Coral Reefs (2013) 32:401–409
DOI 10.1007/s00338-012-0983-z

REPORT

A simple temperature-based model predicts the upper latitudinal limit of the temperate coral *Astrangia poculata*

**J. L. Dimond · A. H. Kerwin · R. Rotjan ·
K. Sharp · F. J. Stewart · D. J. Thornhill**

Received: 6 July 2012 / Accepted: 6 November 2012 / Published online: 23 November 2012

Abstract A few hardy ahermatypic scleractinian corals occur in shallow waters well outside of the tropics, but little is known concerning their distribution limits at high latitudes. Using field data on the growth of *Astrangia poculata* over an annual period near its northern range limit in Rhode Island, USA, we tested the hypothesis that the distribution of this coral is limited by low temperature. A simple model based on satellite sea surface temperature and field growth data at monthly temporal resolution was used to estimate annual net coral growth north and south of the known range limit of *A. poculata.* Annual net coral growth was the result of new polyp budding above ~10 °C minus polyp loss below ~10 °C, which is caused by a state of torpor that leads to overgrowth by encroaching and settling organisms. The model accurately predicted *A. poculata*'s range limit around Cape Cod, Massachusetts, predicting no net growth northward as a result of corals' inability to counteract polyp loss during winter with sufficient polyp budding during summer. The model also indicated that the range limit of *A. poculata* coincides with a decline in the benefit of associating with symbiotic dinoflagellates (*Symbiodinium* B2/*S. psygmophilum*), suggesting that symbiosis may become a liability under colder temperatures. While we cannot exclude the potential role of other coral life history traits or environmental factors in setting *A. poculata*'s northern range limit, our analysis suggests that low temperature constrains the growth and persistence of adult corals and would preclude coral growth northward of Cape Cod.

Keywords Biogeography · Facultative symbiosis · Physiological tolerance · Species range · *Symbiodinium* B2 · *Symbiodinium psygmophilum*

Communicated by Biology Editor Dr. Anastazia Banaszak

J. L. Dimond
Shannon Point Marine Center, Western Washington University,
1900 Shannon Point Rd., Anacortes, WA 98221, USA

A. H. Kerwin
Department of Molecular and Cellular Biology, University of
Connecticut, 91 N. Eagleville Rd, Unit 3125, Storrs,
CT 06269, USA

R. Rotjan
John H Prescott Marine Laboratory, New England Aquarium,
1 Central Wharf, Boston, MA 02110, USA

K. Sharp
Galbraith Marine Sciences Laboratory, Eckerd College,
4200 54th Ave South, St., Petersburg, FL 33711, USA

F. J. Stewart
School of Biology, Georgia Institute of Technology,
310 Ferst Drive, Atlanta, GA 30332, USA

D. J. Thornhill (✉)
Department of Conservation Science and Policy, Defenders of
Wildlife, 1130 17th Street NW, Washington, DC 20007, USA
e-mail: thornhill.dan@gmail.com

Introduction

Scleractinian corals are conspicuously rare in shallow waters outside of the tropics. This may have been true throughout their evolutionary history (Stanley 2003), and there is evidence that the distribution of shallow-water corals is deeply rooted in the obligate endosymbiotic relationships many corals form with dinoflagellates (*Symbiodinium* spp.) that provide photosynthetic energy and enhance calcification (Stanley and Swart 1995; Davy et al. 2012). Temperature, light, and seawater aragonite saturation state—critical factors for photosynthesis and calcification by hermatypic corals—co-vary and decline with increasing latitude, limiting coral growth and reef formation (Kleypas et al. 1999). In contrast, macroalgae become increasingly abundant in shallow waters at higher latitudes due to increased nutrient concentrations and reduced grazing activity (Johannes et al. 1983; Miller and Hay 1996; Miller 1998). Competition with macroalgae for light and space within the photic zone is thus a further impediment to coral success in temperate regions (Miller 1995, 1998; Miller and Hay 1996).

A few hardy, ahermatypic shallow-water scleractinians exist well beyond the latitudinal limits of hermatypic corals (Schuhmacher and Zibrowius 1985). These temperate species tend to engage in facultative symbioses with *Symbiodinium* spp., and under sufficiently high light and temperature, symbiosis can considerably enhance their growth (Jacques et al. 1983; Miller 1995; Dimond and Carrington 2007; Hoogenboom et al. 2010). However, low temperatures during winter months, and generally suboptimal light availability due to water column turbidity, macroalgal shading and reduced solar radiation at higher latitudes means that symbiosis has limited benefit in temperate regions (Jacques et al. 1983; Dimond and Carrington 2007; Ferrier-Pagès et al. 2011). Consequently, temperate corals must rely heavily on heterotrophy to support their growth and metabolic demands (Szmant-Froelich and Pilson 1980; Ferrier-Pagès et al. 2011). Temperate corals may have higher heterotrophic potential than their tropical counterparts because of the higher net productivity of temperate regions (Muller-Parker and Davy 2001) and the potentially higher heterotrophic capacity of temperate scleractinians (Tremblay et al. 2011).

