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Cross-continental shelf trends in $\delta^{13}C$ in coral on the Great Barrier Reef

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ABSTRACT: We studied scleractinian corals from the central region of the Great Barrier Reef, Australia, to determine the degree to which they utilize terrigenous carbon as an ultimate food source. $\delta^{13}C$ was analyzed in both the tissue and zooxanthellae of *Porites lobata* and *Acropora formosa*. Both tissue and zooxanthellae of *P. lobata* have $\delta^{13}C$ values which increase linearly with distance from shore from −16 to −11‰. A similar relationship was found for tissue and zooxanthellae from *A. formosa*, although the variance was higher. Most of the variance observed (72 to 76%) was explained by cross-shelf differences. The correlation between values for tissue and zooxanthellae in both species was highly significant and strongly linear, e.g. 0.926 in *P. lobata*. The slopes of all relationships observed were found to be not significantly different for the 2 species, but the $\delta^{13}C$ values for *A. formosa* were consistently less than for *P. lobata*, by 1 to 2‰. When coral tissue and zooxanthellae were analyzed as homogenates together, the same general cross-shelf trend was found, although the variance was higher, indicating that a crude extract may still be used to indicate general trends. This study implies that inshore corals derive much of their nutrients from terrigenous sources, and that a terrigenous influence on diet is measurable out to the edge of the continental shelf, ca 110 km offshore. Previous data derived from POC (particulate organic carbon) in sediments have implied that the limit of the terrigenous influence was 10 to 20 km. Judging from differences between the 2 species examined, *P. lobata* is less dependent upon autotrophy and more dependent on exogenous carbon sources than *A. formosa*.

KEY WORDS: Stable isotopes · Coral · Carbon · $\delta^{13}C$ · Terrigenous nutrients · Tissue · Zooxanthellae · Great Barrier Reef

INTRODUCTION

Natural trophic links between land and the sea have been the subject of scientific investigation for over 100 yr (e.g. Darwin 1842, 1933, El-Sabh & Silverberg 1990, Elliott & Ducrotoy 1991). The influence of terrigenous sources of nutrients on coastal and oceanic biota has served as a point of controversy in this area for some time. For example, terrigenous nutrients have been linked to phytoplankton production in inshore waters (Subrahmanyan 1959, Revelante & Gilmartin 1982, Revelante et al. 1982), concomitant zooplankton community changes (Calef & Grice 1967, Grahame 1976, Kidd & Sander 1979, Youngbluth 1980, Sammarco & Crenshaw 1984), and nutrient charging of coastal estuaries, salt marshes and wetlands (see Livingston 1985). Terrestrial runoff has also been linked to increased bioerosion of scleractinian corals (Risk & Sammarco 1991), and eutrophication and hypoxia in inshore waters (Birkeland 1987, Turner & Rabalais 1991, Rabalais & Harper 1992, Rabalais et al. 1992).

Coral reefs are known generally to flourish in oligotrophic, nutrient-poor tropical waters; yet Darwin's paradox involves the observation that reefs flourish better closer to shore. Birkeland (1987) has noted that increased nutrient input has a strong influence on the community structure and trophic structure of coral reefs. This may be seen when comparing the reefs of high islands or continental margins with those associated with atolls or low islands. One of the major rea-

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sons that scleractinian corals are successful in oligotrophic waters stems from the symbiotic relationship between the coral tissue and endosymbiotic zooxanthellae. This association has been well studied from a physiological perspective (Muscatine 1986), but it is not known whether there is any relationship between zooxanthellar function, nutrients in the water column, and the source of those nutrients.

The role of terrigenous nutrients in coastal waters is still not completely understood. For example, to what distance from the shoreline can these nutrients be traced as an ultimate food source for benthic organisms? The Great Barrier Reef, Australia, occurs on a continental shelf which is between 20 and 250 km in breadth, depending upon latitude, generally occupying the outer half of the shelf. A number of characteristics have been found to vary significantly across the shelf with distance from shore. Physical attributes which exhibit cross-shelf variation include temperature and salinity (Kenny 1974, Archibald & Kenny 1980, Walker 1981a, b, Wolanski 1981), wind and currents (e.g. Andrews 1983, Andrews & Furnas 1986, Pickard et al. in press), turbidity (Walker & O'Donnell 1981), nature of sediment (Gagan et al. 1987), influence of deeper offshore waters (Andrews & Gentien 1982), and types and concentrations of nutrients (Ikeda et al. 1980). Ecological characteristics also vary significantly with distance from shore, including the community structure of phytoplankton (Revelante & Gilmartin 1982, Revelante et al. 1982), zooplankton (Sammarco & Crenshaw 1984), corals (Done 1982, Sammarco 1983, 1991), algae (Drew 1983), fish (Williams 1982), and other taxa.

Stable isotope ratios of biologically important, lighter elements such as H, C, N, O, and S have been used extensively to decipher metabolic pathways in living and fossil organisms (DeNiro & Epstein 1978) and to elucidate trophic linkages in a variety of ecosystems, ranging from subarctic to tropical in climate (LeBlanc et al. 1989, Muscatine et al. 1989, Risk et al. 1989). Ratios of stable isotopes derived from different types of primary producers differ and therefore make it possible to trace the diets of target organisms. The underlying principle in stable isotope research is the isotopic fractionation which is produced by the slightly varying rates of reaction of the different isotopes based upon the very slight differences in their mass.

