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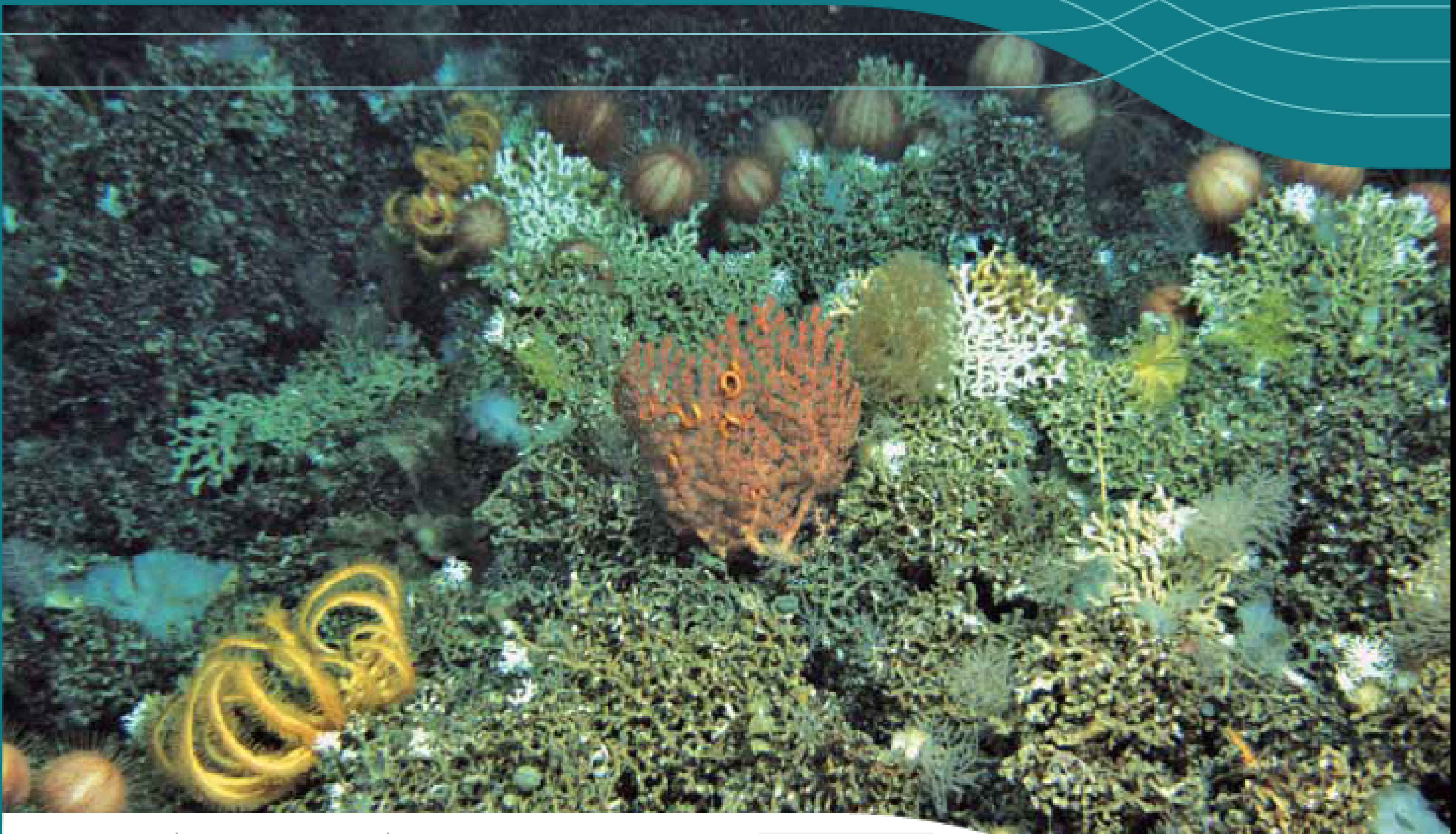

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Adapting to the effects of climate change on Australia's deep marine reserves

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1 NON TECHNICAL SUMMARY

2010/510 Adapting to the effects of climate change on Australia's deep marine reserves.

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OBJECTIVES:

1. To develop practical options for DSEWPAC to manage the impacts of climate change on the South-east Commonwealth Marine Reserve
2. To develop a generic model that can be applied to forecasting the impacts of climate change on other deep sea biota

NON TECHNICAL SUMMARY:

OUTCOMES ACHIEVED TO DATE

To date, this project has
(1) determined that climate change in general, and ocean acidification in particular, is likely to result in the loss over the next century of the cold-water coral reefs that characterize seamounts in the SE Commonwealth Marine Reserve
(2) identified possible refugia habitats along the continental shelf of southern Australia
(3) identified possible adaptation strategies that involve assisted translocation of the reefs and the use of artificial substrates to provide suitable hard ground for coral growth
(4) raised the need with key stakeholders for a workshop to assess the feasibility of these strategies and to consider other options for maintaining the viability of these deepwater ecosystems

Extensive coral reefs formed primarily by a single species, *Solenosmilia variabilis*, occupy seamounts at depths of 1-2 km along Australia's southeastern coast, and have recently been protected in the SE Commonwealth Marine Reserves. These reefs are hotspots of deep ocean biodiversity and productivity, and are a focal habitat for deep-sea fisheries, such as dories and orange roughy. Climate change in general, and ocean acidification in particular, has been identified as a potential threat to the long-term survival of these reefs, as the carbonate saturation horizon - the depth at which calcium carbonate is fully saturated in seawater- shoals, a consequence of increased ocean CO_2. The literature suggests that the coral will struggle to grow its carbonate skeleton in undersaturated conditions. If global CO_2 levels continue to rise as predicted, a shoaling carbonate saturation horizon could push Australia's temperate deepwater reefs to the tops of the seamounts they occupy and, with nowhere else to go, they may simply disappear.

The magnitude of the risk to the reefs in the marine reserves depends on two factors: (1) how sensitive *Solenosmilia variabilis* is to low carbonate levels, and (2) future conditions in the seamount environment. This project assesses these factors, using all available information to determine the corals tolerance limits and using state-of-the-art ocean biogeochemical models to estimate future environmental conditions in the marine reserves. From these analyses, we begin to quantify the risk to the reef, determine critical time frames for developing management responses to mitigate the threat, if any, and help identify mitigation options.

Using a range of approaches, we estimate that established colonies of the coral can persist in water as low as 16% undersaturated ($\Omega = 0.84$, where an Ω of 1.0 is fully saturated). However, the data suggest that long-term viability requires saturation levels no lower than 0.90-0.94 and that extensive reefal development may require saturation levels closer to 1.0. To determine how these values compared with likely future environmental conditions, we downscaled a state-of-the-art coupled ocean-atmosphere biogeochemical model to the reserve location and to the mean depth of the present day reef (1100 m) and predicted saturation states over the next century. The model indicates that under an IPCC "business-as-usual" atmospheric CO_2 scenario, carbonate saturation levels by 2100 at the site of the present day reefs could be as low as 0.77 and as high as 0.92, but most likely will be in the range of 0.83-0.86. Comparison of these values with the coral's tolerance limits suggests that if the IPCC scenario is maintained some *S. variabilis* will survive in the reserves until the turn of the century. However, the corals are likely to be under severe physiological stress and probably will not sustain the extensive reefs that currently characterise the seamount habitats. In practice, global CO_2 levels are rising faster than the IPCC "business-as-usual" model, suggesting strongly that even these predictions for the corals may be optimistic.

Preliminary spatial modelling indicates some coastal habitats may remain suited for the species locally and could serve as refugia for the ecosystem, although this depends very much on both the coral's abilities to tolerate rising ocean temperatures and the availability of suitable hard ground on which to grow. Most shelf edge habitats along the southern Australian coasts are soft or sandy sediment or mudstone, none of which appears to be a suitable substrate for the coral. Local survival of the species, its reefs and associated biota may require assisted translocation of coral colonies and the use of artificial structures to provide suitable hard ground environments. We recommend that a small workshop of relevant stakeholders be convened to consider the feasibility of these options, to canvas other adaptation strategies, and to assess additional implications of our analyses for management of the ecosystems in the SE Commonwealth Marine Reserves.

KEYWORDS: Climate change, Coldwater coral reefs, Ocean acidification, Deep-sea fisheries, Seamounts, SE Commonwealth Marine Reserve.

2 ACKNOWLEDGMENTS

This project was funded by the National Climate Change Adaptation Research Fund (which is jointly support by the Fisheries Research and Development Corporation and the Commonwealth Department of Climate Change) and by the CSIRO Climate Adapatation Flagship. Some elements of the modelling work were supported by the CSIRO Wealth from Oceans Flagship. The project benefited extensively from discussions at the 1st International Marine Conservation Think Tank, on Deep-Sea Coral Research to Enhance Conservation, held in Auckland, NZ in November 2011 and organised by Di Tracey (NIWA) and Tom Hourigan (NOAA), and at the Fifth International Symposium on Deep-Sea Corals, held in Amsterdam in April 2012, at which the results of this work was presented as an invited plenary.

3 BACKGROUND

Ocean acidification results from net uptake by the ocean of carbon dioxide (CO_2) emissions, which causes a decrease in the carbonate ion concentration of ocean waters (Feely, et al., 2004). This decrease has been forecast to hamper production of biogenic carbonates (aragonite and calcite) in the skeletons, shells and tests of marine taxa (Orr et al, 2005; Moy, et al., 2009). Coral reefs in the deep-sea have been identified as particularly vulnerable, on the basis of pre-industrial carbonate levels at the depths and temperatures they inhabit that were already low (Guinotte, et al., 2006; Riegl, et al., 2009; Veron, et al. 2009). Direct tests of this sensitivity have not been done, but in at least one relatively shallow cold-water coral, *Lophelia pertusa*, calcification rates decline as predicted in low pH conditions (Maier, et al., 2009). Deep-water corals may often also have very limited scope for vertical adjustment, potentially being squeezed between seamount summits on the one hand and shoaling saturation horizons, on the other. Even the tops of many seamounts in the SW Pacific that currently support deep-sea coral communities may well be under-saturated in the next 50-100 years (H. Bostock, NIWA, pers. comm.). With nowhere to go, these cold-water reefs could "simply disappear" (Poloczanka, el al., 2007).

This poses an existential threat to the coldwater reefs of the Southeast Commonwealth Marine Reserve. In 2007, the Commonwealth declared the Huon and Tasman Fracture Commonwealth Marine Reserves (CMR) as a key form part of the National Representative System of Marine Protected areas. Relatively little was known about the benthic biodiversity of the deeper sections of these Reserves, but the areas shallower than about 1500 m had been extensively surveyed by the CSIRO and demonstrated to consists of a series of seamounts on which grew extensive coral reefs dominated by the deep-sea scleractinian *Solenosmilia variabilis*. *S. variabilis* supports an extensive and diverse benthic community on the seamounts at depths ranging from roughly 1000 to 1300 m (Koslow et al., 2001; Althaus, et al., 2009; Thresher, et al., submitted ms), and is a focal habitat for orange roughy and dories, both of which support important regional fisheries. Protection of the *S. variabilis* reef was one of the key objectives of the SE Commonwealth Marine Reserve.

Predicting such climate change impacts with confidence is difficult for deep-sea communities, such as the *S. variabilis* reef, due to two major sources of uncertainty: (1) the deep ocean's responses to climate change, which is compounded by short historical instrumental records against which to calibrate and validate predictive models, and (2) biological responses to these changes in the ocean environments. Deep-sea corals are logistically difficult subjects for experimental studies. As a result, environmental tolerances need to be inferred, rather then demonstrated, from present-day distributions, from proxies and from generalisations derived from studies of related shallow-water taxa. Refining these uncertainties is critical to developing effective management responses to climate change impacts that have the potential to severely degrade the conservation and ecological service values of deep-reef ecosystems.