In spite of their high heterotrophic potential, few shallow-water scleractinians are found beyond 40° latitude (Veron 2000). If heterotrophy can sustain these corals at high latitudes, what ultimately limits their distributions? In this study, we evaluate a simple temperature-based model of the growth of *Astrangia poculata*, a widespread scleractinian in shallow waters of the northwest Atlantic that forms a facultative symbiosis with *Symbiodinium psygmophilum* (*Symbiodinium* ITS2 type B2) throughout its range (Thornhill et al. 2008; LaJeunesse et al. 2012). This coral reaches an abrupt northern range limit around Cape Cod, Massachusetts ($\sim$42°N; Peters et al. 1988). Our model is based on a field study of the growth of *A. poculata* near this northern limit (Dimond and Carrington 2007), where it was speculated that low temperatures restrict coral growth further north through a combination of physiological and ecological effects. Here, we test this model and find that it accurately predicts the known geographic range limit of *A. poculata.*

Materials and methods

Range of *A. poculata*

Geographic occurrence data for *A. poculata* were acquired from the Global Biodiversity Information Facility (GBIF; data.gbif.org, accessed 2012-03-22). Data sources included the Ocean Biogeographic Information System, the National Museum of Natural History, the Yale University Peabody Museum, and the Marine Science Institute, University of California, Santa Barbara. The dataset was imported into ArcGIS 10 (ESRI, Redlands, CA, USA) and included a total of 599 observations of *A. poculata* occurrence at 270 distinct locations.

Coral growth data

Growth of *A. poculata* was measured using methods described in detail by Dimond and Carrington (2007). Briefly, symbiotic and asymbiotic *A. poculata* colonies were collected and reattached with underwater epoxy to cleared plots on vertical rock surfaces at two sites at 3 m depth in Narragansett Bay, RI. For 15 months between May 2004 and July 2005, digital photographs of the corals were taken on a quasi-monthly basis and image analysis was used to enumerate coral polyps as a measure of colony growth between sampling intervals. In situ temperature records from dataloggers (Stowaway TidBit loggers, Onset Computer, Bourne, MA, USA) fastened adjacent to experimental plots at 3 m depth permitted analysis of coral growth in relation to average temperatures between sampling intervals. As shown in Dimond and Carrington (2007), the temperature–growth relationship obtained by this method was very similar to laboratory-derived measurements of *A. poculata* $CaCO_3$ deposition by Jacques et al. (1983). In addition to positive growth through polyp budding and skeletal accretion, however, Dimond and Carrington (2007) also documented loss of living coral polyps during the coldest times of the year. This loss was attributed to polyp dormancy and tissue thinning throughout the winter, which had the added consequence of rendering the colony unable to protect itself from sedimentation and the encroachment and settlement of organisms such as barnacles, mussels, and macroalgae. Polyp dormancy, defined here as a persistent contraction of polyps within their calices, was consistently observed in the field during the winter months at temperatures below approximately 5 °C. Growth versus temperature data were fitted with polynomial functions in SigmaPlot 11 (Systat Software Inc., San Jose, CA, USA). These functions were used to predict spatial patterns in coral growth, as described below.

Symbiosis between *A. poculata* and *S. psygmophilum* is facultative, and symbiont densities can range naturally from very low to over 10^7 cm^{-2} (Cummings 1983; Jacques et al. 1983; Dimond and Carrington 2008). While few corals appear to completely lack symbionts, field data suggest a natural break between fully symbiotic and functionally asymbiotic colonies at *Symbiodinium* densities of approximately 10^5 cm^{-2} (Cummings 1983; Dimond and Carrington 2008). Below this threshold density, corals appear visibly pale, and such colonies were selected and designated asymbiotic (=azooxanthellate) by Dimond and Carrington (2007). In contrast, corals designated symbiotic (=zooxanthellate) had full brown pigmentation from *Symbiodinium* densities greater than approximately 10^6 cm^{-2}. Importantly, below this threshold density, *Symbiodinium* have negligible influence on coral calcification and do not provide net photosynthesis (Jacques et al. 1983). Symbiotic states in *A. poculata* appear to be largely stable over time (Dimond and Carrington 2007).

Sea surface temperature data

To estimate *A. poculata* growth potential along the U.S. Atlantic coast, we obtained sea surface temperature (SST) records from NOAA Pathfinder 4 km advanced very high resolution radiometer (AVHRR) satellite data (www.nodc.noaa.gov/SatelliteData/pathfinder4km; Casey et al. 2010). Cloud-screened monthly climatology datasets spanning the years 1981–2008 were imported into ArcGIS 10 for manipulation and analysis.

The suitability of remotely sensed SST data for studies of near-shore benthic ecology was recently evaluated by Smale and Wernberg (2009), who compared AVHRR and MODIS satellite data to in situ dataloggers at 10 m depth at several sites along the coast of Western Australia. Satellite-derived SST was typically 1–2 °C higher than temperatures logged at depth, and AVHRR data provided better correlations with in situ loggers than MODIS data, with correlations ranging from 0.85 to 0.96. Smale and Wernberg (2009) concluded that while satellite SST is not appropriate for fine-scale (e.g., sub-kilometer) studies requiring spatially and temporally explicit shallow subtidal temperatures, it is appropriate for large-scale analyses of broad geographic patterns (Fig. 1).

Analysis of coral growth potential

To estimate growth potential of *A. poculata* along the U.S. Atlantic coast, monthly SST climatology data were extracted along a transect 10 km offshore of the coast at 0.5° latitude intervals from 25 to 45°N (approximately Miami, FL, to Eastport, ME). For each month, symbiotic and asymbiotic coral growth (polyps mo^{-1}) were calculated using the temperature-growth functions obtained in Fig. 2. Monthly estimates were then summed to determine estimated net annual coral growth (polyps yr^{-1}) along the latitudinal transect. As a measure of the potential enhancement effect of symbiosis on coral growth, we also calculated the ratio of symbiotic to asymbiotic growth along the transect.

