, and A. Cemberlis. 1997. Respiration rates in bacteria exceed phytoplankton production in unproductive aquatic systems. *Nature* 385:148-151.
- Dewar, R. C., B. E. Bedlyn, and R. E. McMurtrie. 1999. Acclimation of the respiration / photosynthesis ratio to temperature: insights from a model. *Global Change Biology* 5:615-622.
- Duffy, J. E., and M. E. Hay. 2000. Strong impacts of grazing amphipods on the organization of a benthic community. *Ecological Monographs* 70:237-263.
- Edwards, M., and A. J. Richardson. 2004. Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature* 430:881-884.
- Farquhar, G. D., S. von Caemmerer, and J. A. Berry. 1980. A biochemical model of photosynthetic CO₂ assimilation in leaves of C₃ plants. *Planta* 149:78-90.
- Gaines, S. D., and J. Lubchenco. 1982. A Unified Approach to Marine Plant-Herbivore Interactions .2. Biogeography. *Annual Review of Ecology and Systematics* 13:111-138.
- Gleason, H. A. 1926. The individualistic concept of the plant association. *Bulletin of the Torrey Botanical Club* 53:7-26.
- Hawkins, S. J., and R. G. Hartnoll. 1983. Grazing of intertidal algae by marine-invertebrates. *Oceanography and Marine Biology* 21:195-282.
- Helmuth, B., N. Mieszkowska, P. Moore, and S. J. Hawkins. 2006. Living on the edge of two changing worlds: Forecasting the responses of rocky intertidal ecosystems to climate change. *Annual Review of Ecology, Evolution and Systematics* 37:373-404.
- Hochachka, P. W., and G. N. Somero. 2002. *Biochemical adaptation: Mechanism and process in physiological evolution*. Oxford University Press, Oxford.
- Kareiva, P. 1982. Experimental and mathematical analyses of herbivore movement: quantifying the influence of plant spacing and quality on foraging discrimination. *Ecological Monographs* 52:261-282.
- Kingsolver, J. G. 1989. Weather and the population-dynamics of insects - Integrating physiological and population ecology. *Physiological Zoology* 62:314-334.
- Laska, M. S., and J. T. Wootton. 1998. Theoretical concepts and empirical approaches to measuring interaction strength. *Ecology* 79:461-476.

- Lobban, C. S., and P. J. Harrison. 1997. *Seaweed ecology and physiology*. Cambridge University Press, New York.
- Logan, J. A., J. Regniere, and J. A. Powell. 2003. Assessing the impacts of global warming on forest pest dynamics. *Frontiers In Ecology And The Environment* 1:130-137.
- Lopez-Urrutia, A., E. San Martin, R. P. Harris, and X. Irigoien. 2006. Scaling the metabolic balance of the oceans. *Proceedings of the National Academy of Sciences USA* 103:8739-8744.
- Lubchenco, J., and S. D. Gaines. 1981. A Unified Approach to Marine Plant-Herbivore Interactions. I. Populations and Communities. *Annual Review of Ecology and Systematics* 12:405-437.
- MacArthur, R. 1972. *Geographical Ecology*. Princeton University Press, Princeton, NJ.
- May, R. M. 1973. *Stability and complexity in model ecosystems*. Princeton University Press, Princeton, NJ.
- Menge, B. A., and J. P. Sutherland. 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *The American Naturalist* 130:730-757.
- Morelissen, B., and C. D. G. Harley. 2007. The effects of temperature on producers, consumers, and plant-herbivore interactions in an intertidal community. *Journal of Experimental Marine Biology and Ecology* 348:162-173.
- Osovitz, C. J., and G. E. Hofmann. 2007. Marine macrophysiology: studying physiological variation across large spatial scales in marine systems. *Comparative Biochemistry and Physiology Part A* 147:821-827.
- Padilla-Gamino, J. L., and R. C. Carpenter. 2007. Seasonal acclimatization of *Asparagopsis taxiformis* (Rhodophyta) from different biogeographic regions. *Limnology and Oceanography* 52:833-842.
- Paine, R. T. 1966. Food web complexity and species diversity. *The American Naturalist* 100:65-75.
- Paine, R. T. 1992. Food-web analysis through field measurement of per capita interaction strength. *Nature* 355:73-75.
- Park, T. 1954. Experimental studies of interspecies competition. 11. Temperature, humidity and competition in two species of *Tribolium*. *Physiological Zoology* 27:177-238.
- Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421:37-42.

- Pennings, S. C., and B. R. Silliman. 2005. Linking biogeography and community ecology: Latitudinal variation in plant-herbivore interaction strength. *Ecology* 86:2310-2319.
- Ritchie, M. E. 2000. Nitrogen limitation and trophic vs. abiotic influences on insect herbivores in a temperate grassland. *Ecology* 81:1601-1612.
- Ruesink, J. L. 1998. Variation in per capita interaction strength: Thresholds due to nonlinear dynamics and nonequilibrium conditions. *Proceedings of the National Academy of Sciences USA* 95:6843-6847.
- Ryan, M. G. 1991. Effects of climate change on plant respiration. *Ecological Applications* 1:157-167.
- Sanford, E. 1999. Regulation of keystone predation by small changes in ocean temperature. *Science* 283:2095-2097.
- Sanford, E. 2002. Water temperature, predation, and the neglected role of physiological rate effects in rocky intertidal communities. *Integrative And Comparative Biology* 42:881-891.
- Schneider, C. W., and R. B. Searles. 1991. *Seaweeds of the Southeastern United States: Cape Hatteras to Cape Canaveral*. Duke University Press.
- Schoener, T. W. 1986. Mechanistic approaches to community ecology: a new reductionism? *American Zoologist* 26:81-106.
- Somero, G. N. 2002. Thermal physiology and vertical zonation of intertidal animals: optima, limits and costs of living. *Integrative And Comparative Biology* 42:780-789.
- Taylor, C. R., N. C. Heglund, and G. M. O. Maloiy. 1982. Energetics and mechanics of terrestrial locomotion. I. Metabolic energy consumption as a function of speed and body size in birds and mammals. *Journal Of Experimental Biology* 97:1-27.
- Taylor, R. B., E. E. Sotka, and M. E. Hay. 2002. Tissue-specific induction of herbivore resistance: seaweed response to amphipod grazing. *Oecologia* 132:68-76.
- Thompson, R. C., T. A. Norton, and S. J. Hawkins. 2004. Physical stress and biological control regulate the producer-consumer balance in intertidal biofilms. *Ecology* 85:1372-1382.
- Vasseur, D. A., and K. S. McCann. 2005. A mechanistic approach for modeling temperature-dependent consumer-resource dynamics. *The American Naturalist* 166:184-198.
- Wootton, J. T. 1997. Estimates and tests of per capita interaction strength: diet, abundance, and impact of intertidally foraging birds. *Ecological Monographs* 67:45-64.

Yee, E. H., and S. N. Murray. 2004. Effects of temperature on activity, food consumption rates, and gut passage times of seaweed-eating Tegula species (Trochidae) from California. *Marine Biology* 145:895-903.

CHAPTER 4

EFFECTS OF METABOLIC TEMPERATURE SCALING AND NUTRIENTS ON MARINE FOOD WEBS

Abstract

The ecological effect of variation in physical environmental conditions in marine ecosystems is complex, resulting in contradictory patterns of food web production in response to climate conditions. This complexity hinders a general understanding of factors driving variation in fisheries production and ecological change with climate change. Whole food web responses to one important physical condition, temperature, may be predictable based on general metabolic responses of consumers and producers. The metabolic theory of ecology predicts that differential temperature scaling of photosynthetic- and respiration-based metabolic processes drive systematic, differential responses to temperature across trophic levels, and food web theory suggests that these effects depend on resource availability. We tested the hypothesis that differential temperature scaling of heterotrophic and autotrophic metabolism can explain variation in food web structure and production under different nutrient supply scenarios. Mesocosm experiments using a pelagic marine food web demonstrated that temperature alone can shift food web structure towards greater consumer biomass relative to producer biomass. Shifts in food web structure with temperature were driven by disproportionate increases in grazing relative to primary production. The strength of these temperature effects depended on nutrient levels. These results support a general model of

temperature scaling of food web structure and production based on metabolic theory. The relevance of metabolic theory in realistic nutrient scenarios informs a predictive conceptual framework for community responses to climate change.

Introduction

Physical and biological causes of variation in marine food web productivity have long been a focus of scientific research (Harvey et al. 1935, Schaefer 1965, Ryther 1969). Factors such as nutrient availability, light and temperature drive variation in primary productivity (Platt and Jassby 1976, Keller 1989, Behrenfeld et al. 2006), yet direct causes of variation in secondary productivity at higher trophic levels are less clear (Iverson 1990, Finney et al. 2002). The problem of understanding how food web structure and production responds to environmental change has seemed overwhelmingly complex due to the lack of a general, quantitative and testable mechanism that links food web processes to environmental conditions such as temperature or nutrient availability (McGowan et al. 1998, Brander 2007). This gap hinders a predictive understanding of ecological effects of variation in ocean conditions associated with geography and climate change.

Environmentally driven variation in productivity rates can alter overall food web properties, causing major changes in related ecosystem services such as fish production and carbon sequestration (Cushing 1982, Schindler et al. 1997, McGowan et al. 1998, Finney et al. 2002, Lopez-Urrutia et al. 2006). For example, many studies have compared large-scale variation in food web structure and production to variation in primary production in an effort to improve predictability of fish stocks (Schaefer 1965, Ryther 1969, Iverson 1990, Pauly and Christensen 1995). These analyses leave much variation unexplained, and are limited by

their failure to consider physical or biological factors that drive variation in links between net primary production (NPP) and secondary production (Brander 2007). In another example, pelagic marine food webs in the Atlantic Ocean tend to be net autotrophic (carbon sinks) in colder waters and net heterotrophic (carbon sources) in warmer waters (del Giorgio and Duarte 2002, Lopez-Urrutia et al. 2006). This macroecological pattern has been explained in terms of general metabolic responses to temperature (Lopez-Urrutia et al. 2006), but lacks an experimental test. A few experimental studies suggest that individual responses to temperature alone can explain such a shift in food web structure (Keller et al. 1999, Muren et al. 2005, Sommer et al. 2007), but how this effect compares to constraints of resource limitation and is relevant to field conditions remains to be experimentally tested.

The recently developed Metabolic Theory of Ecology (MTE) provides a general framework for understanding the effects of temperature on all organisms, demonstrating that metabolic responses to temperature are highly conserved across broad taxonomic groups (Gillooly et al. 2001, Brown et al. 2004). Systematic differences in the temperature sensitivity of respiration- and photosynthesis-based metabolism imply that producers and consumers respond differently to environmental temperature (Dewar et al. 1999, Allen et al. 2005, Lopez-Urrutia et al. 2006) (Figure 4.1A). This differential metabolic temperature scaling leads to the prediction that organismal processes such as resource use, growth and reproduction rates scale differently for heterotrophs and autotrophs. Warming generally increases metabolic rate within a range of non-lethal temperatures, affecting respiratory processes more severely than photosynthetic production. Consequently, at higher temperatures, grazing rates should increase faster than increases in primary production (O'Connor Accepted). The result would be reduced standing plant biomass and a shift in

food web structure (i.e., the distribution of biomass along the food chain, Figure 4.1B) and higher productivity at higher trophic levels. This mechanism has been invoked to explain the biogeographic trend towards net heterotrophy in warmer climates in open ocean pelagic food webs (del Giorgio and Duarte 2002, Lopez-Urrutia et al. 2006), and is consistent with patterns observed in spring bloom dynamics, rocky intertidal systems, grasslands and forests (Keller et al. 1999, Ritchie 2000, Logan et al. 2003, Thompson et al. 2004, Rose and Caron 2007, Sommer et al. 2007).

Temperature driven shifts in food web productivity and structure will be limited ultimately by resource availability. Bottom-up dynamics such as nutrient or light limitation may constrain potential temperature effects by limiting the amount of primary production possible at any temperature (Keller 1989, del Giorgio and Peters 1993, 1994, Brown et al. 2004). Light and nutrient limitation directly constrain autotrophic production, while metabolic responses to temperature influence both photosynthetic and respiratory processes, and thus primary and secondary production. The ubiquitous effects of temperature therefore should be different and complementary to effects of resource availability. For example, in resource-limited systems where effects of warming on productivity may be constrained by low nutrient supply, eutrophication may increase the importance of temperature effects. But when nutrients are plentiful, increases in primary and secondary production should increase consumer biomass through bottom-up dynamics (Lindeman 1942, Iverson 1990, Bambach 1993). The well-known balance between bottom-up and top-down processes will regulate changes in food web production as temperatures change, and these changes may be quite predictable in different nutrient scenarios.

To understand the combined effects of general temperature dependence of metabolism and bottom-up regulation of food web production, whole food web responses to variation in both factors need to be assessed. Using a coastal pelagic food web consisting of microbes, phytoplankton and zooplankton, we experimentally tested three hypotheses: 1) small, non-lethal increases in temperature shift the structure of a pelagic marine food web toward greater consumer biomass and reduced primary producer biomass (increased heterotrophic/autotrophic biomass, Figure 4.1), 2) warming increases food web biomass production and 3) this effect is constrained by nutrient availability. We predicted that the temperature-driven shift in food web structure is driven by disproportionate increases in rates of consumption relative to primary production.

Methods

Mesocosm System and Experimental Design

We tested the effect of temperature and its dependence on nutrient supply on food web structure using a factorial experiment with 4 temperature levels and 2 nutrient levels ($n = 5$). Food webs were maintained in 4-L translucent plastic mesocosms in outdoor water tables at IMS from April 23rd to May 1st, 2008 (Figure 4.2). Pilot experiments indicated that 8 days were sufficient to allow zooplankton population growth without exhausting water quality. Mesocosms started with identical conditions of 3 L of filtered seawater containing phytoplankton and microbes at concurrent field densities (6.64 mg Chl a/L and 2.23×10^6 / L, respectively) and an inoculum from the concentrated pool of zooplankton (69/L, consistent with measured field densities (Fulton 1984)). Treatments received either no nutrients (controls) or 20 μ M N and 5 μ M P on Days 0, 2, and 4 (nutrient additions). No addition

controls mimicked conditions in Bogue Sound year round, when nutrient levels are extremely low, and nutrient addition treatments replicated nutrient concentrations in coastal streams after storm events (Piehler, unpublished data).