In this project, we address these issues for the ecologically important reef-forming scleractinian *Solenosmilia variabilis* on seamounts in the SE Commonwealth Marine Reserve. Global biogeographic analyses suggest that the depth distribution of *S. variabilis* is constrained to areas where carbonate levels are above or close to saturation

($\Omega \geq 1$)(Davies & Guinotte, 2011), making it and its associated biota possibly particularly vulnerable to saturation horizons that are shoaling as a result of anthropogenic climate change. In this study, we address both sources of uncertainty in the global predictions. First, we use a suite of indirect approaches to more robustly estimate the tolerance of *S. variabilis* to low carbonate conditions, and second, we apply these tolerance limits to an up-dated predictive model of present and future carbonate saturation state. From these analyses, we determine the distribution of habitats likely to be suitable for the continued presence of the *S. variabilis* reef in the Australian region under a "business as usual" climate change scenario and identify possible refugia for the reef and community, which could be considered for management protection if needed.

4 NEED

Australia's highly endemic deep-water coral communities are under a current and accelerating threat of being squeezed out of existence, between seamount summits typically deeper than 1000 m. and carbonate levels that are falling and pushing the saturation horizon towards the surface. This horizon, below which the reef-forming corals apparently cannot grow (Guinotte et al., 2006), has already shoaled by 50-130 m in the last 200 years due to industrial CO_2 emissions (Thresher, et al., ms). Under-saturated water is likely already encroaching on the reef, which recent surveys found is just below the current saturation horizon (Thresher, et al., 2011), and not above it, as expected. There is real risk that the reef is already stressed and may even be dying. The problem will only get worse. Under a "business-as-usual" scenario, even the tops of the seamounts will be under-saturated in the next 50-100 years. With nowhere to go, Australia's cold-water reefs could "simply disappear" (Poloczanka, el al., 2007).

There are presently no adaptation strategies for dealing with this threat, nor even any research on strategies, even though it challenges the key objectives of the SE Commonwealth Marine Reserve Network, and the survival of deep-sea reefs globally. This project, developed in consultation with DSEWPAC, evaluates the magnitude of the threat to Australia's key reef-forming species, and identifies and tests management options for adapting to it. It addresses NARP priorities for determining ecosystem vulnerability and the feasibility of intervention and adaptation strategies.

5 OBJECTIVES

1. To develop practical options for DSEWPAC to manage the impacts of climate change on the South-east Commonwealth Marine Reserve
2. To develop a generic model that can be applied to forecasting the impacts of climate change on other deep sea biota

6 METHODS

The project's objectives was achieved by (1) developing and validating a biologically realistic model of the distribution of Australia's principal reef-forming deep-sea coral, *Solenosmilia variabilis*, that includes information on its sensitivity to environmental factors such as temperature, salinity and carbonate saturation state, (2) using this model to forecast the coral's potential distribution under different climate change scenarios, (3) identifying possible refugia for the community, which could be considered for management protection, if needed, and (4) liaising closely with DEWHA regarding management implications and strategies.

1. Model development and validation: Details are provided in the appended draft manuscripts. In brief, the spatial forecast model was developed in collaboration with the Marine Conservation Institute (Seattle, USA), NIWA (NZ) and the CERF Marine Biodiversity Hub. MCI has in hand a presence-only model (MaxEnt) that it is using to predict the distribution of modern deep-sea reef-forming corals (Guinotte, et al., Pew Charitable Trusts, Final Report, 2009). This model is immediately available to the project, but is generic, and needs to be customized to *S. variabilis* in the SW Pacific region. NIWA has been analysing and attempting to predict the distribution of corals on NZ seamounts using Boosted Regression Tree Analysis (A. Rowden, pers. comm.) and to relate those distributions to the outputs of global maps of carbonate saturation horizons, roughly downscaled to New Zealand waters (Bostock, et al., Abstract, 4th Internat. Deepsea Coral Symp., 2008). Their model structures are at an early stage of development, and have been discussed with MCBI in the context of a regional comparison of models and integration of results. We will participate in that integration, to develop and validate and optimal forecast model structure. This assessment will be informed by the work of the CERF Marine Biodiversity Hub, which has assessed the accuracy and systematic error of different model classes when used to predict the modern distributions of marine benthos from patchy field data (N. Bax, pers. comm.). The CERF background work will inform the choice of models used in this project, against the background of the amount and reliability of information available of the target species' environmental tolerances (see below) and environmental maps of the region. At the moment, the default model we will use is the MCI model, which is in hand, but we will hold a small workshop in Hobart early in the project (March-April, 2011) to discuss other possible models, the data requirements for each, and their suitability for use in the present project.

   All models will be informed by CSIRO's integrated oceanographic data sets (in particular, the CSIRO Atlas of Regional Seas [CARS], which is being up-graded to include nutrient data), sea bottom topography and substratum maps (accessed via the CERF Marine Biodiversity Hub and GA), and CSIRO's regionally downscaled state-of-the-art ocean carbonate models. The last will be tested and refined against historical measurements made locally (CARINA Group. U.S. Department of Energy, Oak Ridge, Tennessee. doi: 10.3334/CDIAC/otg.CARINA.SO.V1.1, 2010) and against near-bottom and water-column measurements made on and around the Southern Hills seamounts in January 2009 (Thresher, et al., 2011.). Additional carbonate profiles to groundtruth and tune the carbonate model will be obtained near *S. variabilis* reefs off NE Tasmania in November 2010 (ship-time already allocated).

The environmental tolerances of *S. variabilis* are central to developing an accurate predictive model for the species. These tolerances will be determined three ways, as no single assay is likely to be definitive. In aggregate they should provide a good measure of the temperature, salinity, oxygen and carbonate requirements of the species.

a. By documenting the environmental ranges it presently inhabits, globally from information in the literature and personal communications with researchers overseas and locally by comparing the coral's distribution on different seamounts (as determined by in 2008/10 using the ROV Jason and AUV ABE) with concurrent oceanographic measurements (temperature, salinity, oxygen from CTD, and pH and alkalinity from bottle casts). Coral distributions off NE Tasmania, determined using the Jason, will be compared with environmental data to be determined by hydrocasts in Nov. 2010. Apparent distributions (presence/absence data as determined from trawl surveys) for other sites (e.g., Cascade Plateau, Lord Howe Rise) will be compared with data from the CARS database and carbonate saturation levels as determined from a downscaled regional oceanographic model. Results will be integrated with parallel analyses being done by NIWA on *S. variabilis* on NZ seamounts.

b. By comparing historical changes in its depth distribution with concurrent oceanic conditions as inferred from paleo-climate models and skeletal proxies. Our observations indicate that in the past *S. variabilis* was abundant about 200 m deeper on the Southern Hills seamounts than at present (see Koslow, et al., 2002). We suspect this deeper distribution occurred during the Last Glacial Maximum (ca. 15000 yrs Before Present), which was perhaps not coincidentally a period of low atmospheric CO_2. Using specimens we have in hand that were collected from precisely known depths using Jason, we will 1) date the changes in depth distributions of the coral using radiocarbon dating (30-50 specimens dated), 2) compare the history of the changing depth distributions with the timing of changes in environmental conditions in the Southern Ocean as inferred from paleoceanographic models, and 3) determine the environment the coral's lived in from skeletal proxies for temperature (Cohen, et al., in prep) and pH. The elemental analyses of the skeletal fragments will be done using ICP-MS at the Univ. Tasmania Central Sciences Laboratory, dating of colonies will be done in collaboration with the ANU Research School of Earth Sciences (Stewart Fallon), temperature reconstruction from proxies in collaboration with Woods Hole (Anne Cohen), and the pH proxies possibly in collaboration with UWA (J. Trotter). To determine the factors that may have changed over time, and thereby changed the depth distribution of the coral, we will compare the inferred conditions when the corals occurred below their current depths with those there now, and with those in the depth range it presently inhabits.

c. By measuring the coral’s tolerance ranges in the laboratory. The aquarium study will potentially provide the most precise information on tolerances, but will be logistically difficult given the depths at which the corals occur. Live specimens will be collected in November 2010 (ship time already allocated) and transported to Hobart in chilled seawater aquaria. The experimental design will test the interactive effects of water temperature (approximately 2º below to 4º above present conditions) and pH on apparent health (assayed by on the amount of time the polyps are extended). This kind of work has not previously been done on deep-sea corals, so the experimental procedures will have to be developed as the work progresses. We anticipate initially, however, a series of step-wise changes in temperature to define this tolerance range at species normal pH (roughly 8.1), each step being held for 2-4 weeks depending on the responsiveness of the corals. These will be followed by a perpendicular series varying saturation state while maintaining the corals at the species’ typical water temperature (4ºC). The protocol for determining interactive effects, and possibly testing effects of varying salinity, will be determined after the first round of trials. Two cold-water aquaria are available to undertake the work, along with a third that will be used to house control colonies. We have successfully kept two other deep-sea corals (though not yet *S. variabilis*) alive in these aquaria for over a year.

These data will be incorporated into the predictive model(s) of the present day distribution of *S. variabilis* regionally. Model outputs will be tested against its present documented spatial and depth distribution off Southern Australia and in the Tasman Sea, and cooperatively with NIWA, against the distribution of the species on NZ seamounts.

2. The completed model will be driven in forecast mode using a three-dimensional model for ocean carbonate saturation state, that we have in hand, down-scaled to the reef area. The downscaling and ocean forecasting will be done by R. Matear (CSIRO), a world authority on ocean carbonate modelling, at no cost to this project. Projected regional changes in other factors, such as regional productivity, surface and sub-surface temperatures and salinity, will be input as spatially explicit data from other climate forecasts models that have been developed by CSIRO MAR. During the deployment of the predictive model, information will be shared (in a two way process) with the Atlantis modelling group so that consistent environmental properties and impact assessments are used in the two cases.

3. Project output will be a series of maps showing probability distributions of habitat suitable for deep-sea coral reefs in the Australian region, under a range of different climate change scenarios. The use of these maps to guide management decisions has already been discussed with DSEWPAC, and further discussions will be held as the project progresses. Currently, the fate of the reef assumes it has limited options to move into shallower regions, due to the minimum depths of its known seamount habitats. This prediction may be wrong. Swath maps of the SW corner of Tasmania, for example, indicate hard ground in the depth range of 200-1500 m, less than 100 km away from the reefs in the Commonwealth Reserves. This area is unexplored biologically, but could provide a pathway for

the community to move into shallow areas if forced to by climate change. We also know that reef communities similar to those in the Commonwealth Reserves exist outside of the reserves, such as off NE Tasmania and in the Great Australian Bight. The forecast model will be used to determine if areas where the coral is now found will remain suitable for its continued presence and, if not, where, if anywhere regionally, refugia will exist. If so, it will provide managers options of extending protection to them, if needed, to ensure their utility as refugia.

Even if refugia for the *S. variabilis* reef develop locally and can be protected, the long life span of the coral, its likely limited ability to disperse, and the rapid rate of climate change may make it difficult for it to naturally colonize new areas in time to survive. Human-assisted translocation may be required, as has been suggested for some threatened terrestrial communities. We will undertake a desktop evaluation of this option and formulate a research plan to test its potential, as a possible follow-on project.

