



# Multi-century time-series of $^{15}\text{N}$ and $^{14}\text{C}$ in bamboo corals from deep Tasmanian seamounts: evidence for stable oceanographic conditions

Owen A. Sherwood<sup>1,5,\*</sup>, Ronald E. Thresher<sup>2</sup>, Stewart J. Fallon<sup>3</sup>, Diana M. Davies<sup>4</sup>,  
Thomas W. Trull<sup>2,4</sup>

<sup>1</sup>Department of Earth Sciences, Memorial University of Newfoundland, St. John's, Newfoundland A1C 3X9, Canada

<sup>2</sup>CSIRO Marine and Atmospheric Research and Wealth from Oceans and Climate Adaptation Flagships, Castray Esplanade, Hobart, Tasmania 7000, Australia

<sup>3</sup>Research School of Earth Sciences, Australian National University, Bldg 61, Mills Road, Acton, Australian Capital Territory 2000, Australia

<sup>4</sup>Antarctic Climate and Ecosystems Cooperative Research Centre (ACE CRC) and Institute of Antarctic and Southern Ocean Studies (IASOS), University of Tasmania, Private Bag 80, Hobart, Tasmania 7001, Australia

<sup>5</sup>Present address: 4 Hipditch Hill, St. John's, Newfoundland A1A 1A5, Canada

**ABSTRACT:** Bamboo corals (Family Isididae) are an important component of seamount benthos south of Tasmania. Besides having lifespans of up to 400 yr, little is known about their basic ecology, nor how to decode potential climate signals encoded in their skeletons. We explored the stable nitrogen isotope and radiocarbon compositions of the skeletal organic fraction of the genera *Isidella*, *Keratoisis* and *Lepidisis* collected from 3 Tasmanian seamounts. Analyses were performed on tissues and organic node growth rings sampled at a temporal resolution of 1 to 4 yr. Radiocarbon chronologies exhibited nuclear bomb signals characteristic of surface waters and constrained radial growth rates to  $\sim 35 \pm 10 \mu\text{m yr}^{-1}$  for 3 specimens of the genus *Lepidisis* and  $113 \pm 17 \mu\text{m yr}^{-1}$  for 1 specimen of *Isidella*.  $\delta^{15}\text{N}$  values of the living tissue and underlying gorgonin were similar and averaged 9 to 12‰. Records of  $\delta^{15}\text{N}$  from 8 different specimens showed subtle, quasi-decadal patterns over the last  $\sim 100$  yr, although the amplitude of these features ( $\sim 1\%$ ) was similar to the average intra- and inter-colony reproducibility. These results demonstrate the utility of deep-sea corals to track seamount biogeochemical processes over long time scales, and suggest that the extent of nutrient depletion of surface waters and associated trophic dynamics have remained relatively constant in this region over centuries. This provides an important baseline for the evaluation of the impacts of anthropogenic climate change.

**KEY WORDS:** Tasmanian seamounts · Deep-sea corals · Stable isotopes · Radiocarbon · Biogeochemistry

Resale or republication not permitted without written consent of the publisher

## INTRODUCTION

Deep-sea gorgonian corals of the family Isididae form an important component of the benthic macrofauna of the Tasmanian seamounts. The common name for this group, bamboo corals, derives from the bamboo-like alternation of calcite internodes and shorter organic nodes along skeletal axes (Fig. 1). Owing to lifespans of up to

400 yr (Thresher et al. 2004, Andrews et al. 2005, Sherwood & Edinger 2009), there has been growing interest in the both the vulnerability of deep-sea corals to the impacts of bottom trawling (Koslow et al. 2001) and the potential to extract long-term climate records from their skeletons (Thresher et al. 2004, 2007, Roark et al. 2005).

The organic nodes of deep-sea isidid corals are derived from recently exported particulate organic mat-

ter (POM; Griffin & Druffel 1989, Roark et al. 2005). This suggests that geochemical analyses of the organic nodes could be used to track a variety of biogeochemical cycles in overlying surface waters, including pri-

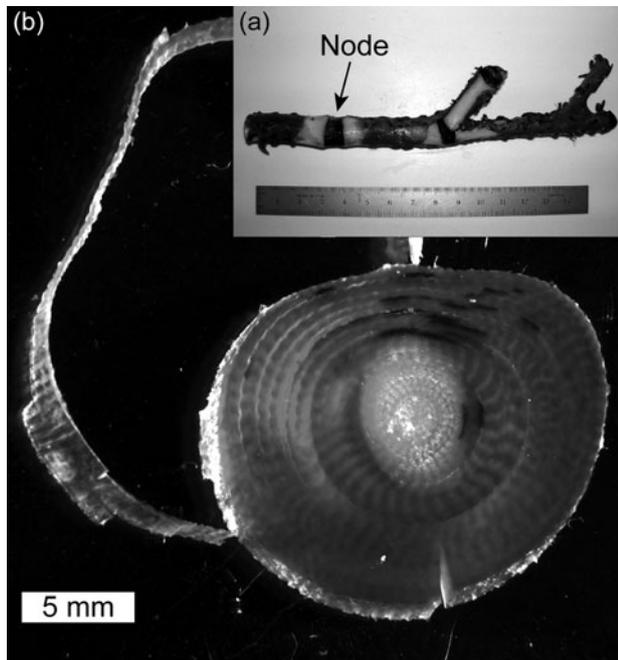


Fig. 1. (a) Piece of a live-collected isidid colony (*Isidella* sp.; I4) showing dark brown organic nodes and white calcite internodes which make up the skeletal axis. Tissue layer remains partially intact around the colony. Ruler is 15 cm long. (b) Section through a decalcified organic node, showing finely laminated, concentric growth rings in the midst of being individually separated

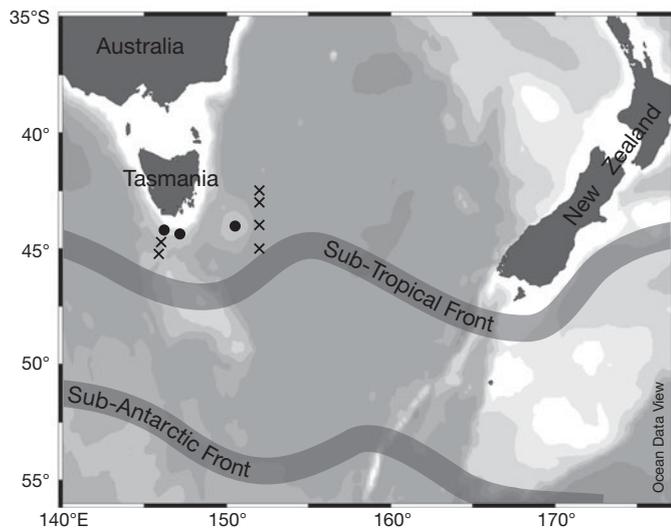


Fig. 2. Coral collection locations (●), from east to west Cascade Plateau, Dory Hill and an unnamed seamount in the southwestern zone; seawater radiocarbon stations (x), taken from the literature. Also shown are the approximate positions of the subtropical and subantarctic fronts.

mary productivity and trophic dynamics (Heikoop et al. 2002, Sherwood et al. 2005). Moreover, by linking these analyses with those from the calcitic internodes, which are derived from dissolved inorganic carbon (DIC) at depth, detailed records of both surface and deep-water processes could be generated from the same coral (Roark et al. 2005, Sherwood et al. 2008a).

