Cross-continental shelf trends in coral $\delta^{15}N$ on the Great Barrier Reef: further consideration of the reef nutrient paradox

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ABSTRACT: In this study, we investigate potential sources of nitrogen for the scleractinian coral *Porites lobata* in a transect across the central region of the Great Barrier Reef, Australia. The experiment followed a 1-way, Model I, nested ANOVA design. We sampled colonies of *P. lobata* from 12 reefs spanning the 110 km wide continental shelf at 5 m depth, and determined the $\delta^{15}N$ signature in tissue extracts (with zooxanthellae; n = 46). The response curve of the $\delta^{15}N$ was found to be curvilinear, yielding a highly significant parabolic relationship with distance from shore (p < 0.001, second-order least-squares polynomial regression). Highest values of $\delta^{15}N$ were observed inshore (5.0 to 5.5‰), lowest values at the mid-shelf (~3.8‰), and high values again offshore (5.2‰). We suggest the following causal factors, based on environmental characteristics and phenomena known to occur in this region: (1) inshore corals may be receiving much of their nitrogen from terrigenous sources; (2) mid-shelf corals may be receiving at least some of their nitrogen from associated algal mats known to possess high rates of nitrogen-fixation in this region, which in turn could lower $\delta^{15}N$ values; and (3) offshore corals may be receiving their nitrogen from seasonal, nutrient-rich, cold-water intrusions or upwellings, documented to occur in this area.

KEY WORDS: $\delta^{15}N$ · Corals · Upwelling · Nutrient sources · Trophic shifts

INTRODUCTION

Although reefs are among the most productive of the world's ecosystems (Whittaker 1975), their existence is generally associated with low nutrient concentrations (Hallock & Schlager 1986). This paradoxical relationship has stimulated a large body of research, beginning with that of Darwin (1842). The apparent health of coral reefs in nutrient-poor waters has, in fact, often been termed 'Darwin's Paradox'. Research in this field has been reviewed by Rougerie & Wauthy (1993).

Research in coral physiology has suggested another coral reef paradox, which until now has been implicit rather than explicit. A large body of work, employing a variety of sophisticated analytical techniques, has been directed toward the energetic relationships between hermatypic corals and their endosymbionts (e.g. Muscatine et al. 1981, 1984, Falkowski et al. 1984, Edmunds & Davies 1986, 1989). A general conclusion of these studies is that common, shallow-water reef corals are able to meet all their metabolic carbon requirements via translocation from zooxanthellae. That is, many of the common reef corals can function facultatively as autotrophs. Similarly, evidence for uptake and assimilation of dissolved inorganic nitrogen (DIN) may be found in coral nutrient budget calculations and in stable isotopic studies of nutrient exchange in corals (Bythell 1988, Falkowski et al. 1993, Eustice et al. 1995, Yamamuro et al. 1995, Heikoop et al. 1998). Uptake of DIN has often been found to be light dependent (Muscatine & D'Elia 1978, Wilkerson & Trench 1986). The corollary of these observations would appear to be that, all other things being equal,

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corals should grow best in clear, offshore waters. This, however, is not always so. Although reefs can be excluded from nearshore areas where siltation is high, nearshore fringing reefs frequently possess corals which are adapted to this type of environment, yielding high cover, growth rates, and coral diversity (see Done 1982 for discussion, Isdale 1983, Edinger 1998). Corals can grow in waters with low nutrient concentrations but can also grow as well or better when nutrients and/or allochthonous organic inputs are higher (Edinger 1998, Edinger et al. unpubl.). Coral populations can also, of course, experience high levels of mortality in regions with high nutrient loadings (e.g. Maragos et al. 1985). Edinger (1998) has referred to the balance between coral growth, reef growth, and nutrient concentration as the 'Janus Effect', after the 2-faced Roman guardian of entrances and exits.

Andrews & Gentien (1982) suggested that in the central region of the Great Barrier Reef, productivity of reefs on the outer continental shelf is driven in part by tidally pumped upwelling, introducing nutrient-rich waters onto the floor of the continental shelf and into the GBR Lagoon. Hallock & Schlager (1986) and Hallock (1988) point out that increased nutrients should result in algal blooms and increased bioerosion. Rougerie & Wauthy (1993) state that reefs require a continuing importation of nutrients, using 'endo-upwelling' at times, which has been observed on some French Polynesian atolls. Endo-upwelling is the process by which nutrient-rich interstitial waters are carried up to a reef from below, driven by a geothermal gradient. The complete relationship between coral nutrition and reef growth remains to be elucidated. Nutrient sources utilized by corals on the Great Barrier Reef need to be more fully characterized.