7 RESULTS/DISCUSSION

Given the logistical difficulties of keeping *S. variabilis* alive in aquaria for experimental studies, we used five indirect indicators of environmental tolerances for the species in Australian waters. Results from these analyses can be summarised as follows:

Inferences from Present Day Distribution
- global - $\Omega_{aragonite}$ probably limiting, at a value between 0.9 and 1.0
- Australia/New Zealand distribution - temperature and/or $\Omega_{aragonite}$ limiting, at 3.0º C and 0.85, respectively
- Stress - *S. variabilis* stressed below $\Omega_{aragonite}$ of approximately 1.0

Inferences from Present Day distribution on Tasmanian seamounts - Minimum temperature 2.85ºC; minimum $\Omega_{aragonite}$ of 0.84

Inferences from Growth rate/skeletal density - Not informative

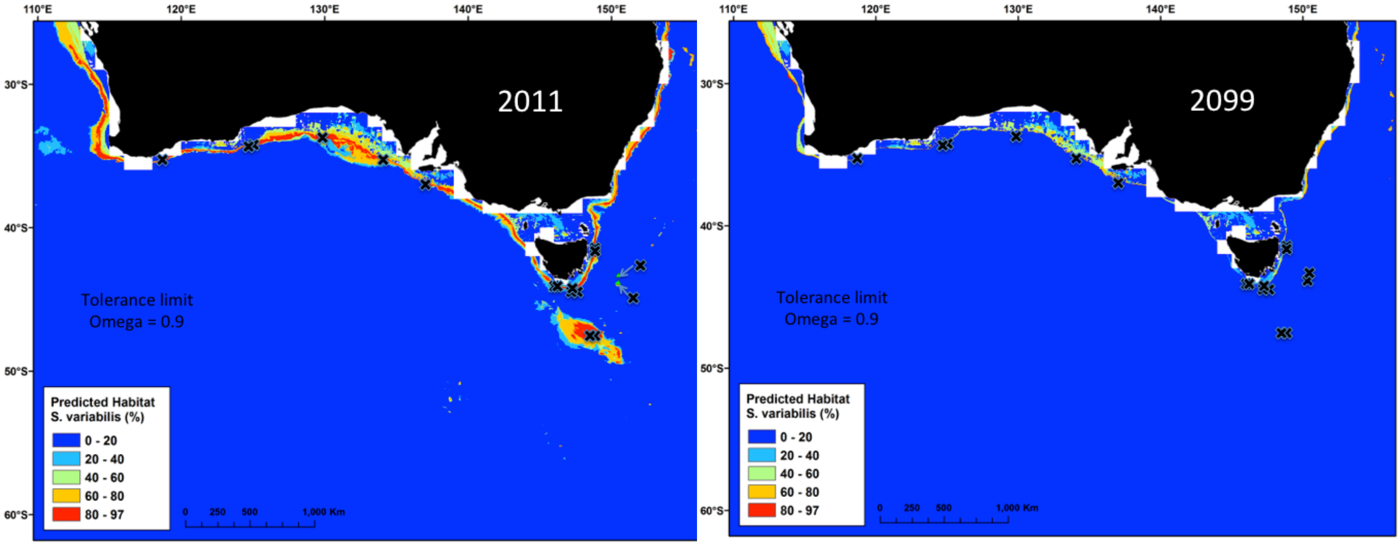
Inferences from aquarium observations: *S. variabilis* prefers higher temperatures and higher pH than solitary scleractinians

Inferences from historical distributions: Proxies suggest conditions during development of sub-fossil reef were similar to those of the modern, shallower reef. Minimum temperature and carbonate saturation states indicated are 3.2ºC and 0.92, respectively.

From these data, we draw several conclusions. First, it is difficult overall to separate a lower depth distribution based on a minimum temperature tolerance from one based on a minimum saturation state tolerance. Second, across several of the assays, minimum temperatures tend to close to 3º C. Third, across assays minimum saturation state ranges from about 0.85 to 1.0. Fourth, direct observations on Tasmanian seamounts indicate that *S. variabilis* presently survives, and appears to be growing, at a temperature of 2.85ºC and a saturation state of 0.84. However, fifth, extensive reef structure occurs only at a higher temperature (3.6º) and higher saturation state (0.91). Finally, sixth, a preference for higher temperatures and higher pH in aquaria by *S. variabilis* than two species of solitary corals is consistent with their distributions in the field (solitaries deeper and hence in cooler water and at lower saturation states than *S. variabilis*)

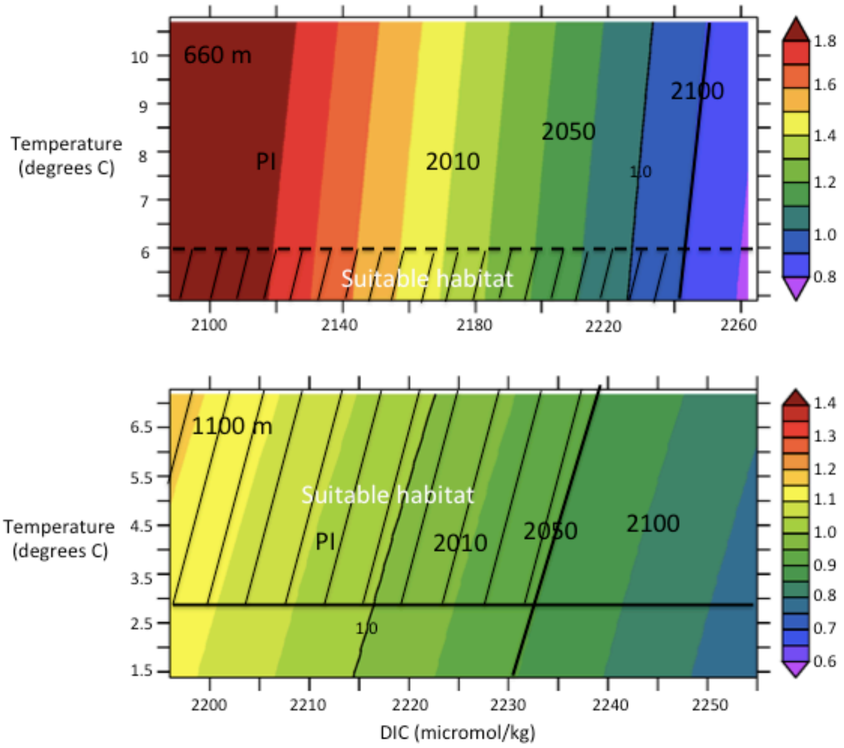
Two approaches were taken to assess the suitability of future conditions in the Reserve area for the continued viability of *S. variabilis* reefs.

First, we downscaled a global model developed explicitly to predict suitable habitats for deep-sea reef forming corals, ran it explicitly in the southern Australian region for *S. variabilis*, and the forced it into a future state using a global model to predict ocean carbonate saturation states. Results are shown below. The model predicts that at an assumed minimum requirement of a saturation state on 0.9 (10% under-saturated), by 2099 none of the current areas occupied by *S. variabilis* reef will be suitable for the species. Some marginally suitable habitat along the continental shelf might become available, however, though this very much depends on the availability of hard ground on which the reefs can form. Most shelf habitat is sedimentary or mud stone, neither of which will apparently support reef development.



Habitat suitability map for southern Australia at present and as predicted in 2099 based on a state-of-the art presence-absence model, a carbonate saturation state distribution at depth derived from Orr et al (2005), and an assumed minimum carbonate tolerance limit for *S. variabilis* of 0.9. Colors indicate predicted degree of habitat suitability (red = highest). X's indicate sites where live S. *variabilis* has been found.

Second, we explicitly modelled conditions on the Tasmanian seamounts (Huon Marine Reserve) both to verify the results above using a regionally specific oceanographic model and to test whether movement of the reef to the seamount peaks would be a useful adaptation strategy. To do these analyses, we used the Australian Community Climate Earth System Simulator-Ocean (ACCESS-o), with a simple marine biogeochemical cycles module (WOMBAT), to predict conditions in 2050 and 2100 for the approximate mid-depth of the modern day reef (1100 m) and at the peak of the shallowest seamount in the Marine Reserve (660 m). Results are shown below.



Forecast aragonite saturation conditions (colour-coded) for the top of the shallowest seamount in the Tasmanian region (660 m depth) in 2050 and 2100 (top), as compared with conditions at 1100 (bottom), based on highest probability estimates of local changes in temperature and carbonate chemistry. Saturation values less than 1 are under-saturated with respect to aragonite; values greater than 1 are super-saturated. Black diagonal lines indicate the estimated tolerance limit of *S. variabilis* to low carbonate saturation levels (0.9). Horizontal line in the bottom figure indicates apparent minimum temperature tolerance (2.85º C). Suitable habitat for the coral is therefore defined by the upper right hand area bounded by the intersection of the two lines and indicated by the thin diagonal lines. The same approach is used in the 660 m analysis, but the dashed line indicates roughly estimated long-term temperature maxima for *S. variabilis* (ca. 6º C), with suitable habitat in the lower right area bounded by the intersection of the two lines. PI = pre-industrial.

From these analyses, we conclude that under the forecast scenario used ("business-as-usual"), (1) conditions will no longer be suitable for reef development at 1100 m by roughly 2050, and (2) conditions at shallower depths are not now and will not become suitable for *S. variabilis* in the future. This is mainly because temperatures at those depths will exceed its maximum tolerances by several degrees.

These forecasts are likely to be conservative. Globally, CO_2 levels are rising faster than the assumed business-as-usual scenario tested here, so that conditions unsuitable for the reef are likely to develop more rapidly than we predict and may be more extreme.

8 BENEFITS AND ADOPTION

This project has significant benefits at three levels:

First, as a result of this project cost-effective management plans may be developed that prevent the loss of Australia's deep-sea coral reef ecosystem, currently threatened by the effects of climate change. The project results indicate strongly that in the absence of management intervention or an unexpectedly large adaptive capacity by the corals, the reefs will degrade and likely go extinct by 2100, with a consequent loss in regional biodiversity and fish habitat.

Second, the results of this project and the decisions made as a result of it will have global implications. The same issues of loss of deep-sea ecosystems due to climate change have been forecast globally, based on relatively crude models. The results of this project will not only provide a template for similar work that will need to be undertaken elsewhere (since the inception of this project, a parallel project that builds on the approaches we developed has since started in NZ), but will also provide a more realistic assessment of the threats posed globally than are currently available. In that regard, we anticipate a high profile technical publication highlighting the global implications of the work.

Third, to date consideration of the impacts of climate change on deep-sea ecosystems has been largely theoretical and conceptual, i.e., vague and ill defined. Management responses have been similarly unfocussed. This project provides robust results and constrained timelines of the magnitude of the threat posed by climate change to a key deep-sea ecosystem. The flow-on from this project is likely to be the first robust consideration world-wide of management options for deep-sea assets in the face of climate change, and hence is likely to serve as a precedent and guide for other countries and agencies that will be facing similar problem sets.

The principal route to adoption locally will be a workshop of key stakeholders to consider feasibility of different management options, discussed below. Internationally, the path to adoption will entail a high profile publication and presentations in international forums.

9 FURTHER DEVELOPMENT

Three further steps are required to fully implement the results of this project.

(1) As noted above, the project's predictions are based on the IPCC "business-as-usual" (A2) scenario for global CO_2 emissions. Data over the last decade indicate that emissions are already exceeding this scenario, and are closer to an intensive carbon use scenario (IPCC A1F1). As a result, the predictions we make regarding the impacts of ocean acidification on viability of Australia's deep reefs are likely to be optimistic. The regional model used to develop these predictions is being revised to allow incorporation of an A1F1 type scenario. The revisions are due to be completed in September/October 2012. For an accurate forecast of the magnitude and timing of impacts of ocean acidification, and hence the time available to develop and implement adaptation strategies, the forecasts need to be run using this more realistic scenario.