The present study examines temporal patterns of bomb- $^{14}\text{C}$  and natural abundance stable nitrogen isotopic compositions ( $\delta^{15}\text{N}$ ) in the organic nodes of deep-sea isidids. Bomb- $^{14}\text{C}$  refers to the radiocarbon produced by atmospheric nuclear weapons testing in the late 1950s and early 1960s. Oceanic uptake of bomb-radiocarbon beginning in the late 1950s provides a dated marker which may be used to establish or validate skeletal chronology (Kalish 1993, Kerr et al. 2005, Sherwood & Edinger 2009). The combination of bomb- $^{14}\text{C}$  and  $\delta^{15}\text{N}$  data allows us to assess carbon and food sources to the skeletons, provides new constraints on deep-sea coral growth rates and makes it possible to evaluate the use of  $\delta^{15}\text{N}$  time series records from isidids for tracking marine biogeochemical processes on and around seamounts and other deep-sea environments over long (decade to century) time scales (Sherwood et al. 2005, Williams et al. 2006, 2007).

## MATERIALS AND METHODS

Analyses were carried out on specimens of deep-water isidid corals of the genera *Isidella*, *Keratoisis* and *Lepidisis* (Family Isididae; see Table 1). Identification to species level was not possible. Specimens were collected by dredge from seamounts south and east of Tasmania, Australia (Fig. 2), from Cascade Plateau (approx. 44.0°S, 150.5°E), Dory Hill (44.33°S, 147.13°E) and an unnamed seamount from the southwestern zone (44.19°S, 146.20°E). Map drawn with ODV software (Schlitzer 2007). All of the specimens were live when collected and were stored in 70% ethanol, except for a large (4 cm diameter) stump of *Keratoisis* (specimen K1) which was probably recently dead when collected and was stored dry. Ethanol preservation of the live-collected specimens was unavoidable, as the specimens originally were preserved for taxonomic identification. While ethanol preservation may induce slight alteration in the isotopic composition of some organism tissues (Sweeting et al. 2004), the durable, cross-linked, fibrillar protein of isidid node material (Sherwood et al. 2006) is likely to resist such alterations.

Nitrogen isotope and radiocarbon analyses were done on the organic nodes sectioned from specimen bases in order to obtain the longest records possible. To test for intracolony reproducibility of isotopic re-

cords, 2 adjacent nodes from the base of specimen T.H17442 and 1 node from 43 cm higher up the same colony were analysed. To isolate samples, nodes were sectioned with a diamond saw to a thickness of approximately 4 mm and immersed in 4% (v/v) HCl to dissolve the calcite fraction. After 4 d of dissolution, sections were transferred to a glass petri dish and immersed in deionised water. Sections were then peeled apart in concentric rings using scalpel and tweezers under a binocular microscope equipped with a digital camera (Fig. 1). Peels were delineated along growth zones, with each sample integrating 1 to 4 individual growth rings (the finest possible resolution using scalpel and tweezers). Specimen K1 was sampled at slightly lower resolution (approx. 5 growth rings per sample) because of its longer, 200 yr lifespan. Photographs were taken after removal of each sample in order to measure exact distances. Samples were transferred to 2 ml polyethylene vials, triple rinsed in deionised water and dried at 50°C over 48 h. Tissue samples were prepared in the same manner as organic node samples.

For nitrogen isotope analysis, approximately 0.5 mg aliquots were weighed into 5 × 5 mm ultralight Sn cups. Analyses were carried out using a Fisons 1500 elemental analyser coupled via a Con-flow II interface to a Finnigan Delta+ isotope ratio mass spectrometer at CSIRO Marine and Atmospheric Research. Combustion CO<sub>2</sub> was removed from the carrier gas stream using a sodium hydroxide scrubber (self-indicating Ascarite 2, Thomas Scientific) during the <sup>15</sup>N analyses to avoid the possibility of CO<sub>2</sub> from previous samples producing CO+ in the source and interfering at specific mass to charge ratios (m/z) 29 and 28 (Brooks et al. 2003). Standardization was by reference to the N<sub>2</sub> lab tank working gas, injected before and after each sample, and by normalization to solid reference materials run after each 6 samples and blank light weight tin cups. Nitrogen isotopic values are reported in the standard δ-notation:  $\delta^{15}\text{N} = [({}^{15}\text{N}/{}^{14}\text{N}_{\text{sample}}/{}^{15}\text{N}/{}^{14}\text{N}_{\text{standard}}) - 1]$ . Values are in per mil (‰) units with respect to the N<sub>2</sub> in air standard. The reference materials were IAEA N1 (ammonium sulphate, RM8547,  $\delta^{15}\text{N} = +0.4\text{‰}$  AIR), N3 (potassium nitrate, RM8549,  $\delta^{15}\text{N} = +4.7\text{‰}$  AIR; Gonfiantini et al. 1995) and casein (standard OAS,  $\delta^{15}\text{N} = +5.94\text{‰}$  AIR; Organic Analytical Standard B2155, batch no. 114859, Elemental Microanalysis). Based on replicate runs of these standards, the estimated precisions were typically 0.1‰ (n = 20). Blank contributions were negligible and no correction was applied. Approximately 6% of the coral samples were analysed in duplicate. The difference between duplicates averaged 0.11‰ (n = 11).

For radiocarbon analysis, decalcified organic node samples were combusted in individual quartz tubes

and reduced to graphite in the presence of iron catalyst. Measurements were performed on graphite targets at the Australian National University Single Stage Accelerator Mass Spectrometer facility. Results include a background and  $\delta^{13}\text{C}$  correction and are reported as  $\Delta^{14}\text{C}$  (±SD), corrected for decay between 1950 and the year of measurement according to Stuiver & Polach (1977). Additional correction for decay since the time of sample formation was not applied, because ages of individual samples were not known *a priori*. Precision of individual  $\Delta^{14}\text{C}$  measurements averaged 6‰ (1 SD).

## RESULTS AND DISCUSSION

### Bomb-<sup>14</sup>C chronologies

Four of the live-collected corals (*Lepidisis*: T.H17442, K1350 and L4; *Isidella*: I4) were analysed for  $\Delta^{14}\text{C}$  and one of these (T.H17442) was analysed in replicate (nodes 3 and 4). Plots of  $\Delta^{14}\text{C}$  versus sample distance from the margin of the growing edge of the coral all showed temporal patterns characteristic of oceanic uptake of bomb-<sup>14</sup>C (Fig. 3). Values of  $\Delta^{14}\text{C}$  averaged  $-66 \pm 7\text{‰}$  (n = 12) during the pre-bomb era, increased rapidly to a maximum of +60 to 90‰ and then decreased to +40 to 65‰.