Most of the research using stable isotopes to trace trophic pathways has been performed in temperate, cooler waters (Chisolm et al. 1982, 1983). There have, however, been several recent studies centered on tropical ecosystems, such as Fry et al. (1983), Rodelli et al. (1984), and Cooper & DeNiro (1989). Muscatine et al. (1989) reported the results of an elegant study of resource partitioning in reef corals based on trends in stable isotopes. A great deal of research has also been devoted to the study of the relationship between scleractinian coral tissue and the zooxanthellae.

Here we have attempted to make use of contrasts in isotopic composition of terrigenous vs marine-derived organic matter in order to test whether terrigenous nutrient usage by corals could be identified and traced across the continental shelf. In addition, we use the isotopic composition of coral tissue to estimate the relative contribution of terrigenous and marine-derived carbon as a function of position on the shelf, i.e. distance from shore.

The study is based on the observation that terrigenous organic carbon, delivered to the shelf in the form of particulate organic matter (POM), has a $\delta^{13}C$ value of about -27‰, typical of C3 plants which dominate the eastern Australian flora (Gagan et al. 1987). Marine-derived organic matter is considerably enriched in $\delta^{13}C$ with respect to terrigenous POM (TPOM), with a $\delta^{13}C$ value of >-18‰ (Gagan et al. 1987). The ^{13}C-enrichment of marine organic matter is partly due to the fact that primary photosynthetic production in the sea makes use of dissolved HCO_3^- which is about 7‰ enriched with respect to atmospheric CO_2, the carbon source for land plants. In addition, kinetic isotopic fractionation during photosynthesis in the terrestrial C3 plants is greater than fractionation between HCO_3^- and marine organic matter. Besides POM, we presume that significant amounts of dissolved organic matter (DOM) are also delivered by rivers (see Herczeg et al. 1989) to the waters of the shelf and could serve as nutrients for bacteria and other heterotrophic microorganisms, thus contributing to the trophic system.

We can make use of these isotopically contrasting nutrients, because it has been shown in various studies (e.g. DeNiro & Epstein 1978) that the weighted average $\delta^{13}C$ of the tissues of heterotrophic animals is very close to that of their diet. Therefore, we can use the $\delta^{13}C$ of animals close to shore to estimate the relative contribution of marine and terrestrial sources to their heterotrophic intake. For corals, this approach is complicated by the fact that they are partly autotrophic, as a result of the presence in their tissues of endosymbiotic algae (zooxanthellae). We shall show, however, that at least for these coral populations, $\delta^{13}C$ values of the zooxanthellae track those of the tissues, and therefore can be considered as a passive compartment of the total coral tissue. We should therefore be able to use $\delta^{13}C$ of total tissue to estimate the percent terrigenous nutrient.

Here we have focused on the variation in $\delta^{13}C$ of corals with distance from the shore, measured as the perpendicular distance to the nearest coastline. In doing so, we assume that, at distances of more than

10 to 20 km away from the coast, discharges by individual rivers or swampy regions are thoroughly dispersed into the seawater of the shelf, although samples collected closer to shore may indicate differential responses, depending on their distance from the mouth of the nearest river or adjacent mangrove swamp.

The objectives of this study were to: (1) attempt to trace the general origin of the diet of 2 scleractinian corals — *Porites lobata* and *Acropora formosa* — across the continental shelf of the central region of the Great Barrier Reef via $\delta^{13}C$ in the coral tissue; (2) identify how that portion of the diet which is terrestrially derived changes with distance from shore; (3) determine the relationship between $\delta^{13}C$ in the tissue and zooxanthellae, respectively, in these 2 coral species; and (4) determine how much variation there is in $\delta^{13}C$ in corals across the continental shelf of the Great Barrier Reef, and how much of the total variance observed is accounted for by inter- vs intra-reef differences between coral colonies.

MATERIALS AND METHODS

All field work was performed in the central region of the Great Barrier Reef, Australia, between 1986 and 1988. Samples of the scleractinian corals *Porites lobata* and *Acropora formosa* were collected from a number of reefs in this region, varying in their distance from shore (Fig. 1): Pandora Reef; Picnic Bay, Magnetic Island; Pioneer Bay, Orpheus Island; Davies Reef; Britomart Reef; Myrmidon Reef; Salamander Reef; Grub Reef; Bray Island; Morinda Shoals; and Little Broadhurst Reef. Samples were collected with hammers and chisels from the apices of *A. formosa* and the tops of *P. lobata* colonies from a water depth of 5 to 8 m. Approximately 150 to 200 cm^2 of material was collected from each head. Each sample yielded at least 2 g (dry wt) of carbon.

All replicates from a given reef were collected within several meters of each other. All samples were taken during austral winter; 2 sets of samples were taken, one in 1986, the other in 1987; in each set, samples were taken within 1 wk of each other. Not all reefs were sampled during the same sampling period.