A geochemical approach is a viable mechanism by which to address questions regarding the nourishment of largely autotrophic corals on shelf-edge reefs versus partially heterotrophic corals in coastal, turbid, nutrient-rich waters. Because of the difference between typical values of $\delta^{13}C$ for terrestrial plants and marine organic matter, $\delta^{13}C$ ratios can be good indicators of ratios of terrestrial to marine carbon within an heterotrophic target organism. In an earlier study (Risk et al. 1994), we reported $\delta^{13}C$ values of the tissues of scleractinian corals across the continental shelf in the central region of the Great Barrier Reef. There we reviewed the importance of stable isotope ratios in palaeodiet studies, as tracers of trophic pathways. We also reported that $\delta^{13}C$ from the tissue of 2 different corals (*Acropora formosa* and *Porites lobata*) revealed strong cross-shelf trends, consistent with autotrophic processes increasing in dominance within these species as distance from shore increased. One conclusion we reached was that corals are not completely autotrophic

but are plastic in their trophic responses to the environment; our data indicated that nearshore corals were obtaining up to one-third of their carbon from terrestrial sources. In a comparative study, Heikoop (1997) found that Risk et al.'s (1994) $\delta^{13}C$ values for *Porites lobata* collected from inshore sites on the Great Barrier Reef were the lowest of any shallow-water corals analyzed from a variety of various Indo-Pacific and Caribbean reefs (< 5 m depth, n = 123).

Most heterotrophic organisms are enriched in ^{15}N on average by about 3.5‰ relative to diet, due to excretion of isotopically light nitrogen (Minagawa & Wada 1984). Due to efficient conservation and recycling of nitrogen between host and zooxanthellae, however, corals, despite being partially heterotrophic, are unlikely to display this trophic level effect (Heikoop et al. 1998). Coral tissues may actually be depleted in ^{15}N, relative to DIN, due to preferential uptake and assimilation of $^{14}NH_4^+$, $^{14}NO_3^-$, etc. by the zooxanthellae; (similar fractionations are seen during nutrient uptake by phytoplankton; see Table 9.4 in Goericke et al. 1994). This fractionation is reduced under conditions of higher irradiance and increased zooxanthella photosynthesis (Muscatine & Kaplan 1994, Heikoop et al. 1998). Under high irradiance conditions, uptake and assimilation of DIN by zooxanthellae strongly deplete the DIN pool within the coral, leading to reduced fractionation relative to the DIN of the surrounding reef environment. The exact relationship between $\delta^{15}N$ in the coral and that of the nitrogenous nutrient sources is not yet known. Production of protein within the coral via autotrophic processes with the assistance of zooxanthellae would involve extraction of nitrogen from seawater, principally in the form of dissolved NH_4^+ and NO_3^- with the former being the preferred species (Franzisket 1974, D'Elia & Webb 1977, Muscatine & D'Elia 1978, Webb & Wiebe 1978, Propp 1982, Burris 1983, Wafar et al. 1985, Wilkerson & Trench 1986, Bythell 1990). Heterotrophic production of protein, on the other hand, would involve the extraction of nitrogen primarily from ingested particulate organic matter (POM), plankton, and the like (Muscatine & Porter 1977). Stable nitrogen isotope ratios are becoming increasingly useful indicators of stress due to sewage in marine and freshwater ecosystems (Sweeney & Kaplan 1980, Risk et al. 1993, Bachtiar et al. 1996) and in studies of productivity and palaeo-productivity (Altabet 1989, Altabet & Francois 1994).

Here, we report the results of analyses of $\delta^{15}N$ in *Porites lobata* sampled in a large-scale cross-shelf transect across the central region of the Great Barrier Reef. The tissue samples used here are derived from the same set used by and reported in Risk et al. (1994). The results will be compared with earlier results derived from our $\delta^{13}C$ study. Based on these combined

data, we will suggest hypotheses regarding the nitrogen sources for the corals and implications for Darwin's Paradox.