The point of initial increase in bomb-<sup>14</sup>C records provides a dated marker because surface waters of the world oceans began taking up bomb-<sup>14</sup>C around 1957 (±3 yr) (Kalish 1993, Grottoli & Eakin 2007, Campana et al. 2008). The timing of the peak in bomb-<sup>14</sup>C varies with local oceanographic conditions, and is therefore less useful as a dated marker if the timing is not known *a priori*. Assuming that recently fixed and exported POM is consumed by the corals with no appreciable time lag (see below), the midpoint between the first datum to exceed the +2 SD level ( $-53\text{‰}$ ) associated with the average pre-bomb  $\Delta^{14}\text{C}$  ( $-66 \pm 7\text{‰}$ ) and the next oldest datum was assigned to the year 1957. The point of initial increase and the year of collection thus provided 2 tie-in points from which growth rates (Table 1) and skeletal chronology were defined. The coral records in Fig. 3 were scaled to a common time axis on the basis of these calculations. While we assumed a constant radial growth rate for the purposes of sclerochronology, radial growth rates probably vary by up to 20%, based on observations of axial asymmetry. This, along with errors in the bomb-<sup>14</sup>C derived growth rate itself, should be taken into consideration when comparing geochemical records and growth rates among different colonies.

Coral-based bomb-<sup>14</sup>C records were compared with 2 other records from the Southern Ocean derived from dated otoliths of fish (Fig. 4). The longest of the otolith

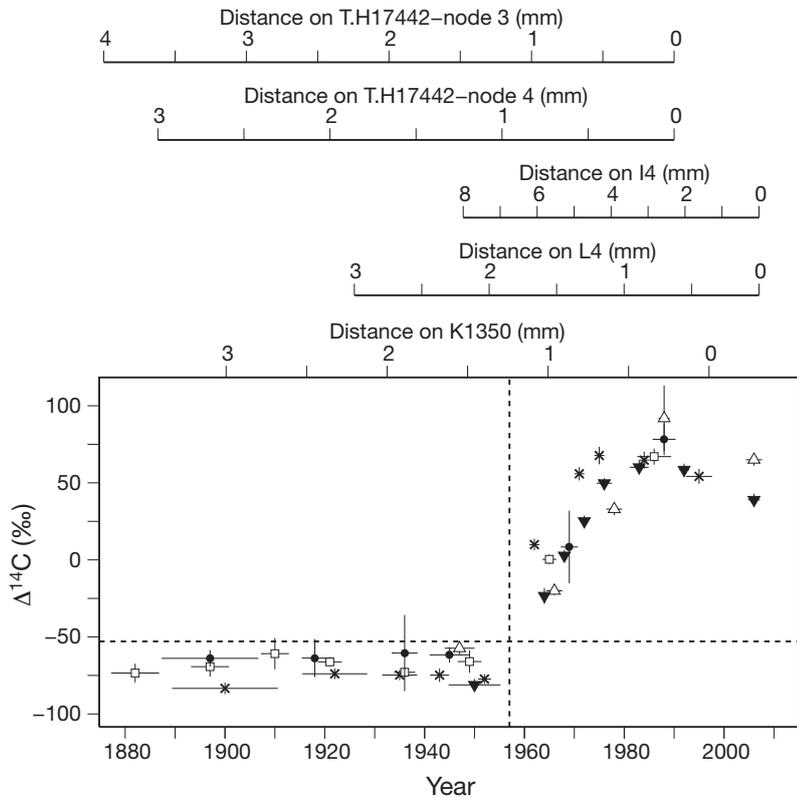


Fig. 3. Records of  $\Delta^{14}\text{C}$  from the organic nodes of 5 live-collected isidids: (●) T.H17442-node 3; (□) T.H17442-node 4; (▼) I4; (△) L4; and (×) K1350. For each record, the mid-point between the first datum to exceed  $-53\text{‰}$  (horizontal line) and the preceding pre-bomb datum was assigned to the year 1957 (vertical line). This and the date of collection defined skeletal chronologies, allowing all of the records to be plotted on a common time scale. Upper horizontal axes indicate skeletal distances for each coral in the plot. Vertical error bars are  $\pm\text{SD}$ ; horizontal error bars represent radial width of individual samples

records was derived from a collection of snapper *Pagrus auratus* from coastal waters of the North Island of New Zealand ( $39^{\circ}\text{S}$ ,  $179^{\circ}\text{E}$ ; Kalish 1993). The closest record to ours in terms of geographic distance was derived from blue grenadier *Macruronus novaezealandiae* from the west coast of Tasmania (Kalish et al. 1997). Based on the assumption that the growth zones in the otoliths of both species form annually,  $\Delta^{14}\text{C}$  data were reported with an age correction for the time since formation (Kalish 1993, Kalish et al. 1997). Our data were not age-corrected because we could not assume an independent chronology *a priori*. The difference between  $\Delta^{14}\text{C}$  and age-corrected  $\Delta^{14}\text{C}$  values was  $0\text{‰}$  in the year 1950, and  $<5\text{‰}$  towards the earlier and later ends of the records, which is negligible over the time period of interest. All of the records exhibited similar pre-bomb levels of  $\Delta^{14}\text{C}$  and patterns of increase, but with important differences in the timing and amplitude of the bomb peak. The otolith records peaked between 1970 (Tasmanian grenadier) and 1980 (New Zealand snapper) with values of approximately  $+100\text{‰}$ . The coral records peaked somewhat later, in the 1980s, with values of  $+60$  to  $90\text{‰}$ , suggesting that the bomb signal in the corals could

Table 1. Summary of collection details, growth rates and bulk  $\delta^{15}\text{N}$  of isidid corals in the present study. nd: no data

Coral ID	Genus	Region	Latitude ( $^{\circ}\text{S}$ )	Longitude ( $^{\circ}\text{E}$ )	Depth (m)	Year of collection	Node	Distance from base of colony (cm)	Radial growth rate ( $\mu\text{m yr}^{-1}$ )	Bulk $\delta^{15}\text{N}$ (‰) mean $\pm$ SD (N)
T.H17442	<i>Lepidisis</i>	Cascade Plateau	44.0	150.5	1000	1990	3	8.5	$35 \pm 13^{\text{b}}$	$12.08 \pm 0.33$ (18)
							4	13	$29 \pm 7^{\text{b}}$	$12.29 \pm 0.45$ (22)
							23	56	$32^{\text{c}}$	$11.75 \pm 0.40$ (5)
T.H17437	<i>Lepidisis</i>	Cascade Plateau	44.0	150.5	1250	1990	2	nd	$33^{\text{d}}$	$11.23 \pm 0.21$ (10)
T.H17441	<i>Keratoisis</i>	Cascade Plateau	44.0	150.5	925	1990	2	nd	$\sim 100^{\text{e}}$	$9.49 \pm 0.41$ (13)
K1 <sup>a</sup>	<i>Keratoisis</i>	Cascade Plateau	44.0	150.5	$\sim 1000$	1990	2	nd	$\sim 100^{\text{e}}$	$9.45 \pm 0.40$ (39)
I1	<i>Isidella</i>	Dory Hill	44.33	147.13	1150	2007	3	9	$113^{\text{f}}$	$11.05 \pm 0.47$ (20)
K1350	<i>Lepidisis</i>	Dory Hill	44.33	147.13	1366	1997	1	4	$31 \pm 4^{\text{b}}$	$11.68 \pm 0.44$ (29)
I4	<i>Isidella</i>	SW zone	44.19	146.20	1140	2007	1	nd	$113 \pm 17^{\text{b}}$	$11.64 \pm 0.25$ (20)
L4	<i>Lepidisis</i>	SW zone	44.19	146.20	1140	2007	4	4.5	$37 \pm 7^{\text{b}}$	$11.82 \pm 0.28$ (16)

