

Temperature related depth limits of warm-water corals

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Abstract. While biogeographical limits of tropical fauna have been studied with increasing latitude, little is known about their lower depth distributions. For non-photosynthetic, warm-water fauna, decreasing temperature with increasing depth eventually limits their depth distribution. However, the nature of this lower thermal threshold, which has habitat management implications, has not been studied to date. In the Au'au Channel, Hawai'i, the temperature regime along a depth gradient near previously identified lower depths limits for warm-water azooxanthellate corals was characterized to determine whether the lower depths limits were consistent with acute stress causing colony mortality or chronic stress inhibiting growth, reproduction, and/or larval settlement. Data suggests that lower depth limits are associated with a minimum required exposure (e.g., 5-7 months) to water >22°C. This lower depth limit appears to be decoupled from the lower temperature limits of colony survival.

Key words: temperature stress; coral biogeography; mesophotic coral ecosystems.

Introduction

Mesophotic coral reef ecosystems (MCE) are warm-water coral reef ecosystems found below the depth limits of traditional SCUBA diving (~40 m) and extend to the lower photic zone which exceed 150 m in some regions (reviewed by Kahng et al. 2010). MCEs are characterized by light-dependent scleractinian corals and associated communities, but also include non-photosynthetic organisms including azooxanthellate gorgonians, antipatharians and sponges (Kahng et al. 2010). Within MCEs sessile invertebrate fauna exhibit depth dependent community structure with dominant taxa changing with depth (Kahng and Kelley 2007; Rooney et al. 2010). This vertical zonation correlates with various environmental factors that change predictably with increasing depth. In exposed locations, wave stress and episodic hydrodynamic disturbance can exclude fragile and slow-growing organisms from shallow water. Similarly, the gradient of light intensity with depth can exclude both light sensitive organisms from shallow water (Jokiel 1980), and obligate photosynthetic organisms from deeper waters (reviewed in Kirk 1994). Additionally, some benthic organisms that are not directly affected by light, may be excluded from well-lit areas due to space competition with faster growing photosynthetic organisms (reviewed in Kahng et al. 2010).

Temperature is another environmental factor that exhibits a predictable pattern with depth, with a rapid decrease below the mixed layer followed by a more

gradual decrease to abyssal depths. For ectothermic tropical organisms, exposure to low temperatures has been shown to limit their geographic distribution at high latitudes (Pörtner 2010). An analogous decrease in temperature with depth eventually limits the distribution of tropical organisms in deeper waters. For sessile organisms such as corals, tolerance to low temperature exposures varies widely by species and geographic location (Kleypas et al. 1999).

In the Au'au Channel between the Hawaiian islands of Maui and Lāna'i, the dominant megabenthic organisms exhibit a distinct vertical zonation with a marked change in faunal composition in the vicinity of the seasonal thermocline at 110-120 m (Kahng and Kelley 2007). The lower depth limits of commercially valuable black corals (*Antipathes griggi* and *A. grandis*) and other heterotrophic, tropical invertebrates (e.g., *Carijoa* sp., *Reteporellina denticulate*, *Triphylozoon* sp.) coincide with this depth zone of transition (Kahng and Kelley 2007; Wagner et al. 2010a).

The fact that multiple tropical organisms have a similar lower depth limit which coincides with the vicinity of the seasonal thermocline suggests that their depth distribution is limited by a common mechanism. Possible explanations for this pattern include (1) bottom-up limitation by factors such as food or oxygen (2) interactions with other organisms through predation or space competition, (3) mechanical disturbances, (4) light limitation, or (5) low temperature stress. Below 120 m, passive

suspension feeders of closely related taxa (e.g., *Acanthopathes undulata*, *Myriopathes* sp., *Stichopathes* spp., *Corallium* sp.) remain conspicuous and highly abundant in adjacent locations (pers. obs.) indicating that food for obligate heterotrophs is not limiting at depth. Around the Main Hawai'ian Islands, oxygen concentrations remain uniformly high (>150 $\mu\text{mol/kg}$) in the upper 500 m of the water column (Emerson et al. 2002). While little is known about the levels of predation on these deep-water species, antipatharians, octocorals, and bryozoans are generally not limited by predators (Sammarco and Coll 1992; Wagner et al. 2009). Additionally, the well-defined lower depth limit of several species makes predation an unlikely driving mechanism, especially given the abundance of closely related taxa at deeper depths. In the Au'au Channel, space competition diminishes sharply below 90 m as habitat-forming taxa such as macroalgae, sponges, scleractinian and antipatharian corals become less abundant and the amount of uncolonized hard substrate increases substantially (Kahng and Kelley 2007). The large aggregations of fragile calcareous fauna such as weakly attached corals (i.e., *Leptoseris* spp.) at 60-80 m suggest a lack of large scale mechanical disturbances at these depths. While endosymbiotic dinoflagellates of the genus *Symbiodinium* have recently been discovered in several Hawaiian antipatharians taxa, their extremely low densities (<92 cells/mm³) indicates that heterotrophic feeding is most certainly the dominant mode of nutrition for Hawaiian black corals (Wagner et al. 2010b). The attenuation of skilophilous (shade loving) fauna (e.g., *Carijoa* sp. and *R. denticulate*) below this lower depth limit rules out light as a contributing factor.