(2) Given the magnitude of the projected impacts of climate change on the viability of the deep-sea reef ecosystem, the implications of this project need to be discussed in detail with all relevant stakeholders, and options canvassed as to possible adaptation strategies. Brief discussions have been held with DSEWPAC, the NERP Biodiversity Hub and CSIRO Climate Adaptation Flagship about the desirability, participant list and rough agenda for such a workshop. Tentatively, one is being planned for November/December 2012.

(3) As a result of this workshop, it is likely that additional information will be required before adaptation strategies can be implemented. As an example, given the long life spans of the corals and their probable infrequent recruitment, it is likely that assisted translocation of coral colonies will be required to seed continental shelf refugium sites with living coral. The logistics of such activities need to be considered in detail, given the likely costs involved, and it is likely that one or more pilot projects will be required to test the logistical feasibility of this and other adaptation activities.

10 PLANNED OUTCOMES

This project will inform DSEWPAC as to how quickly it needs to respond to the threat of climate change to the deep reef, and assess and possibly provide practical adaptation strategies for responding. Specifically, there are two key outputs: an assessment of the environmental tolerances of the principal reef-forming species (*S. variabilis*), and identification of sites that might be refugia for the species under various climate change scenarios. A third, supplemental output will be to assess whether intervention, in the form of seeding these sites, might be a required option and the development of a recommended research plan to assess the feasibility of translocation.

The first output will provide critical information as to the amount of environmental change *S. variabilis* can sustain, and hence the rate at which DSEWPAC needs to respond in implementing adaptation strategies. The second and third will identify practical components of this adaptation strategy.

The path from output to outcomes in this case is relatively direct, and hinges upon maintaining close contact with DSAWPAC and informing them of the results and implications of this research. This will be done in three ways. First, meetings with DSEWPAC managers (who are based in Tasmania) will be held near the end of the project, to inform them directly of the results and implications, to be followed up by a written report. Second, CSIRO is participating, and in some cases initiating, national meetings on impacts of climate change in general, and ocean acidification in particular, on the marine environment. CMAR, for example, will host an international workshop on marine impacts of ocean acidification early in the project (early 2011), most likely in Canberra (details still being finalised). The project, its results and its implications will be presented at this and subsequent fora, to which DSEWPAC, DCC and other relevant managers and policy makers will be strongly encouraged to attend (one of the reasons why the 2011 meeting will be held in Canberra). These for will also facilitate transfer of the skills, methods and results from the project internationally. All four of the participating senior scientists (Thresher, Matear, Guinotte and Fallon) are all also heavily involved in this area of research, and are engaged with a number of international initiatives regarding deep-sea coral ecology and impacts of climate change, which will also ensure wide dissemination and uptake of the results. Third, results of this project will be provided in written form, as part of the extension effort, in the Marine Adaptation Bulletin, and as technical publications.

The first metric of the success of this project will be the quality of the predictive maps of likely future refugia for the deep-reef. This can be assessed technically by sensitivity analyses of the model outputs and through indices of the probabilities associated with predicted habitat suitability.

The second metric will be the extent to which the results of this project are taken up by and inform DSEWPAC deliberations, and their effect on policy development and implementation. As this is likely to be a longer term response to the project, only initial indications from DSEWPAC and policy makers are likely to be available during the current lifetime of the project. In that regard, both DSEWPAC, the NERP Biodiversity Hub and the CSIRO Climate Adaptation Flagship has all expressed strong support for a workshop on assessment and development of adaptation strategies for the deep-reef, tentatively scheduled for November/December 2012.

11 CONCLUSION

This project confirms that climate change in general, and ocean acidification in particular poses an existential threat to the deep-sea coral reef ecosystem currently protected in the SE Commonwealth Marine Reserve. The modelling results are mixed as to whether any refugia for this ecosystem will remain in Australian waters by 2100, particularly if the current actual rate of CO_2 emissions (as opposed to the more conservative ones used in current generation models) is factored into the analysis. In the face of this threat, it is essential that key stakeholders meet to discuss possible adaptation strategies, in what is likely to be a world-first effort to directly confront and manage the impacts of climate change on a deep-sea ecosystem.

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13 COMPLETION CHECKLIST

Provided five bound copies of the final report - ensure that if colour figures are used they are included (in colour) in all five copies?		Y
Provided one unbound double-sided copy of the final report?		Y
Provided an electronic copy of the final report on CD, including a copy of the non technical summary and all materials produced, such as photographs, data sets, manuals, etc.		Y
Confirmed submission of the final financial statement, and transaction report if required, with your financial contact?		Y
Provided two beneficiary responses Will be provided following post-project workshop with key stakeholders, tentatively scheduled for February 2013		I P
Provided your final report distribution list to the FRDC including contact names and postal details (including those listed below)?		Y
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14 INTELLECTUAL PROPERTY

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16.1 PUBLICATIONS

Age and growth of the cold-water scleractinian *Solenosmilia variabilis* and its reef on SW Pacific seamounts

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FOR CORAL REEFS

Abstract Little is known about growth rates of deep-water reef forming corals or the rates at which these reefs accumulate. Such information is critical for determining the resilience of the reefs to anthropogenic impacts such as trawling and climate change. We radiocarbon date live-caught and sub-fossil samples of the bioherm-forming coral *Solenosmilia variabilis* collected from precisely known depths and locations by means of a remotely operated vehicle on seamounts south of Tasmania, Australia. The growth rate of a colony live-caught at 958 m was estimated at 1.1mm linear extension yr^{-1}, and that of a large, recently dead specimen at least 11 mm yr^{-1}. Internal structure of the colony suggests annual deposition of growth increments in its skeletal structure near the growing tips as the skeleton is extended and thickened. The extension rate of the live-caught specimen is similar to those reported in the literature for *S. variabilis* in New Zealand and for other cold-water scleractinians, but that of the sub-fossil appears to be exceptionally high. Dating of additional sub-fossil material indicates *S. variabilis* has been present on Tasmanian seamounts for at least the last 48,000 years, and a reef accumulation rate of 0.12 mm yr^{-1}.

Keywords Demography, Deep-sea, Scleractinia, Age, Growth rate, Holocene, Accumulation rate

Introduction

More species of scleractinian corals occur at depths below than above 50 m (Cairns, 2007), but much less is known about their ecology and demography (Freiwald and Roberts, 2005). Recent surveys document extensive cold-water reefs on seamount and other rocky substrates globally, many of which have been or are likely to be subject to the impacts of deep-water fishing (Pitcher, et al., 2007; Roberts, et al., 2009). Age and growth studies carried out on a few of the deep-water taxa suggest that many are slow-growing and long-lived, usually in excess of a century (Risk, et al., 2002; Andrews, et al., 2002; Adkins et al., 2004; Roark, et al., 2005; Sherwood and Edinger, 2008), which has raised concerns about the resilience of deep-sea coral communities to adverse anthropogenic impacts (Koslow, et al., 2001; Althaus, et al., 2009).

The bioherm-forming colonial coral, *Solenosmilia variabilis*, is widely distributed on seamounts globally (Davies and Guinotte, 2011). In the SW Pacific, it is the dominant reef-forming species, building extensive reefal structure at a depth band of roughly 1000-1300 m on seamounts off NZ and Australia (Koslow, et al., 2001; Thresher et al., submitted ms). These reefs are relatively high is species richness, suggesting that they are important habitat for seamount biota. They are also fragile and easily damaged by near-bottom trawling (Althaus, et al., 2009) and may be particularly susceptible to adverse effects of climate change in general and ocean acidification in particular (Guinotte, et al., 2006). To an extent, this apparent vulnerability depends on the growth rate of the coral and its ability to regenerate after damage and to grow into and colonise new habitat. To begin to quantify this resiliency, we use radiocarbon dating to determine the ages and growth rates of *S. variabilis* collected at precisely known depths and locations off SW Pacific seamounts by means of the remotely operated vehicle *Jason*. We also dated sub-fossil material to provide , for the first time globally, an estimate of the accumulation rate of a deep-water scleractinian reef.

Methods

Field work was carried out and samples obtained from the "Southern Seamount" region south of Tasmania, Australia. The area is described in detail and seamount locations given by Koslow, et al. (2001). The seamounts are of volcanic origin, come to within about 750 m of the surface, and support an extensive benthic community, dominated at depths < 1300 m by the reef-forming scleractinians, *Solenosmilia variabilis* and *Enallopsammia rostrata*, and deeper by hormathiid anemones, bathylasmatid barnacles and isidid gorgonians (Koslow et al., 2001; Althaus, et al., 2009; Thresher, et al., 2011). A large sub-fossil specimen of *S. variabilis* (specimen 2, see below) was trawled from 1140-1200 m depth from Seamount U (44º 19.5' S., 147º 10.8' E.) on 1 April 2007 (Southern Surveyor cruise 2007/2 station 12); trawling details are provided by Althaus, et al., 2009). All other samples were obtained from a survey of the seamounts in December 2008/January 2009 by the Woods Hole Oceanographic Institute ROV *Jason*; for details, see Thresher et al, submitted ms). Samples were taken using a small basket scoop at the end of one of the ROV's manipulator arms. Samples were sorted immediately upon return to the surface. Live caught material was frozen at -70ºC.

The gross skeletal morphology of *S. variabilis* consists of a tubular structure with irregularly spaced but frequent, three-dimensional dichotomous branching (Fig. 3). In most instances, one branch bears a terminal polyp, whereas the other continues developing as the main extension axis. Samples for radiocarbon dating, increment counts and measurements of skeletal dimensions were all taken from the extension axis, at points of relatively uniform diameter just below where the skeleton flares into the next branching. Sampling was done using a Dremel tool, cutting the coral perpendicular to the extension axis. Skeletal diameter was measured using a digital caliper.

Increment analysis

Possible incremental growth structure was examined in Specimen 1, which was alive when caught. Extended sections of the coral were brushed clean of adhering dried organic matter, and then embedded in epoxy (Araldite Kit K3600). Approximate 200 µm sections were cut using a Steuers Accutom saw, which were then attached to glass slides using epoxy. Each specimen was hand ground using a range of fine sandpapers to a thickness of about 25 µm, before being polished using 3 µm grit. Structure was observed and increments counted using a Leica MX16FA dissecting microscope and a Leica DMIRB inverted microscope. Photographs were taken using the Zeiss Axiocam system.

Radiocarbon Sampling and Analysis

Two sets of *S. variabilis* samples were dated using radiocarbon analysis.

1. To assay growth rates of individual colonies, subsamples were taken from the base, tip and intermediate positions of three live-caught colonies. Specimen 1 was 10.7 cm long and was live-caught at 958 m on North Sisters seamount, at 44º 16.6' S., 147º 15.6' E. Specimen 2 was 43 cm long sub-fossil collected by trawl at approximately 1100 m depth on Seamount U, as noted above.