The experiment followed a 3-level nested ANOVA design (Sokal & Rohlf 1981). Three heads of each species of coral were sampled from each reef in a preliminary experiment (1986), six for the later study. Excess skeleton was removed from the corals, and the remaining portions, including their tissue, were frozen on shipboard. Frozen samples were returned to the laboratory and stored for processing later. Some samples were lost during tissue processing, yielding a lower number of replicates than planned.

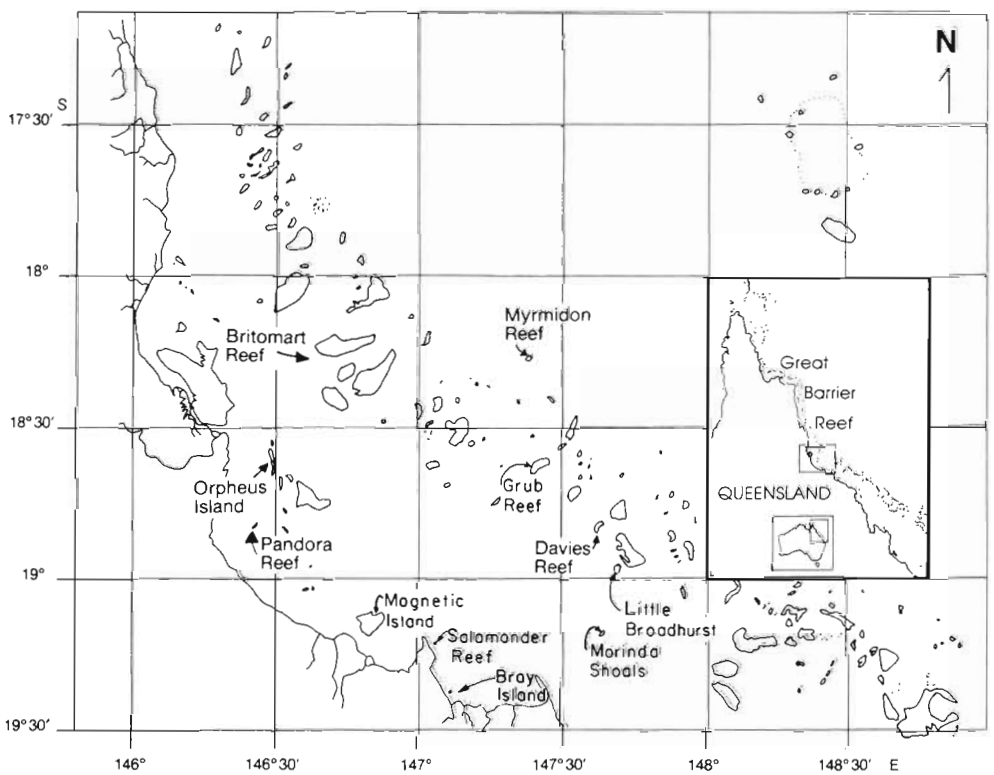

Fig. 1. Central region of the Great Barrier Reef, Australia, depicting the various reefs sampled for corals in this study

The coral samples taken in 1986 were used in a preliminary study, designed to yield information on the degree of isotopic fractionation between the algal tissue and the coral host. This information was later used to help design the larger, cross-shelf study. The 1986 samples were processed in the Department of Chemistry and Biochemistry, James Cook University of North Queensland. Separate coral tissue and zooxanthellar extracts were prepared through repeated centrifugations and then lyophilized. Microscopic examination of the separated materials confirmed clean zooxanthellar samples, free of coral tissue, and vice versa. The samples were then shipped to the Department of Geology at McMaster University for processing. Corals taken on later field trips were freeze-dried, heat-sealed in labeled plastic bags to avoid contamination, and shipped to the Department of Geology, McMaster University, for stable isotope analysis.

Samples in the latter set were subdivided into ≤3 sections; sections were further subdivided into ≤5 replicates. Each replicate was decalcified in dilute HCl. Each sample of decalcified bulk coral tissue (including endosymbiotic algae) was then centrifuged and rinsed in distilled water several times in succession. The resulting pellets were freeze-dried.

All subsamples were loaded into precombusted Pyrex tubes, along with CuO. Tubes were combusted at 550°C for 2 h. The resulting CO_2 gas was analyzed on an isotope-ratio mass spectrometer (VG Micromass 602D). All data are presented in the standard $\delta^{13}C$ notation $\delta^{13}C = [(^{13}C/^{12}C)/(^{13}C/^{12}C)_{std} - 1] \times 1000$ (‰), with respect to the PDB standard. The precision of analysis was ± 0.1‰.

Resulting $\delta^{13}C$ data were analysed using standard parametric and non-parametric statistical methods. Details of statistical results are presented in figure and table legends. Only significant trends will be discussed. With respect to figures, regression lines are shown only for Model I regressions, not for correlations. In cases where Model II regression analyses have been performed, results are presented in the figure legends, but regression lines are not shown (see Sokal & Rohlf 1981).