For closer inspection of estimated growth of *A. poculata* at its northern range limit around Cape Cod, we used the raster calculator tool in ArcGIS 10 to estimate asymbiotic coral growth for each 4 km pixel and each month of the satellite SST monthly climatology data. Asymbiotic coral growth was modeled for this analysis with the rationale that symbiotic corals are relatively uncommon around *A. poculata*'s range limit; a transect from 0 to 15 m depth at Ft. Wetherill, Rhode Island in July 2010 found that 8 % of corals were fully

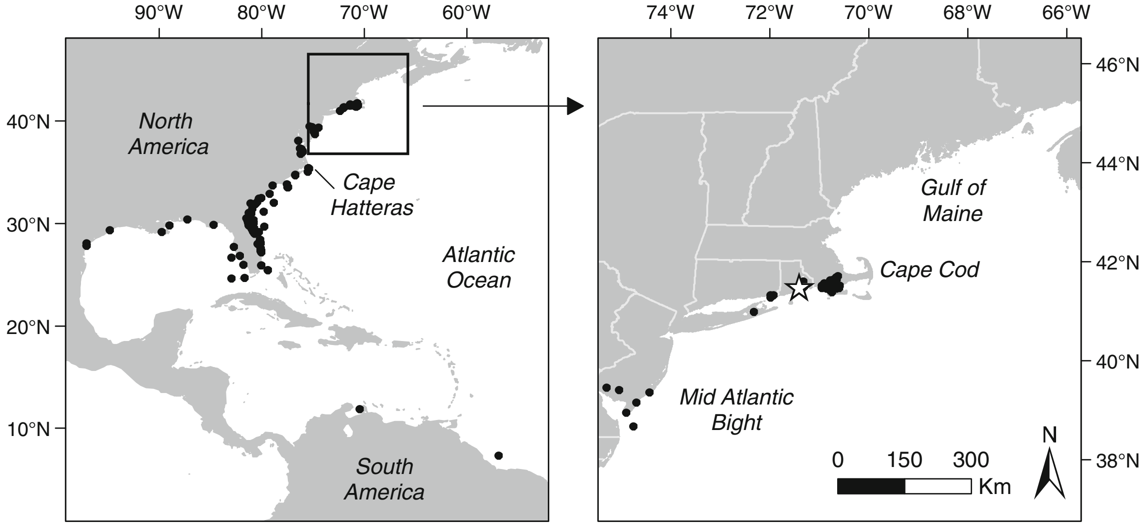

Fig. 1 Geographic occurrences of *Astrangia poculata* from published collection records (*black dots*). *Star* indicates the location of the field study on *A. poculata* growth in Rhode Island, USA (Dimond and Carrington 2007)

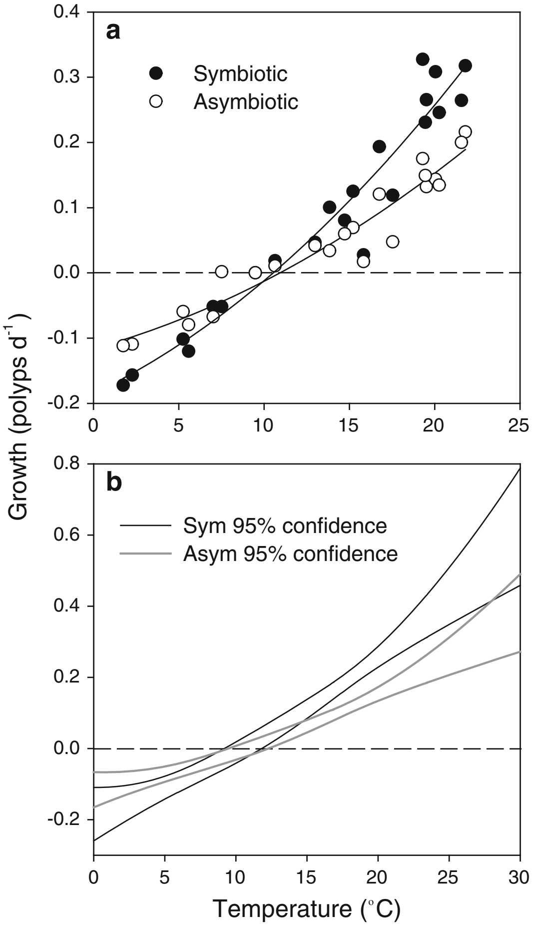

Fig. 2 Temperature versus growth relationships **a** and 95 % confidence bands **b** for symbiotic and asymbiotic *Astrangia poculata* colonies derived from field growth data and in situ temperature dataloggers. Symbiotic: $y = -0.1849 + 0.0125x + 0.0005x^2$, $r^2 = 0.97$, $p < 0.0001$, $n = 22$. Asymbiotic: $y = -0.1161 + 0.0072x + 0.0003x^2$, $r^2 = 0.96$, $p < 0.0001$, $n = 22$

symbiotic, with no clear depth pattern (R. Rotjan, pers obs). Secondly, the predicted benefit of symbiosis drops sharply beyond the range limit (see Results). As above, estimated annual growth was determined by summing estimated monthly growth. We then created a polygon coverage of areas with net growth versus no net growth by reclassifying values as either negative (no net growth) or positive (net growth) and clipping the dataset to a 100 km buffer of the coastline. This buffer distance was chosen primarily for visual clarity rather than to represent *A. poculata* habitat. Our SST-based analysis applies only to shallow near-shore waters and cannot predict deep-water coral growth patterns.

Results

Figure 1 shows geographic occurrences of *A. poculata* published by GBIF. Although lack of observations of *A. poculata* from a given area could reflect lack of sampling effort and should not necessarily be interpreted as an absence, the dataset suggests that *A. poculata* does not occur north of Cape Cod, Massachusetts. This limit is supported by Peters et al. (1988) and by Hargitt (1914), although the latter study mentioned a second-hand account of *A. poculata* occurrence in Casco Bay, Maine. We are unaware of any officially documented reports of *A. poculata* north of Cape Cod, but anecdotal reports suggest that *A. poculata* occasionally occurs in Massachusetts Bay and the Gulf of Maine (D. Thornhill and R. Rotjan, pers. obs.).