<sup>a</sup>Probably dead when collected; <sup>b</sup>Bomb- $^{14}\text{C}$  derived growth rate (present study); <sup>c</sup>Assumed growth rate, based on average of Nodes 3 and 4 from the same coral; <sup>d</sup>Assumed growth rate, based on average of all bomb- $^{14}\text{C}$  dated *Lepidisis* colonies (present study); <sup>e</sup>Assumed growth rate, based on data in Thresher et al. (2007); <sup>f</sup>Assumed growth rate, based on that for colony I4

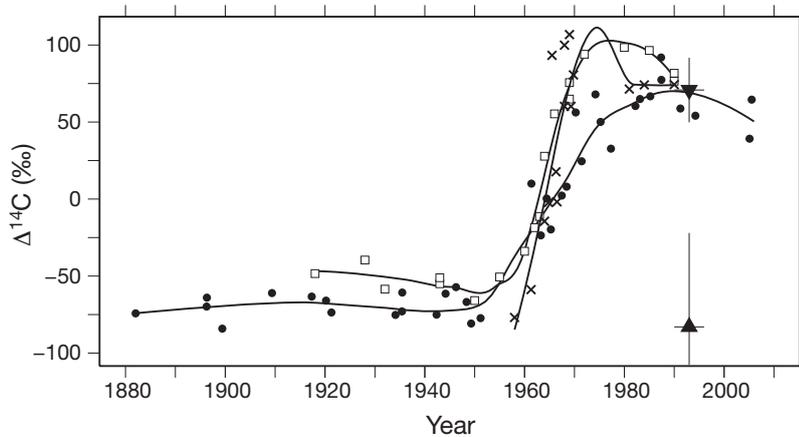


Fig. 4. Comparison of isidid bomb- $^{14}\text{C}$  records ( $\bullet$ ) with those derived from otoliths of fish collected from coastal waters of the North Island of New Zealand ( $\square$ , Kalish 1993) and western Tasmania ( $\times$ , Kalish et al. 1997). Also shown are seawater dissolved inorganic carbon (DIC) data from Tasmanian waters between 42 and 46° S (Lassey et al. 1990, Key et al. 2004): ( $\blacktriangledown$ ) 0–100 m; ( $\blacktriangle$ ) 800–1200 m. Error bars for DIC data are  $\pm\text{SD}$ ; error bars for coral and otolith data are omitted for clarity

be somewhat lagged and attenuated relative to surface waters.

These differences, however, may in part reflect local variability in surface water bomb  $^{14}\text{C}$  contents, given that the corals had very similar  $\Delta^{14}\text{C}$  values to seawater DIC samples collected along meridional transects adjacent to Tasmania, which suggests no attenuation (Fig. 4). One of these transects, from 1990, was located along 152° E, just to the east of the Cascade Plateau (Lassey et al. 1990). The other transect, from 1993, was located at approximately 146° E south of Tasmania (data from GLODAP, Key et al. 2004). Over the latitudinal range of 42 to 46° S, seawater  $\Delta^{14}\text{C}$  values for the upper 100 m averaged  $+71 \pm 21\text{‰}$  ( $n = 11$ ), overlapping with the coral data for the same time period from 1990 to 1993. In contrast, waters from 800 to 1200 m depth had pre-bomb levels of  $\Delta^{14}\text{C}$  ( $-83 \pm 61\text{‰}$ ,  $n = 7$ ). These results reiterate that the skeletal organic fractions of deep-sea octocorals are derived not from DIC at depth, but rather from recently fixed and exported particles (Griffin & Druffel 1989, Roark et al. 2005, Sherwood & Edinger 2009), and validate our assumptions for assigning the point of initial increase to the year 1957.

If the corals feed on a degraded fraction of POM, as potentially indicated by  $\delta^{15}\text{N}$  results (see below), the point of initial increase could have occurred later than 1957, leading to an underestimation of growth rates. Similarity of the reconstructed bomb- $^{14}\text{C}$  records with surface water DIC (Fig. 4) argues against significant delay in the timing of initial increase of skeletal bomb- $^{14}\text{C}$ . Moreover, sinking particles in the Tasman Sea and elsewhere sink to 1000 m water depth within weeks of leaving the euphotic zone (Trull et al. 2001, and references therein).

### Growth rate variability

Isidid growth rates appear to vary widely among different genera, even among those inhabiting the same depth on the same seamount. At radial growth rates of  $\sim 30 \mu\text{m yr}^{-1}$ , *Lepidisis* colonies grew about 3 times slower than colonies of *Keratoisis* and *Isidella* ( $\sim 110 \mu\text{m yr}^{-1}$ ; Table 1). For comparison, bomb- $^{14}\text{C}$ -dated colonies of *Keratoisis ornata* collected off Newfoundland grew at 50 to 75  $\mu\text{m yr}^{-1}$  (Sherwood & Edinger 2009), while samples of *Keratoisis* and *Isidella* from California and the Gulf of Alaska were shown to grow at 55 to 160  $\mu\text{m yr}^{-1}$  (Roark et al. 2005, Andrews et al. 2005). A  $^{210}\text{Pb}$ -dated colony of *Lepidisis* collected off New Zealand grew at 180  $\mu\text{m yr}^{-1}$  (Tracey et al. 2007). While it is not clear why growth rates should

differ so widely among isidid genera living in the same habitat, resource partitioning in order to reduce competition offers a possible explanation. For example, based on stable carbon and nitrogen isotope analysis, different species of deep-sea gorgonians of Newfoundland and Labrador occupy distinct trophic niches with food sources ranging from freshly exported phytodetritus to more degraded and resuspended materials (Sherwood et al. 2008b). Differences in quality and quantity of foods could thus account for growth rate variability. Intergeneric differences in  $\delta^{15}\text{N}$ , however, point to *Keratoisis* as having a different trophic niche compared to *Isidella* and *Lepidisis*.

### Organic node $\delta^{15}\text{N}$

The overall distribution of organic node  $\delta^{15}\text{N}$  values for the Cascade Plateau was bimodal, with *Lepidisis* spp. (T.H17442, T.H17437) averaging  $11.98 \pm 0.53\text{‰}$  ( $n = 55$ ) and *Keratoisis* sp. (T.H14771, K1) averaging  $9.46 \pm 0.40\text{‰}$  ( $n = 52$ ) (Table 1). For the unnamed seamount samples from the southwestern zone,  $\delta^{15}\text{N}$  of *Isidella* (I4) and *Lepidisis* (L4) averaged  $11.72 \pm 0.27\text{‰}$  ( $n = 20$ ). For Dory Hill,  $\delta^{15}\text{N}$  of *Lepidisis* (K1350) and *Isidella* sp. (I1) averaged  $11.43 \pm 0.54\text{‰}$  ( $n = 49$ ). Thus differences in bulk  $\delta^{15}\text{N}$  were distributed among species, with *Keratoisis* spp. having distinctly lower  $\delta^{15}\text{N}$ , and not among seamounts. Analysis of a living tissue sample from K1350 yielded a  $\delta^{15}\text{N}$  value of 11.5‰, indistinguishable from that of the bulk skeleton and indicating no isotopic fractionation between tissue and skeleton, as previously noted in other gorgonians (Heikoop et al. 2002, Sherwood et al. 2005).