Via deductive reasoning, these collective observations suggest that the lower depth limit for various tropical sessile invertebrates is associated with exposure to low temperatures. The physiological basis by which low temperature limits the geographic distribution of sessile, tropical fauna is likely oxidative stress which lowers aerobic capacity (Pörtner 2002). At low levels of chronic stress, spontaneous activity such as feeding, growth and reproduction are adversely affected. Furthermore, physiological effects of low temperature stress on corals can include decreased photosynthetic efficiency, reduced feeding rates, and reduced larval settlement on crustose coralline algae (Saxby et al. 2003; Palardy et al. 2005; Putnam et al. 2008).

At acute levels of low temperature stress, hypoxia is induced with its associated production of oxygen radicals and cellular damage (Pörtner 2002). If prolonged, acute stress eventually causes mortality. For shallow-water corals (<40 m), large-scale

mortalities caused by episodic low temperature disturbances are well documented (Porter et al. 1982; Hoegh-Guldberg et al. 2005). Mesophotic coral reef ecosystems are also subject to a high degree of thermal variability due to incursions of cold, sub-thermocline waters associated with internal waves (Leichter et al. 2006; Sheppard 2009). In Palau, Wolanski et al. (2004) reported daily temperature fluctuations of up to 10°C at 90 m, with cold water incursions as low as 9°C. Such temperatures are known to cause coral mortality (Coles and Fadlallah 1991) and may be responsible for the biologically depauperate biological community on the island slopes at depths between 60-120 m.

Whether the lower depth limits of heterotrophic taxa in the Au'au Channel is due to chronic low temperature stress limiting growth and reproduction, or acute low temperature disturbances causing mortality is not known. In general, little is known about thermal thresholds and their effects on limiting the depth distribution of tropical fauna in deeper waters. The objectives of this study were to (1) characterize the relationship between temperature regime at the lower depth limits of tropical corals on a mesophotic reef in Hawai'i and (2) test whether lower depth limits were consistent with chronic low temperature stress or acute low temperature disturbance.

Material and Methods

Temperature loggers (Onset Stowaway TidBit model TBI32-O5+37) were deployed using the Hawai'i Undersea Research Laboratory (HURL) manned submersible *Pisces IV* on October 24, 2006. The loggers were deployed approximately every 10 m along a 90-150 m depth gradient on the northern slope of the sunken land bridge of the Au'au Channel (20° 57.00-57.02' N, 156° 45.90-45.00' W). The site was chosen based on previous surveys in the area which identified a zone of faunal transition along this depth gradient. Temperature loggers recorded *in situ* temperature every 30 minutes from October 23, 2006 to August 30, 2008. Temperature loggers were retrieved using the HURL *Pisces IV* manned submersible on November 21, 2009 (HURL dive number P4-222).

All temperature loggers were calibrated by immersing them in a bucket of ice and tap water inside a 4°C refrigerator before deployment and after retrieval. The temperature data were contoured separately using Surfer 9.0 software (Golden Software). For each depth the percent of total time spent below and above various temperature thresholds (18- 25°C) were calculated. Corresponding sea surface temperature (SST) data obtained from AVHRR Pathfinder Version 5.2 (PFV5.2) was

obtained from the US National Oceanographic Data Center and GHRSSST (Casey et al. 2010).

In order to investigate periodicity of temperature fluctuations, the time-series temperature data at 100m were de-trended and a Fast Fourier Transform was performed. The logarithm of temperature spectral density was plotted as a function of the logarithm of frequency.

Results

In the Au'au Channel, the 22 month average temperature decreased gradually with increasing depth from 90 to 140 m. A similar trend was observed for the minimum and maximum temperatures. There was no abrupt temperature change at the zone of faunal transition (~115 m). The thermal regime of reefs below 90 m was decoupled from sea surface temperature (SST), and did not exhibit the characteristic SST seasonal pattern (Fig. 1).