Symbiotic and asymbiotic coral growth illustrates the strong temperature dependence of *A. poculata* polyp gain and loss (Fig. 2). Little coral growth was observed below mean temperatures of approximately 10 °C. Symbiotic corals exhibited a clear growth advantage above 10 °C, but below this temperature, the data suggest that they performed poorly relative to asymbiotic colonies, actually losing polyps at a faster rate (Fig. 2a). For clarity, 95 % confidence bands for the coral growth functions are shown in Fig. 2b. These bands are extrapolated beyond the extent of the data, hence their widening at higher values.

Estimated coral growth along the U.S. Atlantic coast based on temperature alone shows a strong latitudinal effect (Fig. 3). For this analysis, coral growth was extrapolated beyond the extent of the data, so it should be noted that summertime coastal temperatures south of New Jersey (~40°N) exceed those observed in our Rhode Island dataset. Despite considerable overlap of 95 % confidence limits for predicted symbiotic and asymbiotic coral growth over much of the range, general patterns suggest interesting trends and contrasts. Most significantly, this analysis predicted net polyp loss north of 41.9°N for asymbiotic corals and 43.0°N for symbiotic corals. Symbiotic coral growth exceeds asymbiotic coral until 43.6°N, after which asymbiotic coral growth exceeds that of symbiotic corals; this pattern is also illustrated by the ratio of symbiotic to asymbiotic coral growth, which drops sharply below 1 at 43.6°N. This ratio remains relatively high and stable at southerly locales until dropping precipitously north of ~40°N.

Closer examination of spatial patterns of estimated *A. poculata* growth around its northern range limit shows that the model accurately predicts the coral's actual range limit in terms of areas with and without predicted net growth (Figs. 1, 4). *Astrangia poculata* is effectively absent north of the southern coast of Cape Cod, making Buzzards Bay and Nantucket Sound the northernmost coastal waters with persistent documented populations of *A. poculata*. The model suggests that cold water intrusion along the outer Cape Cod coast may act as a barrier to coral growth there and further north. Although the model does predict net asymbiotic coral growth within part of Cape Cod Bay, there are no published records of *A. poculata* there.

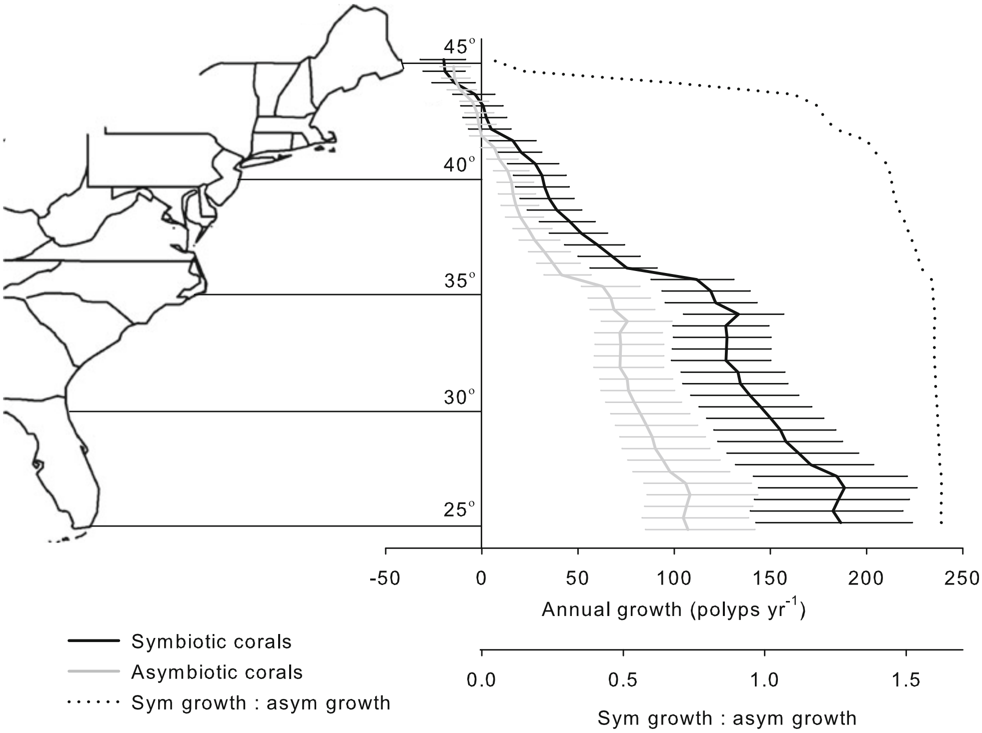

Fig. 3 Latitudinal trends in predicted annual symbiotic and asymbiotic coral growth (±95 % confidence limits) along the U.S. Atlantic coast (*solid lines*), and the predicted benefit of symbiosis expressed as the ratio of symbiotic coral growth to asymbiotic coral growth (*dotted line*)

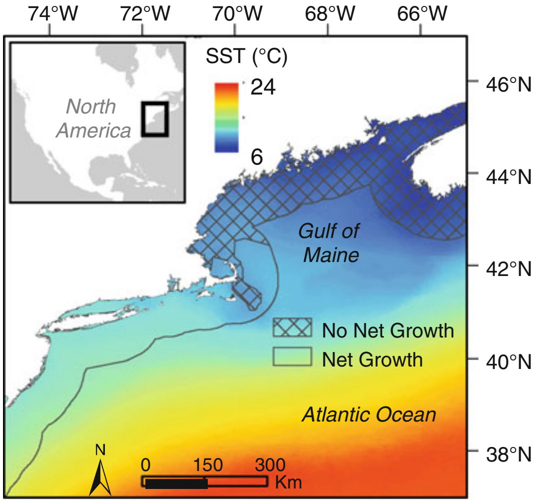

Fig. 4 Spatial patterns of predicted net growth of *Astrangia poculata* around its known range limit (Cape Cod, Massachusetts), with sea surface temperature (SST) climatology as a backdrop