The  $\delta^{15}\text{N}$  of deep sinking POM in the subantarctic zone south of Tasmania averages 2 to 3‰ (Lourey et al. 2003; Fig. 5). If the corals were feeding directly on these food sources, they would be expected to have a  $\delta^{15}\text{N}$  of 5 to 6‰, based on an approximate 3‰ trophic level enrichment (Minagawa & Wada 1984, Wada et al. 1987). The observed higher coral  $\delta^{15}\text{N}$  values (9 to 12‰) could occur in several ways. (1) The corals could be feeding on sinking POM, but with larger trophic level enrichment than expected. This appears unlikely, because nitrogen is recycled more efficiently in deep-sea ecosystems, and thus trophic fractionation would be expected to be less, not greater, than the canonical 3‰ (e.g. Iken et al. 2001). (2) Food sources could be derived from north of the subtropical front, located between  $\sim 40$  to  $45^\circ\text{S}$ , where  $\delta^{15}\text{N}$  of POM appears to be higher because of more complete nitrate utilization (Altabet & Francois 1994, DiFiore et al. 2006; Fig. 5), although the oligotrophic conditions of those waters argues against them as a dominant source of food. (3) A significant proportion of the corals' diet could come from degraded POM fractions, as observed for *Keratois ornata* living near the Grand Banks of Newfoundland in the northwest Atlantic (Sherwood et al. 2008b). The  $\delta^{15}\text{N}$  of suspended POM increases significantly (on the order of 3 to 5‰) with depth through the mesopelagic zone (Saino & Hattori 1987, Altabet 1988) as the particles are degraded by microbial activity (Macko & Estep 1984), and this is reflected in animals which feed on these fractions (Mintenbeck et al. 2007). (4) The corals may feed on zooplankton, as observed in deep-sea gorgonians of Antarctica (Orejas et al. 2003).

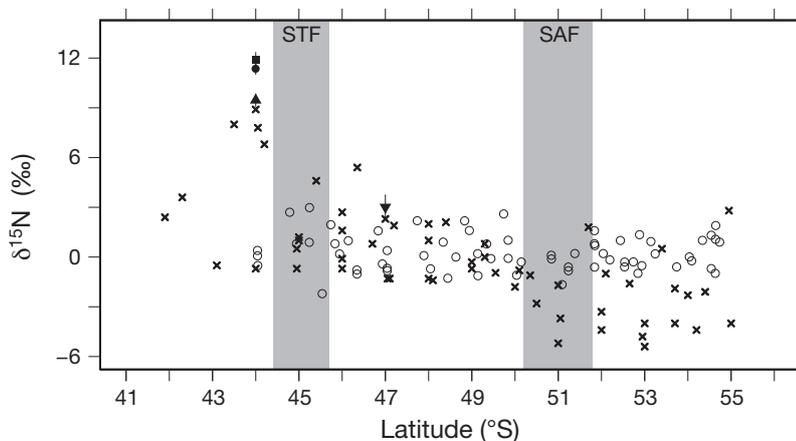


Fig. 5. Distribution of  $\delta^{15}\text{N}$  of surface water suspended POM with latitude south of Tasmania: (o) Sep–Dec; (x) Jan–March. Also shown, flux-weighted mean  $\delta^{15}\text{N}$  (▼) of sediment trap POM collected at  $47^\circ\text{S}$  at 1060 m water depth (data from Lourey et al. 2003). Mean coral  $\delta^{15}\text{N}$ —(■) *Lepididisis*; (●) *Isidella*; and (▲) *Keratois*—indicate up to 3 trophic levels between trap POM and corals. Vertical grey bands indicate approximate positions of the subtropical (STF) and subantarctic fronts (SAF). Vertical error bars on coral data points are  $\pm\text{SD}$

This would introduce 1 or 2 additional trophic steps, with a corresponding 3 to 6‰ increase in  $\delta^{15}\text{N}$ . We consider feeding on degraded POM and/or zooplankton to be the most likely explanation for the high  $\delta^{15}\text{N}$  in the present study. Additional data, particularly from lipid and fatty acid analyses (e.g. Kiriakoulakis et al. 2004, Hamoutene et al. 2008), would help to verify this hypothesis.

### $\delta^{15}\text{N}$ time series

Because the skeletal organics of deep-sea isidids are derived ultimately from recently exported particles, transmitted to the corals via one or more trophic intermediaries, time series records of  $\delta^{15}\text{N}$  from this fraction have the potential to record a variety of biogeochemical processes in overlying surface waters (Sherwood et al. 2005, Williams et al. 2006, 2007). In order to evaluate the potential usefulness of this proxy, we examined both intra- and intercolony reproducibility of  $\delta^{15}\text{N}$  records.

To examine intracolony reproducibility, 3 nodes were isolated from *Lepididisis* specimen T.H17442 from the Cascade Plateau. Nodes 3, 4 and 23 were sectioned 8.5, 13 and 56 cm, respectively, from the base of the colony. Using bomb- $^{14}\text{C}$  derived growth rates (Table 1), nodes 3 and 4 showed reasonable similarity in  $\delta^{15}\text{N}$  with a broad peak centered around the year 1960 and a trough centered on 1920 (Fig. 6a). The maximum offset between contemporaneous values (around year 1950) was 1.2‰, which far exceeded the analytical reproducibility (0.1‰). It remains unclear what proportion of this offset can be attributed to improper alignment of the chronologies (owing to error and non-linearity of radial growth rates) versus real differences in  $\delta^{15}\text{N}$  among contemporaneous samples. Sampling at higher resolution may introduce additional variability. For node 23, we assumed a growth rate of  $32\ \mu\text{m}\ \text{yr}^{-1}$  based on the average growth rates for nodes 3 and 4. The  $\delta^{15}\text{N}$  record for node 23 was 0.5 to 1‰ depleted relative to the records for nodes 3 and 4. Again, it is unclear what proportion of this offset may be attributed to chronological error. Ongoing investigations of skeletal growth banding coupled with bomb- $^{14}\text{C}$  and  $^{210}\text{Pb}$  dating may help to improve dating precision.