2. As a first attempt to determine the accumulation rate of the reef as a whole, as opposed to the growth of individual colonies, we dated samples collected from a large, apparent cut in the reef we found near the peak of seamount K1, at 1231 m depth (44º 17.566' S., 147º 23.212' E)(Figure 1). The ROV pilot estimated the cut to be about 2/3rds of a meter deep and about twice that wide. One edge was sheer and vertical, the other more gradual, with the cut itself oriented across the top of the reef. From discussions with local researchers and fishers, it is likely the cut dated from 1997, when CSIRO targeted the top of K1 for biological sampling (see Koslow, et al., 2001). The Lewis (1999) dredge used had a mouth 0.6 m deep and 1.2 m wide, which is consistent with our observations. To assess the accumulation rate of the reef, we took two samples from the cut. One was made by digging the mesh basket into the approximate mid-point of the vertical wall of the cut; the second by brushing away loose fragments and then digging the basket into the bottom of the cut. We also selected for dating several well eroded and, we suspected, old samples collected opportunistically elsewhere on the shallower (<1400 m) seamount complex to begin to gauge the maximum age of the *S. variabilis* reef locally.

The method for specimen handling and analysis was similar for all both sample sets. Each coral sample was subjected to physical pretreatments. The outer surfaces were ground off with a dental drill to expose clean white calcium carbonate. The inside was also drilled out to remove the interior dissepiments, resulting in a hollow tube. The hollow tube was coarsely crushed into ~0.25mm chunks and subjected to a 0.1M HCl leach in which ~50% of the outside material was removed. The resulting clean carbonate was rinsed 5x in 18 MΩ water (Milli-Q™) until near neutral pH was achieved.

A further subsample of 8-10mg of $CaCO_3$ was loaded into a 10 ml serum vial (BD Vacutainers ®) and evacuated, before CO_2 was liberated by the introduction of 85% orthophosphoric acid (Ajax UNIVAR, Analytical Grade). The CO_2 was then passed through a cryogenic water trap, measured for % carbon yield and transferred to an individual graphite reactor assembly. In the presence of hydrogen and using Fe powder as a catalyst and a temperature of 570C the CO_2 is converted to graphite, the resulting water from the reaction is trapped using Mg Perchlorate. The graphite is then loaded into Al cathode sample holders for $^{14,13,12}C$ isotope analysis on the single stage Accelerator Mass Spectrometer located at the Research School of Earth Sciences, The Australian National University (Fallon et al., 2010). All samples were normalized to Oxalic Acid I (Stuiver and Polach, 1977) and background subtracted using ^{14}C free $CaCO_3$. Conversion of radiocarbon years to calendar years was preformed using OXCAL 4.1 (http://c14.arch.ox.ac.uk/oxcal/). The quoted uncertainty on the radiocarbon age (at 1 sigma) is reported in Table 1, using the convention of Stuiver and Polach, 1977).

Leaching Experiment

In order to test whether our results were being influenced by any outer coatings on the samples we prepared a larger sample and only mechanically treated the outside and inside of the sample as explained above. An aliquot of sample (~35mg) was loaded into the glass septa sealed vial, enough orthophosphoric acid was added to evolve ~25% of the $CaCO_3$ sample, this was repeated 3 additional times so that we had four samples, the samples containing 0-25%, 25-50%, 50-75% and 74-100% of the material. This successive leaching technique has been used in ^{14}C studies of surface exposed corals to assess the effect of overgrowth contamination. Our results suggest that there is little to no effect of overgrowth on the radiocarbon age with all samples being within error (Figure 2).

Results

Age and growth

In order to use radiocarbon to understand deep-sea coral growth rates the radiocarbon age must be calibrated to calendar age. This is due to variations in ^{14}C production in the atmosphere over time. The other more critical component of the radiocarbon age is the reservoir the carbon originates from. In the ocean the carbon that is incorporated into the $CaCO_3$ skeleton is derived from the dissolved inorganic carbon (DIC) pool. Because carbon in seawater DIC is separated from the atmosphere, radioactive decay without ^{14}C replenishment occurs. In general the radiocarbon reservoir age of seawater increases with depth. We also estimate the reservoir age using the outer growing measurements from live collected corals.

Radiocarbon dating of three sections from live-caught specimen 1 indicates a reservoir age of 630 years (radiocarbon age of outermost section analysed), a colony age of approximately 95 years, possible non-linear growth, and an average linear extension rate of ~1.1mm yr^{-1} (Figure 3e). For the Hill U sub-fossil sample (specimen 2), we are less confident with the reservoir age, so we used two (800 and 1000 years) within the range suggested by regional oceanographic data (Lassey et al 1990) to test the influence of reservoir age on the extension rate (Figure 4c). Seven sub-samples were taken from the colony, ranging from the base to the last growing section (marked by a bifurcation into two terminal polyps). Regardless of reservoir age, a linear regression suggests the 43 cm long sample coral is only ~38 years old, providing a mean estimated linear extension of ~11mm yr^{-1}. We emphasize that this is a minimum extension rate. Within measurement error there is no significant difference between age estimates for the base and outer tip of the sample (Figure 4c), i.e., growth rate could not be resolved within the roughly 50-year measurement error.

Increment structure

Thin sectioning of specimen 2 revealed an internal structure that consists of inward projecting septa surrounded by a calcium carbonate wall that was spanned by prominent radially oriented crystal bundles. Both the septa and the skeletal wall had a fine incremental structure, the former suggestive of an infilling and thickening process and the latter skeletal thickening by deposition of annuli. The annuli were extremely low contrast, difficult to visualise, photograph or count and had an average width of about 200 μm (Figure 3a and b). The number of annuli increased non-linearly from the tip to the base of the specimen (Figure 3d), ranging from 5-11 (range of counts) in a section cut 8 mm from the tip of the coral to 65-70 near the base. Longitudinal differences in the number of counted annuli correlated with changes in the diameter of the skeleton, both increasing from the tip to about 60 mm from the tip and stabilising thereafter (Figure 3d).

Reef age and accumulation rate

The mean estimated ages (radiocarbon, model-adjusted) of three samples collected at the base of the cut in K1 ranged from 5135 to 5748 years BP, averaging 5522 years (minimum and maximum for any given specimen, 4885 and 5968 years BP, respectively). This assumes a reservoir age of 1100 years, the modern value at that depth. Mean estimated ages for three samples extracted from the approximate mid--point of the cut ranged from 2590 to 3184 years BP, averaging 2801 years (minimum and maximum for individuals ranging from 2337 to 3400 years). Assuming an age of 0 years BP at the top of the cut, the regression between depth into the cut and the age of the coral fragments is linear ($R^2 = 0.98$) and has a slope of 0.12 mm/year (95% CI 0.10 - 0.138 mm yr^{-1}) (Figure 6A).

The oldest *S. variabilis* fragment we dated was 47395 - 49000 years old, collected at 1500 m and uncorrected for a reservoir age. The modern radiocarbon reservoir age at 1500 m is about 1200 years.

Discussion

The extension rate of the live-caught *S. variabilis* we examined, at ~1.1 mm yr^{-1}, is similar to those reported for a live-caught and two recent sub-fossil samples in New Zealand by Neil, et al. (ms) (0.25-1.56 mm yr^{-1}) and to the only other reported *in situ* growth rate for a deep-water bioherm-forming scleractinian (~5 mm yr^{-1} for a North Atlantic specimen of *Enallopsammia rostrata*, by Adkins, et al., 2004). More work has been done on the shallow cold-water species *Lophelia pertusa*, for which extension rates of up to 25 mm $year^{-1}$ have been reported (Roberts, et al., 2009). Relatively high extension rates (up to 18 mm $year^{-1}$) have also been reported for Mediterranean Sea specimens of *Madrepora oculata* held in relatively warm aquaria (11.5-12.5° C) (Orejas, et al., 2008), though a subsequent study suggested an average extension rate for the species of about 5 mm $year^{-1}$ (Orejas, et al., 2011).

The internal structure for the live caught *S. variabilis* is also consistent with a ca. 1 mm extension rate per year. Internal banding (annuli) have previously been reported in a North Atlantic specimen of *Enallopsamia rostrata*, by Adkins et al (2004), which also presented evidence that the annuli formed at roughly decadal intervals. We found very fine (ca. 200 µm), very faint annuli in the skeleton of *S. variabilis*. The number of annuli was often difficult to ascertain, but increased from less than 10 close to the growing tip of the colony to about 60-70 50-60 mm from the tip and remained at about that level to the base of the sample (155 mm from the tip). At the same time, the diameter of the colony, all of which was covered with live tissue, increased from about 4 mm near the tip (excluding the flared calyx around the terminal polyps) to increase to just over 5 mm about 50-60 mm from the tip and remaining about the same thereafter to the base of the sample. We interpret these observations as follows: Initial extension of the colony is relatively rapid as a new terminal polyp forms. Thereafter, the colony increases both in length (further extension) and skeletal width, as new aragonite matrix is deposited on the skeleton, presumably strengthening it. This deposition, we suggest, is annual, up to a point. This is suggested by the rough correspondence between distance from the terminal tip and the number of counted increments, with an implied extension rate of ca. 1 mm yr^{-1}, i.e., similar to that indicated by the radiocarbon analysis. Thickening of the skeleton, however, stops at a distance about 50-60 mm from the growing tip, beyond which both the number of counted increments and skeletal diameter are stationary (Figure 6). This proposed growth framework provides a logical basis for colony growth, but also implies that annually deposited increments in this deep-water species are an unreliable means of aging specimens beyond a certain point, even if the logistical difficulties of working with such low resolution annuli could be resolved.

The oldest sample we examined, a sub-fossil *S. variabilis* dating from 300-500 years BP (depending on assumed reservoir age), appears to have an exceptionally fast extension rate. We estimate a minimum extension rate of about 11 mm yr^{-1}, i.e., about 10 times faster than modern conspecific specimens, but also note that the age model does not provide an upper limit to the extension rate. This growth rate appears to be exceptional compared with those of the live-caught sample we examined, with other reported growth rates for *S. variabilis* (Neil, et al., ms), and with respect to growth rates for other deep-water scleractinians (Risk, et al., 2002; Adkins, et al., 2004). Samples taken at the base and tip of the colony, 43 cm apart, do not differ significantly in age, suggesting either a problem with the radiocarbon dating (possibly related to changing reservoir ages or a previously unreported plateau in local atmospheric radiocarbon) or exceptionally fast growth rates for the species in the recent past. Multiple cleaning of the specimen did not significantly alter the age estimate of the sample, allowing us to discount any age distortions due to, for example, ferromanganese oxide accumulation on the specimen.

Dating of the older material allows allows us to provide a first ever estimate of accumulation rates for a deep-water hermatypic coral assemblage. Based on the ages of the samples collected at the mid-point and base of the trawl cut at the top of seamount K1, we estimate an accumulation rate of about 0.12 mm yr^{-1}, which corresponds to about 1 meter every 8.1K yrs. Accumulation rates have been estimated for shallower hermatypic mounds for two North Atlantic scleractinians, *Lophelia pertusa* and *Oculina vericosa*, based on a combination of dating and acoustic estimates of reef/mound thickness (reviewed by Roberts, et al., 2009). These estimates are orders of magnitude higher than we calculated for the South Pacific *S. variabilis* reef. This could reflect regional differences in productivity, in water temperatures (modern temperatures for the North Atlantic sites are 3-5ºC higher than the 3-4º C. typical of the *S. variabilis* sites) or absolute coral extension rates (higher in *L. pertusa*) which in turn could also be a function of productivity or water temperature. The slow accumulation rates for the *S. variabilis* reef is also consistent with qualitative observations of thick reef complexes (we estimate reef mounds off NE Tasmania at 2-3 m thick, for example) and the apparent longevity of the reef. Our oldest sample dated thus far for the reef complex is just under 50 K yrs BP, pre-dating the Last Glacial Maximum and suggesting the seam,ounts have been occupied by *S. variabilis*, albeit perhaps intermittently, throughout the Holocene (see also Thiagarajan, et al., submitted ms, for a parallel analysis of South Pacific *Desmophyllum dianthus*).