Discussion

The results of our analysis suggest that the seasonally integrated net growth of *A. poculata* colonies is constrained by low temperature north of Cape Cod. Simply put, the effect of increasing latitude on *A. poculata* annual net growth is to reduce favorable conditions and increase unfavorable conditions. Although biogeographic limits can arise from the complex interplay of demographic, ecological, and environmental factors (Gaston 2009; Sexton et al. 2009), temperature is a key factor governing organism physiology and therefore plays a significant role in the biogeography of many organisms (Pörtner 2002). Our analysis did not test alternative hypotheses for the upper latitudinal limit of *A. poculata* and therefore may oversimplify the processes that influence *A. poculata* biogeography. Nevertheless, our results demonstrated that latitudinal temperature patterns alone could successfully predict this coral's distribution. We also provide evidence that while associating with symbiotic dinoflagellates remains largely beneficial for *A. poculata* around its range limit, the benefit of symbiosis declines sharply at higher latitudes.

Astrangia poculata exhibits metabolic characteristics similar to tropical corals when acclimated to tropical temperatures (Jacques et al. 1983), so warmer and longer summers should be favorable for *A. poculata* growth. Calcium carbonate deposition rates of *A. poculata* in the laboratory were highly temperature-dependent (Jacques et al. 1983) and very similar to the seasonal polyp budding rates observed in the field by Dimond and Carrington (2007). The steep increase in growth rates observed in both studies at higher temperatures may be due in part to the fact that *A. poculata* respiration is largely constant between 11.5 and 23 °C (Jacques et al. 1983). This ability of *A. poculata* to regulate its respiration rates across a broad range of temperatures may allow increased energy input to growth as temperature increases (Jacques et al. 1983). Above 23 °C, however, *A. poculata* respiration rates increase (Jacques et al. 1983), which probably limits the amount of energy available for growth. Because of this and because energy sources may not be sufficient to keep up with energy demand, particularly at higher temperatures (e.g., Fitt et al. 2000), our extrapolated analysis of growth at southerly latitudes beyond the range of temperatures in our dataset is purely theoretical and should be interpreted with caution. Moreover, our analysis does not account for potential local adaptation to either lower or higher temperature regimes other than those in our Rhode Island dataset. Anecdotal reports of *A. poculata* north of Cape Cod, for example, could reflect local adaptation of a small population to colder temperatures. Local thermal adaptation has been observed in tropical corals (Smith-Keune and van Oppen 2006) and *Symbiodinium* (Howells et al. 2011), and broadcast spawning species such as *A. poculata* generally have greater potential for local adaptation (Szmant-Froelich et al. 1980; Sanford and Kelly 2011).

During the winter, a state of torpor characterized by contracted polyps, slowed respiration rate, and growth cessation allows *A. poculata* to conserve energy albeit at the cost of starvation, tissue thinning, and loss of living surface area to competitors (Jacques et al. 1983; Peters et al. 1988; Grace 1996; Dimond and Carrington 2007). Colder, longer winters such as those occurring north of Cape Cod therefore result in a prolonged state of torpor that exacerbates polyp loss to competitors. Polyp expansion is not only necessary for feeding, but also protects *A. poculata* from burial by sediment (Peters and Pilson 1985) and is probably also critical for defense of space from both settling and neighboring sessile organisms. For the temperate northeastern Pacific cup coral *Balanophyllia elegans*, for example, maintaining tentacular contact with neighboring sessile invertebrates is an effective defense against their encroachment (Bruno and Witman 1996). Among the more destructive sessile invertebrates frequently found in contact with *A. poculata* on southern New England rocky reefs are boring clionid sponges (J. Dimond pers. obs.). Rützler (2002) found that the ability of Caribbean reef corals to defend themselves against clionid sponges was compromised when corals were stressed by either high or low temperatures. In addition to sponges and other invertebrates, seaweeds are the dominant competitor for space at the shallowest depths on temperate reefs, and under algal canopies, *A. poculata* adopts a flat encrusting morphology to avoid excessive algal abrasion (Miller and Hay 1996; Grace 2004). The detrimental effects of algal competition are further illustrated by the temperate coral *Oculina arbuscula* (likely a regional moniker of *O. varicosa*, Eytan et al. 2009) which co-occurs with *A. poculata* south of Cape Hatteras (~35°N). This species grows only in a branching morphology even at shallow depths, but benefits considerably from the grazing activity of the crab *Mithrax forceps*, which consumes seaweeds adjacent to the coral and gains protection from predators by closely associating itself with the coral's branches (Stachowicz and Hay 1999). *Oculina arbuscula* may succumb to the effects of restricted growth and interspecific competition northward of Cape Hatteras in a similar manner to what we predict for *A. poculata* at its range limit around Cape Cod.

Cape Cod is a well-known biogeographic boundary where many species reach their northern, and to a lesser extent, southern range limits (Engle and Summers 2000; Wares 2002; Hale 2010). Pleistocene glaciation of the New England coast reached its southern terminus at Cape Cod and may have affected contemporary distributions and gene flow of coastal species, but oceanographic conditions including both temperature and currents are also very likely to play a role in setting species' range limits around Cape Cod (Wares 2002). Western Gulf of Maine and Mid-Atlantic Bight coastal circulation is predominantly southward (Churchill et al. 2005; Lentz 2008), which may create unfavorable conditions for northward larval dispersal around Cape Cod (Wares 2002). On the other hand, larvae originating from coastal areas south of Cape Hatteras can be transported far northward by the Gulf Stream and its warm-core rings (Hare et al. 2002), probably as far north as the Scotian Shelf based on the high frequency of expatriated subtropical fish larvae often found there (Markle et al. 1980). Independent of larval dispersal limitation, however, low temperature has been found to limit species' ranges northward of Cape Cod by three primary factors, summarized by Sanford et al. (2006): 1) inability to survive winter temperatures; 2) inability to reproduce at cooler temperatures; and 3) inability to successfully compete for resources with northern species. Although coastal wintertime temperatures north of Cape Cod reach similar lows as those observed to the south, low temperature conditions persist for longer periods of time at increasing latitudes, and thus, exposure duration is probably at least as important a consideration as temperature per se. With this caveat, and the fact that we did not test *A. poculata* performance in the presence of the suite of potential competitors occurring north of Cape Cod, our results are consistent with hypotheses 1 and 3.