To examine intercolony reproducibility, 2 additional colonies from the Cascade Plateau were analysed (Fig. 6a). For *Lepididisis* specimen T.H17437, we

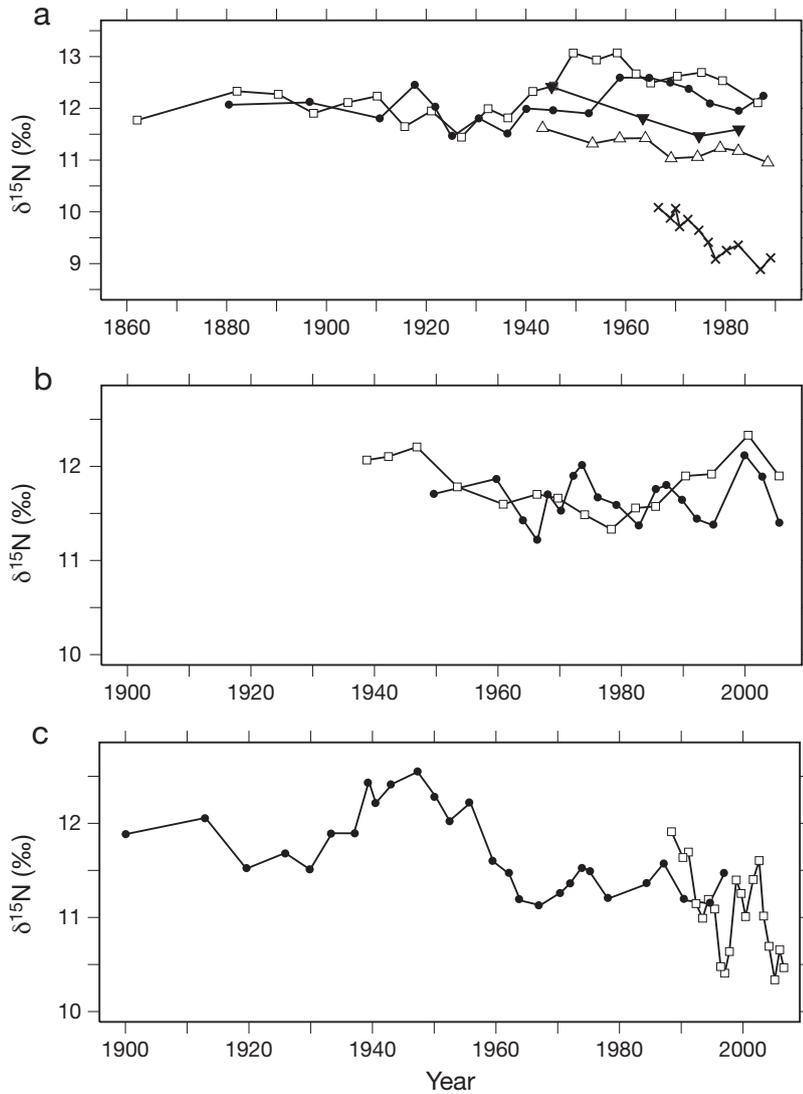


Fig. 6. Records of  $\delta^{15}\text{N}$  from the organic nodes of isidids. (a) Cascade Plateau: (●) T.H17442-node 3; (□) T.H17442-node 4; (▼) T.H17442-node 23; (△) T.H17437 and (×) T.H17441. (b) Dory Hill: (●) I4 and (□) L4. (c) Southwestern zone: (●) K1350 and (□) I1. Note differences in x-axis scales

assumed a radial growth rate of  $33 \mu\text{m yr}^{-1}$ , based on the average for other *Lepidisis* colonies dated by bomb- $^{14}\text{C}$ . The  $\delta^{15}\text{N}$  record from T.H17437 appeared similar to that of T.H17442-node 23, but was  $\sim 0.4\%$  depleted. Specimen T.H17441 represented a different genus, *Keratoisis*, and we assumed a growth rate of  $\sim 100 \mu\text{m yr}^{-1}$  based on previous work (Thresher et al. 2007). While  $\delta^{15}\text{N}$  values were lower in T.H17441 ( $\sim 9.5\%$ ), the  $\delta^{15}\text{N}$  record followed a similar pattern of decreasing  $\delta^{15}\text{N}$  to that of T.H17442-node 23 and T.H17437.

Intercolony reproducibility was also examined for corals from 2 other seamounts. Specimens I4 (*Isidella*) and L4 (*Lepidisis*) were collected from an unnamed seamount in the southwestern zone off Tasmania. The

$\delta^{15}\text{N}$  record for I4 exhibited 4 quasi-decadal peaks between 1950 and 2007 (Fig. 6b). The record for L4 did not exhibit the same peaks, but was broadly similar in terms of the mean and amplitude of  $\delta^{15}\text{N}$ . Colonies K1350 and I1 were collected from the Dory Hill seamount. Colony K1350 exhibited a broad peak in  $\delta^{15}\text{N}$  centered around 1950, with values dropping by  $1\%$  thereafter (Fig. 6c). This trend was continued with the record for specimen I1, although there was little temporal overlap between the 2 records.

The  $\delta^{15}\text{N}$  records from all colonies were compared with additional data for an approximately 200 yr old stump of *Keratoisis* from Cascade Plateau (specimen K1; Fig. 7). Data from recent specimens of *Isidella* and *Lepidisis* showed broad similarity in terms of mean values and trends. Values for *Keratoisis* averaged about  $2\%$  lower and indicated no trend over the past  $\sim 250$  yr. Subtle, quasi-decadal features were evident in the records; however, the amplitude of these features within individual records ( $0.5$  to  $1.5\%$ ) was of the same magnitude as the apparent intra- and intercolony variations. The causes of the quasi-decadal features remain unclear. One hypothesis is that latitudinal movements of the subtropical convergence zone associated with quasi-decadal climate variability (Thresher 2002, Ridgway 2007) alternately brings oligotrophic subtropical waters (higher in  $\delta^{15}\text{N}$  of  $\text{NO}_3$ ) and nitrate-rich subantarctic waters (lower in  $\delta^{15}\text{N}$  of  $\text{NO}_3$ ; DiFiore et al. 2006) into the study area. The  $\delta^{15}\text{N}$  signature is then incorporated into export production and reflected in the corals.

The range in  $\delta^{15}\text{N}$  values in the corals can be combined with observed latitudinal gradients in  $\delta^{15}\text{N}$  of  $\text{NO}_3$  to estimate possible movement of the boundary between oligotrophic subtropical and nutrient-rich subantarctic waters. Using gradients observed near  $43$  to  $45^\circ\text{S}$  south of Tasmania (DiFiore et al. 2006) suggests frontal movements of less than  $1^\circ$  of latitude. Alternatively, the minimal changes in the coral  $\delta^{15}\text{N}$  can be translated into possible changes in the oligotrophic state of overlying surface waters; correlations between  $\delta^{15}\text{N}$  and  $[\text{NO}_3]$  (Lourey et al. 2003, DiFiore et