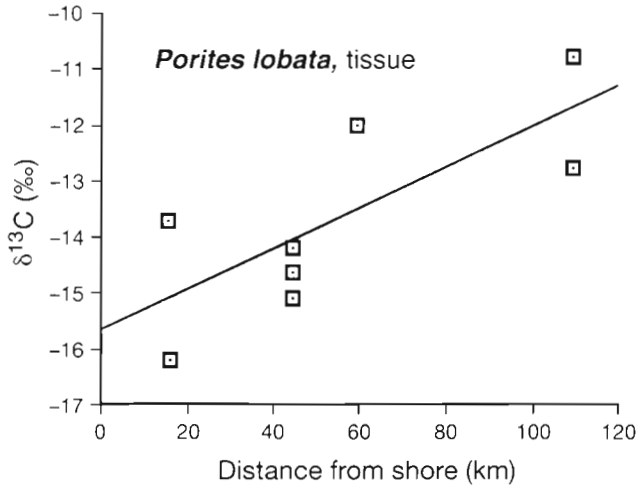

Fig. 2. *Porites lobata*. Scattergram showing $\delta^{13}C$ in isolated coral tissue (zooxanthellae-free) as a function of distance from shore. $\delta^{13}C$ increases in significant linear fashion with distance from shore ($p < 0.05$, $Y = 0.0462X - 15.977$)

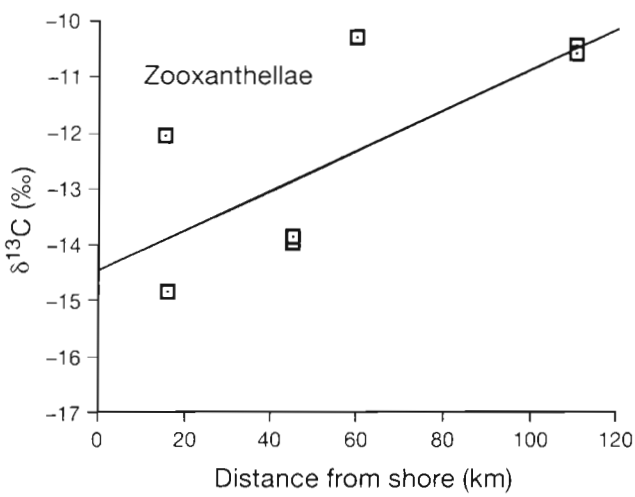

Fig. 3. Scattergram depicting $\delta^{13}C$ in isolated zooxanthellae (free of coral tissue) from *Porites lobata* as a function of distance from shore. Significant positive correlation between $\delta^{13}C$ and distance from shore ($p < 0.05$, Pearson's product-moment correlation coefficient = 0.713). $\delta^{13}C$ increases significantly in linear fashion with distance from shore ($p < 0.05$, linear regression analysis; $Y = 0.035X - 14.525$). Significant difference between reefs ($p < 0.001$, 1-way ANOVA)

RESULTS

Trends in coral tissue and zooxanthellae

In this section, we will refer to the analyses taken during the 1986 cruise, from which separate coral tissue and zooxanthellar extracts were prepared. With respect to *Porites lobata*, $\delta^{13}C$ in both the isolated coral tissue (Fig. 2) and the isolated zooxanthellae (Fig. 3) show highly significant correlations with distance from shore, ranging in both cases from near-shore values of ca −16‰ to offshore values of ca −10 to −11‰. There was no significant difference between the slopes of the linear regressions for the tissue and the zooxanthellae.

The $\delta^{13}C$ values for the coral tissue and zooxanthellae from the same individuals are also linearly correlated in

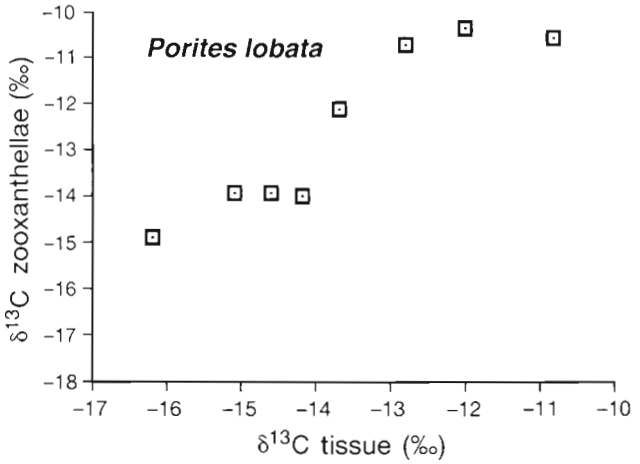

Fig. 4. Scattergram depicting positive correlation between $\delta^{13}C$ in coral tissue extracts and zooxanthellae extracts isolated from the same colonies of *Porites lobata* across the continental shelf of the central region of the Great Barrier Reef. Significant positive correlation (Pearson's product-moment correlation = 0.926, $p < 0.001$). Significant positive linear regression ($p < 0.001$, Model II linear regression analysis, $Y = 1.04\,X + 1.72$)