Reproductive limitations to *A. poculata*'s distribution were not examined in our analysis but deserve consideration. Coral gametogenesis, for example, could become limited at higher latitudes and lower temperatures. Although gametogenesis in *A. poculata* begins in early spring, the coldest time of year in southern New England coastal waters, it is not complete until late summer and may be dependent on a sufficiently warm summer to be completed before water temperatures begin to drop again in the autumn (Szmant-Froelich et al. 1980). Szmant-Froelich et al. (1980) found that *A. poculata* kept in the laboratory at 20–22 °C and fed regularly were able to spawn year-round, suggesting that *A. poculata* gametogenesis was controlled by either temperature or food availability. Spawning during late summer in natural populations may also be critical for larval development, which is likely to be temperature-dependent. The fiddler crab *Uca pugnax* also reaches its northern range limit around Cape Cod, and this limit appears to be determined by the inability of larvae to develop at the lower temperatures commonly encountered north of Cape Cod (Sanford et al. 2006). It is important to recognize that other life history characteristics may limit the competency of *A. poculata* at higher latitudes, but here we argue that temperature effects on adult persistence are sufficient to control the coral's range regardless of reproductive success or early life history stage survival.

Does temperature alone cause the considerable seasonal changes in coral growth observed in the field, and can latitudinal changes in temperature alone predict coral growth and persistence? Two additional factors influencing coral growth are light availability and aragonite saturation state, both of which co-vary seasonally and latitudinally with temperature (Kleypas et al. 1999). If we consider only asymbiotic corals, light availability can be excluded as a factor limiting *A. poculata*'s range. Aragonite saturation state has been implicated as a limiting factor for the growth of both tropical reef corals (Kleypas et al. 1999) and deep-sea scleractinians (Cairns 2007). Aragonite saturation state generally declines with increasing latitude (Kleypas et al. 1999) and also changes seasonally (Holcomb et al. 2010). In Woods Hole, Massachusetts, the northern range limit of *A. poculata*, seawater aragonite saturation state varies from approximately 1.5 in winter to 2.5 in summer (Holcomb et al. 2010). Holcomb et al. (2010, 2012) found that reduced seawater aragonite saturation state resulting from experimental CO_2 enrichment generally decreased *A. poculata* calcification, but nutrient supplementation could offset the effects of low aragonite saturation, and female corals were more negatively affected than males. Experiments with two other temperate corals, *Cladocora caespitosa* (Rodolfo-Metalpa et al. 2010) and *Oculina arbuscula* (Ries et al. 2010), have shown that these corals are fairly robust to changes in aragonite saturation. Ries et al. (2010) found that *O. arbuscula* can maintain steady calcification rates until aragonite becomes under saturated (<1). This suggests that aragonite saturation state is unlikely to affect the range limit of *O. arbuscula* since supersaturating conditions persist well northward of Cape Hatteras. Even in the Gulf of Maine, aragonite saturation remains well above 1 except where periodic large discharges of freshwater occur around river mouths (Salisbury et al. 2008). It seems unlikely that the abrupt northern range limit of *A. poculata* around Cape Cod is delineated by changes in aragonite saturation state alone, but since temperature affects aragonite saturation state, the two factors may act synergistically in limiting *A. poculata* growth northward.

Our analysis suggests that *A. poculata*'s range limit coincides with a sharp decline in the benefit of associating with *Symbiodinium.* This is due to limited growth enhancement by symbiosis at lower summer temperatures and, intriguingly, an augmented polyp loss effect associated with symbiosis during colder months, suggesting that symbiotic dinoflagellates may incur costs during stressful winter periods. Thornhill et al. (2008) demonstrated that *Symbiodinium ITS2* type B2 (recently described as *S. psygmophilum,* LaJeunesse et al. 2012), the symbiont lineage associated with *A. poculata*, is remarkably tolerant of low temperatures in comparison with tropical symbiont types. Despite this, the maximum photochemical efficiency of photosystem II of *S. psygmophilum* declined to approximately 0 at 10 °C (Thornhill et al. 2008). Additionally, *S. psygmophilum* had no measureable effect on the growth of *A. poculata* below 6.5 °C (Jacques et al. 1983). This symbiont species does, however, continue to divide at temperatures as low as 3 °C and in prolonged darkness (Dimond and Carrington 2008), suggesting that it may become heterotrophic and draw resources from its host during the winter (e.g., Steen 1986). This hypothesis is supported by the observations that asymbiotic *A. poculata* had higher tissue mass per unit area than symbiotic corals, particularly during the winter (Cummings 1983), and that asymbiotic corals were less susceptible than symbiotic corals to tissue damage during experimental starvation and sedimentation stress (Peters and Pilson 1985). In spite of the potential negative effects of symbiosis on the host under suboptimal conditions, our analysis also suggests that, at shallow depths with adequate light penetration (Jacques et al. 1983), symbiosis can provide a valuable boost for *A. poculata* growing near its range limit.