MATERIALS AND METHODS

Sampling locations, collecting techniques, and sample processing methods for these corals are presented in Risk et al. (1994), and the reader is referred there for complete details. In Risk et al. (1994), we presented data on δ^{13}C isotopic analyses of extracts of tissue, zooxanthellae, and a combination of the 2, respectively, from 2 species of scleractinian coral—*Porites lobata* and *Acropora formosa*. In this paper, we present data only for combined tissue-zooxanthellae extracts of *Porites lobata*; *A. formosa* sample sizes were generally too small to analyze.

Due to the myriad of nitrogen sources available to a coral in unknown proportions, it is difficult to measure the isotopic composition of source nitrogen in a meaningful fashion. The obvious alternative is to measure the δ^{15}N of the coral under conditions in which fractionation will be minimized. This will at least yield relative variations in δ^{15}N of total source nutrient, which in turn will be strongly influenced by δ^{15}N of new nitrogen sources to the reef. Autotrophic corals, collected under conditions of high illumination meet this requirement of minimal fractionation (cf. Heikoop et al. 1998).

Coral samples used in this study were collected in 1988 on a cross-shelf transect in the central region of the Great Barrier Reef (Fig. 1). The experimental reefs were as follows: Pandora Reef; Picnic Bay, Magnetic Island; Pioneer Bay, Orpheus Island; Davies Reef; Britomart Reef; Eagle Reef; Anzac Reef; Salamander Reef; Grub Reef; Bray Island; Morinda Shoals; and Little Broadhurst Reef. The site nearest to shore was Bray Island, only 0.5 km from the mainland. Eagle and Anzac Reefs were well offshore. Magnetic and Orpheus Islands were inshore to midshelf continental islands capable of introducing terrigenous components onto their fringing reefs. The sample sites were generally the same as those used in Risk et al. (1994), except in that study, the furthest offshore site was Myrmidon Reef. Here, the Myrmidon Reef samples proved to be too small to analyze; here, offshore sites are represented by Eagle and Anzac Reefs.

This experiment followed a 1-way, multiple level, nested ANOVA design (Sokal & Rohlf 1981). At least 3 corals were collected with a hammer and chisel from a depth of 5 m at each reef. All corals were a dark brown color morph, in order to help control for any potential variations in zooxanthellae populations. Since the coral samples were all drawn from the same species, thickness of coral tissue was not a consideration here. That is, no variation in magnitude of nitrogen isotopic fractionation could be expected to occur as a result of variable resistance to diffusion of nitrogen species, as has been suggested for uptake of DIC (cf. Muscatine et al. 1989).
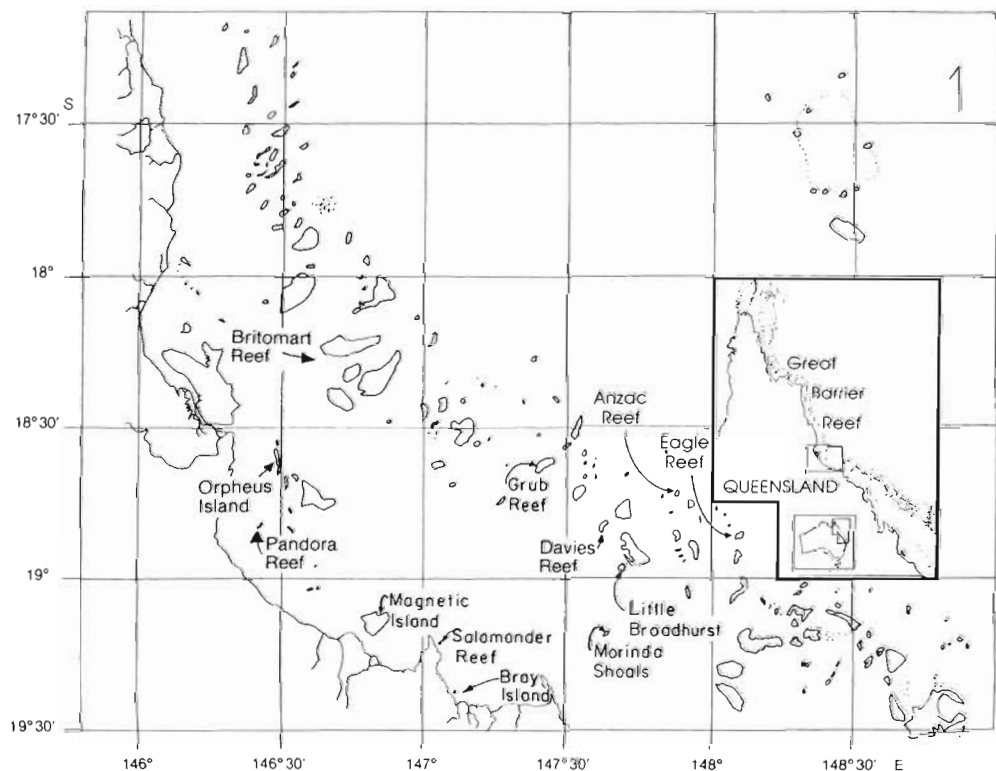