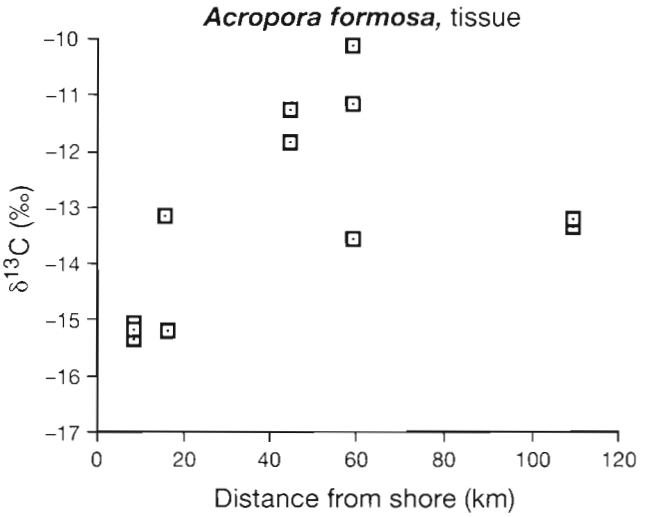

Fig. 5. *Acropora formosa*. Scattergram depicting $\delta^{13}C$ in isolated coral tissue (zooxanthellae-free) as a function of distance from shore. Significant positive correlation ($r = 0.398$, $p < 0.05$) and significant differences between reefs ($p < 0.05$, nested 1-way ANOVA)

a highly significant manner (Fig. 4). Pearson's product-moment correlation coefficient was 0.926 ($p < 0.001$).

A nested analysis of variance revealed that of the total variance observed in the $\delta^{13}C$ of coral tissue collected in this initial study, 76.6% was accounted for by differences between reefs across the continental shelf, and 23.4% was accounted for by differences between coral colonies within reefs (Table 1). With respect to zooxanthellae in *Porites lobata*, 99.9% of the total variance observed was accounted for by differences between reefs (Table 1). The remainder was explained by variance between coral colonies within reefs.

With respect to *Acropora formosa*, a similar relationship was found in the correlation between $\delta^{13}C$ in the coral tissue and distance from shore ($r = 0.398$, Fig. 5). The cross-shelf pattern, however, exhibited a higher degree of variance and a less pronounced cross-shelf trend than that observed for *Porites lobata*.

Zooxanthellar $\delta^{13}C$ values also exhibited a strong correlation with distance from shore (Fig. 6). This relationship was linear, and virtually identical to the relationship found to occur in the zooxanthellae of *Porites lobata*.

A highly significant linear relationship was found between the $\delta^{13}C$ values for isolated coral tissue and zooxanthellae in *Acropora formosa*, just as was found in *Porites lobata*.

Of the total amount of variance observed in the $\delta^{13}C$ values of *Acropora formosa* tissue, 71.6% was accounted for by differences between reefs across the

Table 1. *Porites lobata* and *Acropora formosa*. Proportion of total observed variance (%) in $\delta^{13}C$ accounted for by inter-reef/cross-shelf and inter-coral/within-reef differences. Results shown for *P. lobata* and *A. formosa* where coral tissue and zooxanthellar extracts were separated; results also shown for *P. lobata* for combined extracts. Variance components attributable to inter-replicate/within-coral differences also shown for *P. lobata*

Species	Source of variance	Extract type		
		Coral tissue	Zooxanthellae	Combined coral tissue and zooxanthellae
P. lobata	Between reefs	76.6	99.9	45.2
	Between corals/within reefs	23.4	0.1	23.0
	Between replicates/within corals	–[a]	–[a]	31.8
A. formosa	Between reefs	71.6	75.8	–[b]
	Between corals/within reefs	28.4	24.2	–[b]

[a]Preliminary samples did not include replicates within corals. [b]*A. formosa* was not sampled during the 1987 cruise

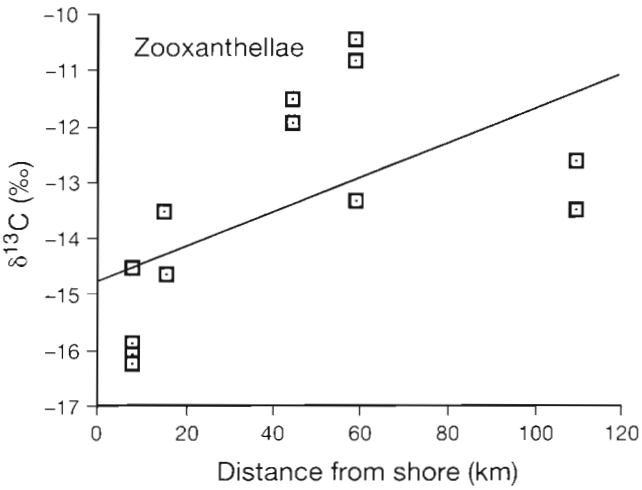

Fig. 6. Scattergram depicting $\delta^{13}C$ in isolated zooxanthellae extracts (free of coral tissue) from *Acropora formosa* as a function of distance from shore. Significant positive correlation ($p < 0.05$, $r = 0.573$, Pearson's product moment correlation coefficient). Significant positive linear regression ($p < 0.05$, linear regression analysis). Significant difference between reefs ($p < 0.01$, 1-way ANOVA). No significant difference between slopes of regressions in coral tissue or zooxanthellae in either species of coral ($p > 0.05$ in all cases; all possible pairwise comparisons of regression coefficients shown in Figs. 2, 3, 5 & 6)

continental shelf, whereas 28.4 % was accounted for by differences between coral colonies within reefs (Table 1). Similar values were observed in the zooxanthellae, with inter-reef differences explaining 75.8 % of the total observed variance and inter-colony differences explaining 24.2 % of the variance (Table 1).