Here, we have provided support for two hypotheses concerning the biogeography of *A. poculata* which may apply to shallow-water temperate corals in general. We show that latitudinal declines in temperature (1) not only limit favorable conditions for coral growth, but also exacerbate unfavorable conditions that cause corals to lose surface area to competitors and (2) may be associated with a shift to net costs of associating with symbiotic dinoflagellates. Gradual northward range shifts in response to climatic warming would be predicted based on the first hypothesis, but in the meantime, further investigation into latitudinal variation in the costs and benefits of associating with symbiotic dinoflagellates would be worthwhile from both an ecological and evolutionary perspective.

Acknowledgments We thank T. Lemos-Eskin and C. Marks for diving assistance. This study was conceived at the January 2012

Astrangia Workshop hosted by Ocean Genome Legacy in Ipswich, Massachusetts and funded in part by the Philip Goelet Foundation. We are grateful to J. Churchill and two anonymous reviewers whose helpful comments improved the manuscript.

References

Bruno JF, Witman JD (1996) Defense mechanisms of scleractinian cup corals against overgrowth by colonial invertebrates. J Exp Mar Biol Ecol 207:229–241

Cairns SD (2007) Deep-water corals: an overview with special reference to diversity and distribution of deep-water scleractinian corals. Bull Mar Sci 81:311–322

Casey KS, Brandon TB, Cornillon P, Evans R (2010) The past, present and future of the AVHRR Pathfinder SST program. In: Barale V, Gower JFR, Alberotanza L (eds) Oceanography from space: revisited. Springer, New York, pp 323–341

Churchill JH, Pettigrew NR, Signell RP (2005) Structure and variability of the Western Maine Coastal Current. Deep-Sea Res II 52:2392–2410

Cummings C (1983) The biology of *Astrangia danae*. PhD thesis, University of Rhode Island, Kingston, p 147

Davy SK, Allemand D, Weis VM (2012) Cell biology of cnidarian-dinoflagellate symbiosis. Microbiol Mol Biol Rev 76:229–261

Dimond J, Carrington E (2007) Temporal variation in the symbiosis and growth of the temperate scleractinian coral *Astrangia poculata*. Mar Ecol Prog Ser 341:161–172

Dimond J, Carrington E (2008) Symbiosis regulation in a facultatively symbiotic temperate coral: zooxanthellae division and expulsion. Coral Reefs 27:601–604

Engle VD, Summers JK (2000) Biogeography of benthic macroinvertebrates in estuaries along the Gulf of Mexico and western Atlantic coasts. Hydrobiologia 436:17–33

Eytan RI, Hayes M, Arbour-Reily P, Miller M, Hellberg ME (2009) Nuclear sequences reveal mid-range isolation of an imperilled deep-water coral population. Mol Ecol 18:2375–2389

Ferrier-Pagès C, Peirano A, Abbate M, Cocito S, Negri A, Rottier C, Riera P, Rodolfo-Metalpa R, Reynaud S (2011) Summer autotrophy and winter heterotrophy in the temperate symbiotic coral *Cladocora caespitosa*. Limnol Oceanogr 56:1429–1438

Fitt WK, McFarland FK, Warner ME, Chilcoat GC (2000) Seasonal patterns of tissue biomass and densities of symbiotic dinoflagellates in reef corals and relation to coral bleaching. Limnol Oceanogr 45:677–685

Gaston KJ (2009) Geographic range limits: achieving synthesis. Proc R Soc B 276:1395–1406

Grace SP (1996) The effects of water flow on *Astrangia poculata*. University of Rhode Island, Kingston, MS thesis, p 146

Grace SP (2004) Ecomorphology of the temperate scleractinian *Astrangia poculata*: coral–macroalgal interactions in Narragansett Bay (Rhode Island). PhD thesis, University of Rhode Island, Kingston, p 182

Hale SS (2010) Biogeographical patterns of marine benthic macroinvertebrates along the Atlantic coast of the Northeastern USA. Estuaries Coasts 33:1039–1053

Hare JA, Churchill JH, Cowen RK, Berger TJ, Cornillon PC, Dragos P, Glenn SM, Govoni JJ, Lee TN (2002) Routes and rates of larval fish transport from the southeast to the northeast United States continental shelf. Limnol Oceanogr 47:1774–1789

Hargitt CW (1914) The Anthozoa of the Woods Hole region. Bull US Bureau Fish 32:223–254

Holcomb M, McCorkle DC, Cohen AL (2010) Long-term effects of nutrient and CO_2 enrichment on the temperate coral *Astrangia poculata* (Ellis and Solander, 1786). J Exp Mar Biol Ecol 386:27–33

Holcomb M, Cohen AL, McCorkle DC (2012) An investigation of the calcification response of the scleractinian coral *Astrangia poculata* to elevated $p\mathrm{CO}_2$ and the effects of nutrients, zooxanthellae and gender. Biogeosciences 9:29–39

Hoogenboom MO, Rodolfo-Metalpa R, Ferrier-Pagès C (2010) Co-variation between autotrophy and heterotrophy in the Mediterranean coral *Cladocora caespitosa*. J Exp Biol 213:2399–2409

Howells EJ, Beltran VH, Larsen NW, Bay LK, Willis BL, van Oppen MJH (2011) Coral thermal tolerance shaped by local adaptation of photosymbionts. Nature Climate Change 2:116–120

Jacques TG, Marshall N, Pilson MEQ (1983) Experimental ecology of the temperate scleractinian *Astrangia danae*. II. Effect of temperature, light intensity and symbiosis with zooxanthellae on metabolic rate and calcification. Mar Biol 76:135–148

Johannes RE, Weibe WJ, Crossland CJ, Rimmer DW, Smith SV (1983) Latitudinal limits to coral reef growth. Mar Ecol Prog Ser 11:201–208

