

The Physiological Mechanisms of Acclimatization in Tropical Reef Corals(1). RUTH D. GATES and PETER J. EDMUNDS.
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The Physiological Mechanisms of Acclimatization in Tropical Reef Corals

Abstract:

SYNOPSIS. The ability of scleractinian corals to survive changes that are predicted in the global environment over the next century will lie in their physiological mechanisms of acclimatization. Corals display rapid modifications in behavior, morphology and physiology enabling them to photoacclimate to changing light conditions, a scenario that demonstrates considerable biological flexibility. Here we argue that the acclimatization mechanisms in corals are fundamentally similar to those exhibited by other invertebrate taxa. We discuss protein metabolism as a mechanism underlying acclimatization responses in reef corals, and explore the relationship between protein turnover, metabolic rate, growth rate, and acclimatization capacity. Our preliminary analyses suggest that corals with low growth rates ($\mu\text{Ca}/\text{mgN}/\text{h}$) and high metabolic rates ($\mu\text{O}_2/\text{cm}^2/\text{hr}$), such as the massive species, acclimatize more effectively than those with high growth rates and low metabolic rates, a feature that is characteristic of branching species. We conclude that studies of protein turnover, combined with temporally relevant investigations into the dynamic aspects of coral dinoflagellate symbioses will provide considerable insight into why corals exhibit such a high level of variation in response to the same environmental challenge. Furthermore, a more detailed understanding of acclimatization mechanisms is essential if we are to predict how a coral assemblage will respond to present and future environmental challenges.

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INTRODUCTION

There is concern regarding the ability of scleractinian corals and reef communities to tolerate changes in the global environment predicted to result from $[\text{CO}_2]$ emissions and global warming. In the marine

environment, these changes are likely to be manifest as increases in surface sea water temperatures, intensities of ultraviolet radiation and rates of sea-level rise, and a decrease in aragonite saturation state (Gattuso et al., 1999; Pittock, 1999). The intensity and frequency of El Nino/Southern Oscillation events (ENSO) and tropical cyclones may increase, resulting in riverine flooding and regional incidents of lower salinity, elevated turbidity and high nutrient levels (Pittock, 1999).

To gain insight into the responses of coral reef communities to these predicted environmental challenges, it is necessary to assess how such changes might impact the physiology of the organisms within the reef, particularly the hermatypic corals. The organismic response to physical change is affected by both the magnitude of the change and the rate at which the environment shifts. The present predictions forecast major changes in the global environment on a temporal scale of decades to centuries (Pittock, 1999) and, as such, the ability of individual corals to tolerate the changing conditions will lie in their physiological mechanisms of acclimatization. Acclimatization refers to compensatory changes in the metabolism of an organism exposed to multiple natural variations in the environment, such as those resulting from changing seasons (Prosser, 1973). Thus, acclimatization represents the physiological response of an organism to a suite of co-occurring, and temporally variable environmental stimuli which range from gradual to abrupt in onset and from mild to acute in magnitude and/ or duration. Given that the frequency of sexual reproduction in reef corals is greater than the predicted temporal scale of global climate change, adaptation will also play a fundamental role in determining how coral populations will respond to changing environmental conditions, a subject that is discussed in detail elsewhere (Kinzie, 1999; Lasker and Coffroth, 1999).

While the persistence of many coral species through geologic time provides compelling evidence that they can adapt to a changing global environment (Veron, 1995), there are only a few examples that demonstrate corals rapidly acclimatize to changes in their physical environment in the present. The best documented of these is photoacclimation, where modifications in organismic behavior, morphology, physiology and biochemistry allow corals to acclimatize to changes in solar radiation during growth (reviewed by Barnes and

Chalker, 1990; Falkowski et al., 1990; Brown, 1997a), or experimental transplantation (Dustan, 1979). On modern reefs, corals exhibit resilience to both seasonal changes in light and temperature regimes (Gates, 1990; Hoegh-Guldberg and Salvat, 1995; Barnes and Lough, 1996; Brown, 1997a, b; Fitt et al., 1998), and acute shifts associated with meteorological events such as ENSO (Lang et al., 1992; Glynn, 1993; Fitt and Warner, 1995; Brown, 1997a, b). Corals also experience, and withstand, widely fluctuating environmental conditions occurring over a diurnal cycle. Oxygen concentrations adjacent to living corals change from hyperoxic during the day, to hypoxic at night (Shashar et al., 1993; Kuhl et al., 1995), with oxygen, pH, and light levels in the tissues exhibiting marked differences from those on the surrounding reef (Kuhl et al., 1995). These data emphasize that corals routinely occupy a physically heterogeneous environment and suggests they should possess a high degree of biological flexibility.