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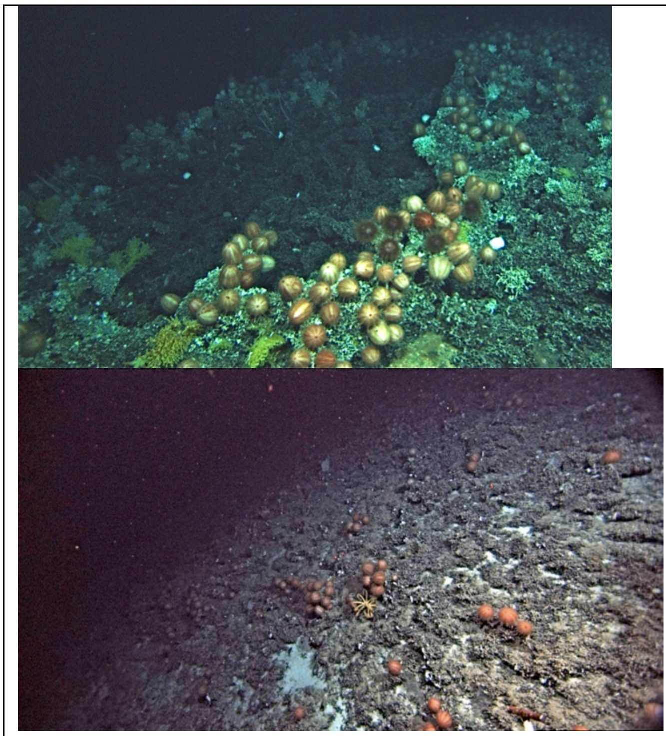

Figure 1. Left. Modern reef and 0.67 m deep trawl cut on the peak of seamount K1. Depth 1231 m. Right. Seascape of dead *Solenosmilia* reef at 1480m on Seamount A1.

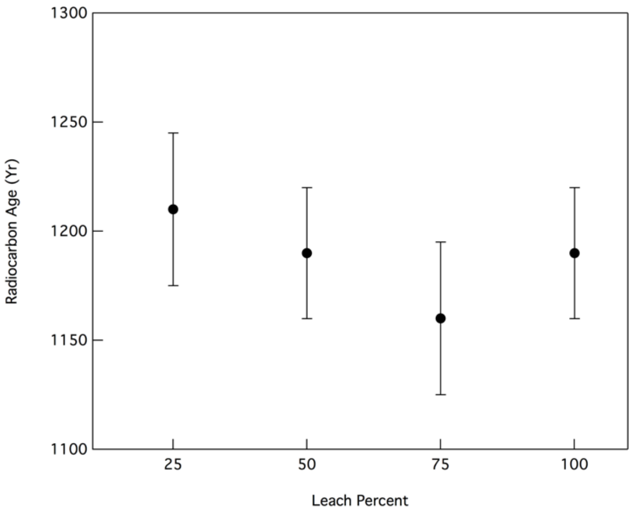

Figure 2. Radiocarbon age of single sample after collecting the first 25%, then successive 25% of CO^2 evolved from sample.

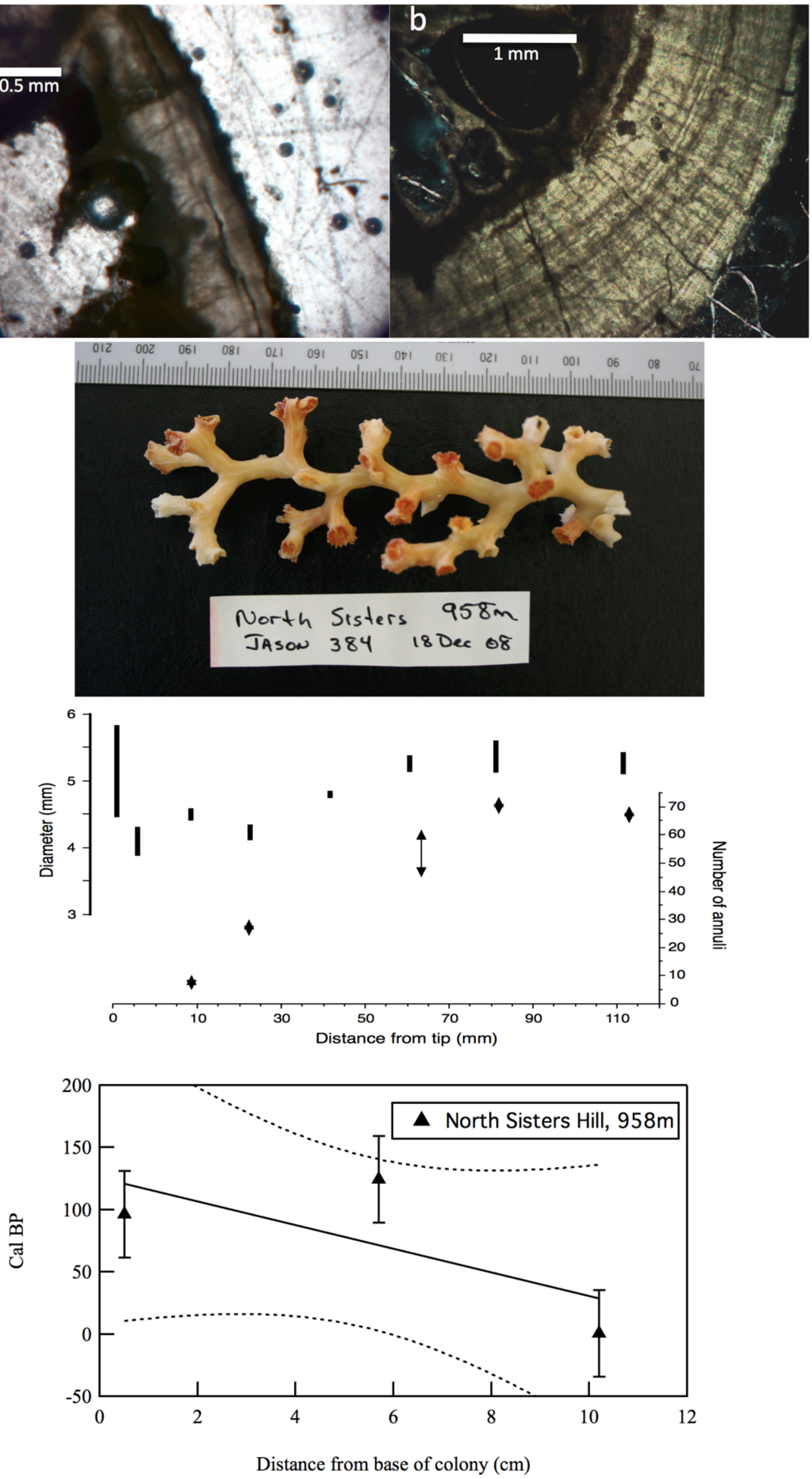

Figure 3. *S. variabilis* specimen 1. a and b) Transmitted light microphotographs of sections taken 8 mm from the terminal polyp and 5 mm from the fragment base c) Live collected specimen. d) Skeletal diameter (thick bars, indicating minimum and maximum) and number of counted skeletal annuli (fine bars with arrows) as a function of position along the extension axis. Arrows indicate the range of counts in each section. e) Calendar calibrated radiocarbon age; regression indicates an age of ~95 years and extension rate of ~1.1 mm yr^{-1}.

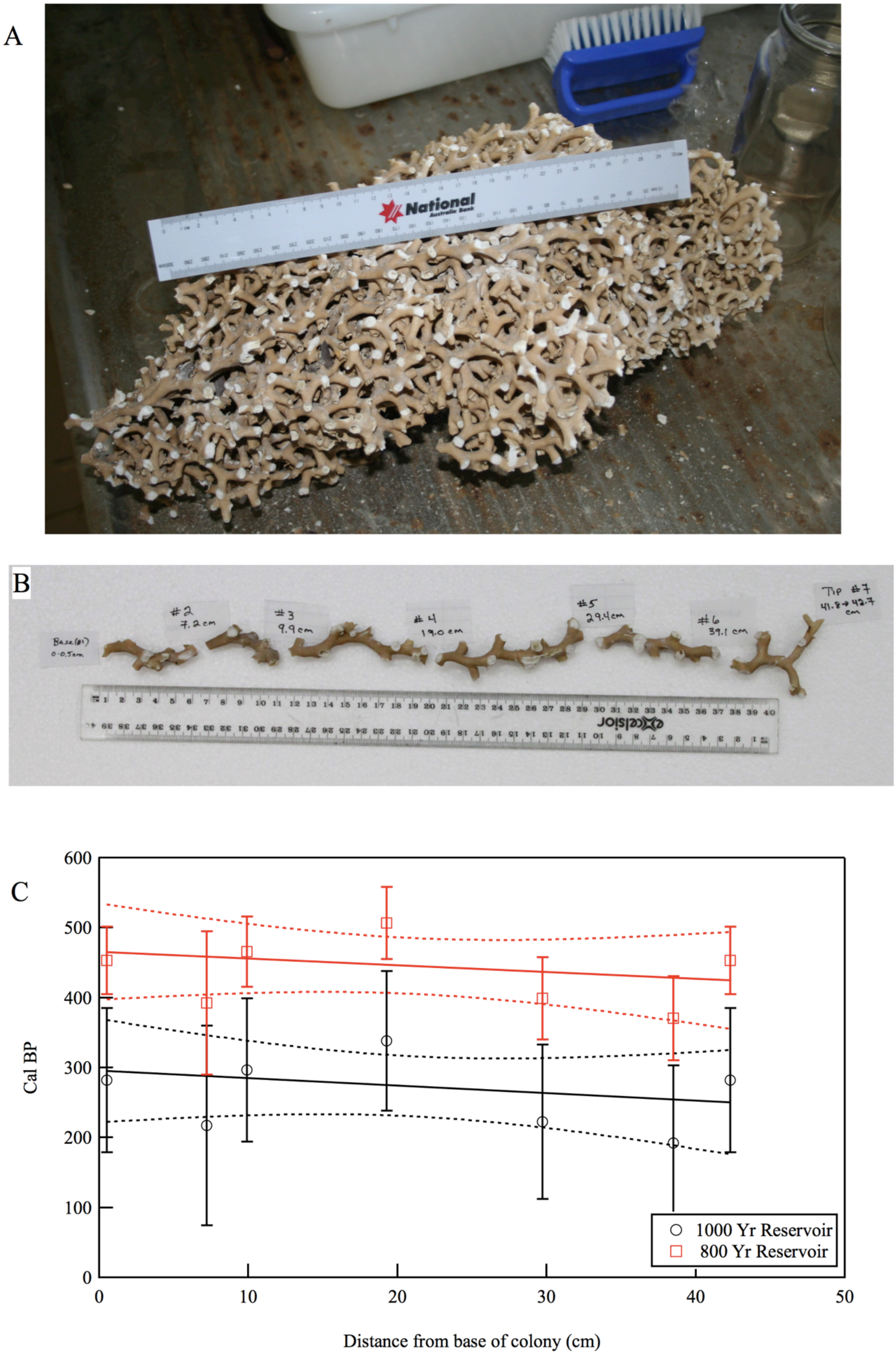

Figure 4. *S. variabilis* specimen 2. a) Sub-fossil sample. The ruler lies immediately above the section removed for dating. b) Excised section, showing locations of sections removed for dating. c) Calendar calibrated radiocarbon age results using a reservoir of 800 ± 50 (squares) and 1000 ±50 (circles) and the resulting linear regressions (95% CI). Both results suggest coral extension rates of ~11 mm yr^{-1}, but also extension rates that may be faster than can be resolved by radiocarbon dating.