Temperatures were maintained using water baths. We maintained temperature levels at ambient Bogue Sound water temperature, +2, +4 and +6 °C in a blocked design with temperature blocked by water table (Table 4.1, Figure 4.2). Temperatures in Bogue Sound range from approximately 7 – 32 °C throughout the year, and increase from about 18 – 28 °C between early April and late June (Figure 4.3). Temperatures were monitored regularly using a hand thermometer and continuously using ibutton Thermochron dataloggers (Dallas semiconductor, Dallas, Texas, USA). Nutrient addition and control replicates were randomly arranged in water tables. Mesocosms were covered with Plexiglass to block UV radiation and minimize evaporation and one layer of window screen to reduce light levels to those similar to 0.5-1.0 m depth (approximately 900 μM photons / m^2 / s midday on a sunny day, Piehler, unpublished data). Each mesocosm received air through an air stone to maintain oxygen levels and water mixing.

We collected zooplankton, phytoplankton and microbes from the Bogue Sound Estuary at the University of North Carolina's Institute of Marine Sciences (IMS) in Morehead City, NC, on 4/23/07 in the mid-morning just before high tide. Phytoplankton and microbes were separated from particulates and zooplankton using a 63- μm filter, and zooplankton were collected using a 63- μm net. Zooplankton and the phytoplankton and microbes were stored in separate coolers for less than one hour prior to the start of the experiment.

Sampling food web structure, production and primary productivity

We measured effects of temperature and nutrient treatments on standing stocks of primary and secondary producers, and on rates of primary productivity. Biomass response variables were measured at the start of the experiment (t_0) and eight days (t_8) after the start of the experiment. Initial conditions were estimated by randomly sampling aliquots ($n=5$) from the pools of phytoplankton / microbes and zooplankton, before initial additions to the mesocosms.

Phytoplankton biomass was estimated by quantifying chlorophyll a concentrations in 50 mL aliquots of each replicate. Phytoplankton was concentrated on Whatman GF/F glass fiber filters (25mm diameter, 0.7 μm nominal pore size) and chlorophyll a was extracted using 10 mL acetone. Pigment levels were determined using a Turner Designs Trilogy fluorometer using the non acidification module (Welschmeyer 1994). Carbon biomass was estimated using a conversion factor of 55 mg C per mg Chla (Gasol et al. 1997). Nutrient (NH_4 , PO_4 , NO_3 and total nitrogen (TN)) concentrations were quantified using the filtrate from the same water samples used to estimate phytoplankton abundance. Nutrients were quantified with a Lachat Quick-Chem 8000 automated ion analyzer using standard protocols (Lachat Instruments, Milwaukee, WI, USA: NO_2/NO_3 Method 31-107-04-1-C, NH_4 Method 31-107-06-1-A, PO_4 Method 31-115-01-3-C, and TN Method 31-107-04-3-B).

We estimated consumer density and biomass. Zooplankton were sorted from water remaining in the mesocosm after other sampling (2768 mL) using a 63 μm mesh and preserved in 4.5% sucrose Formalin. In the laboratory, zooplankton were counted and identified to lowest taxonomic level possible at 40X magnification. Body length was estimated for a subset of individuals counted, and biomass (ash free dry weight, AFDW) was

determined for a subset of each replicate. Carbon biomass was estimated by multiplying AFDW by 0.5 (J. Cebrian, personal communication). Microbes were collected in 3 mL aliquots and preserved in glutaraldehyde. Subsamples were stained with DAPI for 10 minutes before 1 mL of sample, combined with 1 mL of sterilized deionized water, was filtered onto 0.22 μm black polycarbonate filters. Filters were then mounted onto microscope slides and viewed under oil immersion on an epifluorescence microscope at 1000x magnification. Approximately 400 cells were counted per slide to estimate microbial abundance using the equation

$$\text{Bacteria/mL} = (\text{membrane conversion factor} \times N)/D$$

where N is the average number of bacteria per field of view, the membrane conversion factor is the filtration area per field of view area, and D is the dilution factor. Carbon biomass was estimated by multiplying counts by 20 fg C / bacterium.

Final maximum primary productivity was estimated using photosynthesis versus irradiance (P-I) relationships for ambient, +2 and +6 °C. Maximum photosynthesis per unit chlorophyll biomass (P_M^B) and the initial slope of the PI curve (\pm 95% confidence intervals) were calculated according to Jassby and Platt (1976). P-I relationships were determined using the Lewis and Smith (1983) photosynthetron method. Water samples (60 mL) were collected from each replicate mesocosm and pooled for each temperature x nutrient treatment. Samples of 5 mL from this pool were spiked with ^{14}C -bicarbonate (Amersham, Inc.) to a final concentration of 0.8 $\mu\text{Ci mL}^{-1}$ (See Appendix C for additional detail). Samples were incubated for 45 minutes at varied irradiances generated by two Cool-Lux 75

W projector lamps using a combination of neutral density filters, distance from light source, and angle of incidence (see Lewis and Smith (1983) for further detail). One mL of 50% HCl was added to the samples which were then placed on a shaker table overnight to purge unincorporated ^{14}C . Ten mL of Ecolume (ICN Inc.) scintillation cocktail was added to each vial, which were stored in the dark for 12 hours and were then counted in a Beckman model LS 5000TD liquid scintillation counter. Counts per minute were converted to disintegrations per minute using internal quench curves from a calibrated ^{14}C -toluene standard. Dissolved inorganic carbon concentration in seawater in all treatments was determined by a Shimadzu TOC 5000A total carbon analyzer.

Effects of temperature and nutrient levels on response variables were analyzed using a two-way ANOVA. Zooplankton biomass data and heterotroph to autotroph biomass ratio data were log transformed to meet the assumptions of ANOVA. All statistical analyses were performed in R (v. 2.7.0). P-I curve fitting was performed in SAS.

Results

Small differences in temperature (Table 4.1) altered food web structure so that the ratio of heterotrophic to autotrophic biomass increased from low to high temperatures (Figure 4.4A, Table 4.2). This trend occurred regardless of nutrient treatment (Table 4.2), although the peak ratio occurred at a lower temperature in the low nutrient treatment than in the high nutrient treatment. At high nutrient levels, declines in phytoplankton standing stock and increases in zooplankton and bacteria biomass drive this trend in H/A (Figure 4.4, Table 4.2). At lower nutrient levels, consumer biomass increases were reversed at the highest temperature (Figure 4.4C-D).

Food web biomass production and productivity were affected by nutrients and temperature. Total standing stock of the whole food web increased with nutrient addition and declined with temperature only in nutrient addition treatments (Figure 4.4E, Table 4.2). Primary productivity was limited in the nutrient control treatments, evidenced by lower P-I curve parameters for the initial slope (α) and maximum photosynthesis per unit chlorophyll biomass (P_M^B) relative to nutrient addition treatments (Figure 4.5, Table 4.3). Effects of temperature on productivity depended on nutrient availability. When nutrients were augmented, P_M^B was higher at +6 °C relative to the ambient temperature treatment, while in low nutrient conditions P_M^B was unaffected by temperature.

Increasing zooplankton biomass with temperature and nutrients was driven by population growth of calanoid and cyclopoid copepods (Figure 4.6, Table 4.2). Nauplii density increased 6-fold over the temperature gradient in the nutrient addition treatments, but in the low nutrient treatments population density peaked at an intermediate temperature and declined at the highest temperature.

Discussion

The community-level effects of temperature-dependent food web processes and nutrient limitation support a predictive conceptual framework for understanding broader ecological change in marine ecosystems. Our experiments demonstrate that small increases in temperature shift food web structure towards increased consumer biomass relative to producer biomass, consistent with predictions based on the metabolic theory of ecology (hypothesis 1). Shifting food web structure was a consequence of differential temperature scaling of producer and consumer processes. Increased grazing pressure with temperature

reduced standing phytoplankton biomass, in spite of increased primary productivity (Figures 4.4 and 4.5). Stronger consumer effects and greater consumer biomass were driven by higher density, and not increased individual size or a shift in species composition (Figure 4.6). This pattern is consistent with our hypothesis that temperature affected change on a metabolic, individual level rather than through competitive exclusion or other species interactions. Although temperature-driven changes in food web structure have been observed many times (Keller et al. 1999, Muren et al. 2005, Sommer et al. 2007), these are generally attributed to differential effects of light and nutrient limitation across trophic levels, or the combined effects of resource limitation and temperature (Richardson and Schoeman 2004, Muren et al. 2005). Our experiments demonstrate that temperature alone can shift food web structure and change overall standing biomass. Furthermore, the magnitude of this effect depends on nutrient availability.

Shifts in food web structure were accompanied by a decrease in overall biomass, contrary to our prediction based on bottom-up control of food web production (hypothesis 2). The decline in total biomass is, however, consistent with stronger top down control of food web structure in a context of abundant nutrients (Carpenter et al. 2001). Disproportionate increases in secondary production relative to primary production lead to consumption (grazing) of primary production faster than it can be produced. Trophic transfer efficiencies of approximately 10% (Slobodkin 1959) imply that overall food web biomass will decline as primary production is converted to higher trophic levels without compensatory increases in primary production. However, total food web production is rarely of interest. Rather, secondary or tertiary production (i.e., harvestable fish) are studied more carefully. Metabolic

temperature scaling increases secondary production when nutrients are abundant, but this effect is muted when nutrients are limiting (Figure 4.4).

Whole food web effects of temperature scaling depend on resource availability (hypothesis 3). At all temperatures, nutrient limitation constrained primary productivity (Figure 4.5) and limited food web production from the bottom up. This effect was strongest at higher temperatures, when higher rates of primary productivity depleted nutrients more rapidly, exhausting supplies and more severely limiting production (Figure 4.4). In addition to directly limiting primary production, nutrient concentrations can indirectly influence phytoplankton standing stock through effects of altered elemental composition on phytoplankton growth and grazing rates (Goldman et al. 1979, Elser et al. 2000, Sterner and Elser 2002). For example, low nutrient supplies can increase C:nutrient, leading to reduced phytoplankton growth rates (Droop 1974, Sterner and Hessen 1994) and lower quality food for consumers (Sterner and Elser 2002). Alternatively, increased algal growth rates have been associated with decreased C: nutrient and increased food quality for grazers (the growth rate hypothesis, (Elser et al. 2003)). Whether such growth rate - induced changes in elemental composition occur with temperature-dependent increases in growth rate is unclear. If so, increased food quality could reduce zooplankton grazing rates and/or enhance their growth rates (DeMott et al. 1998, Elser et al. 2001). Therefore, either by constraining production altogether, or by indirectly affecting growth or consumption rates, nutrient availability can interact with metabolic temperature scaling to reduce phytoplankton standing stocks and regulate food web structure from the bottom up.

Food web structure and standing stocks are related to productivity of pelagic food webs throughout the world's oceans and lakes. These food webs are the basal trophic levels

supporting nearly all fisheries and are the engines of the biological oceanic component of the global carbon cycle. In coastal systems, pelagic food webs are highly productive, and are often nutrient rich either due to natural oceanographic processes or anthropogenic influences (Ryther 1969, Ryther and Dunstan 1971). The ecosystem effects of slight warming over short time scales may be amplified in these systems at critical times of year, such as during spawning seasons or the spring bloom. Because important consumers such as fish larvae are often food-limited (Morgan 1995), temperature-dependent increases productivity when nutrients are abundant could lead to much greater survival and growth at higher trophic levels. For example, in our experiment, warming increased productivity and boosted zooplankton abundance over temperature differences observed over days to weeks in the coastal North Carolina system, well within the range of annual variation. Temperature effects were strongest under nutrient enrichment, suggesting that such effects may be further exacerbated during storm events when normally very low nutrient levels temporarily increase.

This experiment validates mechanistic predictions grounded in MTE and food web theory (FWT) to predict change in food web structure and production. The combined theory provides a conceptual framework for understanding temporal change in food web structure associated with environmental change. In pelagic marine ecosystems, nutrient concentrations and temperature tend to be negatively correlated. Nutrient availability to phytoplankton is determined by inputs to sunlit surface waters of deeper, cooler nutrient-rich water through mixing or upwelling. Thus, we often find cooler, nutrient rich ecosystems and relatively warmer, nutrient poor systems. This pattern occurs on very broad geographic scales (i.e., cold temperate or polar systems relative to tropical systems), on smaller scales within oceans

and seas (i.e., the North Sea, Richardson and Schoeman 2004), and over time within a single region (McGowan et al. 1998, Hunt et al. 2002). According to the MTE-FWT conceptual framework, small increases in sea surface temperature should cause small declines or no change at all in primary productivity and standing stocks in nutrient limited systems such as stratified areas with a shallow thermo- or pycnocline. Nutrient limitation would constrain secondary productivity and biomass stocks from the bottom up. In contrast, when nutrients are plentiful, as in upwelling or well-mixed systems, warming should increase productivity leading to increased biomass production across trophic levels, shifted food web structure and stronger top-down control of phytoplankton standing stock.

Documented ecosystem change with climate change is consistent with these predictions of opposite effects of warming on food web structure depending on nutrient availability within three major pelagic ecosystems (McGowan et al. 1998, Hunt et al. 2002, Richardson and Schoeman 2004). In the North Sea, for example, warming between 1958 and 2002 has increased phytoplankton abundance in cooler, nutrient rich regions, while warming has caused phytoplankton abundance to decline in warmer, more stratified and nutrient limited regions (Richardson and Schoeman 2004). Whether temperature influenced entire food web structure is unclear at this point, because the study only looked at plankton and not top consumers. However, O'Brien et al. (2000) report increased cod abundance with warming in cooler, northern regions of the North Sea and declines with warming in the southern region, consistent with the plankton pattern and the framework. In the Pacific Ocean, warming in the California Current system has decreased secondary production, while warming in the cooler, nutrient rich Alaskan Gyre has increased consumer production

(McGowan et al. 1998). Similar patterns have been observed in the Bering Sea (Hunt et al. 2002).