Most organisms, including corals, respond to environmental challenges in a manner that reflects the frequency, severity and duration of the disturbance. As such, the impact of environmental shifts on physiological processes will range from subtle, in response to frequent and/or minor disturbances, to severe, in response to more extreme disturbance. Such perturbations provide general examples of "stress responses" where "stress" denotes a reduction in fitness resulting from the impairment of structure and function by environmental factors (Calow, 1989), a scenario which involves a net reduction in surplus energy that can be allocated to reproduction (Koehn and Bayne, 1989). Shifts in protein metabolism necessary to repair and/or stabilize impacted physiological processes drive some of these energetic costs, and enable the organism to acclimatize to the changing conditions (Koehn and Bayne, 1989; Hawkins, 1991). While mildly harmful conditions may only result in minor increases in energy cost, engaging biochemical repair systems that are able to keep pace with accruing damage, more extreme conditions are likely to result in the death of the organism, due to the energy constraints associated with an inability to repair damage at the rate it is accrued (Kirkwood, 1981).

The response of corals to more extreme environmental challenge, a phenomenon known as coral bleaching, has received a considerable

amount of attention (for detailed review see Brown, 1997a, b). This response is elicited by a diversity of environmental factors including anomalously high or low sea water temperatures, variations in visible and ultraviolet radiation, fluctuations in salinity, high sedimentation, and low light levels (Hoegh-Guldberg and Smith, 1989; Gleason and Wellington, 1993; Glynn, 1993; Brown, 1997a, b). Bleached corals undergo an array of physiological and biochemical changes. These include a reduction in symbiotic dinoflagellate and chlorophyll content, variation in respiration (Hoegh-Guldberg and Smith, 1989) and photosynthetic rates (Hoegh-Guldberg and Smith, 1989; Iglesias-Prieto et al., 1992; Fitt and Warner, 1995), and changes in biochemical composition (Fitt et al., 1993), nutritional strategy (Porter et al., 1989), growth (Goreau and MacFarlane, 1990), reproduction (Szmant and Gassman, 1990) and cellular structure (Gates et al., 1992).

Coral bleaching is generally considered detrimental to affected corals, and much research has focused on the negative aspects of this phenomenon such as bleaching-associated mortality (Lasker et al., 1984). However, corals routinely recover from the loss of symbionts, as long as the events are of relatively short duration or intensity (Lang et al., 1992; Fitt and Warner, 1995). In addition, regional and local intra- and inter-specific variation in the bleaching response of corals to the same environmental disturbance is common (Edmunds, 1994; Rowan et al., 1997). Further, corals intermittently exhibit visual signs of bleaching which correlate with seasonal variations in sea water temperature (Gates, 1990), and similar changes in coloration have now been shown to correspond to seasonal variations in dinoflagellate densities (Stimson, 1997; Fitt et al., 1998). Such observations suggest that coral bleaching may represent one extreme of a range of physiological processes that characterize the acclimatization biology of corals. If this is the case, our understanding of how corals will respond to predicted changes in the global environment will be greatly enhanced by identifying and explicitly studying the physiological processes that are associated with acclimatization in reef corals.

The physiological responses of symbiotic cnidarians to environmental disturbance has recently been the subject of rigorous review (Brown, 1997a). Our paper will not duplicate that review, but will focus on the acclimatization biology of reef corals and highlight one avenue of

investigation that might be valuable in understanding how corals respond to environmental challenges. Specifically, we present evidence both from a re-evaluation of the coral literature and from our own research, that implicates protein metabolism as a central component of the acclimatization biology in tropical reef corals. Although this statement may appear somewhat naive given what is known about acclimatization mechanisms in other systems, protein metabolism (and its correlates) has received little attention by coral reef biologists. With this in mind, we explore the relationship between protein turnover, metabolic rate and growth rate and consider how these parameters might relate to the capacity of a coral to acclimatize. Lastly, we discuss aspects of the symbiosis between corals and their autotrophic dinoflagellates, which may play an important role in the physiology of the acclimatization response in reef corals.