Fig. 1. Map of the central region of the Great Barrier Reef, depicting the various reefs sampled for corals in this study

Several replicate tissue samples were taken from the top of each coral head. Tissue samples (with their associated skeletal material) were frozen at −20°C and, upon reaching the laboratory, were decalcified with dilute HCl and treated with mercuric chloride to protect the tissue from bacterial degradation. This dilute acid treatment has been shown to have no effect on coral tissue $\delta^{15}N$ (Heikoop 1997, Heikoop et al. 1998). The resulting samples of coral tissue (including zooxanthellae) were centrifuged and washed several times to produce pellets which were freeze-dried for isotopic analysis. The $\delta^{15}N$ of separated zooxanthellae and host tissue from shallow (<10 m) *Porites* are very similar, presumably reflecting a largely autotrophic diet (Muscatine & Kaplan 1994).

All samples were loaded into pre-combusted Pyrex® tubes with CuO, evacuated, and combusted at 550°C. The N_2 gas produced was distilled from CO_2 and water and analyzed on a VG Micromass 602D mass spectrometer. Precision of analysis was ±0.1‰. Data are presented as $\delta^{15}N$ values with respect to atmospheric N in the standard $\delta^{15}N$ notation, where

$$\delta^{15}N(‰) = \frac{^{15}N/^{14}N_{sample} - ^{15}N/^{14}N_{atm.\ N_2}}{^{15}N/^{14}N_{atm.\ N_2}} \times 1000$$

RESULTS

A total of 46 samples were analyzed. There were highly significant differences in $\delta^{15}N$ values between reefs (p < 0.001, 1-way nested ANOVA, Fig. 2). The response was found to be curvilinear with respect to distance across the continental shelf. Values were highest inshore (5.0 to 5.5‰), lowest ~60 km from shore at the mid-shelf (~3.8‰), and high again offshore (5.2‰). A second-order polynomial regression was found to be highly significant (p < 0.001), yielding a significant parabolic relationship between $\delta^{15}N$ and distance from shore.

The variance around these values was relatively small, with the highest variance being observed at the most inshore site. The curvilinear relationship of the means to each other across the shelf was quite clear, with surprisingly small amount of scatter, except, once again, at the inner shelf sites.

To facilitate discussion and comparison of these trends, the $\delta^{13}C$ values from Risk et al. (1994) are presented in Fig. 3. By comparison, the means of $\delta^{13}C$ values across the shelf were highly significantly linear. There too, the clearest evidence of a linear relationship between the means was offshore, with the highest scatter amongst means being inshore. The highest variance around a mean was also found inshore in that analysis.
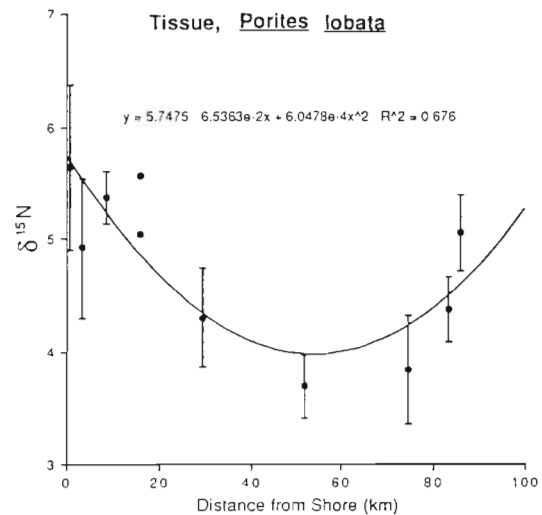