Differential temperature scaling among heterotrophs and autotrophs provides a simple, mechanistic explanation for observed biogeographic variation in food web structure (Lopez-Urrutia et al. 2006), and serves as a general model for understanding ecosystem change with climate conditions. The temperature scaling mechanism is general and relatively invariant among taxonomic groups (Gillooly et al. 2001), and therefore may explain broad biogeographic variation in ecosystem structure and even nutrient availability. For example, algal standing biomass is extremely low and highly grazed in tropical marine ecosystems (Carpenter 1986), while cooler, temperate systems have high algal standing stocks (Gaines and Lubchenco 1982). Theoretical work and meta-analyses have found this mechanism to explain variation in pelagic food web structure in open ocean systems in the Atlantic (Lopez-Urrutia et al. 2006), and our results now experimentally confirm this mechanism.

Changing temperature will influence marine ecosystems in many ways, including altering physical properties such as stratification, and causing species range shifts and altered timing of life cycle events (Beaugrand et al. 2002, Parmesan 2006). Such ecological changes can be important, causing mismatch between consumers and their prey (Cushing 1982, Philippart et al. 2003, Edwards and Richardson 2004, Sommer et al. 2007). However, temperature scaling of food web properties is a general response that will occur regardless of species composition. It can be incorporated into predictions of ecological variation, thus providing one of the few mechanistic, general models for ecosystem change with geography or climate. The conceptual framework outlined here reinforces predictions that effects of

climate change on ecosystem processes will vary among regions (Walther et al. 2002). Future warming will likely increase secondary productivity and fish harvests in nutrient-rich regions, but may cause declines in more stratified, oligotrophic systems. These are not paradoxical responses, and the general effects of temperature in different nutrient contexts explain why different parts of the same ecosystem can respond differently to warming. Implications of temperature effects on food webs for the ocean's role in carbon cycling are unclear, due in part to the mosaic of nutrient-rich and nutrient-poor regions of the world's oceans, and to temperature-driven shifts in the threshold dividing net heterotrophy from net autotrophic (carbon sinks from carbon sources) (Lopez-Urrutia et al. 2006). Effects of climate change at the regional scale will likely involve changes in ecosystem structure or function that may be understood in terms of an experimentally validated, general mechanistic theory.

Tables.

Table 4.1. Experimental conditions in temperature and nutrient treatments.

Values are mean (\pm s.d.) for final day of experiment (Day 8). Significant differences among treatments (one-way anova, $P < 0.01$) indicated by *. Temperature treatments were significantly different, and water table was not a significant factor (two-way ANOVA: temperature $df=1$, $F = 567.98$, $P < 0.001$, block $df = 1$, $F = 0.76$, $P = 0.384$, temperature x table $df = 1$, $F = 1.391$, $P = 0.240$).

Temperature Treatment				
Treatment	Ambient	+2 °C	+4 °C	+6 °C
Temperature °C *	20.4 (\pm 0.06)	22.7 (\pm 0.06)	24.0 (\pm 0.60)	26.4 (\pm 0.48)
Salinity *	34.7 (\pm 0.82)	36.4 (\pm 1.51)	36.4 (\pm 1.65)	38.2 (\pm 1.81)

Table 4.2. Statistical results of two-way ANOVA analyses on the effects of temperature and nutrient levels on biomass standing stocks in an experimental food web.

Response	Source	df	MS	F	P
Phytoplankton C biomass	Temperature	1	14.782	33.544	< 0.001
	Nutrients	1	56.152	127.424	< 0.001
	Temperature*Nutrients	1	14.699	33.357	< 0.001
	Error	36	0.441		
Microbe C biomass	Temperature	1	6.385 x 10 ⁻⁷	19.017	< 0.001
	Nutrients	1	1.892 x 10 ⁻⁶	52.364	< 0.001
	Temperature*Nutrients	1	4.705 x 10 ⁻⁷	14.013	< 0.001
	Error	36	3.357 x 10 ⁻⁸		
Zooplankton C biomass	Temperature	1	6.926	11.056	0.002
	Nutrients	1	6.798	10.851	0.002
	Temperature*Nutrients	1	4.504	7.189	0.011
	Error	36	0.627		
Heterotroph / Autotroph C biomass	Temperature	1	18.402	21.285	<0.001
	Nutrients	1	9.908	11.460	0.002
	Temperature*Nutrients	1	13.416	15.517	<0.001
	Error	36	0.865		

Total C biomass (mg/L)	Temperature	1	0.938	19.568	<0.001
	Nutrients	1	8.380	174.861	<0.001
	Temperature*Nutrients	1	0.950	19.825	<0.001
	Error	36	0.048		
Zooplankton average length (um)	Temperature	1	3	<0.001	0.984
	Nutrients	1	93345	14.448	<0.001
	Temperature*Nutrients	1	992	0.154	0.697
	Error	36	6461		
Calanoid density	Temperature	1	9193.7	18.434	< 0.001
	Nutrients	1	13468.9	27.006	< 0.001
	Temperature*Nutrients	1	3960.5	7.941	0.008
	Error	36	498.7		
Cyclopoid density	Temperature	1	105.13	1.375	0.249
	Nutrients	1	1155.63	15.120	<0.001
	Temperature*Nutrients	1	235.44	3.080	0.088
	Error	36	76.43		
Harpacticoid density	Temperature	1	12.50	2.059	0.160
	Nutrients	1	16.90	2.783	0.104

	Temperature*Nutrients	1	2.00	0.329	0.570
	Error	36	6.07		
Nauplii density	Temperature	1	58277	12.518	0.001
	Nutrients	1	121000	25.992	<0.001
	Temperature*Nutrients	1	56919	12.227	0.001
	Error	36	4655		

Table 4.3. Parameters for photosynthesis-irradiance (P-I) curves.

Initial slope (α) and maximum photosynthesis per unit chlorophyll biomass (P_m^B) (mean \pm 95% confidence intervals) (Jassby and Platt 1976).

	α (mg C * [mg Chl a] ⁻¹ hr ⁻¹ / W m ⁻²)	P_m^B (mg C/[mg Chl a]/hr)
No nutrients		
Ambient	0.00354 (0.00268-0.00439)	1.8354 (1.7004-1.9704)
+2 °C	0.00411 (0.00358-0.00464)	1.846 (1.777-1.915)
+6 °C	0.0038 (0.00305-0.00455)	1.7785 (1.6754-1.8816)
Nutrient addition		
Ambient	0.00862 (0.00564-0.0116)	2.2013 (1.966-2.4367)
+2 °C	0.00632 (0.00458-0.00807)	2.3241 (2.0676-2.5806)
+6 °C	0.00629 (0.00522-0.00732)	2.6623 (2.4693-2.8553)

Figures.

Figure 4.1. Conceptual models of temperature effects on food web structure.

A) Temperature ($1/kT$ for T in Kelvin) dependence of photosynthesis- (PS, slope = -0.32 eV) and respiration- (R, slope = -0.65 eV) based mass-normalized resting metabolism ($\text{mmol O}_2/\text{d pg C}^{\text{th}}$) (Adapted from Allen et al., 2005, Lopez-Urrutia et al., 2006). Predicted temperature ($^{\circ}\text{C}$) effects on food web structure: B) the ratio of heterotrophic to autotrophic biomass standing stock and C) relative consumer and producer biomass visualized as compartments in a trophic pyramid.

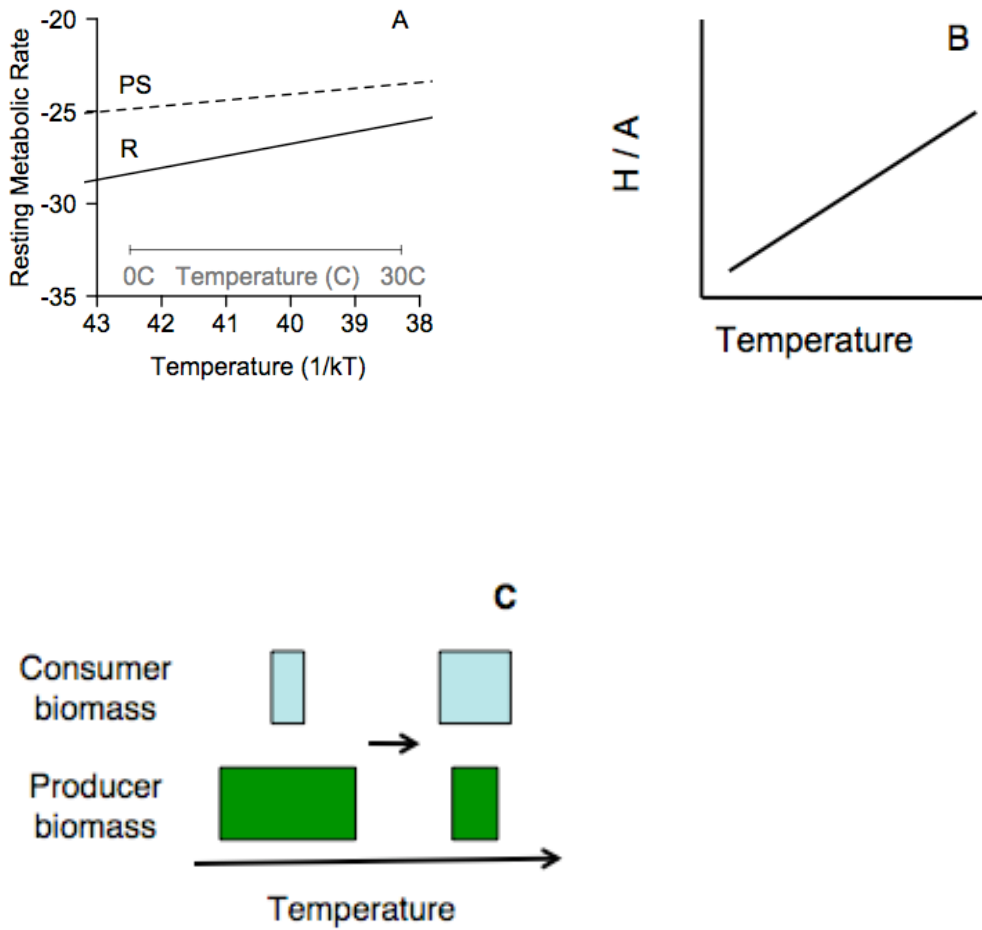


Figure 4.2. Experimental mesocosm set up.

Four temperature levels and two nutrient treatments. Temperature treatments were randomly assigned to block within each row of four tables. Nutrient treatments were randomly assigned to replicates within temperature level.



Figure 4.3. Observed temperatures in Bogue Sound.

Observations from UNC's Institute of Marine Sciences between March 2007 and May 2008 (Piehler, Bogue Watch). The experiment took place April 23 – May 1, 2008.

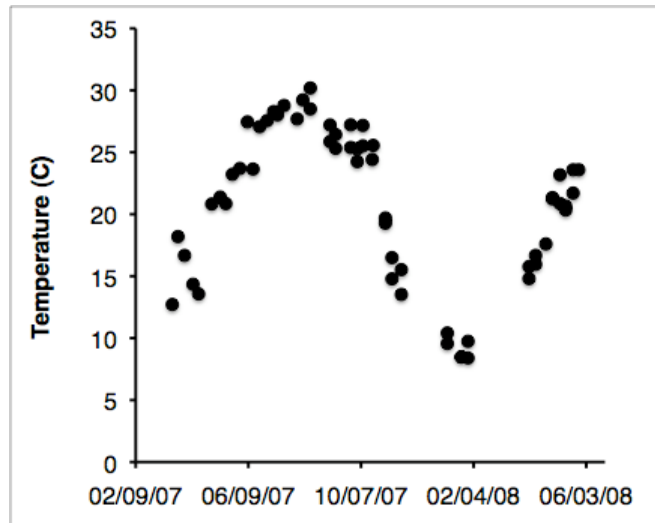
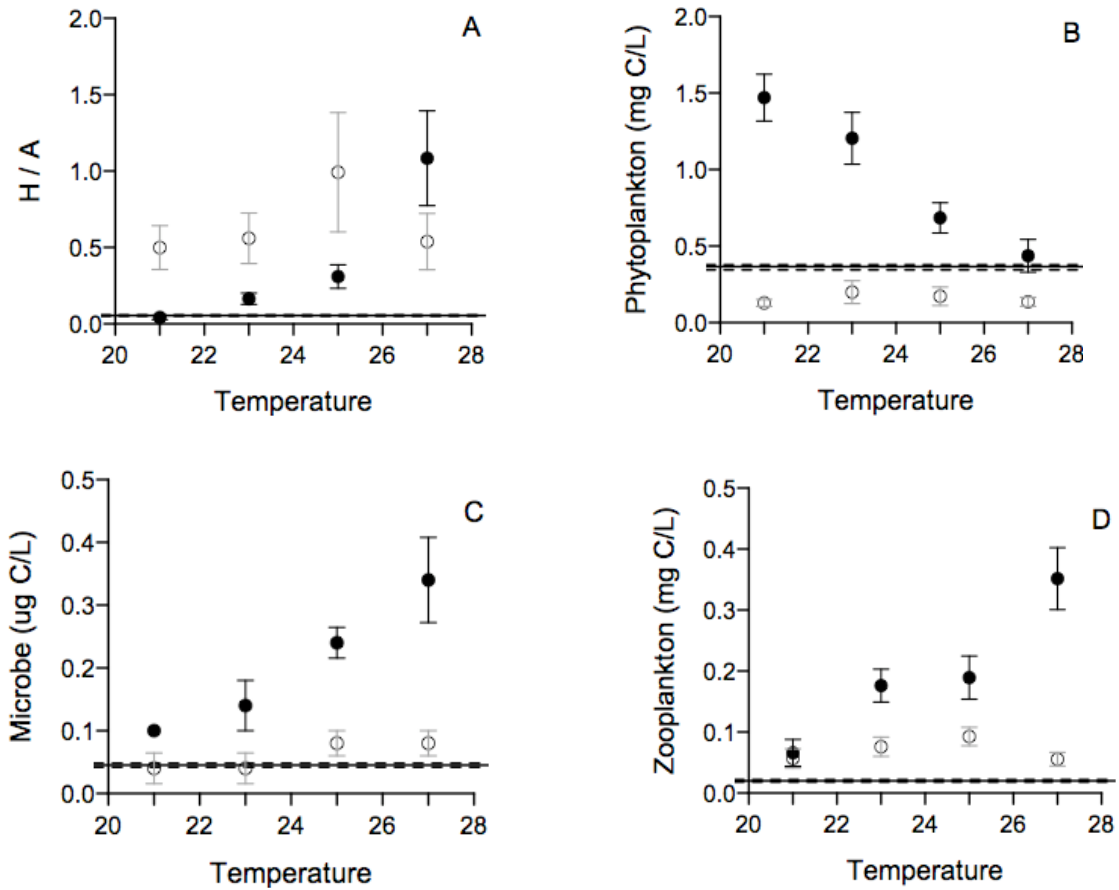


Figure 4.4. Experimental effects of temperature and nutrients on a pelagic food web.