PROTEIN METABOLISM IN CORALS AND OTHER TAXA

General properties

The general properties of protein metabolism are common to both prokaryotes and eukaryotes (Hawkins, 1991), and protein turnover is responsible for the dynamic ability of biological systems to acclimatize (Schoenheimer, 1942). Even though all proteins undergo constant renewal over an organism's life span, there are marked differences in the rates of renewal of individual proteins, and in the renewal rates of the same protein located in different tissues (Mayer, 1987; Bradshaw, 1989; Hawkins, 1991). In mammals, a minimum of 77% of total protein synthesis is allocated to protein turnover rather than net deposition and in marine mussels, fish, and mammals, a conservative estimate of heat loss due to protein turnover is near 18-26% (Hawkins, 1991).

A re-evaluation of the coral literature in this context reveals many compelling examples that confirm the prominence of protein metabolism in the biology of corals. For example, a suite of mycosporine-like amino acids (MAAs) screens UV radiation and protects corals from cellular and molecular damage (Jokiel and York, 1982; Gleason and Wellington, 1993). Glycoproteins may be central to the mediation of host-symbiont recognition (Markell and Trench, 1993). A heterogeneous pool of free

amino acids, identified as a "host factor" in *Pocillopora damicornis* (Gates et al., 1995), and several other reef corals (Gates, unpublished), sustains the metabolic competency of isolated symbiotic dinoflagellates in vitro, and induces the translocation of metabolites from these dinoflagellates to the surrounding medium (Gates et al., 1995; Gates et al., 1999). Thus proteins and their constituent amino acids occupy highly diverse functional roles in reef corals, a scenario which, by default, implicates protein turnover in the maintenance of these metabolic processes.

Protein metabolism and environmental challenge

a) Induction of heat shock proteins.--In the majority of organisms exposed to environmental variation, a number of ubiquitous physiological responses are elicited which are associated with acclimatization, the most common being the induction of heat shock proteins (hsps; Morimoto et al., 1994). Hsps are induced by a number of stressors, but are best characterized by their role in thermal tolerance at the cellular level (Parsell and Lindquist, 1994). Hsps function as molecular chaperones, preventing the aggregation of non-native proteins, helping refold reversibly heat damaged proteins, and assisting in the insertion of proteins into organelles (Hartl, 1996; Roberts et al., 1997).

The relationship between environmental tolerance, constitutive levels, and induction rates of hsps is not known in corals, although the presence and/or induction of hsps has been demonstrated in a number of symbiotic coral species exposed to environmental change, including *Goniopora djiboutiensis* and *G. pandoraensis* (hsp 70; Sharp, 1995; Sharp et al., 1997), *Montastraea faveolata* (hsps 27, 28, 33, 74, 78, 90 and 95; Black et al., 1995), *M. annularis* (hsp 70; Hayes and King, 1995), *M. franksi* (hsp 70; Fig. 1) and *Acropora grandis* (hsp 35, 60 and 70; Fang et al., 1997). Interestingly, intertidal *G. djiboutiensis* exhibit high constitutive levels of hsp 70 in comparison to their subtidal con-specifics, and corals transplanted from sub-tidal to inter-tidal locations increase constitutive expression of hsp 70 within 32 days (Sharp et al., 1997). These results suggest that constitutive levels may correlate strongly with environmental disturbance within the habitat, a result and conclusion similar to that described for field acclimatized *Mytilus californianus* (Roberts et al., 1997).

[Figure 1 ILLUSTRATION OMITTED]

Our own work (in collaboration with Virginia Weis) provides further insight into the temporal aspects of hsp 70 induction in corals. While hsp 70 expression in *Montastraea franksi* remains constant in corals maintained at ambient temperature, those exposed to a 2-3 [degrees] C increase in temperature exhibit elevations in hsp 70 expression after 6 hr maintenance at temperature (Fig. 1). Expression returns to control levels after 12 hr despite continued exposure to the experimental thermal regime (Fig. 1). This provides strong evidence that changes in protein turnover during the initial exposure to elevated temperature provides this coral with the biological flexibility to acclimatize to the elevation in sea water temperature, at least over the first 24 hr (Figs. 1, 2). Interestingly, the expression of hsp 70 increases again at 48 hr, a result that indicates another shift in protein turnover perhaps associated with an attempt to acclimatize to the more chronic level of temperature stress.