Fig. 2. *Porites lobata*. $\delta^{15}N$ values of tissue extracts in an extensive cross-shelf survey. Means and 95% confidence intervals shown; (individual values presented in one case). Highly significant difference in $\delta^{15}N$ values between reefs (p < 0.001, 1-way nested ANOVA). Note the pronounced curvilinear relationship between $\delta^{15}N$ and distance from shore, described by a highly significant second-order equation: $y = (6.047 \times 10^{-4})x^2 - (6.5363 \times 10^{-2})x + 5.7475$; (p < 0.001, least-square polynomial regression analysis)
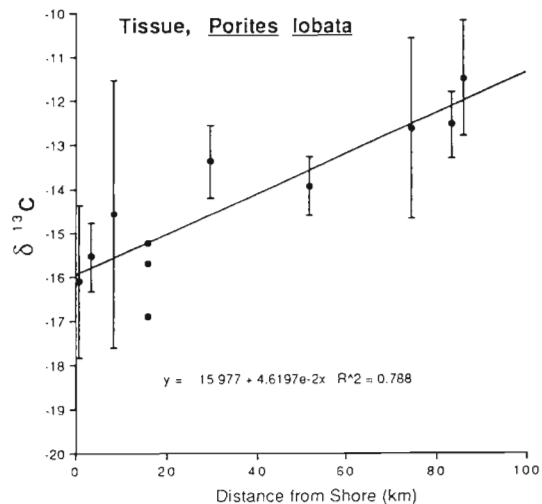

Fig. 3. *Porites lobata*. $\delta^{13}C$ values of tissue extracts in a similar cross-shelf survey. Extracts represent a combination of both coral tissue and zooxanthellae, highly correlated in separate $\delta^{13}C$ values (Risk et al. 1994). Means and 95% confidence intervals shown; (individual values 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 analysis). Significant difference in $\delta^{13}C$ between reefs (p < 0.01, nested ANOVA) and between corals within reefs (p < 0.05). Significant positive linear relationship (p < 0.001, linear regression analysis, $y = 0.041x - 15.6$) (reprinted from Risk et al. 1994, with permission). No significant correlation between $\delta^{13}C$ and $\delta^{15}N$ values (see Fig. 2) (p > 0.05, Pearson's product-moment correlation analysis). Reprinted from Risk et al. (1994), with permission

The $\delta^{15}N$ data collected here were also analyzed in conjunction with the sister $\delta^{13}C$ data gathered from the same samples in an earlier study. The 2 characters were found to be not significantly correlated ($r^2 = 0.060$, $p > 0.05$, Pearson's Product-Moment Correlation Analysis).

DISCUSSION AND CONCLUSIONS

Because all corals studied here are growing under shallow-water, high-irradiance conditions, and since we have evidence to support their being largely autotrophic (Risk et al. 1994), it is likely that fractionation was reduced and the relative differences in $\delta^{15}N$ were being driven by relative differences in the isotopic composition of nutrient sources. A gradient in the degree of autotrophy versus heterotrophy across the shelf could be identified via an isotopic signal if the autotrophic and heterotrophic food sources were isotopically distinct.

The $\delta^{15}N$ values from Australian *Porites lobata* measured here are among the lightest known for shallow-water (<5 m depth) *Porites* in the Indo-Pacific (Heikoop 1997). This is particularly true for our mid-shelf corals. These low values may be influenced by 3 factors. Firstly, many of the nutrient influxes into the Great Barrier Reef most likely have a relatively low $\delta^{15}N$. These include natural terrigenous sources, agricultural runoff, mangrove detritus, nitrogen fixation, and upwelling of deep-water nitrate (Minagawa & Wada 1986, Owens 1987, Liu & Kaplan 1989, Newell et al. 1995, Primavera 1996, Marguillier et al. 1997, also see discussion below). Secondly, reduced irradiance related to latitude of collection may have slightly increased light-related zooxanthellar fractionation of DIN (cf. Muscatine & Kaplan 1994, Heikoop et al. 1998) relative to other corals in a related broad, geographic comparative study (Heikoop 1997). Under low levels of illumination, less depletion of the internal DIN pool will occur and nitrogen isotopic fractionation can be more fully expressed. Thirdly, and related to this, our collections were made during the austral winter when surface irradiation was lower than at the other sites and may have increased fractionation relative to DIN in our samples (cf. Heikoop et al. 1998).