Effect of temperature ($^{\circ}\text{C}$) on mean (+ s.e.) A) ratio of heterotroph to autotroph biomass, the carbon biomass of B) phytoplankton, C) microbes, D) zooplankton, and E) entire food web in nutrient addition (\bullet) and no-addition control (\circ) treatments. Initial conditions (means + s.e.) indicated by horizontal lines.



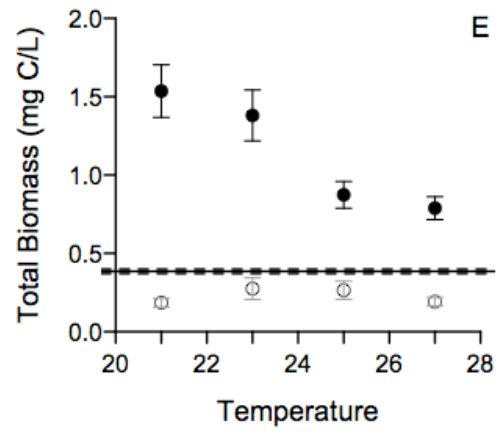


Figure 4.5. Effects of temperature and nutrients on primary productivity.

Effects of temperature ($^{\circ}\text{C}$) on primary productivity approximated as (A) mean ($\pm 95\%$ CI) maximum photosynthesis per unit chlorophyll biomass (P_M^B) in nutrient addition (\bullet) and no-addition control (\circ) treatments and (B) P-I curves for nutrient addition (black lines) and no-addition control (gray lines) for ambient, +2 and +6 $^{\circ}\text{C}$ treatments (solid, dashed and dotted lines, respectively).

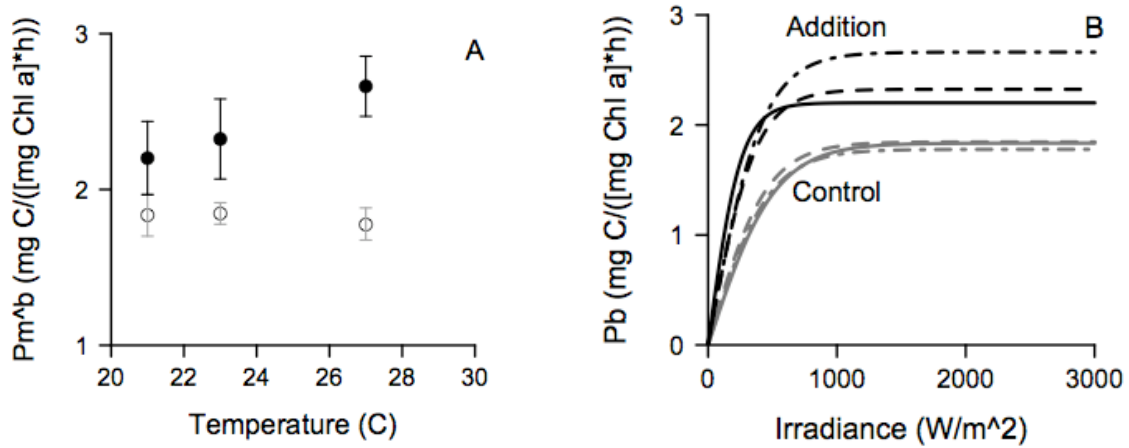
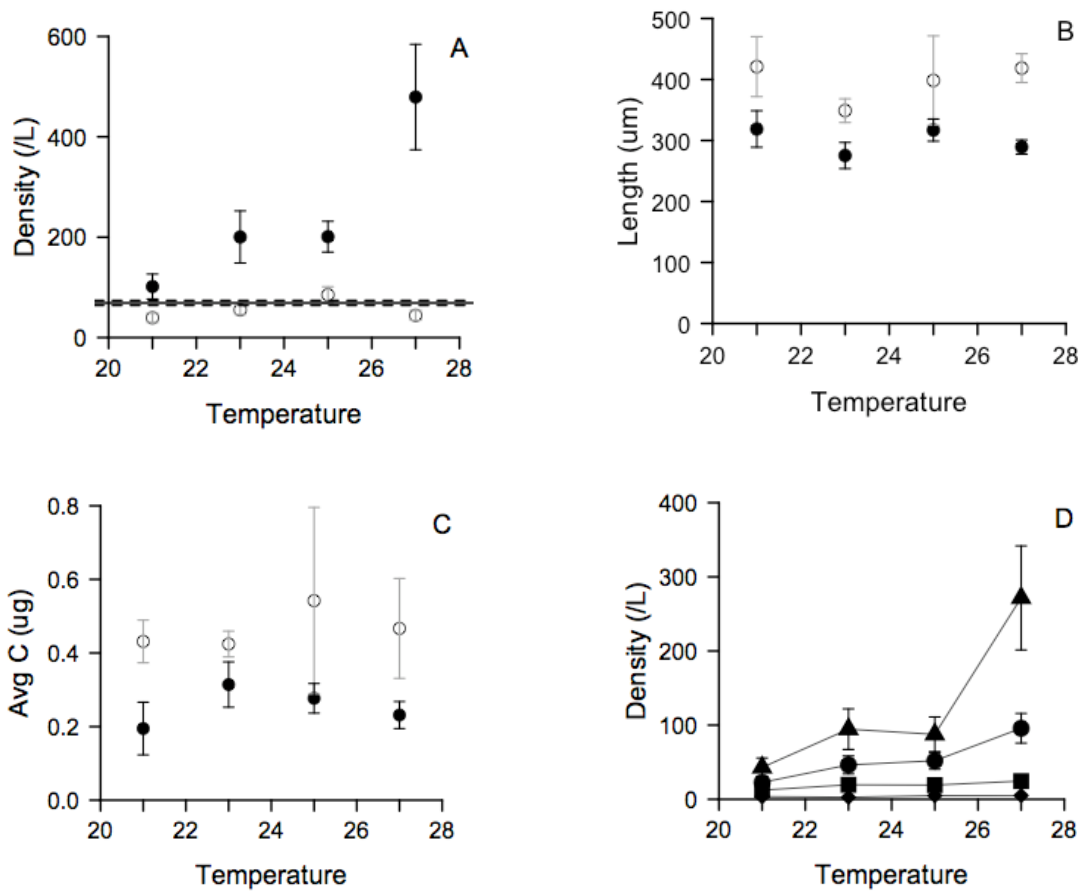
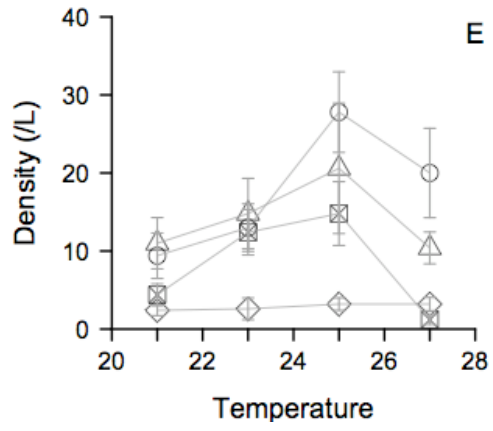


Figure 4.6. Experimental effects of temperature and nutrients on zooplankton.

Effect of temperature ($^{\circ}\text{C}$) on zooplankton size, density and taxonomic composition. Mean \pm se A) density and B) average length (μm), and C) average size ($\mu\text{g C}$), and densities of nauplii \blacktriangle , calanoids \bullet , cyclopoids \blacksquare and harpacticoids \blacklozenge in D) nutrient (filled symbols) and E) no nutrient (open symbols) treatments. Initial conditions (means \pm s.e.) indicated by horizontal lines.





References

- Allen, A. P., J. F. Gillooly, and J. H. Brown. 2005. Linking the global carbon cycle to individual metabolism. *Functional Ecology* **19**:202-213.
- Bambach, R. K. 1993. Seafood Through Time - Changes In Biomass, Energetics, And Productivity In The Marine Ecosystem. *Paleobiology* **19**:372-397.
- Beaugrand, G., P. C. Reid, F. Ibanez, J. A. Lindley, and M. Edwards. 2002. Reorganization of North Atlantic marine copepod biodiversity and climate. *Science* **296**:1692-1694.
- Behrenfeld, M. J., R. T. O'Malley, D. A. Siegel, C. R. McClain, J. L. Sarmiento, G. C. Feldman, A. J. Milligan, P. G. Falkowski, R. M. Letelier, and E. S. Boss. 2006. Climate-driven trends in contemporary ocean productivity. *Nature* **444**:752-755.
- Brander, K. M. 2007. Global fish production and climate change. *Proceedings of the National Academy of Sciences of the United States of America* **104**:19709-19714.
- Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage, and G. B. West. 2004. Toward a metabolic theory of ecology. *Ecology* **85**:1771-1789.
- Carpenter, R. C. 1986. Partitioning herbivory and its effects on coral reef algal communities. *Ecological Monographs* **56**:345-364.
- Carpenter, S. R., J. J. Cole, J. R. Hodgson, J. F. Kitchell, M. L. Pace, D. Bade, K. L. Cottingham, T. E. Essington, J. N. Houser, and D. E. Schindler. 2001. Trophic cascades, nutrients, and lake productivity: whole-lake experiments. *Ecological Monographs* **71**:163-186.
- Cushing, D. H. 1982. *Climate and Fisheries*. Academic Press, New York, NY.
- del Giorgio, P. A., and C. M. Duarte. 2002. Respiration in the open ocean. *Nature* **420**:379-384.
- del Giorgio, P. A., and R. H. Peters. 1993. Balance between phytoplankton production and plankton respiration in lakes. *Canadian Journal of Fisheries and Aquatic Sciences* **50**:282-289.
- del Giorgio, P. A., and R. H. Peters. 1994. Patterns in planktonic P:R ratios in lakes: Influence of lake trophic and dissolved organic C. *Limnology and Oceanography* **39**:722-787.
- DeMott, W. R., R. D. Gulati, and K. Siewertsen. 1998. Effects of phosphorus-deficient diets on the carbon phosphorus balance of *Daphnia magna*. *Limnology and Oceanography* **43**:1147-1161.

- Dewar, R. C., B. E. Bedlyn, and R. E. McMurtrie. 1999. Acclimation of the respiration / photosynthesis ratio to temperature: insights from a model. *Global Change Biology* **5**:615-622.
- Droop, M. R. 1974. The nutrient status of algal cells in continuous culture. *Journal of the Marine Biological Association of the U.K.* **54**:825-855.
- Edwards, M., and A. J. Richardson. 2004. Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature* **430**:881-884.
- Elser, J. J., K. Acharya, M. Kyle, J. Cotner, W. Makino, T. Markow, T. Watts, S. Hobbie, W. Fagan, J. Schade, J. Hood, and R. W. Sterner. 2003. Growth rate-stoichiometry couplings in diverse biota. *Ecology Letters* **6**:936-943.
- Elser, J. J., K. Hayakawa, and J. Urabe. 2001. Nutrient limitation reduces food quality for zooplankton: *Daphnia* response to seston phosphorus enrichment. *Ecology* **82**:898-903.
- Elser, J. J., R. W. Sterner, E. Gorokhova, W. F. Fagan, T. A. Markow, J. B. Cotner, J. F. Harrison, S. E. Hobbie, G. M. Odell, and L. J. Weider. 2000. Biological stoichiometry from genes to ecosystems. *Ecology Letters* **3**:540-550.
- Finney, B. P., I. Gregory-Eaves, M. S. V. Douglas, and J. P. Smol. 2002. Fisheries productivity in the northeastern Pacific Ocean over the past 2,200 years. *Nature* **416**:729-733.
- Fulton, R. S., III. 1984. Distribution and community structure of estuarine copepods. *Estuaries* **7**:38-50.
- Gaines, S. D., and J. Lubchenco. 1982. A unified approach to marine plant-herbivore interactions .2. Biogeography. *Annual Review of Ecology and Systematics* **13**:111-138.
- Gasol, J. M., P. A. del Giorgio, and C. M. Duarte. 1997. Biomass distribution in marine planktonic communities. *Limnology and Oceanography* **42**:1353-1363.
- Gillooly, J. F., J. H. Brown, G. B. West, V. M. Savage, and E. L. Charnov. 2001. Effects of size and temperature on metabolic rate. *Science* **293**:2248-2251.
- Goldman, J. C., J. J. McCarthy, and D. G. Peavey. 1979. Growth-rate influence on the chemical composition of phytoplankton in oceanic waters. *Nature* **279**:210-215.
- Harvey, H. W., H. N. Cooper, M. V. Lebour, and F. S. Russell. 1935. Plankton production and its control. *Journal of the Marine Biological Association of the U.K.* **20**:407-440.
- Hunt, G. L. J., P. Stabeno, G. Walters, E. Sinclair, R. D. Brodeur, J. M. Napp, and N. A. Bond. 2002. Climate change and control of the southeastern Bering Sea pelagic ecosystem. *Deep-Sea Research II* **49**:5821-5853.