[Figure 2 ILLUSTRATION OMITTED]

b) Regulation of enzyme activity.--Another response that is characteristic of organismic acclimatization is the regulation of enzyme activity (Hochachka and Somero, 1984). For example, reef corals regulate the activity of antioxidant enzymes to ameliorate the deleterious effects of oxygen radicals generated in their tissues in response to environmental change (Lesser, 1997). Following exposure to elevated temperature and UV radiation, increased activities of superoxide dismutase (SOD) and catalase (CAT) have been directly measured in the coral *Pocillopora damicornis* exposed to differential flow regimes (Lesser et al., 1994), and in the soft-bodied symbiotic cnidarians *Anthopleura elegantissima* (Dyken and Shick, 1982, 1984) and *Palythoa caribaeorum* (Lesser et al., 1990), and in freshly isolated and cultured symbiotic dinoflagellates (Lesser et al., 1990; Lesser, 1996; Matta and Trench, 1991). Interestingly, aposymbiotic individuals of the sea anemone *Aiptasia pulchella* maintain high activities of SOD and CAT relative to symbiotic con-specifics. This result suggests enzymatic regulation and acclimatization to what appears to be a chronic state of oxidative stress in the animal tissues that is independent of the symbiotic dinoflagellates (Nii and Muscatine, 1997).

c) Additional observations.--The ability of corals to increase and decrease expression levels of hsp 70, and effectively regulate the activity of antioxidant enzymes clearly reflects the intrinsic biological flexibility of reef corals with respect to their environment. Additional evidence lends added weight to the suggestion that protein turnover in reef coral is highly dynamic and sensitive to environmental challenge. Over a 24 hour period, the amount of soluble protein in the tissues of *Acropora cervicornis* can vary by 43% (Kendall et al., 1983). *Montastraea franksi* exhibits similar changes in soluble protein (Fig. 2), and amino acids (Fig. 3), and there is a tendency for changes in both these parameters to become more profound as a result of exposure to elevated sea water temperatures (Figs. 2, 3). Suharsono et al. (1993) report rapid changes in lysosomal latency in symbiotic sea anemones exposed to elevated sea water temperatures, and concentrations of MAAs in *Fungia repanda* undergo measurable compensatory changes within a week of exposure to altered solar UV radiation in the field (Drollet et al., 1997). Additionally, the cellular mechanisms responsible for the loss of symbionts during a bleaching event, such as necrosis, apoptosis, exocytosis and host cell detachment (Gates et al., 1992; Brown et al., 1995; Le Tissier and Brown, 1996), all indirectly implicate shifts in protein turnover. These results strongly suggest that corals have the capacity to rapidly modify protein expression as a response to both acute and chronic changes in environmental conditions. As such, it is likely that corals exhibit high rates of protein turnover.

[Figure 3 ILLUSTRATION OMITTED]

Protein turnover, metabolic rate and growth rate correlates

Protein turnover directly reflects organismic genotype and is responsible for some profound organismic traits (Hawkins, 1991). For example, in *Mytilus edulis*, the fastest growing and largest individuals have low, and efficient protein turnover, an energetic saving that results in low metabolic rate and high growth rate. Slow growing individuals exhibit the opposite trend (Bayne, 1987; Hawkins, 1991). Recently, these discrepancies have been traced, in part, to differences in lysosomal protease activity (Hawkins and Day, 1996). Rates of protein turnover are also directly related to an organism's ability to acclimatize (Hawkins,

1991); mussels that exhibit high rates of protein turnover, high metabolic rates and low growth rates, are able to acclimatize to changing conditions more rapidly. In contrast, those with slower, more efficient protein turnover, low metabolic rates and high growth rates acclimatize more slowly (Bayne, 1987; Hawkins, 1991).