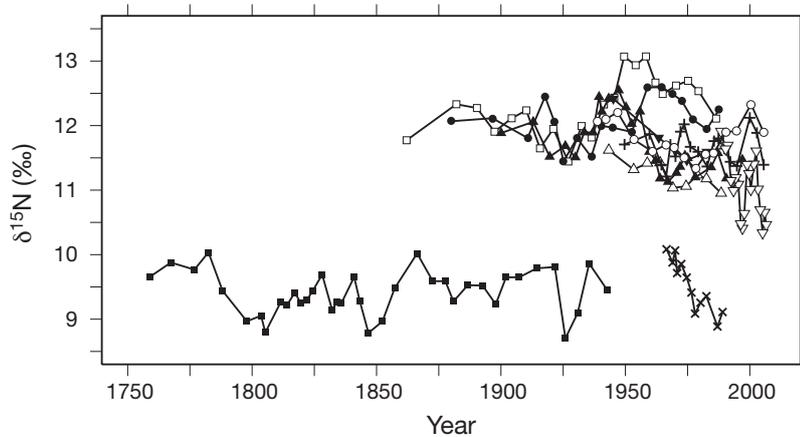


Fig. 7. Comparison of all  $\delta^{15}\text{N}$  records from isidids from all 3 seamounts plotted on a common time scale. (●) T.H17442-node 3; (□) T.H17442-node 4; (▼) T.H17442-node 23; (△) T.H17437; (×) T.H17441; (+) I4; (○) L4; (▲) K1350; (▽) I1 and (■) K1

al. 2006) suggest changes of no more than about 10% in surface water  $[\text{NO}_3]$ , and thus considerable constancy in environmental conditions over the past century. This includes constancy in the trophic relations that connect the surface water nitrate supply to the organic food on which the corals feed at depth. These observations provide an important baseline against which future climate change in the region can be evaluated. This is particularly important in light of models of anthropogenic  $\text{CO}_2$  driven ocean warming that suggest this region will experience greater warming than elsewhere (Lyne et al. 2005), and observations in surface waters further north along the eastern coast of Tasmania that suggest a recent increase in the southward delivery of warm, salty Eastern Australian Current waters (Ridgway 2007, Hill et al. 2008).

Finally, the long-term stability of the organic  $\delta^{15}\text{N}$  signal in K1 (Fig. 7) contrasts with substantial changes in its skeletal calcite (internodal) composition over the same period (Thresher et al. 2004). This difference is consistent with a surface-derived dietary source for the organic node material, as compared with effects of ambient environmental conditions, at ca. 1000 m depth, on skeletal composition.

## CONCLUSIONS

Uptake of bomb- $^{14}\text{C}$  in deep-sea isidids sampled from the Tasmanian seamounts at 900 to 1400 m water depth indicates that the seamount ecosystems may be tightly coupled with surface productivity. While bomb- $^{14}\text{C}$  levels in isidids originate from recently fixed and exported particles,  $\delta^{15}\text{N}$  data suggest this material is transmitted to the corals via one or more trophic intermediaries in the form of microbially degraded POM

and/or zooplankton. Quasi-decadal features in the coral  $\delta^{15}\text{N}$  time series suggest the possible influence of decadal regional climate variability on seamount biogeochemistry, although improved sclerochronological precision is required to fully decode these signals. The limited overall range of  $\delta^{15}\text{N}$  variations indicates constancy of oceanographic conditions and ecosystem trophic dynamics over the past century, which provides a baseline for the evaluation of future impacts. The high precision with which the  $\delta^{15}\text{N}$  timeseries were obtained ( $\sim 0.1\text{‰}$  analytical uncertainty) and the interspecimen reproducibility (better than  $1\text{‰}$ ) in comparison to expected trophic effects ( $\sim 3\text{‰}$  per level), potential subtropical/sub-

antarctic frontal movements (several ‰) and changes in the extent of nutrient depletion (also several ‰) make it clear that  $\delta^{15}\text{N}$  in deep-sea corals offers the capacity to provide sensitive records of oceanographic change.

**Acknowledgements.** We thank A. Williams, K. Gowlett-Holmes and G. Walker-Smith for the coral samples, and P. Alderslade for taxonomic assistance. O.A.S. was supported by an Endeavour Research Fellowship, R.E.T. by the CSIRO Wealth from Oceans and Climate Adaptation Flagships and T.W.T. and D.M.D. by the Australian Commonwealth Cooperative Research Centres Program. Sample collection was supported by CSIRO, the Australian Fisheries Research and Development Corporation and the Australian Department of Environment and Heritage. This is a contribution from the CSIRO Wealth from Oceans and Climate Adaptation Flagships.

## LITERATURE CITED

- Altabet MA (1988) Variations in nitrogen isotopic composition between sinking and suspended particles: implications for nitrogen cycling and particle transformation in the open ocean. *Deep-Sea Res A* 35:535–554
- Altabet MA, Francois R (1994) Sedimentary nitrogen isotopic ratio as a recorder for surface ocean nitrate utilization. *Global Biogeochem Cycles* 8:103–116
- Andrews AH, Cailliet GM, Kerr LA, Coale KH, Lundstrom C, DeVogelaere AP (2005) Investigations of age and growth rate for three deep-sea corals from the Davidson Seamount off central California. In: Freiwald A, Roberts JM (eds) *Cold-water corals and ecosystems*. Springer-Verlag, Berlin, p 1021–1038
- Brooks PD, Geilmann H, Werner RA, Brand WA (2003) Improved precision of coupled  $^{13}\text{C}$  and  $^{15}\text{N}$  measurements from single samples using an elemental analyser. *Rapid Commun Mass Spectrom* 17:1924–1926
- Campana SE, Casselman JM, Jones CM (2008) Bomb radiocarbon chronologies in the Arctic, with implications for the age validation of lake trout (*Salvelinus namaycush*) and other Arctic species. *Can J Fish Aquat Sci* 65:733–743