- Iverson, R. L. 1990. Control of marine fish production. *Limnology and Oceanography* **35**:1593-1604.
- Jassby, A. D., and T. Platt. 1976. Mathematical Formulation of Relationship between Photosynthesis and Light for Phytoplankton. *Limnology and Oceanography* **21**:540-547.
- Keller, A. A. 1989. Modeling the effects of temperature, light and nutrients on primary productivity: An empirical and a mechanistic approach compared. *Limnology and Oceanography* **34**:82-95.
- Keller, A. A., C. A. Oviatt, H. A. Walker, and J. D. Hawk. 1999. Predicted impacts of elevated temperature on the magnitude of the winter-spring phytoplankton bloom in temperate coastal waters: A mesocosm study. *Limnology and Oceanography* **44**:344-356.
- Lewis, M. R., and J. C. Smith. 1983. A small volume, short-incubation-time method for measurement of photosynthesis as a function of incident irradiance. *Marine Ecology-Progress Series* **13**:99-102.
- Lindeman, R. L. 1942. The trophic-dynamic aspect of ecology. *Ecology* **23**:399-418.
- Logan, J. A., J. Regniere, and J. A. Powell. 2003. Assessing the impacts of global warming on forest pest dynamics. *Frontiers In Ecology And The Environment* **1**:130-137.
- Lopez-Urrutia, A., E. San Martin, R. P. Harris, and X. Irigoien. 2006. Scaling the metabolic balance of the oceans. *Proceedings of the National Academy of Sciences USA* **103**:8739-8744.
- McGowan, J. A., D. R. Cayan, and L. M. Dorman. 1998. Climate-ocean variability and ecosystem response in the Northeast Pacific. *Science* **281**:210-216.
- Morgan, S. G. 1995. Life and Death in the Plankton: Larval mortality and adaptation. Pages 279-322 in L. R. McEdward, editor. *Ecology of Marine Invertebrate Larvae*. CRC Press, Inc., Boca Raton, FL.
- Muren, U., J. Berglund, K. Samuelsson, and A. Andersson. 2005. Potential effects of elevated sea-water temperature on pelagic food webs. *Hydrobiologia* **545**:153-166.
- O'Brien, C. M., C. J. Fox, B. Planque, and J. Casey. 2000. Fisheries: Climate variability and North Sea cod. *Nature* **404**:142-142.
- O'Connor, M. I. Accepted. Warming strengthens an herbivore-plant interaction: linking individual responses to temperature with changes in community structure. *Ecology*.
- Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution and Systematics* **37**:637-639.

- Pauly, D., and V. Christensen. 1995. Primary production required to sustain global fisheries. *Nature* **374**:255-257.
- Philippart, C. J. M., H. M. van Aken, J. J. Beukema, O. G. Bos, G. C. Cadee, and R. Dekker. 2003. Climate-related changes in recruitment of the bivalve *Macoma balthica*. *Limnology and Oceanography* **48**:2171-2185.
- Platt, T., and A. D. Jassby. 1976. Relationship between Photosynthesis and Light for Natural Assemblages of Coastal Marine-Phytoplankton. *Journal Of Phycology* **12**:421-430.
- Richardson, A. J., and D. S. Schoeman. 2004. Climate impacts on plankton ecosystems in the Northeast Atlantic. *Science* **305**:1609-1613.
- Ritchie, M. E. 2000. Nitrogen limitation and trophic vs. abiotic influences on insect herbivores in a temperate grassland. *Ecology* **81**:1601-1612.
- Rose, J. M., and D. A. Caron. 2007. Does low temperature constrain growth rates of heterotrophic protists? Evidence and implications for algal blooms in cold waters. *Limnology and Oceanography* **52**:886-895.
- Ryther, J. H. 1969. Photosynthesis and fish production in the sea. *Science* **166**:72-76.
- Ryther, J. H., and W. M. Dunstan. 1971. Nitrogen, phosphorus, and eutrophication in coastal marine environments. *Science* **171**:1008-&.
- Schaefer, M. B. 1965. The potential harvest of the sea. *Transactions of the American Fisheries Society* **94**:123-128.
- Schindler, D. E., S. R. Carpenter, J. J. Cole, J. F. Kitchell, and M. L. Pace. 1997. Influence of Food Web Structure on Carbon Exchange between Lakes and the Atmosphere. *Science* **277**:248-251.
- Slobodkin, L. B. 1959. Energetics in *Daphnia pulex* populations. *Ecology* **40**:232-243.
- Sommer, U., N. Aberle, A. Engel, T. Hansen, K. Lengfellner, M. Sandow, J. Wohlers, E. Zollner, and U. Riebesell. 2007. An indoor mesocosm system to study the effect of climate change on the late winter and spring succession of Baltic Sea phyto- and zooplankton. *Oecologia* **150**:655-667.
- Sterner, R. W., and J. J. Elser. 2002. *Ecological Stoichiometry: the biology of elements from molecules to the biosphere*. Princeton University Press, Princeton, NJ.
- Sterner, R. W., and D. O. Hessen. 1994. Algal nutrient limitation and the nutrition of aquatic herbivores. *Annual Review of Ecology and Systematics* **25**:1-29.
- Thompson, R. C., T. A. Norton, and S. J. Hawkins. 2004. Physical stress and biological control regulate the producer-consumer balance in intertidal biofilms. *Ecology* **85**:1372-1382.

Walther, G. R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J. M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. *Nature* **416**:389-395.

Welschmeyer, N. A. 1994. Fluorometric analysis of chlorophyll a in the presence of chlorophyll b and pheopigments. *Limnology and Oceanography* 39:1985-1992.

APPENDIX A: SUPPLEMENTARY METHODS AND FIGURES TO CHAPTER 1

Temperature control of larval dispersal and implications for marine ecology, evolution, and conservation

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This Appendix includes:

Supplementary Methods

Supplementary Figures and Legends

Supplementary Tables

SUPPLEMENTARY METHODS

Additional detail on data compilation:

We searched BIOSIS and ISI Web of Science online databases for relevant articles and identified additional articles using their cited references. Our goal was not to find all relevant articles, but to build a database of sufficient size and taxonomic diversity to test our hypothesis. When multiple studies for a single species met our criteria, we chose the study that reported a greater number of unique test temperatures.

We used the following criteria to include data: 1) studies reported PLD (hatching to metamorphosis or settlement) at multiple temperatures for a single species, 2) other environmental factors (e.g., salinity, food availability) were constant and within the species' normal range, 3) temperatures were non-lethal, and 4) the interval between maximum and

minimum test temperatures exceeded 1.5 °C. We extracted the following information for each species: temperature treatments, mean planktonic larval duration at each temperature (we used the minimum or median value when necessary), normal temperature range for the species, geographic location of collection, and larval size.

Incorporation of larval mass

Data on larval mass were sparse. Larval size at metamorphosis was most commonly available as maximum or standard larval length (mm), and for this dataset values range over three orders of magnitude (0.2 – 26.8 mm). There is no convincing or standard method for converting larval length to volume for most species, so a quantitative estimate of the potential effect of mass on *PLD* requires further research.

Potential effects of larval size on model selection (in reference to main text, line 123).

Larval size could modify the temperature dependence of *PLD* in two ways. Systematic bias would occur if larvae tested at different temperatures were collected from different regions and had adapted their size to native temperature conditions (Conover and Schultz 1995). The studies we included tested the effect of temperature on larvae collected at a single location, so this kind of counter-gradient variation does not occur in our dataset. Variation in size with temperature could also occur due to phenotypic plasticity resulting in larger larvae at colder temperature treatments (Atkinson 1994). Of 17 studies in our analysis that tested for an effect of temperature on larval size, only seven report a significant effect. Therefore, for a subset of species in this analysis, temperature may affect *PLD* indirectly through its effects on size in addition to the direct effects of temperature.

Temperature measurement error as a source of error in our model (in reference to discussion of variance in main text, line 163):

Because these studies are peer-reviewed, we consider measurement error to be minimal and evenly distributed among species. There are two types of measurement error that could influence variance in *PLD* about the regression line for any particular species. One type is thermometer error, which we assume to be relatively minor. A possibly more important source of variation is fluctuation in treatment temperature between measurement times. This could occur if, for example, temperature fluctuated overnight but measurements were always made during the day.

Composite multilevel model including mean ln(temperature) and developmental mode as predictors:

This is the multilevel model referred to in Fig 1.4 (main text) and Tables A1.6 and A1.7.

$$\text{Level 1: } \ln(PLD_{ij}) = \beta_{0i} + \beta_1 * (\ln(T_{ij} / T_c)) + \beta_2 * (\ln(T_{ij} / T_c))^2 + \varepsilon_{ij}, \quad \varepsilon_{ij} \sim N(0, \sigma^2)$$

$$\text{Level 2: } \beta_{0i} = \beta_3 + \beta_3 * (\text{Mean } \ln(T_i)) + \beta_4 * (\text{developmental mode}_i) + u_{0i}, \quad \text{Eqn A1.1}$$

$$u_{0i} \sim N(0, \tau^2)$$

Percent variance explained by mean ln(temperature) (Pseudo R-squared).

In multilevel models there is no direct equivalent to the R^2 of ordinary linear regression. We calculated a pseudo- R^2 value as described by Singer and Willett (2003). This value estimates the amount of variance explained by a model relative to a null model of the

same form. We entered mean $\ln(\text{temperature})$ in our model as a level-2 predictor for the intercept, β_{0i} . The pseudo- R^2 we calculate here measures the reduction in the intercept variance, τ^2 , that occurs when mean $\ln(\text{temperature})$ and developmental mode are added to the model given in Eqn 1.4 to produce Eqn A1.1.

Predicting the Trajectories of New Species

One of the attractive features of multilevel models is that they typically outperform classical regression in predictive accuracy (Ashartous and de Leeuw 2005, Gelman 2006). Using the multilevel model we've developed one can directly predict the PLD of any species used in building the model at a temperature that was not observed. With additional data (one or more observations) it is also possible to use this model to predict the PLD of a marine species that was not among those used in estimating the model. The validity of such a prediction hinges on whether the temperature model we've proposed is truly universal. In this section we explain how to use our model to make predictions for new species.

The exponential-quadratic model we've proposed is shown in its generic composite form below.

$$\ln(PLD)_{ij} = \beta_0 + u_{0i} + \beta_1 * (\ln T_{ij} - \ln T_c) + \beta_2 * (\ln T_{ij} - \ln T_c)^2 + \varepsilon_{ij}$$

where $u_{0i} \sim N(0, \tau^2)$ and $\varepsilon_{ij} \sim N(0, \sigma^2)$. Based on this the average PLD–temperature trajectory for species i is the following:

$$\ln(PLD)_{ij} = \beta_0 + u_{0i} + \beta_1 * (\ln T_{ij} - \ln T_c) + \beta_2 * (\ln T_{ij} - \ln T_c)^2$$

or, written as a level-1 model

$$\ln(PLD)_{ij} = \beta_{0i} + \beta_1 * (\ln T_{ij} - \ln T_c) + \beta_2 * (\ln T_{ij} - \ln T_c)^2 \quad \text{Eqn A1.2}$$

where $\beta_{0i} = \beta_0 + u_{0i}$. The terms β_0 , β_1 , and β_2 are fixed effects while u_{0i} is a random effect that is unique for species i . Before Eqn A1.2 can be used to make predictions for a new species, the random effect for that species needs to be estimated from data. Because random effects are random variables rather than population parameters, it is more correct to speak of “predicting” random effects rather than “estimating” them, a convention that we adopt here. Our discussion of the prediction of random effects closely parallels Fitzmaurice *et al.* (2004), pp. 206–210 (Fitzmaurice *et al.* 2004).

From Eqn A1.2 we see that predicting u_{0i} is equivalent to predicting β_{0i} so we’ll focus on this latter quantity instead. It can be shown that the best linear unbiased predictor (BLUP) of β_{0i} is a linear combination of the population-averaged estimate $\hat{\beta}_0$ and the ordinary least squares estimate $\hat{\beta}_0^{OLS}$.

$$\hat{\beta}_{0i} = w_i * \hat{\beta}_0^{OLS} + (1 - w_i) * \hat{\beta}_0. \quad \text{Eqn A1.3}$$

The OLS estimate $\hat{\beta}_0^{OLS}$ is the ordinary regression estimate obtained by using only the n_i observations available for species i while $\hat{\beta}_0$ is the population estimate obtained from the

multilevel model we present using all the available species. The weight w_i appearing in Eqn A1.3 is a ratio of the between species variability to the sum of the within- and between-species variabilities. These quantities are listed in Table A1.2. For a mixed model with a single random effect (i.e., equation A1.2) this ratio is the following.

$$w_i = \frac{n_i * \tau^2}{n_i * \tau^2 + \sigma^2} \quad \text{Eqn A1.4}$$

where again n_i is the number of temperature observations available for species i . To use eqn S4 we substitute estimates of τ^2 and σ^2 obtained from the multilevel model. Generally REML (restricted maximum likelihood) estimates of variance components are preferred over maximum likelihood (ML) estimates for this purpose because they tend to be less biased. For our data the differences between the REML and ML estimates of the variance components turn out to be fairly small, so we don't bother further with this distinction in what follows.

$\hat{\beta}_{0i}$ as given by Eqn A1.3 is called a shrinkage estimate because it causes the OLS estimate $\hat{\beta}_0^{OLS}$ to be more or less “shrunk” toward the population-averaged value $\hat{\beta}_0$ depending on the relative magnitudes of τ^2 , σ^2 , and the sample size n_i of the full, multi-species database. If most of the variability in the data occurs between species then w_i assigns more weight to the OLS estimate. If on the other hand within species variability is dominant, the shrinkage estimate will more closely resemble the population-averaged value.

Observe that there is no restriction on size of n_i ; it can be as small as one. Just as with τ^2 , larger values of n_i will move the shrinkage estimate closer to the OLS estimate.

We illustrate the methodology with an example. Suppose we have the following data for the chiton *Tonicella lineata* that consists of two observations at two different temperatures.

Table A1.1. Data for new species

Temperature	PLD
10.0	3.83
12.5	2.75

This species actually occurs in our database and was used in fitting the model, but for point of illustration we'll treat it as a new species. This will also allow us to check our work. Parameter estimates from the exponential-quadratic multilevel model obtained using all 69 species and $T_c = 15$ are the following.