The generalizations of the *Mytilus* model may provide powerful insight into inter- and intra-specific variation in the responses of reef corals to environmental stress (Gates, 1990; Glynn, 1993; Edmunds, 1994). Although there are strong anecdotal observations that corals with high growth rates have the tendency to undergo rapid bleaching (Suharsono and Brown, 1990; Jokiel and Coles, 1990; Glynn, 1993; Hoegh-Guldberg and Salvat, 1995), there has been no direct experimental evaluation of the relationship between growth rate and metabolic rate in reef corals. Nevertheless, a non-exhaustive survey of the literature provides some support for the inverse relationship between growth rates and metabolism (Fig. 4). This relationship, although tentative, suggests that corals with low growth rates and high metabolic rates (e.g., *Siderastrea siderea*; D on Fig. 4) exhibit high rates of protein turnover and an ability to acclimatize readily. In contrast, those with high growth rates and low metabolic rates (e.g., *Acropora cervicornis*; A on Fig. 4), exhibit lower rates of protein turnover and a reduced capacity to acclimatize. The proposed relationship between growth rates, metabolic rates and acclimatization capacities is also supported by intra-specific differences in the propensity of corals to bleach, assuming that coral bleaching is at one extreme of the range of acclimatization responses. As mentioned above, there are numerous reports of an increased incidence of coral bleaching in fast growing branching species as compared to the slower growing massives (Suharsono and Brown, 1990; Jokiel and Coles, 1990; Glynn, 1993; Brown, 1997a), although it should be noted that the relationship between metabolic rate and growth form is only one of several features of the comparative biology of these corals that are different.

[Figure 4 ILLUSTRATION OMITTED]

The data used to examine the inverse relationship between metabolic rate and growth rate (Fig. 4) were culled from a variety of sources, and represent a small number of coral species growing in water depths

between 2 and 10 m. In the compiling of this figure, it became apparent to us that few studies in the coral literature lend themselves to inter-specific comparative analysis, a problem which reflects among-study differences in the techniques used to collect and normalize data. Additionally, growth studies in corals generally use skeletal characteristics as indices of growth, yet changes in tissue biomass are most likely to reflect differences in protein metabolism, and are thus of greater relevance to the relationship between protein turnover, metabolic rate and growth rate. Currently it is difficult to relate skeletal growth to tissue growth because of the poorly understood interaction between the two, and the ongoing debate concerning the mechanisms of calcification (Gattuso et al., 1999; Marshall, 1996). However, this should underscore the potential importance of the relationship between metabolic rate and growth rate as a tool for advancing our understanding of physiological mechanisms of acclimatization in reef corals.

To our knowledge, there have been no attempts to quantify protein turnover in reef corals, therefore, it is impossible to know whether turnover is related to metabolism and growth rate as described for *Mytilus* (Bayne, 1987; Hawkins, 1991). RNA/DNA ratios provide a measure of protein synthesis (Dortch et al., 1983; Barber et al., 1990), thus we have used this technique to investigate protein synthesis in the reef coral *Madracis mirabilis*. The preliminary results demonstrate that both growth rates, and RNA/DNA ratios vary by a factor of 5 among the 10 clonal genotypes used in the study, confirming that there are unusually large intrinsic metabolic differences among corals of any one species (Edmunds, 1994; Bruno and Edmunds, 1997; Edmunds et al., in review). This observation is consistent with the hypothesis that individual coral colonies differ in their rates of protein turnover, tissue growth and capacity to acclimatize to changing environmental conditions.

HOST--DINOFLAGELLATE INTERACTIONS

Symbiotic composition

So far, we have discussed acclimatization mechanisms in the coral host alone, yet the response of symbiotic corals to changing environments reflects the physiological capacities of both symbiotic partners. This