- DiFiore PJ, Sigman DM, Trull TW, Lourey MJ, Karsh K, Cane G, Ho R (2006) Nitrogen isotope constraints on subantarctic biogeochemistry. *J Geophys Res* 111:C08016
- Gonfiantini R, Stichler W, Rozanski K (1995) Standards and intercomparison materials distributed by the International Atomic Energy Agency for stable isotope measurements. International Atomic Energy Agency, Vienna, p 1–18
- Griffin S, Druffel ERM (1989) Sources of carbon to deep-sea corals. *Radiocarbon* 55:533–542
- Grottoli AG, Eakin CM (2007) A review of modern coral  $\delta^{18}\text{O}$  and  $\Delta^{14}\text{C}$  proxy records. *Earth Sci Rev* 81:67–91
- Hamoutene D, Puestow T, Miller-Banoub J, Wareham V (2008) Main lipid classes in some species of deep-sea corals in the Newfoundland and Labrador region (Northwest Atlantic Ocean). *Coral Reefs* 27:237–246
- Heikoop JM, Hickmott DD, Risk MJ, Shearer CK, Atudorei V (2002) Potential climate signals from the deep-sea gorgonian coral *Primnoa resedaeformis*. *Hydrobiologia* 471: 117–124
- Hill KS, Rintoul SR, Coleman R, Ridgeway KR (2008) Wind forced low frequency variability of the East Australia Current. *Geophys Res Lett* 35:L08602
- Iken K, Brey T, Wand U, Voigt J, Junghans P (2001) Food web structure of the benthic community at the Porcupine Abyssal Plain (NE Atlantic): a stable isotope analysis. *Prog Oceanogr* 50:383–405
- Kalish JM (1993) Pre- and post-bomb radiocarbon in fish otoliths. *Earth Planet Sci Lett* 114:549–554
- Kalish JM, Johnston JM, Smith DC, Morison AK, Robertson SG (1997) Use of the bomb radiocarbon chronometer for age validation in the blue grenadier *Macruronus novaezealandiae*. *Mar Biol* 128:557–563
- Kerr LA, Andrews AH, Munk K, Coale KH, Frantz BR, Cailliet GM, Brown TA (2005) Age validation of quillback rockfish (*Sebastes maliger*) using bomb radiocarbon. *Fish Bull* 103: 97–107
- Key RM, Kozyr A, Lee K, Wanninkhof R and others (2004) A global ocean carbon climatology: results from Global Data Analysis Project (GLODAP). *Global Biogeochem Cycles* 18:GB4031. doi:10.1029/2004GB002247
- Kiriakoulakis K, Bett B, White M, Wolff GA (2004) Organic biogeochemistry of the Darwin Mounds, a deep-water coral ecosystem, of the NE Atlantic. *Deep-Sea Res I* 51: 1937–1954
- Koslow JA, Gowlett-Holmes K, Lowry JK, O'Hara T, Poore GCB, Williams A (2001) Seamount benthic macrofauna off southern Tasmania: community structure and impacts of trawling. *Mar Ecol Prog Ser* 213:111–125
- Lassey KR, Manning MR, Sparks RJ, Wallace G (1990) Radiocarbon in the sub-tropical convergence east of Tasmania: an interim report. DSIR Physical Sciences Report No. 11, Department of Science and Industrial Research, Lower Hutt
- Lourey MJ, Trull TW, Sigman DM (2003) Sensitivity of  $\delta^{15}\text{N}$  of nitrate, surface suspended and deep sinking particulate nitrogen to seasonal nitrate depletion in the Southern Ocean. *Global Biogeochem Cycles* 17:1081
- Lyne V, Thresher R, Rintoul S (2005) Regional impacts of climate change and variability in south-east Australia. CSIRO Marine and Atmospheric Research, Hobart
- Macko SA, Estep MLF (1984) Microbial alteration of stable nitrogen and carbon isotopic compositions of organic matter. *Org Geochem* 6:787–790
- Minagawa M, Wada E (1984) Stepwise enrichment of  $^{15}\text{N}$  along food chains: further evidence and relation between  $\delta^{15}\text{N}$  and animal age. *Geochim Cosmochim Acta* 48: 1135–1140
- Mintenbeck K, Jacob U, Knust R, Arntz WE, Brey T (2007) Depth-dependence in stable isotopic ratio  $\delta^{15}\text{N}$  of benthic POM consumers: the role of particle dynamics and organism trophic guild. *Deep-Sea Res I* 54:1015–1023
- Orejas C, Gili JM, Arntz W (2003) Role of small-plankton communities in the diet of two Antarctic octocorals (*Primnoisis antarctica* and *Primnoella* sp.). *Mar Ecol Prog Ser* 250:105–116
- Ridgeway KR (2007) Long-term trend and decadal variability of the southward penetration of the East Australian Current. *Geophys Res Lett* 34:L13613
- Roark EB, Guilderson TP, Flood-Page S, Dunbar RB, Ingram BL, Fallon SJ, McCulloch M (2005) Radiocarbon-based ages and growth rates of bamboo corals from the Gulf of Alaska. *Geophys Res Lett* 32:L04606. doi:10.1029/2004GL 021919
- Saino T, Hattori A (1987) Geographical variation in the water column distribution of suspended particulate organic nitrogen and its  $^{15}\text{N}$  natural abundance in the Pacific and its marginal seas. *Deep-Sea Res I* 34:807–827
- Schlitzer R (2007) Ocean Data View. Available at <http://odv.awi.de>
- Sherwood OA, Edinger EN (2009) Ages and growth rates of some deep-sea corals of Newfoundland and Labrador. *Can J Fish Aquat Sci* 66:142–152
- Sherwood OA, Heikoop JM, Scott DB, Risk MJ, Guilderson TP, McKinney RA (2005) Stable isotopic composition of deep-sea gorgonian corals *Primnoa* spp.: a new archive of surface processes. *Mar Ecol Prog Ser* 301:135–148
- Sherwood OA, Scott DB, Risk MJ (2006) Late Holocene radiocarbon and aspartic acid racemization dating of deep-sea octocorals. *Geochim Cosmochim Acta* 70:2806–2814
- Sherwood OA, Edinger EN, Guilderson TP, Ghaleb B, Risk MJ, Scott DB (2008a) Late Holocene radiocarbon variability in Northwest Atlantic slope waters. *Earth Planet Sci Lett* 275:146–153
- Sherwood OA, Jamieson RE, Edinger EN, Wareham VE (2008b) Stable C and N isotopic composition of cold-water corals from the Newfoundland and Labrador continental slope: examination of trophic, depth and spatial effects. *Deep-Sea Res I* 55:1392–1402
- Stuiver M, Polach HA (1977) Discussion: reporting of  $^{14}\text{C}$  data. *Radiocarbon* 19:355–363
- Sweeting CJ, Polunin NVC, Jennings S (2004) Tissue and fixative dependent shifts of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  in preserved ecological material. *Rapid Commun Mass Spectrom* 18: 2587–2592
- Thresher RE (2002) Solar correlates of southern hemisphere mid-latitude climate variability. *Int J Climatol* 22: 901–915
- Thresher RE, Rintoul SR, Koslow JA, Weidman C, Adkins J, Proctor C (2004) Oceanic evidence of climate change in southern Australia over the last three centuries. *Geophys Res Lett* 31:L07212
- Thresher RE, MacRae CM, Wilson NC, Gurney R (2007) Environmental effects on the skeletal composition of deep-water gorgonians (*Keratoisis* spp.; Isididae). *Bull Mar Sci* 81:409–422
- Tracey DM, Neil H, Marriot P, Andrews AH, Cailliet GM, Sanchez JA (2007) Age and growth of two genera of deep-sea bamboo corals (Family Isididae) in New Zealand waters. *Bull Mar Sci* 81:393–408
- Trull TW, Bray SG, Manganini SJ, Honjo S, Francois R (2001) Moored sediment trap measurements of carbon export

in the subantarctic and polar frontal zones of the Southern Ocean, south of Australia. *J Geophys Res* 106: 31489–31509

Wada E, Terazaki M, Kabaya Y, Nemoto T (1987)  $^{15}\text{N}$  and  $^{13}\text{C}$  abundances in the Antarctic Ocean with emphasis on the biogeochemical structure of the food web. *Deep-Sea Res A* 34:829–841

Williams B, Risk MJ, Ross SW, Sulak KJ (2006) Deep-water antipatharians: proxies of environmental change. *Geology* 34:773–776

Williams B, Risk M, Stone R, Sinclair D, Ghaleb B (2007) Oceanographic changes in the North Pacific Ocean over the past century recorded in deep-water gorgonian corals. *Mar Ecol Prog Ser* 335:85–94

*Submitted: February 27, 2009; Accepted: May 27, 2009*

*Proofs received from author(s): September 23, 2009*