Table A1.2. Parameter estimates

Parameter	Estimate	Standard Error
β_0	3.1671863	0.10692115
β_1	-1.3439341	0.04640600
β_2	-0.2775613	0.04096706

τ^2	0.75299956	—
σ^2	0.02296691	—

To make use of Eqn A1.3 we need $\hat{\beta}_0^{OLS}$. To obtain it we first solve for β_{0i} in eqn A1.2.

$$\beta_{0i} = \ln(PLD)_{ij} - \beta_1 * (\ln T_{ij} - \ln T_c) - \beta_2 * (\ln T_{ij} - \ln T_c)^2 \quad A1.5$$

Using Table A1.1 and the parameter estimates from Table A1.2, Eqn A1.5 yields the following two separate estimates of β_{0i} .

```
mod1<-lme(log(PLD) ~ I(log(temp)-log(15))+I((log(temp)-log(15))^2),
random=~1|species,data=inverts.red,method='ML')
b0i.func<-function(x) log(x[2])-fixef(mod1)[2]*(log(x[1])-log(15))-
fixef(mod1)[3]*(log(x[1])-log(15))^2
b0i.func(c(10,3.83))
I(log(temp) - log(15))
0.843578
b0i.func(c(12.5,2.75))
I(log(temp) - log(15))
0.7757992
```

The ordinary least squares estimate of β_{0i} is just the mean of these two values. Note: If Table A1.1 consisted of only one temperature observation for the new species then the OLS estimate would be the single value obtained from applying Eqn A1.5 to this one observation.

```
b0.OLS<-mean(c(b0i.func(c(10,3.83)),b0i.func(c(12.5,2.75))))
```

```
b0.OLS
```

```
[1] 0.8096886
```

The term $\hat{\beta}_0$ needed in Eqn A1.3 is just the population-averaged value reported in Table A1.2. Next we calculate the weights.

```
as.numeric(VarCorr(mod1)[1,1])->tau2
```

```
as.numeric(VarCorr(mod1)[2,1])->s2
```

```
wi<-2*tau2/(2*tau2+s2)
```

Finally we can apply Eqn A1.3.

```
wi*b0.OLS+(1-wi)*fixef(mod1)[1]
```

```
(Intercept)
```

```
0.845101
```

This is the same answer returned by R that is obtained when we extract the fixed and random effects and sum the results.

ranef(mod1)[[1]][67]+fixef(mod1)[1]

(Intercept)

0.845101

Because between-species variability dominates the within-species variability for our data, i.e. $\tau^2 \gg \sigma^2$, the shrinkage estimate ends up being very close to the OLS estimate even though we have only two temperature observations for the new species.

The individual trajectory (empirical Bayes estimate) for *Tonicella lineata* is the following.

$$\ln(PLD)_{ij} = 0.845101 - 1.3439341 * (\ln T_{ij} - \ln 15) - 0.2775613 * (\ln T_{ij} - \ln 15)^2$$

We can also write the trajectory in the uncentered form,

$$\ln(PLD)_{ij} = \gamma_0 + \gamma_1 * \ln T_{ij} + \gamma_2 * (\ln T_{ij})^2,$$

by multiplying things out and grouping terms. Alternatively, the following transformation equations can be used.

$$\gamma_0 = \beta_0 - \beta_1 * \ln 15 + \beta_2 * (\ln 15)^2$$

$$\gamma_1 = \beta_1 - 2\beta_2 * \ln 15$$

$$\gamma_2 = \beta_2$$

For our example the transformation equations yield the following uncentered equation for *Tonicella lineata*, predicted from the model based on the multi-species database reported here.

$$\ln(PLD)_{ij} = 2.449036 + 0.1593659 * \ln T_{ij} - 0.2775613 * (\ln T_{ij})^2$$

Figure A1.1. Conceptual diagram of implications of a general effect of temperature on larval development rate.

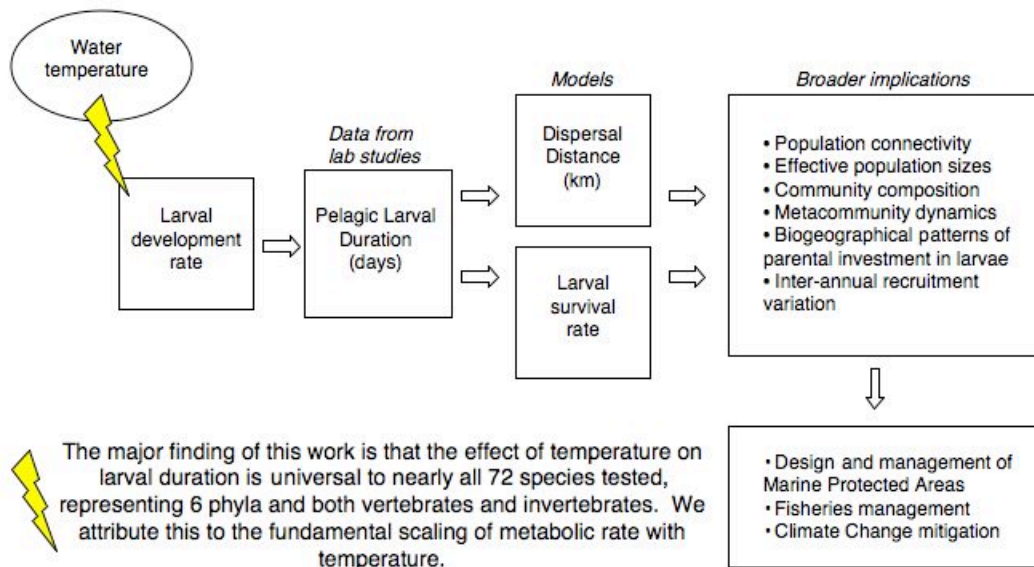


Figure A1.2. Comparison of Arrhenius model and statistical model.

Box plot comparing species-specific slope estimates in the Arrhenius model (see Figure 1.3, main text) using a random slopes and intercepts model. Slopes in this model estimate the activation energy (eV)(Brown et al. 2004). Points are empirical Bayes estimates of the slopes for individual species when the random effects are incorporated in the estimates (population value plus random effect). Black square and error bars on the right indicate the 95% confidence interval for the population value of the slope. The blue dotted line represents the predicted mean for all ectotherms -0.62 eV (Gillooly et al. 2001).

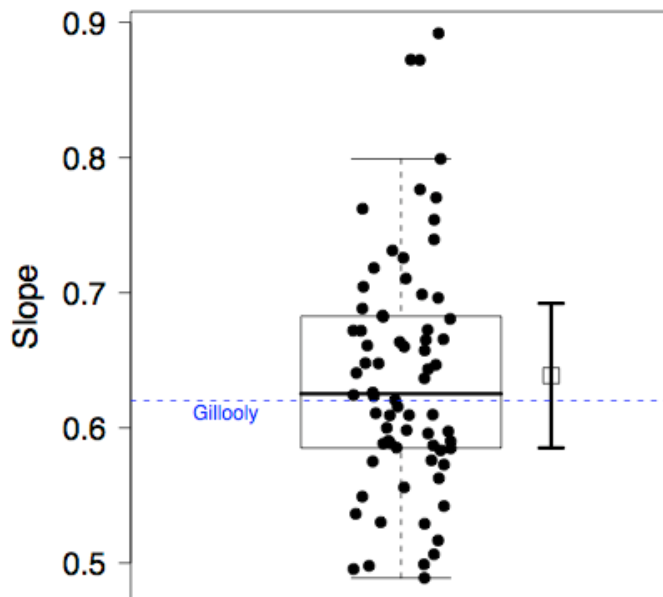


Figure A1.3. Comparison of UTD model and statistical model.

Comparison of population-averaged log-linearized models of two forms plotted on an arithmetic scale: an exponential model quadratic in temperature on a log-log scale (solid line; Eqn 1.2, main text) and universal temperature dependence (UTD) model (dashed line; Eqn 1.3 main text). Although the UTD model ranked third of the three models we tested (Table A1.5), the functional forms of the mechanistic UTD model (Eqn 1.3) and the descriptive exponential-quadratic model (Eqn 1.2) are similar over most of the temperature range.

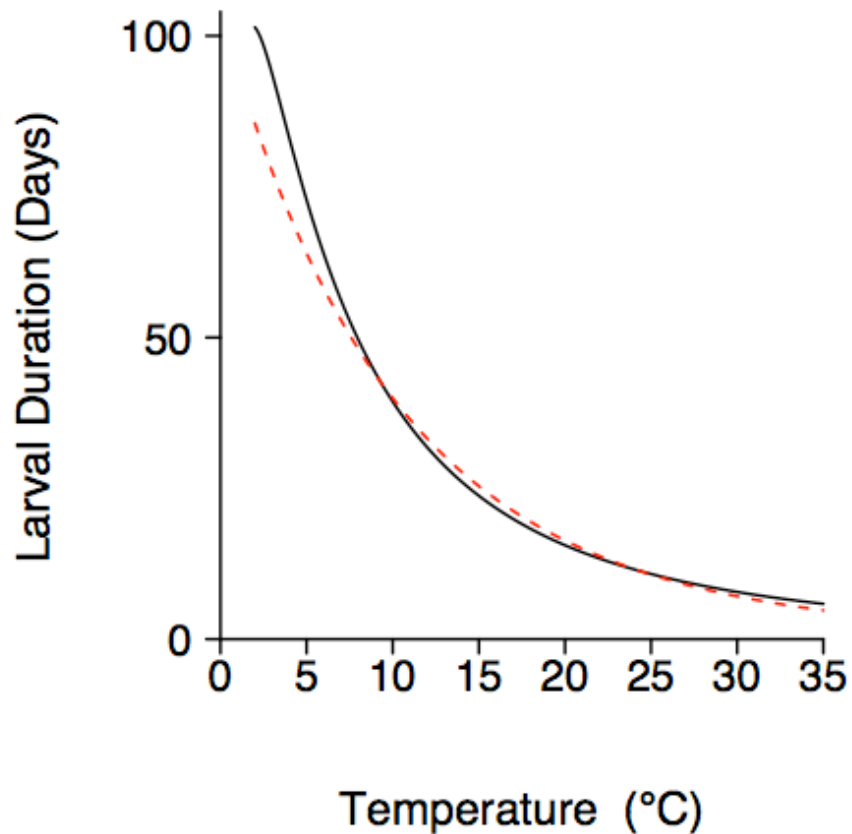


Table A1.3. Summary of species characteristics

		Total	Polar	Temperate	Tropical	L	P
Total		72	8	52	12		
Developmental Type	Lecithotrophic	16	5	9	2		
	Planktotrophic	56	3	43	10		
Phylum	Brachiopoda	1	0	1	0	1	0
	Arthropoda	39	4	31	4	4	35
	Echinodermata	4	0	3	1	2	2
	Chordata	6	1	3	2	0	6
	Mollusca	17	0	13	4	6	11
	Annelida	5	3	1	1	3	2

Table A1.4. Studies used in analyses.

Developmental mode refers to whether larvae need to feed from the environment (plankotrophic - P) or carry nourishment in yolk sacs (lecithotrophic – L). Temp (°C) are the temperature treatments for which PLD was recorded that met our criteria and were included in our study. PLD values are reported here as in the original publications.

Phylum	Species	Develop- mental Mode	Temp (°C)	PLD (d)	Reference
Annelida	Circeus spirillum	L	5	16	Ushakova (2003)
			10	16	
			15	4	
	Hydroides elegans	P	15	8.0	Qiu & Qian (1997)
			20	6.5	
			25	5.0	
			30	3.5	
	Nereis virens	L	5	15.0	Ushakova & Sarantchova (2004)
			10	9.5	
			17	4.5	
Scolecolepides viridis	P	10	42	George (1966)	
		20	26		
Spirorbis spirorbis	L	5	16	Ushakova (2003)	

			10	7	
			15	7	
Arthropoda	<i>Armases miersii</i>	L	23.9	19.3	Schuh & Diesel
			29.3	11.0	(1995)
	<i>Balanus amphitrite</i>	P	15	16	Anil <i>et al.</i> (1995)
			20	13	
			23	9	
			25	8	
			27	9	
	<i>Balanus eburneus</i>	P	20	10.8	Scheltema &
			25	8.4	Williams (1982)
			30	3.9	
	<i>Balanus trigonus</i>	P	18	10	Thiyagarajan (2003)
			21	7	
			24	5	
			28	4	
	<i>Callianassa tyrrhena</i>	P	14	16.6	Thessalou-Legaki
			18	7.6	(1990)
			22	5.1	
			25	3.2	
	<i>Cancer gracilis</i>	P	10	67.0	Sulkin & McKeen
			15	34.2	(1994)
			20	23.4	

Cancer irroratus	P	10	50	Johns (1981)
		15	26	
		18	19	
		21	17	
		24	17	
Cancer oregonensis	P	10	71.7	Sulkin & McKeen
		15	34.8	(1994)
Cancer magister	P	10	68.9	
		15	38.5	
Cancer productus	P	10	59.2	Sulkin & McKeen
		15	33.6	(1994)
		20	28.2	
Carcinus maenas	P	12	63.1	Dawirs (1986)
		15	42.2	
		18	30.5	
		25	23.5	
Chthamalus stellatus	P	18.9	16	Burrows <i>et al.</i>
		22.6	15	(1999)
Chthamalus	P	17.6	13	Burrows <i>et al.</i>
montagui		18.9	11	(1999)
		22.6	11	
Elminius modestus	P	6	42	Harms (1984)
		12	16	

		18	10	
		24	7	
Eriocheir sinensis	P	12	94.0	Anger (1991)
		15	61.0	
		18	44.5	
Hemigrapsus	P	15	53.0	Epifanio <i>et al.</i>
sanguineus		20	20.8	(1998)
		25	15.6	
Homarus	P	10.0	110	MacKenzie (1988)
americanus		12.2	65	
		14.8	45	
		18.0	34	
		21.5	24	
Hyas araneus	P	6	103.6	Anger (1983)
		12	55.4	
		18	35.5	
Limulus	L	20	118	Laughlin (1983)
polyphemus		25	52	
		30	23	
Lithodes santolla	L	3	129.0	Anger <i>et al.</i> (2004)
		6	60.1	
		9	43.4	
		12	32.9	

		15	19.3	
Lysmata seticaudata	P	20	31.8	Calado <i>et al.</i> (2005)
		26	19.5	
Menippe mercenaria	P	25	41	Brown <i>et al.</i> (1992)
		30	28	
Mithrax caribbaeus	P	22	14	Larez <i>et al.</i> (2000)
		25	12	
		28	9	
Necora puber	P	15	48.5	Valdes <i>et al.</i> (1991)
		20	31.6	
		25	28.0	
Pagurus bernhardus	P	6	109	Dawirs (1979)
		12	51	
		18	33	
Pagurus criniticornis	P	30	13.3	Blazkowski &
		25	20.5	Moreira (1986)
		20	27.0	
Palaemonetes	P	20	23.0	Antonopoulou &
longirostris		25	16.5	Emson (1989)
Palaemonetes pugio	P	20	31.8	McKenney & Neff
		25	17.5	(1979)
		30	14.5	
Palaemonetes	P	15	22.5	Antonopoulou &

varians		20	15.0	Emson (1989)
		25	11.0	
Palaemonetes	P	20.3	30.2	Sandifer (1973)
vulgaris		25.4	16.6	
		30.6	15.7	
Pandalus borealis	P	2.5	97	Rasmussen & Tande
		4.3	70	(1995)
Panopeus herbstii	P	20	34	Sastry (1970)
		25	26	
Paralomis granulosa	L	3	117.4	Anger <i>et al.</i> (2003)
		6	55.2	
		9	41.2	
		12	30.8	
		15	24.3	
Parthenope serrata	P	25	30	Yang (1971)
		20	45	
Rhithropanopeus	P	20	33	Costlow <i>et al.</i>
harrisii		25	18	(1966)
		30	13	
Scylla serrata	P	20	37.7	Hamasaki (2003)
		23	24.6	
		26	17.7	
		29	13.0	