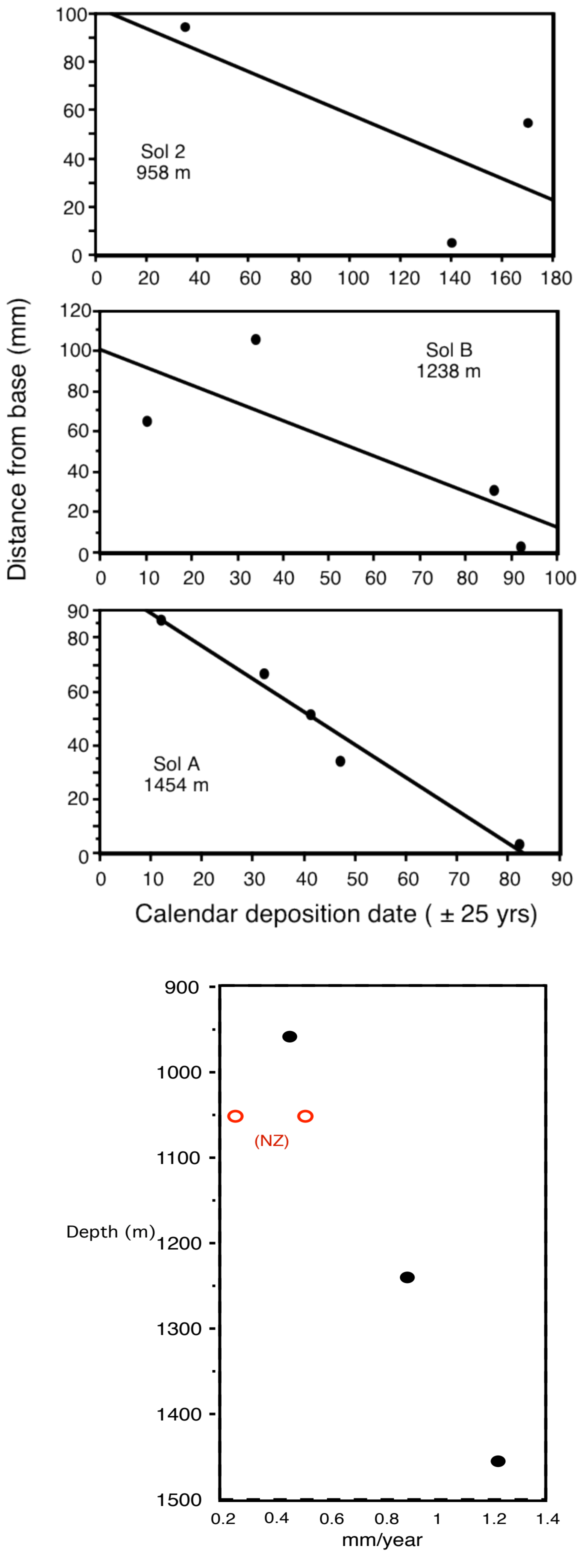

Figure 5. Top: Length at age plots for three live-caught *S. variabilis*. Bottom. Relationship between capture depth and growth rate

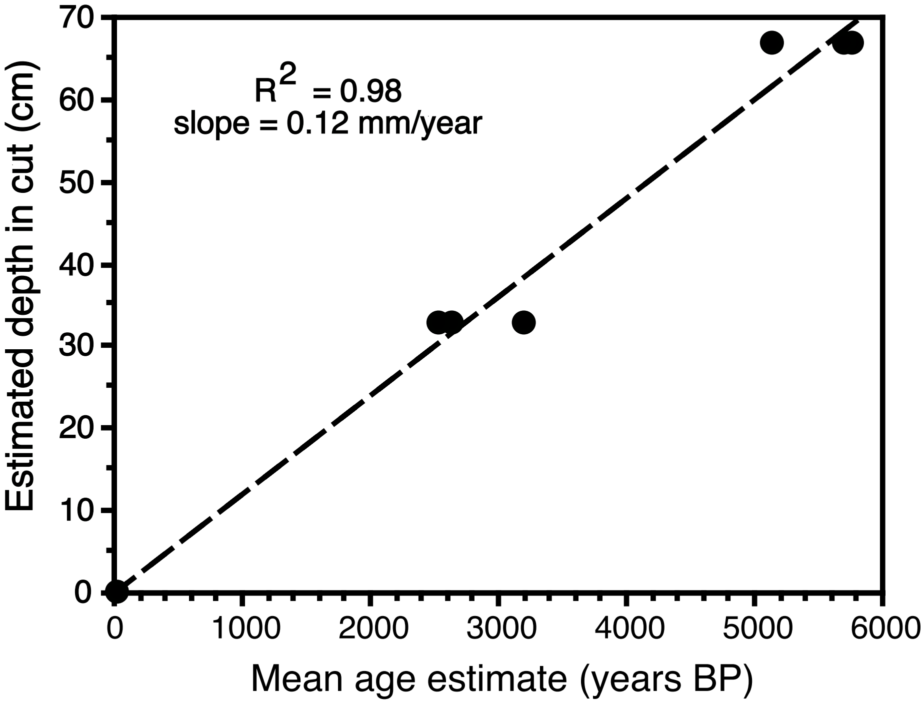

Figure 6. A. Calendar ages of sub-fossil *S. variabilis* fragments collected by ROV from the base and approximate mid-point of the trawl cut in K1.

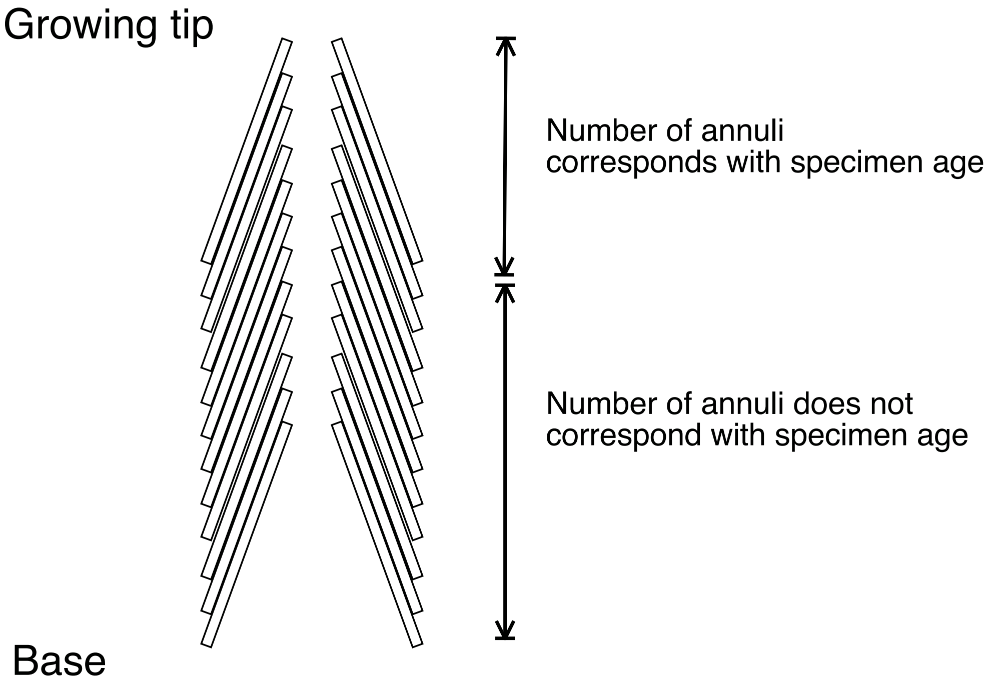

Figure 6. Diagram of the proposed skeletal growth of *S. variabilis*. Each year, a new layer of atagonite is deposited over the existing skeleton near the growing tip, resulting in a thickening and strengthening of the linear growth form. This process is maintained for a period of several decades, after which further thickening ceases. As a result, the number of growth increments close to the growing tip reflects annual ages, whereas those further along the extension axis indicate thage at which thickening stopped.

16.2 PUBLICATIONS

Impacts of ocean acidification on the viability of coldwater reefs off SE Australia: predicting impacts in a data-poor environment

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Abstract

Global models suggest that increasingly acidic oceans will have an extremely adverse effect on the long-term viability of mant cold-water coral reefs. However, predicting these impacts with confidence is difficult due to large uncertainties regarding the deep ocean's responses to climate change and even larger uncertainties with regard to the coral's response to these changes. We address these issues in the context of the future viability of the reef-forming scleractinian, *Solenosmilia variabilis*, on seamounts in a marine protected area off southeastern Australia. Using a range of approaches, we estimate that established colonies of the coral can persist in saturation levels ($\Omega_{aragonite}$) as low as 0.84, but that long-term viability probably requires saturation levels no lower than 0.9-0.94 and that extensive reefal development may require saturation levels closer to 1.0. To determine the likely future environmental conditions in the seamount area, we use a state-of-the-art coupled ocean-atmosphere biogeochemical model, downscaled to the seamount enviroment and the mean depth of the present day reef (1100 m). The model indicates that under a "business-as-usual" atmospheric CO_2 scenario, likely carbonate levels by 2100 at the seamounts will be 0.83-0.86, with a possible range of 0.77 - 0.92 if all sources of uncertainty are included. These values are likely to be under-estimates, as global CO_2 levels are rising faster than the IPCC "business-as-usual" predictions. The combination of relatively high tolerance limits and low predicted enviromental carbonate levels suggests *S. variabilis* reefs will not be viable in the southeastern Australian seamount region by 2100. Spatial modeling indicates some coastal habitats may remain suited for the species locally, but maintanence of the species and its reefs may require assisted translocation of coral colonies and the use of artificial structures to provide suitable hard ground environments.

Key words: Anthozoa, Aragonite Saturation Horizon, Cold-water coral reef, Climate change, Scleractinia, Seamount

Introduction

Ocean acidification results from net uptake by the ocean of carbon dioxide (CO_2) emissions, which causes a decrease in the carbonate ion concentration of ocean waters (Feely, et al., 2004). This decrease has been forecast to hamper production of biogenic carbonates (aragonite and calcite) in the skeletons, shells and tests of marine taxa (Orr et al, 2005; Moy, et al., 2009). Coral reefs in the deep-sea have been identified as particularly vulnerable, on the basis of pre-industrial carbonate levels at the depths and temperatures they inhabit that were already low (Guinotte, et al., 2006; Turley, et al., 2007; Riegl, et al., 2009; Veron, et al. 2009). Direct tests of this sensitivity have not been done, but in at least one relatively shallow cold-water coral, *Lophelia pertusa*, calcification rates decline as predicted in low pH conditions (Maier, et al., 2009). Deep-water corals may often also have very limited scope for vertical adjustment, potentially being squeezed between seamount summits on the one hand and shoaling saturation horizons, on the other. Even the tops of many seamounts that currently support deep-sea coral communities may well be under-saturated in the next 50-100 years (H. Bostock, NIWA, pers. comm.). With nowhere to go, these cold-water reefs could "simply disappear" (Poloczanka, el al., 2007).

Predicting such climate change impacts with confidence is difficult for deep-sea communities due to two major sources of uncertainty: (1) the deep ocean's responses to climate change, which is compounded by short historical instrumental records against which to calibrate and validate predictive models, and (2) biological responses to these changes in the ocean environments. Deep-sea corals are logistically difficult subjects for experimental studies. As a result, enironmental tolerances need to be inferred, rather then demonstrated, from present-day distributions, from proxies and from generalisations derived from studies of related shallow-water taxa. Refining these uncertainties is critical to developing effective management responses to climate change impacts that have the potential to severely degrade the conservation and ecological service values of deep-reef ecosystems.