Risk et al. (1994) concluded that the low $\delta^{13}C$ values observed inshore indicated that these corals were directly or indirectly receiving a substantial portion of their nutrients from terrigenous sources known to have concomitantly low $\delta^{13}C$ and known to be abundant in the region — e.g. partially decayed plant detritus delivered from extensive mangrove forests. It is likely that nitrogen from this material will also affect, directly or indirectly, the isotopic composition of inshore corals. Terrestrial nitrogen is generally depleted in ^{15}N relative to marine nitrogen (terrestrial/freshwater nitrogen has an average $\delta^{15}N$ of approximately 4‰; see Table 2 and Fig. 5 in Owens 1987). Mangrove detritus has a low $\delta^{15}N$, with mean values typically ranging from approximately 1 to 5‰ (Newell et al. 1995, Primavera 1996, Marguillier et al. 1997). As mangrove leaves decompose and become a more readily available food source, the leaves, or their associated microbes, may become even more depleted in the heavy isotope of nitrogen (Zieman et al. 1984). Anthropogenic N from fertilizers and sewage will also introduce light N relative to marine organic matter to inshore reefs (see Rau et al. 1981, Fig. 3.2 in Macko and Ostrom 1994, and references therein, respectively). Clearly, however, a portion of the inshore corals' nutrition would also have been obtained from marine heterotrophic sources (zooplankton, etc.) and/or from nutrients translocated from the zooxanthellae.

As distance from shore increases, nitrogen fixation becomes increasingly important (Sammarco 1983, Wilkinson & Sammarco 1983, Wilkinson et al 1984). Nitrogen fixation will introduce light nitrogen into the reef system with a value about 0‰ (cf. Minagawa & Wada 1986). Similarly, Yamamuro et al. (1995) found low $\delta^{15}N$ values for corals at Palau and Ishigaki (4 to 6‰) and they suggest that nitrogen fixation on the reefs in their study area may have had a significant influence on their values.

With respect to the outer shelf, Andrews & Gentien (1982) demonstrated the presence of large-scale upwellings or cold-water intrusions in the central region of the Great Barrier Reef (our study region), originating at the edge of the continental shelf and progressing shoreward around the reefs. These intrusions were found to be rich in nutrients. Andrews & Gentien (1982) suggested that these cold-water intrusions were supplying nutrients to shelf-edge reefs. Deep-water nitrate from areas free of denitrification is isotopically light in the Eastern Pacific (~5‰; Liu & Kaplan 1989), compared to nitrate in the photic zone of the open ocean. This predominance of a nitrogen source of low $\delta^{15}N$, compared to open ocean nitrate (~7 to 10‰; Minagawa & Wada 1986; enriched due to preferential uptake of $^{14}NO_3^-$ by marine phytoplankton) is probably contributing to the absolute low $\delta^{15}N$ values seen in these shelf-edge Australian corals when compared to other Indo-Pacific corals. This nutrient source is relatively enriched in ^{15}N, of course, compared to nitrogen fixed by algal mats at the mid-shelf. Endo-upwelling of deep-water currents carrying nitrogen may be important for barrier reefs like that of Australia as well (Rougerie & Wauthy 1993).

There was higher variance around and between the means of the $\delta^{15}N$ values found inshore. This can be explained by the combination of terrigenous influ-

ences and those of continental islands found between the mid-shelf and the shore. With respect to the near-shore sites, the higher variability in $\delta^{15}N$ of these corals could have resulted from the wide variety of terrestrial nutrient sources available, including mangrove detritus, dissolved and particulate fluvial nitrogen, and anthropogenic pollution. The islands are located tens of kms offshore, being exposed to clearer waters less influenced by runoff; yet they are capable of introducing N with an isotopic signature similar to that of the coastal environment due to terrigenous nutrients which they themselves introduce into their own surrounding waters and fringing reefs.

In the offshore environments, the $\delta^{15}N$ values of open-ocean DIN will be lowered by the input of additional nitrogen sources with low $\delta^{15}N$ (see above). The minimum value of $\delta^{15}N$, 3.8‰, was reached ~50 km from shore. This would require a dominant nutrient source with very low $\delta^{15}N$, such as nitrogen fixed by cyanobacterial mats (Sammarco 1983, Wilkinson & Sammarco 1983, Wilkinson et al. 1984, Fig. 4). Since nitrogen fixation would introduce nitrogen with $\delta^{15}N$ values lower than either terrestrial or upwelled nitrogen, mid-shelf reefs may be expected to have the lowest coral tissue $\delta^{15}N$ in the cross-shelf trend. As one moves from the mid-shelf to the shelf edge, upwelled nitrogen probably becomes an increasingly more important influence on the coral $\delta^{15}N$ values (Fig. 4). It is possible that variation in light availability, and thus zooxanthellar photosynthesis, may be influencing the observed trend; this is unlikely, however, since the lowest irradiance may be found on inshore reefs (Done 1982) with the highest $\delta^{15}N$ values. Moreover, zooxanthellae often compensate for low light conditions through increased density, thereby minimizing differences in photosynthetic potential (Saunders & Muller-Parker 1997, Stimson 1997, but also see Masuda et al. 1993).