	Semibalanus	P	6	20	Harms (1984)
	balanoides		12	12	
			18	10	
	Sesarma cinereum	P	20	37	Costlow <i>et al.</i>
			25	31	(1960)
			30	21	
	Uca pugilator	P	22	19.4	Christy (1989)
			24	19.6	
			28	14.7	
Brachiopoda	Laqueus	L	5	9	Pennington (1999)
	californianus		10	7	
			15	5	
Chordata	Amphiprion	P	25	12.3	Green & Fisher
	melanopus		28	9.0	(2004)
	Clupea harengus	P	6	6	McGurk (1984)
	pallasi		8	5	
			10	4	
	Gadus morhua	P	4	56	Otterlei <i>et al.</i> (1999)
			6	40	
			8	33	
			10	27	
			12	25	
			14	23	

	Pseudopleuronectes	P	5	80	Laurence (1975)
	americanus		8	49	
	Sprattus sprattus	P	5	3	Nissling (2004)
			13	1	
	Upeneus tragula	P	25	12.0	McCormick &
			30	9.2	Molony (1995)
Echino-	Dendraster	P	12	8.29	McEdward (1985)
dermata	excentricus		17	4.46	
			22	2.63	
	Echinaster type I	L	20	22	Watts <i>et al.</i> (1982)
			25	12	
			30	14	
	Echinaster type II	L	20	22	Watts <i>et al.</i> (1982)
			25	17	
			30	13	
	Lytechinus	P	18	39.5	Roller & Stickle
	variegatus		23	24.5	(1993)
	Cardium edule	P	15	28	Kingston (1974)
			20	22	
Mollusca	Chlamys hastata	P	16	34	Hodgson & Bourne
			12	42	(1988)
	Crassostrea	P	23.0	18	Loosanoff & Davis
	virginica		30.0	10	(1963)

		23.5	18	
Crepidula fornicata	P	18	42	Pechenik (1984b)
		24	24	
Crepidula plana	P	12	71.9	Lima & Pechenik
		20	31.2	(1985)
		25	28.9	
		29	18.1	
Haliotis asinina	L	25	2.7	Sawatpeera <i>et al.</i>
		28	2.0	(2001)
		31	1.7	
Haliotis fulgens	L	25.5	3	Leighton (1974)
		22.5	4	
Haliotis sorenseni	L	20	7	Leighton (1972)
		18	11	
		12	18	
		14	15	
		16	13	
Mactra solidissima	P	22	19	Loosanoff & Davis
		14	35	(1963)
Mopalia muscosa	L	16	26.6	Pechenik (1984a)
		11	19.9	
Mytilus edulis	P	16	16	Bayne (1965)
		11	39	

Nassarius obsoletus	P	17.5	21	Scheltema (1967)
		23.0	16	
		25.2	10	
Ostrea lurida	L	24	7	Loosanoff & Davis
		18	16	(1963)
Perna viridis	P	24	37.5	Nair & Appukuttan
		27	22.0	(2003)
		29	16.6	
		31	19.0	
Strombus gigas	P	24	24	Davis (2000)
		28	22	
		32	16	
Tivela mactroides	P	22	20.9	De Severeyn <i>et al.</i>
		25	16.7	(2000)
		28	13.0	
Tonicella lineata	L	10.0	3.8	Barnes (1972)
		12.5	2.7	

Table A1.5. AIC comparison of three models of temperature dependence of PLD.

For 72 species, Δ_i = difference in AIC of the current model from that of the lowest AIC value of among all tested models, ω_i = Akaike weight, a normalized relative likelihood for each model. Akaike weights (ω_i) can be interpreted as the probability under repeated sampling that a model is the best model among the set of models under consideration (Burnham and Anderson 2002). Equation numbers refer Methods of main text.

Model	AIC	Log-likelihood	Δ_i	ω_i
Linearized power law (Eqn 1.1): random intercepts and slopes	180.63	-84.32	16.77	0.000
Linearized power law with quadratic in temperature (Eqn 1.2): random intercepts, 'slopes', and quadratic term	163.86	-71.93	0	1.000
Universal Temperature Dependence (Eqn 1.3): random intercepts and 'slopes'	182.13	-85.06	18.27	0.000

Table A1.6. Model comparison for cold adaptation using likelihood ratio tests.

Using a random intercepts model (Eqn 1.4, main text; repeated as Eqn A1.7 in Table A1.8, below) as a baseline for 69 species, we tested whether some of the species-level variation in intercepts can be explained by the mean $\ln(\text{test temperature})$ for each species and/or a species' developmental mode (lecithotrophic vs planktotrophic). Reported values are for variable-added-last likelihood ratio tests. See Fig 1.4, main text.

Within-species predictors	Species-level predictors	AIC	Log-likelihood	P-value
$\ln(\text{temperature}),$ $(\ln(\text{temperature}))^2$		132.00	-61.00	—
$\ln(\text{temperature}),$ $(\ln(\text{temperature}))^2$	mean $\ln(\text{temperature})$	120.89	-54.44	<0.001
$\ln(\text{temperature}),$ $(\ln(\text{temperature}))^2$	mean $\ln(\text{temperature}),$ developmental mode	113.50	-49.74	0.002
$\ln(\text{temperature}),$ $(\ln(\text{temperature}))^2$	mean $\ln(\text{temperature}),$ developmental mode, mean $\ln(\text{temperature})$ * developmental mode	115.14	-49.57	0.559

Table A1.7. Effects of temperature, mean test temperature and developmental mode on PLD.

Multilevel model of individual- and species-level effects of temperature, mean ln(temperature tested) and developmental mode on PLD (Eqn A1.1, centered at 15 °C). Different parameter values for β_0 , β_1 , β_2 are obtained when mean ln(temperature tested) and developmental mode are not included in the model (Fig 1.1B, main text, Table A1.6; Table 11 in S.I. 2 of O’Connor et al, 2007).

Summary of Fixed Effects

Individual (Level-1) parameter	Species (Level-2) regression model	Parameter	Estimate	Standard Error
Intercept (β_{0i})	Intercept	β_0	0.511	0.598
	Mean ln(test temperature)	β_3	0.739	0.209
	Developmental mode	β_4	0.714	0.225
Rate of change: ln(temperature) (β_{1i})		β_1	- 1.368	0.047
Curvature: ln(temperature) ² (β_{2i})		β_2	- 0.283	0.041

Summary of Random Effects

Variance Components	Parameter	Estimate
Level-1 (within species)	σ^2	0.023
Level-2 (between species in initial status)	τ^2	0.543

Table A1.8. Log-likelihood ratio tests for exponential models quadratic in temperature on a log-log scale for 72 species.

P-values are for modified incremental likelihood ratio tests that compare the model in one row with the model that appears immediately above it. We follow the methodology outlined in Verbeke and Molenberghs (2000, pp. 70-71) (Verbeke and Molenberghs 2000), for carrying out these tests. See also p. 26 of the supplementary text of O'Connor et al., 2007.

Eqn	Model: Linearized power law model quadratic in temperature	Model description	Log-likelihood	P-value
A1.6	$\ln(\text{PLD}_{ij}) = \beta_0 + \beta_1 * \ln(T_{ij}/T_c) + \beta_2 * (\ln(T_{ij}/T_c))^2 + \epsilon_{ij}$	No random effects	-263.27	—
A1.7*	$\ln(\text{PLD}_{ij}) = \beta_0 + \beta_1 * \ln(T_{ij}/T_c) + \beta_2 * (\ln(T_{ij}/T_c))^2 + u_{0i} + \epsilon_{ij}$	Random intercepts only	-81.10	<0.001
A1.8	$\ln(\text{PLD}_{ij}) = \beta_0 + \beta_1 * \ln(T_{ij}/T_c) + \beta_2 * (\ln(T_{ij}/T_c))^2 + u_{0i} + u_{1i} * \ln(T_{ij}/T_c) + \epsilon_{ij}$	Random intercepts and 'slopes'	-76.14	0.007
A1.9	$\ln(\text{PLD}_{ij}) = \beta_0 + \beta_1 * \ln(T_{ij}/T_c) + \beta_2 * (\ln(T_{ij}/T_c))^2 + u_{0i} + u_{1i} * \ln(T_{ij}/T_c) + u_{2i} * (\ln(T_{ij}/T_c))^2 + \epsilon_{ij}$	Random intercepts, slopes and quadratic coefficients	-71.93	0.038

*same form as Eqn 4 in the main text.

Table A1.9. Modified log-likelihood ratio tests for UTD model.

Testing for needed random effects in the UTD model (Eqn 1.3, main text) for full dataset (72 species, Tables A1.3, A1.4). We follow the methodology outlined in Verbeke and Molenberghs (2000, pp. 70-71) (Verbeke and Molenberghs 2000), for carrying out these tests. See also p. 26 of S.I. 2 of O'Connor et al., 2007.

Eqn	Model: Universal Temperature Dependence (UTD)	Model description	Log-likelihood	P-value
A1.10	$\ln\text{PLD}_{ij} = \beta_0 + \beta_1 * (1 / (k*(T_{ij}+273))) + \varepsilon_{ij}$	No random effects	-263.04	—
A1.11	$\ln\text{PLD}_{ij} = \beta_{0i} + \beta_1 * (1 / (k*(T_{ij}+273))) + u_{0i} + \varepsilon_{ij}$	Random intercepts only	-85.15	<0.001
A1.12	$\ln\text{PLD}_{ij} = \beta_{0i} + \beta_1 * (1 / (k*(T_{ij}+273))) + u_{0i} + u_{1i} / (k*((T_{ij}) + 273)) + \varepsilon_{ij}$	Random intercepts and 'slopes'	-80.04	0.004

References

- Anger, K. 1983. Temperature and the larval development of *Hyas araneus* L. (Decapoda: majaidae); extrapolations of laboratory data to field conditions. *Journal of Experimental Marine Biology and Ecology* **69**:203-215.
- Anger, K. 1991. Effects of Temperature and Salinity on the Larval Development of the Chinese Mitten Crab *Eriocheir-Sinensis* Decapoda Grapsidae. *Marine Ecology Progress Series* **72**:103-110.
- Anger, K., G. A. Lovrich, S. Thatje, and J. A. Calcagno. 2004. Larval and early juvenile development of *Lithodes santolla* (Molina, 1782) (Decapoda: Anomura: Lithodidae) reared at different temperatures in the laboratory. *Journal of Experimental Marine Biology and Ecology* **206**:217-230.
- Anger, K., S. Thatje, G. Lovrich, and J. Calcagno. 2003. Larval and early juvenile development of *Paralomis granulosa* reared at different temperatures: Tolerance of cold and food limitation in a lithodid crab from high latitudes. *Marine Ecology Progress Series* **253**:243-251.
- Anil, A. C., K. Chiba, K. Okamoto, and H. Kurokura. 1995. Influence of temperature and salinity on larval development of *Balanus amphitrite*: Implications in fouling ecology. *Marine Ecology Progress Series* **118**:159-166.
- Antonopoulou, E., and R. Emson. 1989. The combined effects of temperature and salinity on survival, moulting and metamorphosis of the larval stages of three species of palaemonid prawns. Pages 339-347 in J. S. Ryland and P. A. Tyler, editors. *Reproduction, Genetics and Distributions of Marine Organisms*. 23rd European Mar. Biol. Symposium. Olsen & Olsen, Fredensborg.
- Ashartous, D., and J. de Leeuw. 2005. Prediction in multilevel models. *Journal of Educational and Behavioral Statistics* **30**:109-139.
- Atkinson, D. 1994. Temperature and Organism Size - A biological law for ectotherms? *Advances in ecological research* **25**:1-58.
- Barnes, J. R. 1972. Ecology and reproductive biology of *tonicella lineata* (Wood, 1815)(Mollusca: Polyplacophora). Ph.D. Oregon State University, Corvallis.
- Bayne. 1965. Growth and the delay of metamorphosis of the larvae of *Mytilus edulis*. *Ophelia* **2**:1-47.
- Blaszowski, C., and G. S. Moreira. 1986. Combined effects of temperature and salinity on the survival and duration of larval stage of *Pagurus criniticornis* (Dana) (Crustacea: Paguridae). *Journal of Experimental Marine Biology and Ecology* **103**:77-86.

- Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage, and G. B. West. 2004. Toward a metabolic theory of ecology. *Ecology* **85**:1771-1789.
- Brown, S. D., T. M. Bert, W. A. Tweedale, J. J. Torres, and W. J. Lindberg. 1992. The effects of temperature and salinity on survival and development of early life stage Florida stone crabs *Menippe mercenaria* (Say). *Journal of Experimental Marine Biology and Ecology* **157**:115-136.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference. Springer-Verlag, New York.
- Burrows, M. T., S. J. Hawkins, and A. J. Southward. 1999. Larval development of the intertidal barnacles *Chthamalus stellatus* and *Chthamalus montagui*. *Journal of the Marine Biological Association of the U.K.* **79**:93-101.
- Calado, R., J. Figueredo, R. Rosa, M. L. Nunes, and L. Narciso. 2005. Effects of temperature, density and diet on development, survival, settlement synchronism, and fatty acid profile of the ornamental shrimp *Lysmata seticaudata*. *Aquaculture* **245**:221-237.
- Christy, J. H. 1989. Rapid development of megalopae of the fiddler crab *Uca pugilator* reared over sediment implications for models of larval recruitment. *Marine Ecology Progress Series* **57**:259-266.
- Conover, D. O., and E. T. Schultz. 1995. Phenotypic similarity and the evolutionary significance of countergradient variation. *Trends in Ecology & Evolution* **10**:248-252.
- Costlow, J. D., C. G. Bookhout, and R. J. Monroe. 1960. The effects of salinity and temperature on larval development of *Sesarma cinereum* (Bosc) reared in the laboratory. *Biological Bulletin* **188**:183-202.
- Costlow, J. D., C. G. Bookhout, and R. J. Monroe. 1966. Studies on the larval development of the crab, *Rhithropanopeus harrisi* (Gould). I. The effect of salinity and temperature on larval development. *Physiological Zoology* **39**:81-100.
- Davis, M. 2000. The combined effects of temperature and salinity on growth, development, and survival for tropical gastropod veligers of *Strombus gigas*. *Journal of Shellfish Research* **19**:883-889.
- Dawirs, R. R. 1979. Effects of temperature and salinity on larval development on *Pagurus bernhardus* (Decapoda, Paguridae). *Marine Ecology Progress Series* **1**:323-329.
- Dawirs, R. R., and A. Dietrich. 1986. *Journal of Experimental Marine Biology and Ecology* **99**:133-147.
- de Severeyn, Y. G., H. Severeyn, W. Grant, and Y. Reverol. 2000. Effect of water temperature on larval development of the bivalve mollusk *Tivela mactroides*: Evaluation in the laboratory and via simulation. *Ecological Modelling* **129**:143-151.