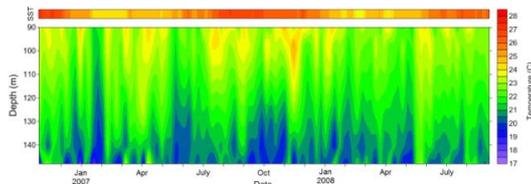


Figure 1: Temperature-depth contour from October, 2006 to August, 2008 in the Au'au Channel, Hawaii. Temperature recorded every 30 min.

Depths between 90-120 m experienced regular, short-term fluctuations of up to 4°C. The periodicity of these fluctuations correlated most strongly with diurnal and semidiurnal (M_2) frequencies and their associated harmonics (Fig. 2).

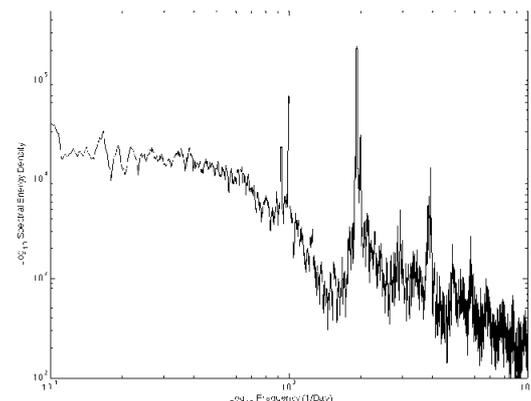


Figure 2: Power spectral density ($^{\circ}\text{C}^2$ cycle-per-day) as a function of frequency (d^{-1}) at 100 m depth for the period October 24, 2006 to August 30, 2008.

Time integrated exposure to low temperatures did not reveal exposures which are known to be lethal to

Hawaiian corals (Coles and Jokiel 1977; Jokiel and Coles 1977) in the vicinity of the zone of faunal transition (~115 m). Potentially lethal temperatures $\leq 18.0^{\circ}\text{C}$ were only recorded at depths ≥ 140 m. At 130 m, the cumulative annual exposure to temperatures $< 19.0^{\circ}\text{C}$ was only 42 hours.

Time integrated temperature exposures indicate that the zone of faunal transition (~115 m) correlates to a sharp decrease in exposure to a temperature $> 22^{\circ}\text{C}$ (Fig. 3). The percentage of time exposed to temperatures $> 22^{\circ}\text{C}$ decreased from 70% at 110 m to ~30% at 120 m. This transition zone coincides with the disappearance of many warm-water invertebrate species and their replacement by other closely related taxa.

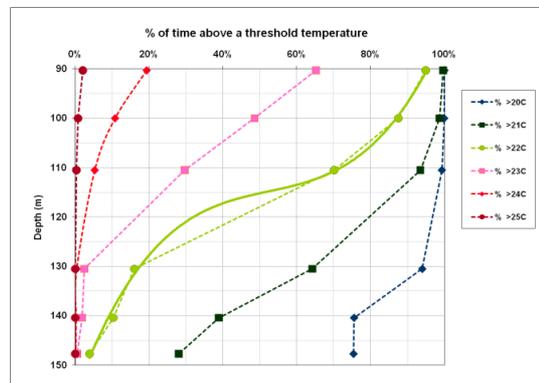


Figure 3: Percent of time above a threshold temperature at each depth from October 24, 2006 to August 30, 2008.

Discussion

The benthic fauna on mesophotic reefs in the Au'au Channel, Hawai'i are frequently exposed to short-term, temperature fluctuations caused by internal waves propagating along the insular island shelf and pushing deeper, cooler waters to shallower depths (Rudnick et al. 2003). Because the magnitude of these temperature fluctuations can exceed the seasonal range of SST, single temperature-depth profiles must be interpreted with due caution.

For ectothermic animals, physiological tolerances and mortality are associated with time-dependent exposures to minimum or maximum temperature thresholds forming thermal tolerance windows (Pörtner 2002). Hence, average temperature for a given location is not necessarily a good indicator of biogeographical limits, especially if the ambient temperature range is large. At the zone of faunal transition in the Au'au Channel (~115 m), the average temperature is $\sim 22^{\circ}\text{C}$. The gradual change in average temperature above and below this depth is not likely the cause of the well-defined and sharp transition of sessile benthic fauna.

Likewise, an exposure limit to a low temperature threshold (i.e., acute thermal stress limit causing mortality) does not appear to be consistent with the lower depth limit of tropical fauna at ~115 m. Sessile fauna at this depth do not experience exposures to low temperatures which are known to be lethal to Hawaiian corals. In Hawai'i's enclosed, shallow-water lagoons, corals are regularly subject to prolonged exposures to temperatures as low as 21°C during winter months without any visible adverse effects. Jokiel and Coles (1977) demonstrated that exposure to 18°C for 1-2 weeks can cause mortality in the Hawaiian reef corals. In the Au'au Channel, substantial exposures to 18°C do not occur until a depth of 140 m, where the cumulative exposure is less than 2.5 days per year.