added biological range is addressed by Buddemeier and Fautin (1993) who propose that coral bleaching represents an adaptive strategy involving the constant shuffling of symbiont genotypes to create an association best suited to the prevailing conditions. Although never directly tested, several of the pre-requisites required to support this hypothesis have now been met. There is growing evidence of physiological differences among the symbionts of different corals (Fitt and Warner, 1995; Warner et al., 1996). In addition, the symbionts of reef corals represent three related Symbiodinium clades (A, B and C) based on restriction-fragment length polymorphisms (RFLPs) in the gene sequences encoding for small 18s subunit ribosomal RNA (Rowan and Powers, 1991; Banaszak et al., 1993). The level of irradiance appears to dictate the distribution of the Symbiodinium clades, both with depth on the reef, and in the tissues of *Montastraea faveolata* and *M. annularis*. While clades A and B predominate in shallow water corals and in areas of the colonies receiving high irradiance, clade C inhabits deep water corals and more shaded locations within the colony (Rowan and Knowlton, 1995). This distribution suggests that the Symbiodinium clades exhibit differences in their physiological optima. Further, the taxonomic assemblages of the symbionts within *M. faveolata* and *M. annularis* are dynamic and undergo changes as the corals bleach in response to elevated sea water temperatures and increased irradiances (Rowan et al., 1997). Coral tissues containing Symbiodinium clade C bleaches more readily than those containing clades A or B. This suggests that the coral preferentially lose clade C, suggesting this clade has a more limited physiological range than clades A and B (Rowan et al., 1997). In contrast to the "polymorphic" (coral hosts containing multiple symbiotic taxa) examples from the Caribbean, Symbiodinium clade C has now been identified as the only symbiotic clade present in the majority of coral species sampled in the Eastern and Australian Pacific (Baker and Rowan, 1997; Loh et al., 1999). The exceptions are *Acropora longicyathus* (clade A and C) and *Pavona decussata* (clade B and C) sampled at One Tree Island, on The Great Barrier Reef (Loh et al., in 1999.) It is impossible to interpret the implications of the apparent decrease in the diversity of individual associations, or the abundance of clade C containing symbioses in the Pacific, as neither the physiological range of the Pacific Symbiodinium clades, nor the temporal variability of these symbiotic associations has been demonstrated.

At this point, our understanding of the biogeographical forces governing the taxonomic composition of coral symbiosis is limited. However, there is no doubt that the existence of multiple Symbiodinium clades, each potentially exhibiting a different physiological optima, provides corals with the opportunity to attain an expanded range of physiological flexibility which will ultimately be reflected in their response to environmental challenge.

Interactive physiology and symbiotic communication

Little is known regarding the interactive physiology of scleractinian symbioses or the relative contribution of each symbiotic partner to fundamental aspects of the biology of the intact association such as metabolic rate, growth rate or response to environmental stress. To gain some insight into the role of dinoflagellate physiology as it relates to the propensity of a coral to bleach, Calavetta (1998) investigated the extent of bleaching in four colonies of *Agaricia agaricites*. The differential response of each coral colony to a specific temperature regime was examined by sampling at specific intervals, characterizing the extent of bleaching, and comparing these results with the physiological response of the dinoflagellates isolated from the coral at each sampling interval (Fig. 5; details in Calavetta, 1998). The results show that intact coral colonies respond differently to elevated temperatures (P [is less than] 0.001), and that there is a significant relationship between aspects of coral physiology and that of its symbionts (Fig. 5; $r = -0.314$, $P = 0.029$, $n = 48$). Thus, corals that bleach less readily have high concentrations of symbionts, chlorophyll and soluble protein (per unit area), and contain dinoflagellates whose physiology is characterized by high photosynthetic efficiency ($[\alpha]$) and low saturation irradiance ($[I_{sub.k}]$). Conversely, corals that exhibit a greater propensity to bleach contain dinoflagellates with lower photosynthetic efficiency that require higher saturation irradiances (Calavetta, 1998). Although there is a statistically significant relationship between the physiology of the coral and its symbionts, there is a large amount of variation that remains unaccounted for and how this variation maps onto the genetic identity of the symbionts is unknown. Nonetheless, these results demonstrate that within a species, corals harbor dinoflagellate populations whose physiology is not only variable, but also an important feature in determining how the intact association responds to

environmental stress.

[Figure 5 ILLUSTRATION OMITTED]

The above example leaves little doubt that the cumulative physiology of a coral dinoflagellate symbiosis is the result of the dynamically intertwined physiologies of the symbiotic partners. As discussed earlier, protein metabolism plays a key role in coral acclimatization and as in non-symbiotic organisms, amino acids for protein metabolism are taken up directly from the environment, released by the catabolism of food, and recycled following protein breakdown. However, corals also acquire translocated essential amino acids from their symbiotic dinoflagellates (Fitzgerald and Szmant, 1997; Swanson and Hoegh-Guldberg, 1999). These amino acids are cyclically available and appear to be rapidly incorporated into host proteins (Gates and Muscatine, unpublished data), although it is unknown whether they are incorporated randomly, or are used to synthesize specific proteins in the host. This supply of amino acids will be changed by environmental conditions that elicit shifts in nutrient uptake, photosynthetic and respiratory pathways. As such, the extent to which the host is dependent on these amino acids for the synthesis of proteins required for acclimatization will dictate the ramifications of the environmental disturbance on the intact association.