Comparison between species

When all 4 cross-shelf relationships are compared, i.e. tissue and zooxanthellae in either species vs distance from shore, they were all found to exhibit linear slopes of about 0.03 to 0.04‰ per km. These slopes were not significantly different from each other ($p > 0.05$, multiple comparison of regression coefficients). Intercepts of both of the zooxanthellar/distance-from-shore relationships (−14.5‰) were also not significantly different ($p > 0.05$, ANCOVA). The same was the case for the intercepts of the tissue/distance-from-shore relationships, i.e. they were not significantly different for the 2 species. The intercepts for tissues of both species were identical. When comparing the intercepts for the tissue vs zooxanthellae relationships, however, they were found to differ significantly from each other by 1 to 2‰ (Fig. 4 vs Fig. 7) ($p < 0.001$, ANCOVA). That is, for a given distance from shore, the *Porites lobata* zooxanthellae value was, on the average, about 1 to 2‰ higher than that for *Acropora formosa* zooxanthellae. This is important and will be discussed below.

The cross-shelf survey: *Porites lobata*

Having demonstrated in the above study (Figs. 4 & 7) that coral tissue and zooxanthellae values were highly correlated, a more extensive cross-shelf study was pursued, using whole-coral tissue homogenates of *Porites lobata* containing both coral tissue and zooxanthellae. The study was expanded to encompass a greater number of samples collected from a larger number of reefs, over the same region as the earlier study.

There was a significant difference between reefs as a whole with respect to $\delta^{13}C$ in the *Porites lobata* extracts ($p < 0.01$, nested ANOVA). In addition, the $\delta^{13}C$ values increased in a highly significant linear manner with distance from shore (Fig. 8; $p < 0.001$, linear regression analysis).

In this part of the study, differences between reefs accounted for 45.2 % of the total variance observed in the *Porites lobata* $\delta^{13}C$ values ($p < 0.01$, 2-level nested ANOVA). There were significant differences between coral colonies within a reef ($p < 0.05$), and this source of

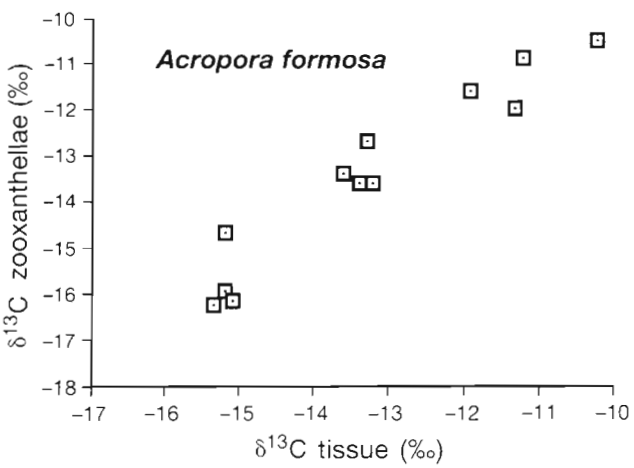

Fig. 7. Scattergram depicting relationship between $\delta^{13}C$ in the coral tissue and zooxanthellae isolated from colonies of *Acropora formosa* sampled from reefs across the continental shelf of the Great Barrier Reef. Highly significant positive correlation ($r = 0.960$, Pearson's product-moment correlation coefficient, $p < 0.001$). Significant positive linear relationship ($p < 0.001$, Model II linear regression analysis, $Y = 1.14\,X + 1.73$). No significant difference between slopes of this linear relationship and that for *Porites lobata* ($p > 0.05$, comparison of regression coefficients); see Fig. 4. Significant difference, however, between intercepts of Model II regression lines in this figure vs Fig. 4 ($p < 0.001$, ANCOVA); *A. formosa* significantly lower than *P. lobata*

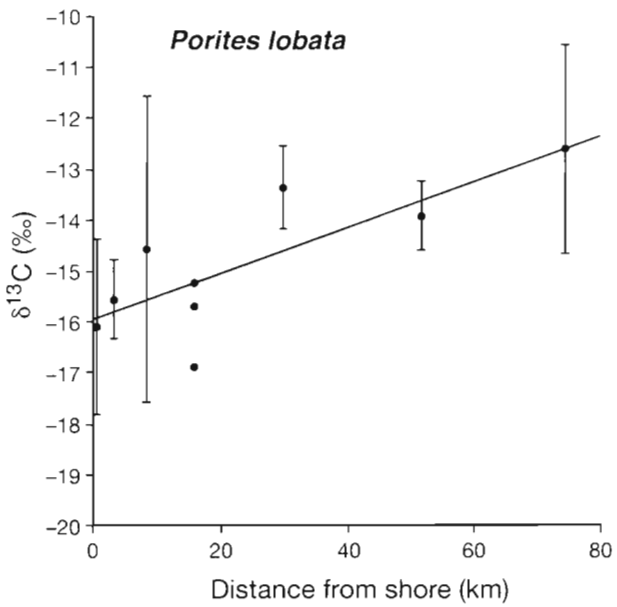

Fig. 8. *Porites lobata*. $\delta^{13}C$ values of tissue extracts in an extensive cross-shelf survey. (Extracts represent a combination of both coral tissue and zooxanthellae.) Means and 95% confidence intervals presented (individual values presented in one case). Significant positive correlation between $\delta^{13}C$ and distance from shore ($r = 0.576$, $p < 0.05$, Pearson's product-moment correlation coefficient). Significant difference in $\delta^{13}C$ between reefs ($p < 0.01$, 2-level nested ANOVA) and between corals within reefs ($p < 0.05$). Significant positive linear relationship ($p < 0.001$, linear regression analysis, $Y = 0.041\,X - 15.6$)

variance accounted for 23.0% of the total observed variance. The variance between subsamples within coral heads was relatively high, accounting for 31.8% of the total observed variance.