- Epifanio, C. E., A. I. Dittel, S. Park, S. Schwalm, and A. Fouts. 1998. Early life history of *Hemigrapsus sanguineus*, a non-indigenous crab in the Middle Atlantic Bight (USA). *Marine Ecology Progress Series* **170**:231-238.
- Fitzmaurice, G. M., N. M. Laird, and J. H. Ware. 2004. *Applied Longitudinal Data Analysis*. Wiley, New York.
- Gelman, A. 2006. Multilevel (hierarchical) modeling: what it can and cannot do. *Technometrics* **48**:432-435.
- George, J. D. 1966. Reproduction and early development of the spionid polychaete *Scolecoides viridis* (Verrill). *Biological Bulletin* **130**:76-93.
- Gillooly, J. F., J. H. Brown, G. B. West, V. M. Savage, and E. L. Charnov. 2001. Effects of size and temperature on metabolic rate. *Science* **293**:2248-2251.
- Green, B. S., and R. Fisher. 2004. Temperature influences swimming speed, growth and larval duration in coral reef fish larvae. *Journal of Experimental Marine Biology and Ecology* **299**:115-132.
- Hamasaki, K. 2003. Effects of temperature on the egg incubation period, survival and development period of the mud crab *Scylla serrata* (Forsk.) (Brachyura: Portunidae) reared in the laboratory. *Aquaculture* **219**:561-572.
- Harms, J. 1984. Influence of water temperature on larval development of *Elminius modestus* and *Semibalanus balanoides* (Crustacea, Cirripedia). *Helgolander Meeresuntersuchungen* **38**:123-134.
- Hodgson, C. A., and N. Bourne. 1988. Effect of temperature on larval development of the spiny scallop *Chlamys hastata* (Sowerby) with a note on metamorphosis. *Journal of Shellfish Research* **7**:349-358.
- Johns, D. M. 1981. Physiological studies on *Cancer irroratus* larvae. I. Effects of temperature and salinity on survival, development rate and size. *Marine Ecology Progress Series* **5**:75-83.
- Kingston, P. 1974. Some observations on the effects of temperature and salinity upon the growth of *Cardium edule* and *Cardium glaucum* larvae in the laboratory. *Journal of the Marine Biological Association of the U.K.* **54**:309-317.
- Larez, M. B., J. L. Palazon-Fernandez, and C. J. Bolanos. 2000. The effect of salinity and temperature on the larval development of *Mithrax caribbaeus* Rathbun 1920 (Brachyura: Majidae) reared in the laboratory. *Journal of Plankton Research* **22**:1855-1869.
- Laughlin, R. 1983. The effects of temperature and salinity on larval growth of the horseshoe crab *Limulus polyphemus*. *Biological Bulletin* **164**:93-103.

- Laurence, G. C. 1975. Laboratory growth and metabolism of the winter flounder *Pseudopleuronectes americanus* from hatching through metamorphosis at three temperatures. *Marine Biology* **32**:223-229.
- Leighton, D. L. 1972. Laboratory observations on the early growth of the abalone, *Haliotis sorenseni*, and the effect of temperature on larval development and settling success. *Fishery Bulletin* **70**:373-381.
- Leighton, D. L. 1974. The influence of temperature on larval and juvenile growth in 3 species of Southern California abalones. *Fishery Bulletin* **72**:1137-1145.
- Lima, G. M., and J. A. Pechenik. 1985. The influence of temperature on growth rate and length of larval life on the gastropod, *Crepidula plana* (Say). *Journal of Experimental Marine Biology and Ecology* **90**:55-71.
- Loosanoff, V. L., and H. C. Davis. 1963. Rearing of bivalve mollusks. *Advances in Marine Biology* **1**:1-136.
- MacKenzie, B. R. 1988. Assessment of temperature effects on interrelationships between stage durations, mortality and growth in laboratory-reared *Homarus americanus* Milne Edwards larvae. *Journal of Experimental Marine Biology and Ecology* **116**:87-98.
- Manoj Nair, R., and K. K. Appukuttan. 2003. Effect of temperature on the development, growth, survival and settlement of green mussel *Perna viridis* (Linnaeus, 1758). *Aquaculture Research* **34**:1037-1045.
- McCormick, M. I., and B. W. Molony. 1995. Influence of water temperature during the larval stage on size, age and body condition of a tropical reef fish at settlement. *Marine Ecology Progress Series* **118**:59-68.
- McEdward, L. R. 1985. Effects of Temperature on the Body Form Growth Electron Transport System Activity and Development Rate of an Echinopluteus. *Journal of Experimental Marine Biology and Ecology* **93**:168-182.
- McGurk, M. D. 1984. Effects of delayed feeding and temperature on the age of irreversible starvation and on the rates of growth and mortality of Pacific herring larvae. *Marine Biology* **84**:13-26.
- McKenney, C. L., Jr., and J. M. Neff. 1979. Individual effects and interactions of salinity, temperature and zinc on larval development of the grass shrimp *Palaemonetes pugio*. Part 1: Survival and developmental duration through metamorphosis. *Marine Biology* **52**:177-188.
- Nissling, A. 2004. Effects of temperature on egg and larval survival of cod (*Gadus morhua*) and sprat (*Sprattus sprattus*) in the Baltic Sea - implications for stock development. *Hydrobiologia* **514**:115-123.

- O'Connor, M. I., J.F. Bruno, S.D. Gaines, B.S. Halpern, S.E. Lester, B.P. Kinlan and J.M. Weiss. 2007. Temperature control of larval dispersal: implications for marine ecology, evolution and conservation. *Proceedings of the National Academy of Sciences of the United States of America* **104**: 1266-1271.
- Otterlei, E., N. Gunnar, A. Folkvord, and S. O. Stefansson. 1999. Temperature- and size-dependent growth of larval and early juvenile Atlantic cod (*Gadus morhua*): A comparative study of Norwegian coastal cod and northeast Arctic cod. *Canadian Journal of Fisheries and Aquatic Sciences* **56**:2099-2111.
- Pechenik, J. A. 1984a. Influence of temperature and temperature shifts on the development of chiton larvae, *Mopalia muscosa*. *Journal of Invertebrate Reproduction and Development* **7**:3-12.
- Pechenik, J. A. 1984b. The relationship between temperature, growth rate, and duration of planktonic life for larvae of the gastropod *Crepidula fornicata* (L.). *Journal of Experimental Marine Biology and Ecology* **74**:241-257.
- Pennington, J. T., M. N. Tamburri, and J. P. Barry. 1999. Development, temperature tolerance, and settlement preference of embryos and larvae of the articulate brachiopod *Laqueus californianus*. *Biological Bulletin* **196**:245-256.
- Qiu, J. W., and P. Y. Qian. 1997. Combined effects of salinity, temperature and food on early development of the polychaete *Hydroides elegans*. *Marine Ecology Progress Series* **152**:79-88.
- Rasmussen, T., and K. Tande. 1995. Temperature-dependent development, growth and mortality in larvae of the deep-water prawn *Pandalus borealis* reared in the laboratory. *Marine Ecology Progress Series* **118**:149-157.
- Roller, R. A., and W. B. Stickle. 1993. Effects of temperature and salinity acclimation of adults on larval survival, physiology, and early development of *Lytechinus variegatus* (Echinodermata: Echinoidea). *Marine Biology (Berlin)* **116**:583-591.
- Sandifer, P. A. 1973. Effects of temperature and salinity on larval development of grass shrimp *Palaemonetes vulgaris* (Decapoda: caridae). *Fishery Bulletin* **71**:115-123.
- Sastry, A. N. 1970. Culture of brachyuran crab larvae using a re-circulating sea water system in the laboratory. *Helgolander Meeresuntersuchungen* **20**:406-416.
- Sawatpeera, S., E. S. Upatham, M. Kruatrachue, Y. P. Chitramvong, P. Sonchaeng, T. Pumthong, and J. Nugranad. 2001. Larval development in *Haliotis asinina* Linnaeus. *Journal of Shellfish Research* **20**:593 - 601.
- Scheltema, R. S. 1967. The relationship of temperature to the larval development of *Nassarius obsoletus* (Gastropoda). *Biological Bulletin* **132**:253-265.

- Scheltema, R. S., and I. P. Williams. 1982. Significance of temperature to larval survival and length of development in *Balanus eburneus*. *Marine Ecology Progress Series* **9**:43-49.
- Schuh, M., and R. Diesel. 1995. Effects of salinity, temperature, and starvation on the larval development of *Armases* (equals *Sesarma*) *miersii* (Rathbun, 1897), a semiterrestrial crab with abbreviated development (Decapoda: Grapsidae). *Journal of Crustacean Biology* **15**:205-213.
- Singer, J. D., and J. B. Willett. 2003. *Applied longitudinal data analysis*. Oxford University Press, New York.
- Sulkin, S. D., and G. McKeen. 1994. Influence of temperature on larval development of four co-occurring species of the brachyuran genus *Cancer*. *Marine Biology (Berlin)* **118**:593-600.
- Thessalou-Legaki, M. 1990. Advanced larval development of *Callinassa tyrrenhia* (Decapoda: Thalassinidea) and the effect of environmental factors. *Journal of Crustacean Biology* **10**:659-666.
- Thiyagarajan, V., H. Tilmann, and P. Y. Qian. 2003. Combined effects of temperature and salinity on larval development and attachment of the subtidal barnacle *Balanus trigonus* Darwin. *Journal of Experimental Marine Biology and Ecology* **287**:223-236.
- Ushakova, O. O. 2003. Combined effect of salinity and temperature on *Spirorbis spirorbis* L. and *Circeus spirillum* L. larvae from the White Sea. *Journal of Experimental Marine Biology and Ecology* **296**:23-33.
- Ushakova, O. O., and O. L. Sarantchova. 2004. The influence of salinity on fertilization and larval development of *Nereis virens* (Polychaeta, Nereidae) from the White Sea. *Journal of Experimental Marine Biology and Ecology* **301**:129-139.
- Valdes, L., M. T. Alvarez-Ossorio, and E. Gonzalez-Gurriaran. 1991. Influence of Temperature on Embryonic and Larval Development in *Necora-Suber* Brachyura Portunidae. *Journal of the Marine Biological Association of the United Kingdom* **71**:787-798.
- Verbeke, G., and G. Molenbergs. 2000. *Linear mixed models for longitudinal data*. Springer-Verlag, New York.
- Watts, S. A., R. E. Scheibling, A. G. Marsh, and J. B. McClintock. 1982. Effect of temperature and salinity on larval development of sibling species of *Echinaster* (Echinodermata) *asteroidea* and their hybrids. *Biological Bulletin* **163**:348-354.
- Yang, W. T. 1971. The larval and post larval development of *Parthenope serrata* reared in the laboratory and the systematic position of the Parthenopinae Crustacea: Brachyura. *Biological Bulletin* **140**:166-189.

APPENDIX B: SUPPLEMENTARY METHODS TO CHAPTER 3

Warming strengthens an herbivore-plant interaction: linking individual responses to temperature with changes in community structure

Prior to initial weighing, *Sargassum* was rinsed in fresh water to remove potential invertebrate grazers, trimmed of senescent tissue and spun 15 revolutions in a salad spinner to remove excess water. At the end of each experiment, algae was spun and weighed again. Amphipods were removed from the algae by hand picking and a freshwater rinse, and either live sorted (*Experiment 1A*) or preserved in 70% ethanol for counting and sorting by size class (*Experiments 1B* and *2*). Counts of the smallest size classes are unreliable because they would not be consistently retained during algae removal and rinsing procedure.

Algal holdfasts or stipes were attached to a small piece of Vexar mesh with a cable tie, and anchored to the bottom of 6-L plastic mesocosms. Temperature-conditioned, gravel-filtered seawater dripped into a small dump bucket above each mesocosm at a rate of 0.2 L / min, and emptied with a splash approximately twice per minute creating wave action in the mesocosm. The water in each mesocosm completely exchanged approximately every 30 minutes, maintaining fresh nutrient and oxygen levels. We rotated mesocosms daily to avoid potentially confounding effects of variation in light intensity among different positions on the table. We recorded temperature in each block of mesocosms hourly using ibutton dataloggers (Dallas Instruments Thermochron ibutton) and daily using hand-held thermometers. Thus we maintained 4-5 temperature levels, ranging from 24.5 – 28.9 °C.

APPENDIX C: SUPPLEMENTARY METHODS TO CHAPTER 4

Detailed methods for determining primary productivity

Three samples for time zero (T0) radioactivity measurements contained sample water 500 μl of buffered formalin that was added to each vial immediately after the addition of labeled seawater. T0 samples were used to correct for uptake of ^{14}C label that occurred during experimental setup. Three vials for measurement of total radioactivity added (Tc) were prepared by adding 500 μl of phenethylamine (PEA) and 50 μl labeled sample water into a 20 ml scintillation vial.

Irradiance ($\mu\text{moles quanta m}^{-2} \text{ s}^{-1}$) in each position of the photosynthetron was measured using a Biospherical Instruments Model QSL-100 irradiance meter with a QSL-101 4π sensor. For each measurement, the sensor was inserted into a 20 ml glass scintillation vial that contained 5 ml of water. Temperature was maintained during the incubations with a circulating water bath. The temperature was set to the experimental temperature for each treatment.