It has been suggested that increased concentration of DIN might increase the expression of zooxanthellar fractionation, i.e. preferential utilization of ^{14}N is more fully expressed (Muscatine & Kaplan 1994, Heikoop et al. 1998). Variation in DIN concentration is unlikely to have influenced coral tissue $\delta^{15}N$ in this cross-shelf transect, however, because the lowest values are found in mid-shelf corals, where nutrient input is expected to be lowest.

The relative differences in nitrogen isotopic values of corals across the continental shelf of the Great Barrier Reef most likely reflect varying inputs of nitrogen sources that supplement nitrogen in open ocean seawater along each part of the shelf. The isotopic values of these inputs would influence both the overall low $\delta^{15}N$ values of these corals and the curvilinear trend observed across the shelf. The introduction of these nutri-
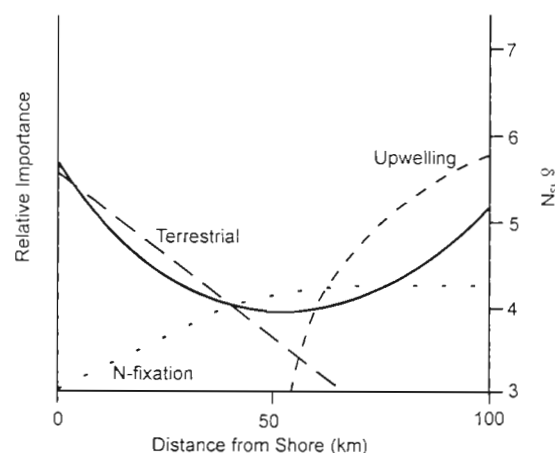

Fig. 4. Schematic diagram of relative importance of nutrient sources across the central Great Barrier Reef. Terrestrial nitrogen (long-dashed line) dominates inshore, while N-fixation (short dash) and upwelled nitrogen (medium dash) are more important nutrient sources in mid-shelf and outer-shelf reefs, respectively. Refer to text for potential isotopic values of these inputs. The solid line shows the cross-shelf trend in $\delta^{15}N$ of coral tissue for comparison. Right-hand axis only applies to the solid curve representing $\delta^{15}N$ of coral tissue. Approximate spatial distributions of the various nutrient fluxes across the shelf based upon nutrient studies by Andrews & Gentien (1982), Wilkinson et al. (1984), and Risk et al. (1994)

ents might help explain how these corals exhibit high productivity when surrounded by oligotrophic seas (see Andrews & Gentien 1982). It is the wide expanse of the shelf that allowed us to observe subtle changes in the $\delta^{15}N$ values of the corals and thus infer potential differential influences on those values. On a narrower shelf, the $\delta^{15}N$ signals derived from land or other sources would probably have been masked via mixing with open ocean nitrate. The clear gradient to lower values of $\delta^{15}N$ from nearshore to mid-shelf implies a decrease in terrigenous nitrogen as a source of nutrition. This trend is supported by a concomitant increase in $\delta^{13}C$ in the corals over the same distance in the same region (Risk et al. 1994), implying a shift to a more fully autotrophic mode of nutrition at the mid-shelf.

The results of both sets of isotope analyses ($\delta^{13}C$ and $\delta^{15}N$) yields implications for the sustainable management of coral reefs. They indicate that terrestrial activities which alter the source and nature of organic matter delivered to the ocean will also affect corals on nearby reefs. Our data also show that the $\delta^{15}N$ in coral tissue can serve as an indicator of local shifts in nitrogen sources and sinks for coral reefs in the central region of the Great Barrier Reef. Further studies of this problem are merited, especially long-term investigations of seasonal fluctuations in the isotopic composition of coral tissues in this region and the waters in which they occur

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