The $\delta^{13}C$ values exhibited a strong linear increase with distance from shore (Fig. 8). The slope of the line (0.041‰ per km) is close to that obtained in the preliminary 1986 study (0.036‰ per km; Risk et al. 1989). The $\delta^{13}C$ value at the intercept (shoreline value) was −16‰, identical to that for the 1986 study. Most significantly, there was no indication of the curve becoming asymptotic with distance offshore using the available data, even though the outermost reef (Myrmidon) is 110 km from land.

DISCUSSION

Terrigenous carbon as a food source for corals

All the data presented here show highly significant trends of increasing $\delta^{13}C$ in coral tissue and zooxanthellae with distance from the coast. This is true of both coral species examined here as well as for their respective zooxanthellar symbionts. These trends are consistent with a model of utilization by the corals of terrigenous, isotopically light carbon, in decreasing amounts with distance from the coast. The linear trends continue to distances of more than 100 km offshore, indicating that terrigenous matter is a significant source of carbon for corals out to the edge of the reef.

We can place some limits on the nature of the terrigenous component by comparison with the study of Gagan et al. (1987), who found that $\delta^{13}C$ of POM in marine sediments increased linearly with distance from shore, from −25‰ near the coast to −18‰ at 10 km from shore; the latter value persisted to the outer limits of their survey, at 50 km from shore. No such steep rise in $\delta^{13}C$ is observed in our data (although our spatial resolution is less than that of Gagan et al. 1987). On the other hand, we observe a continued rise in $\delta^{13}C$ across the shelf, where $\delta^{13}C$ of POM remains constant. We suppose therefore that POM of the shelf sediment does not represent the organic matter which is available to the corals, but rather is dominated by the non-biodegradable component of plant detritus. The corals must be consuming, in a heterotrophic manner, organic matter which does not survive in particulate form within the shelf sediments; this organic matter would appear to contain a mixture of land- and sea-derived carbon. The former may consist principally of TDOM which enters the food web via assimilation by marine micro-organisms (e.g. bacteria). This component also enters the shelf via rivers and disperses across the shelf, being progressively diluted by marine-derived nutrients with increasing distance from shore.

We can estimate the proportion of the terrigenous nutrient in coral tissue as follows. The seaward limit in $\delta^{13}C$ of tissue is about −11‰ for both species. This is identical to the value observed by Allison et al. (1991) for corals from the Maldive Islands, which are remote from any source of terrigenous nutrient, and where terrestrial vegetation could not be a significant carbon source. We can therefore assume that such totally marine corals are consuming a diet whose $\delta^{13}C$ value is close to −11‰. We shall take this to represent the pure marine end-member of the carbon supply. The purely terrigenous component can be assumed to have a value close to −27‰, the value of C3 vegetation which dominates the near-shore and interior regions of the adjacent Australian land mass. A major contributor to TDOM and TPOM would be mangroves which provide detritus with a $\delta^{13}C$ of −27‰ (Gagan et al. 1987).

As noted earlier, the autotrophic component of the coral diet must also be included in any isotopic mass balance. We have shown, however, that the $\delta^{13}C$ values of zooxanthellae follow those of the host coral tissue, displaced by about +2 ‰. There would appear to be some

fractionation occurring between the zooxanthellae and the coral tissue. Contrary to expectation, they do not appear to be strongly controlled by the $\delta^{13}C$ of dissolved HCO_3^- of seawater, which is assumed to remain approximately constant across the shelf. We can therefore consider the zooxanthellae as simply another compartment of the coral tissue, which is too small in mass to displace the total $\delta^{13}C$ of the tissue. This is also indicated by the similarity of the intercepts of $\delta^{13}C$-distance regressions for bulk *Porites lobata* tissue of Fig. 8 with that for zooxanthellae-free tissue in Fig. 2.

The reasons for the extremely low intra-reef variance of zooxanthellar $\delta^{13}C$ values are not yet understood, but the zooxanthellae are clearly receiving their carbon from more 'predictable' and less variable sources than their associated host coral tissue.

In modeling this system, the coral can be treated as if it were predominantly heterotrophic, and a linear mixing model, as discussed for example by Schwarcz (1991), can be used. The proportion of terrigenous nutrient, X_T, is given by the relation:

$$X_T = \frac{\delta_{mar} - \delta_{tissue}}{\delta_{mar} - \delta_{ter}}$$

where $\delta_{ter} = \delta^{13}C$ of the terrestrial food source (-27‰) and $\delta_{mar} = \delta^{13}C$ of the marine food source (-11‰); $\delta_{tissue} = \delta^{13}C$ of the coral tissue. From these estimates, we conclude that the most landward *Porites lobata* obtains one-third of its carbon from terrestrial sources, while more seaward corals utilize linearly decreasing amounts of this nutrient.