Kleypas JA, McManus JW, Meñez LAB (1999) Environmental limits to coral reef development: Where do we draw the line? Am Zool 39:146–159

LaJeunesse TC, Parkinson JE, Reimer JD (2012) A genetics-based description of *Symbiodinium minutum* sp. nov. and *S. psygmophilum* sp. nov. (Dinophyceae), two dinoflagellates symbiotic with Cnidaria. J Phycol. doi:10.1111/j.1529-8817.2012.01217.x

Lentz SJ (2008) Observations and a model of the mean circulation over the Middle Atlantic Bight continental shelf. J Phys Oceanogr 38:1203–1221

Markle DF, Scott WB, Kohler AC (1980) New and rare records of Canadian fishes and the influence of hydrography on resident and nonresident Scotian Shelf ichthyofauna. Can J Fish Aquat Sci 37:49–65

Miller MW (1995) Growth of a temperate coral: effects of temperature, light, depth, and heterotrophy. Mar Ecol Prog Ser 122:217–225

Miller MW (1998) Coral/seaweed competition and the control of reef community structure within and between latitudes. Oceanogr Mar Biol Annu Rev 36:65–96

Miller MW, Hay ME (1996) Coral–seaweed–grazer–nutrient interactions on temperate reefs. Ecol Monogr 66:323–344

Muller-Parker G, Davy SK (2001) Temperate and tropical sea anemone symbioses. Invertebr Biol 120:104–123

Peters EC, Pilson MEQ (1985) A comparative study of the effects of sediment on symbiotic and asymbiotic colonies of the coral Astrangia danae Milne Edwards and Haime, 1849. J Exp Mar Biol Ecol 92:215–230

Peters EC, Cairns SD, Pilson MEQ, Wells JW, Jaap WC, Lang JC, Vasleski CE, St. Pierre Gollahon L (1988) Nomenclature and biology of *Astrangia poculata* (=*A. danae*, =*A.astreiformis*) (Cnidaria: Anthozoa). Proc Biol Soc Wash 101:234–250

Pörtner HO (2002) Climate change and the physiological basis of temperature dependent biogeography: systemic to molecular hierarchy of thermal tolerance in animals. Comp Biochem Physiol 132A:739–761

Ries JB, Cohen AL, McCorkle DC (2010) A nonlinear calcification response to CO_2-induced ocean acidification by the temperate coral *Oculina arbuscula*. Coral Reefs 29:661–674

Rodolfo-Metalpa R, Martin S, Ferrier-Pages C, Gattuso JP (2010) Response of the temperate coral *Cladocora caespitosa* to mid and long-term exposure to $p\mathrm{CO}_2$ and temperature levels projected for the year 2100 AD. Biogeosciences 7:289–300

Rützler K (2002) Impact of crustose clionid sponges on Caribbean reef corals. Acta Geol Hispanica 37:61–72

Salisbury J, Green M, Hunt C, Campbell J (2008) Coastal acidification by rivers: a threat to shellfish? EOS Trans Am Geophys Union 89:513–514

Sanford E, Kelly MW (2011) Local adaptation in marine invertebrates. Annu Rev Mar Sci 3:509–535

Sanford E, Holzman SB, Haney RA, Rand DM, Bertness MD (2006) Larval tolerance, gene flow, and the northern geographic range limit of fiddler crabs. Ecology 87:2882–2894

Schuhmacher H, Zibrowius H (1985) What is hermatypic? A redefinition of ecological groups in corals and other organisms. Coral Reefs 4:1–9

Sexton JP, Mcintyre PJ, Angert AL, Rice KJ (2009) Evolution and ecology of species range limits. Annu Rev Ecol Evol Syst 40:415–436

Smale DA, Wernberg T (2009) Satellite-derived SST data as a proxy for water temperature in nearshore benthic ecology. Mar Ecol Prog Ser 387:27–37

Smith-Keune C, van Oppen M (2006) Genetic structure of a reef-building coral from thermally distinct environments on the Great Barrier Reef. Coral Reefs 25:493–502

Stachowicz JJ, Hay ME (1999) Mutualism and coral persistence: the role of herbivore resistance to algal chemical defense. Ecology 80:2085–2101

Stanley GD (2003) The evolution of modern corals and their early history. Earth-Sci Rev 60:195–225

Stanley GD, Swart PK (1995) Evolution of the coral-zooxanthellae symbiosis during the Triassic: A geochemical approach. Paleobiology 21:179–199

Steen RG (1986) Evidence for heterotrophy by zooxanthellae in symbiosis with *Aiptasia pulchella*. Biol Bull 170:267–278

Szmant-Froelich A, Pilson MEQ (1980) The effects of feeding frequency and symbiosis with zooxanthellae on the biochemical composition of *Astrangia danae* Milne Edwards & Haime 1848. J Exp Mar Biol Ecol 48:85–97

Szmant-Froelich A, Yevich P, Pilson MEQ (1980) Gametogenesis and early development of the temperate coral *Astrangia danae* (Anthozoa: Scleractinia). Biol Bull 158:257–269

Thornhill DJ, Kemp DW, Bruns BU, Fitt WK, Schmidt GW (2008) Correspondence between cold tolerance and temperate biogeography in a western Atlantic *Symbiodinium* (Dinophyta) lineage. J Phycol 44:1126–1135

Tremblay P, Peirano A, Ferrier-Pagès C (2011) Heterotrophy in the Mediterranean symbiotic coral *Cladocora caespitosa*: comparison with two other scleractinian species. Mar Ecol Prog Ser 422:165–177

Veron JEN (2000) Corals of the world, Vol 1–3. Australian Institute of Marine Science, Townsville

Wares JP (2002) Community genetics in the northwestern Atlantic intertidal. Mol Ecol 11:1131–1144