In situ observations support the hypothesis that mortality associated with acute low temperature stress does not determine the lower depth limit of tropical fauna in the Au'au Channel. Toppled colonies of the tropical black coral *A. grandis* have been observed living on their sides at a depth of 150 m on the sand at the base of a vertical escarpment (pers. obs.). Collective visual evidence indicates that slabs of carbonate substrata with the colonies attached fell from an overhanging ledge at ~100 m. Colony branches in direct contact with the sand and within the benthic boundary layer (of a few cm) were dead and fouled with epifauna indicating a prolonged existence at its current position.

Near their lower depth distribution of ~115 m, colonies of *A. griggi* and *A. grandis* attached to permanent substrata are relatively small in size (< 50 cm in height) and disproportionately fouled with large sponges and hammerhead oysters. In contrast, conspecific colonies of equivalent size at depths shallower than 100 m are uniformly free of large fouling organisms. These observations are consistent with chronic low temperature stress limiting growth and possibly coral cleaning mechanisms near a lower depth limit. Slower growing colonies at this depth would have greater time exposure to fouling organisms compared to similar sized (and faster growing) colonies at shallower depths. While the reproductive status of tropical black corals have not been examined at their lower depth limit, the stunted nature of their growth and the general relationship between coral colony size and reproductive maturity and fecundity (Grigg 1976; Parker et al. 1997) suggest that they may be less fecund than their larger conspecifics at shallower depths.

These observations and the sharp attenuation of tropical azooxanthellate corals with depth near ~115m are consistent with a minimum required, time integrated exposure above a threshold temperature. In other words, the lack of exposure to warm water may

set the lower depth limit of heterotrophic tropical corals. In the Au'au Channel, this thermal threshold appears to be associated with a minimum exposure (e.g., 5-7 months) to temperatures >22°C which may represent the threshold required for reproduction (e.g., gametogenesis) but not survival.

Seawater temperatures appear to control the reproductive cycles of many warm-water anthozoans. In the Great Barrier Reef, the annual timing of mass coral spawning has been linked to the rise of maximum sea water temperatures (Harrison and Wallace 1990). Additionally, delayed spawning has been recorded in higher-latitude populations where seasonal rise in temperatures are delayed (van Woesik 1995; Wilson and Harrison 2003). Due to delayed warming at deeper depths, depth-related differences also occur in the onset of gametogenesis and the timing of the reproductive season (Tsounis et al. 2006; Gori et al. 2007). Across a latitudinal gradient, a longer exposure to warm water has been positively correlated with the duration of the reproductive season, colony fecundity and levels of recruitment (Harriott 1999; Hughes et al. 1999; de Putron and Ryland 2009).

For tropical black corals, a minimum threshold temperature >22°C may be required for gonad development, and a minimum duration of exposure may be required for gonads to mature. For anthozoans, the time required for oogenesis is generally longer than spermatogenesis but varies widely by species (Kahng et al. 2011). For tropical black corals, a lack of warm water exposure likely prevents colonies from completing gametogenesis and ultimately reproducing. Reproduction has been characterized for very few antipatharians: oogenesis requires 3-4 months for *A. griggi* in Hawaii (Wagner et al. 2011). These time requirements for oogenesis are consistent with a minimum developmental threshold temperature >22°C and the observed lower depth limit at ~115 m. Large, suspension feeding fauna including antipatharians with ramose morphologies occur in patchy abundance at depths >120 m. These observations suggests that food availability is not limiting and support the hypothesis that thermal regime is responsible for the sharp change in community structure with increasing depth.

The apparent decoupling of the lower depth distribution of warm-water, benthic fauna from their temperature survival limits, may be a product of natural selection and larval behavior. Genes from individual colonies growing below the minimum thermal threshold for reproduction would eventually exit the gene pool causing strong selection for larval behavior that leads to settlement within habitats where reproduction is possible, not just growth and survival. While many studies have been performed on

coral larval behavior in response to high temperature exposure, relatively few studies have examined behavior in response to low temperatures. For the zooxanthellate scleractinian *Stylophora pistillata*, Putnam et al. (2008) reported reduced larval settlement at 23°C versus 25°C and 29°C. Temperature related larval behavior may ultimately set the lower depth limit for tropical black corals. For non-photosynthetic, warm-water species in general, this type of thermal threshold may be responsible for limiting distributions at high latitudes as well as with depth.

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