In addition to their role in protein metabolism, free amino acids have been implicated as regulatory molecules in some tropical symbioses, controlling the synthesis and translocation of photosynthetically derived metabolites, specifically glycerol, from the dinoflagellates to the host (Gates et al., 1995; Gates et al., 1999). Glycerol is generally considered to be a substrate for host respiration, and as such, is thought to be respired rapidly. However, we have enzymatically measured glycerol concentrations in the tissues of *Montastraea franksi* (Fig. 6) and other tropical corals (data not shown), and these data demonstrate that corals maintain high levels of glycerol in their tissues under normal conditions (Fig. 6). While the functional significance of this finding has not been assessed, we speculate that glycerol may play a fundamental role in the osmoregulation of these symbioses, as has been demonstrated in other systems. If this is the case, changes in the availability of free amino acids will influence the synthesis and translocation of glycerol, which may

negatively impact the osmoregulatory capacity of the intact association and result in changes in animal cellular structure. Our data show that concentrations of free amino acids and glycerol are sensitive to elevations in sea water temperature (Figs. 3, 6). Furthermore, damage to the endoderm of corals in the early stages of bleaching is limited to cells containing zooxanthellae (LeTissier and Brown, 1996), and the array of cellular mechanisms implicated in coral bleaching (Gates et al., 1992; Brown et al., 1995) would be consistent with osmoregulatory dysfunction in the host.

[Figure 6 ILLUSTRATION OMITTED]

Our understanding of the biological communication between corals and their symbiotic zooxanthellae is in its infancy, however the preliminary observations presented in this section leave no doubt that these relationships are labile, complex, and physiologically diverse. Further, the intimate association between tropical reef corals and a diversity of symbiotic dinoflagellates provides an opportunity to modify the physiological performance of an intact association by "shuffling" symbiont genotypes. Such physiological plasticity is likely to be a highly advantageous characteristic when considering how corals will respond to changes in the global environment.

CONCLUSIONS AND FUTURE DIRECTIONS

Reef corals exposed to environmental disturbance display physiological responses that are indicative of acclimatization, such as the induction of heat shock proteins (Fig. 1) and the regulation of enzyme activity (Brown, 1997a). By analogy with other systems, it is likely that the rate of protein turnover controls the capacity of a given coral to acclimatize; corals with high rates of protein turnover will readily acclimatize as compared to those with low rates. Although it has never been directly measured in corals, the rate of protein turnover is intrinsically linked to growth and metabolic rates, measures that are available for some species. The relationship between these parameters suggests that corals with low growth rates and high metabolic rates will exhibit high rates of protein turnover, and a greater ability to acclimatize compared to those with high growth and low metabolic rates. In general, these data indicate that

branching corals may be less able to acclimatize than massive forms, although the range of acclimatization capacities within a species is not known.

Although this discussion is weighted toward the animal host, it is clear that the complex interactions between corals and their symbiotic dinoflagellates are likely to result in an added range of acclimatization mechanisms. As such, these symbioses may be particularly well equipped to modify function, survive, and reach new physiological equilibria in the face of a diverse set of temporally variable environmental challenges.

Our understanding of acclimatization in reef corals is largely inferred by analogy with other, more thoroughly studied invertebrate taxa, a phenomenon which is driven by the lack of directly relevant information and the nature of much of the coral literature. Most studies on coral physiology concentrate on a single species, and report the measurement of well established variables, normalized to any one of several arbitrarily selected and easily measured parameters. While this approach has been highly successful in understanding the biology of individual species, it has resulted in data sets that do not lend themselves to inter-, or intra-specific comparisons. Further, the highly dynamic nature of coral physiology indicates that normalization to parameters such as surface area, and single point determinations of protein content, may not offer sufficient resolution to examine subtle but important aspects of coral physiology.

To identify general trends in the biology of scleractinian corals there is an urgent need for studies of a wider diversity of species, the use of a suite of standardized techniques, and the normalization of data to physiologically and temporally relevant parameters. To specifically address questions relating to acclimatization, a better understanding of fundamental aspects of coral biology

such as protein turnover, metabolic rate and tissue growth rates is needed. An evaluation of how these parameters vary inter- and intra-specifically could provide us with a powerful tool with which to understand the response of corals to changes in the global environment.

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