This model assumes that the 'marine' component on the shelf is isotopically identical to that in the open sea. In effect, this represents that part of the trophic system which is derived by photosynthesis utilizing 'normal' marine HCO_3^-. To the extent that $\delta^{13}C$ of this component changes on the shelf, the marine end-member (δ_{mar}) will also change. Rau et al. (1992) have shown that the $\delta^{13}C$ of phytoplankton increases as dissolved CO_2 of seawater decreases from spring to summer. In the present study, we have not monitored such changes and cannot estimate the extent to which these contribute to the shift in $\delta^{13}C$ of coral tissue. If, however, the mechanism discussed by Rau et al. (1992) were the principal control on $\delta^{13}C$ of coral tissue, then we would also expect that change in $\delta^{13}C$ of POM across the shelf would follow approximately the same gradient as that observed in the corals. To the contrary, the data of Gagan et al. (1987) show that, beyond 10 km from shore, $\delta^{13}C$ of POM in sediment is isotopically uniform. Therefore, we do not believe that $[CO_2(aq)]$ depletion caused an increase in offshore $\delta^{13}C$ values in the corals. Rather, this appears to have been caused by seaward decrease in the availability of a terrigenous nutrient capable of being consumed by corals. The precise nature of this nutrient and the route of its transfer through the food web is unclear at this time, but may include bacteria and other micro-organisms which consume DOM and are in turn consumed by the coral.

Comparison of trends noted in *Porites lobata* vs *Acropora formosa* $\delta^{13}C$ values across the shelf permits some deductions to be made regarding balance between autotrophy and heterotrophy in these corals. The resultant regression lines exhibit the same slope with distance from shore; therefore, the metabolic shift from onshore heterotrophic augmentation of diet towards a greater degree of autotrophy offshore is comparable. The difference in intercepts, however, suggests that *A. formosa* is 'more autotrophic' than *P. lobata*. The shoreline value of $\delta^{13}C$ for *A. formosa* is -14‰; that for *P. lobata* is -15.6‰. *P. lobata* appears to be more dependent upon or at least consume more terrestrial carbon than *A. formosa*.

Examination of the nested ANOVA results also reveals an interesting pattern in the case of *Porites lobata*. Within-reef variance of $\delta^{13}C$ in the zooxanthellae is negligible. It would appear that, on any given reef, the populations of zooxanthellae in *P. lobata* have near-identical mixing values, and that these values may be different from those on neighboring reefs. *P. lobata* broods its larvae, and zooxanthellar transmission occurs directly from the egg, possibly helping to explain this low variance.

It has been suggested (L. Muscatine pers. comm.) that the observed trends in $\delta^{13}C$ in coral and zooxanthellar tissue across the continental shelf of the Great Barrier Reef are due to differences in the level of photosynthesis across the shelf, due in turn to differences in turbidity across the shelf. We believe that the observed trends are due to the source of the corals' food, not changes in photosynthesis, particularly since the trend we have noted is not closely related to that known for turbidity in this region. If, however, photosynthesis does vary across the shelf and has affected the changes we have observed in $\delta^{13}C$ ratios, we believe its contribution has been small in comparison to that derived from trophic sources.

Risk & Sammarco (1991) showed that the density of *Porites lobata* skeletons showed a pronounced offshore trend of density increasing with distance from shore. They suggested that this may reflect a trend to increased autotrophy offshore. When we compare the data of Risk & Sammarco (1991) with Fig. 8 here, we find the linear relationships between $\delta^{13}C$ and distance from shore, and that between skeletal density and distance from shore, to be very similar. Perhaps skeletal density is at least a partial indicator of the trophic status of a coral, as well as being an indicator of other environmental factors (e.g. wave energy, turbidity, etc.).

CONCLUSIONS

On the basis of the $\delta^{13}C$ data analyzed here, we conclude that:

(1) There are strong cross-shelf trends in the $\delta^{13}C$ values of coral tissue and zooxanthellae in *Porites lobata* in the central region of the Great Barrier Reef. $\delta^{13}C$ values average approximately −18‰ inshore to −11‰ offshore.

(2) As much as one-third of the diet of inshore corals may be derived ultimately from terrestrial sources, indicating a substantial heterotrophic orientation in their feeding biology. It is possible that the process responsible for yielding the $\delta^{13}C$ values observed in these corals involves direct uptake by the coral of dissolved organic matter of terrestrial origin, although this remains to be confirmed.

(3) $\delta^{13}C$ values of zooxanthellae closely followed those of host coral tissue. Zooxanthellar values were, however, 1 to 2‰ higher in *Porites lobata* than in *Acropora formosa*; thus, *A. formosa* may be more autotrophic than *P. lobata*.

(4) The cross-shelf trend appears to be driven by changes in the isotopic ratios of the coral tissue. Zooxanthellar carbon may be derived from the coral tissue as opposed to the dissolved carbonate in the seawater.

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