In this study, we address these issues for the ecologically important reef-forming scleractinian *Solensomilia variabilis* on seamounts off Tasmania, Australia. *S. variabili*s supports an extensive and diverse benthic community on the seamounts at depths ranging from roughly 1000 to 1300 m (Koslow et al., 2001; Althaus, et al., 2009; Thresher, et al., submitted ms). The seamounts are of volcanic origin and come to within 660 m of the surface. Global biogeographic analyses suggest that the depth distribution of *S. variabilis* is constrained to areas where carbonate levels are above or close to saturation ($\Omega_{aragonite} \geq 1$)(Davies & Guinotte, 2011), making it and its associated biota possibly particularly vulnerable to saturation horizons that are shoaling as a result of anthropogenic climate change. In this study, we address both sources of uncertainty in the global predictions. First, we use a suite of indirect approaches to more robustly estimate the tolerance of *S. variabilis* to low carbonate conditions, and second, we apply these tolerance limits to an up-dated predictive model of present and future carbonate saturation state. From these analyses, we determine the distribution of habitats likely to be suitable for the continued presence of the *S. variabilis* reef in the Australian region under a "business as usual" climate change scenario and identify possible refugia for the reef and community, which could be considered for management protection if needed.

Methods

Tolerance ranges

We employ five appraoches to infer the limits of *S. variabilis* tolerances of low carbonate conditions: (1) documenting and assessing the environmental ranges it inhabits globally, based primarily on information in the literature and global databases, (2) comparing the coral's distribution on seamounts locally with concurrent oceanographic measurements, as determined in situ sampling using an ROV, (3) analysis of coral skeletal density and growth rates, (4) measuring the coral's behavioural responses to varying conditions in laboratory aquaria, and (5) analysis of historical depth distributions.

For the global analysis, data were compiled for 32 environmental parameters from sources that included ship CTD data, satellites (e.g. MODIS), climatologies such as the World Ocean Atlas, and modeled data (see Davies and Guinotte, 2011 for details). The majority of source data were available as gridded datasets partitioned into bins at standardised depth levels (z-layers), and ranged in depth from 0 to 5500 m (z-binned datasets, e.g. temperature), whilst others were available as only a single layer at the surface (e.g. surface primary productivity). For zbinned datasets, it was assumed that the conditions found at a specific gridded depth were representative of conditions at that area of seafloor. This allows for the creation of continuous representations of seafloor conditions by extrapolating each z-bin to the corresponding area of seafloor at that depth using an up scaling approach. The resultant dataset had a spatial resolution of a 30-arc second, approximately 1 km^2. Detailed interrogation of the data was limited to those variables that contributed significantly to describing the present day distribution of *S. variabilis* globally: depth, salinity, temperature, dissolved oxygen levels, surface productivity and modern (1995) carbonate saturation levels ($\Omega_{aragonite}$)(see Davies & Guinotte, 2011).

Distributional data, samples from precisely known depths for skeletal and growth rate analysis, and water samples taken close to the substrata for water chemistry analyses were obtained using the ROV *Jason*. Dive details are provided in Thresher, et al. (2011 and in press). In aggregate, the dives spanned a depth range of 729 to 4011 m, and covered a range of seamounts and rocky substrata in the Tasmanian seamount region. Maximum depth of live, dead and sub-fossil *S. variabilis* was determined from notes made on each dive, from analysis of high-resolution photographs made during the dives, and from samples collected for taxonomic, paleoclimatic and ecological studies. Salinity and temperature were continuously recorded by Jason's on board instruments. Carbonate chemistry close to the seamount was determined from 11 water samples collected 2-3 m above the substratum using *Jason*'s on-board Niskin bottle sampler. Samples were taken opportunistically during the dive program, were obtained from a number of seamounts, and in aggregate covered a depth range of 951 to 3501 m. Water samples were analysed for total dissolved inorganic carbon by coulometry and for total alkalinity by potentiometric titration following standard procedures (Dickson, et al., 2007). The accuracy and precision of both methods is estimated to be +/- 2 μmol/kg, based on duplicate analyses and comparison with certified reference material from Scripps Institution of Oceanography. The saturation states for aragonite and calcite were calculated at *in situ* pressure using Lewis and Wallace (1998), with carbonate equilibrium constants from Mehrbach, et al. (1973), as refit by Dickson and Millero (1987).

Skeletal densities were measured by weighing sections from the coral's growing tips, oven-dried overnight at 35° C., on a Ohaus Explorer balance and determining their volumes by water displacement in a graduated cylinder. The sections were cut longitudinally before weighing and determination of volume, to expose inner septa and minimise air trapped inside the skeleton. Growth rates were determined using $_{14}$C analysis of the base, tip and intermediate segments cut from relatively long continuous growth sections cut from large coral colonies. For details, see Fallon, et al. (ms). Growth rates were determined for three colonies whose depth distributions jointly spanned the araonite saturation horizon (ASH).

The aquarium study was based on specimens collected using Jason in January 2009 and by trawl in November 2010. The corals were maintained in two 240 l aquaria held at temperatures of roughly 3-6 C° using TECO refrigeration units. The water was filtered using recirculation through a fine synthetic mesh to trap larger particles and by using Dymax protein skimmers. The aquaria were maintained in the dark by means of opaque plastic covers. Corals were fed approximately weekly with a mixture of commercially available fine particulate "coral food" (Reef-roids [Polylab] and Pro-coral reef snow [Tropic Marin]) pre-mixed with chilled aquarium water. Water conditions in the aquaria were measured weekly, using a YSI model 63 salinity/conductivity/pH/temperature probe. Each time water conditions were measured, the corals were scored as being open (polyps extended) or closed, which we used as a behavioural index of their condition. Growth rates of the corals are so slow (see Adkins, et al., 2004; Fallon, et al., ms) that other potential response parameters were deemed impractical.

Specimens for the historical analysis were collected from precisely known depths using the *Jason*. Colonies were dated using $_{14}$C analysis and assuming reservoir ages are the same as in the modern ocean. Each coral sample was subjected to physical pretreatments. The outer surfaces were ground off with a dental drill to expose clean white calcium carbonate. The inside was also drilled out to remove the interior dissepiments, resulting in a hollow tube. The hollow tube was coarsely crushed into ~0.25mm chunks and subjected to a 0.1M HCl leach in which ~50% of the outside material was removed. The resulting clean carbonate was rinsed 5x in 18 MΩ water (Milli-Q™) until near neutral pH was achieved. A further subsample of 8-10mg of $CaCO_3$ was loaded into a 10 ml serum vial (BD Vacutainers ®) and evacuated, before CO_2 was liberated by the introduction of 85% orthophosphoric acid (Ajax UNIVAR, Analytical Grade). The CO_2 was then passed through a cryogenic water trap, measured for % carbon yield and transferred to an individual graphite reactor assembly. In the presence of hydrogen and using Fe powder as a catalyst and a temperature of 570C the CO_2 is converted to graphite, the resulting water from the reaction is trapped using Mg Perchlorate. The graphite is then loaded into Al cathode sample holders for ^{14,13,12}C isotope analysis on the single stage Accelerator Mass Spectrometer located at the Research School of Earth Sciences, The Australian National University. All samples were normalized to Oxalic Acid I (Stuiver and Polach, 1977) and background subtracted using ^{14}C free $CaCO_3$. Conversion of radiocarbon years to calendar years was preformed using OXCAL 4.1 (http://c14.arch.ox.ac.uk/oxcal/).

Environmental proxies in the *S. variabilis* skeleton were tested for by measuring and testing for correlations between metal/Ca ratios in coral samples from known depths against enviromental conditions at the site of collection, as determined by Jason instrumentation and the water sampling described above. Approximate 50-100 mg samples were taken from the growing tips of each specimen, oven-dried overnight at 35° C. and weighed on a Ohaus Explorer balance. The samples were dissolved in 20 ml of 0.5M EDTA (pH adjusted to 8.0), until completely gone (minimum 10 days). 50 μl of the solution was withdrawn from each sample, after gently swirling to ensure good mixing and allowing to settle for 10 minutes or so, and used to replace 50μl of Milli-Q water in capped nutrient vials that had been filled to the 10 ml mark (hence a 200X dilution). Sample chemistry was determined by high resolution ICP-MS, using as an internal standard 100 ppb of indium and NIST certified water samples to verify calibration accuracy. Parallel analyses were done on radiocarbon dated sub-fossil samples and the proxies used to estimate conditions when the corals were alive.

Spatial modeling

Spatial distribution of modern and forecasts habitats suitable for *S. variabilis* in the temperate Australian region were made using Maxent modeling, an analysis of tolerance limits for *S. variabilis* from the global environmental data set referred to above, and predicted carbonate saturation conditions at 1000 m depth derived from Orr, et al. (2005). For model details, see Davies and Guinotte (2011). In brief, Maxent is a presence-only approach that assumes the best approach to determining an unknown probability distribution (in this case, the distribution of *S. variabilis*) is to maximize entropy based on constraints derived from environmental variables. The algorithm is supplied within a Java software package (Maxent version 3.2.1). The default model parameters were used as they have performed well in other studies (a convergent threshold of 1025, maximum iteration value of 500 and a regularisation multiplier of 1). Although Maxent is reasonably robust with respect to covariation of environmental parameters, an *a priori* variable selection process was used to reduce covariation. Variables were selected based on a literature search of environmental factors known or thought to influence cold-water coral growth and survival. Strong correlations between variables (0.7) were addressed by omitting one of the environmental variables (except for aragonite saturation state and temperature). The importance of each variable in the model was assessed using a jack-knifing procedure that compared the contribution of each variable (when absent from the model) with a second model that included the variable. For *S. variabilis*, the final significant environmental predictors retained by the model were depth (m), dissolved oxygen, aragonite saturation state, phosphate concentrations, surface productivity (particulate organic carbon concentrations), salinity, slope of the substratum and temperature. The final habitat suitability maps were produced by applying the calculated models to all cells in the study region, using a logistic link function to yield a habitat suitability index (HSI) between zero and one. Modern day distributions were tested against known records of *S. variabilis* in the southern Australian region. To forecast impacts of ocean acidification on future habitat suitability, the Australian habitat suitability map was overlaid with saturation states at 1000 m depth predicted for 2099, based on Orr, et al. (2005).

Point modeling

To forecast conditions specifically at the location of the Tasmanian seamounts, we used the Australian Community Climate Earth System Simulator-Ocean (ACCESS-o) (O'Kane et al 2012) with a simple marine biogeochemical cycles module (WOMBAT, Oke et al., 2012). ACCESS-o employs a tripolar grid with a nominal resolution of 1 degree, with the following three refinements: tripolar Arctic north of 65N; equatorial refinement to 1/3 ° between 10S and 10N; Mercator (cosine dependent) implementation for the Southern Hemisphere, ranging from 0.25 at 78S to 1 at 30S. The refinements in the Southern Ocean enable the model capture important dynamics that are missing in coarser resolution models (O'Kane et al 2012).

The climate change projections use the initial ocean state and atmospheric forcing fields generated by the fully coupled ACCESS simulations for the RCP 2.4, 4.6 and 8.5 scenarios (low, medium and high scenarios). The ACCESS-o simulations are then used to project the impact of climate change and rising CO2 on the acidification of the ocean. Key variables that we use to describe the acidification of the ocean are the aragonite and calcite saturation state and depth where this value equals 1.

Results

Tolerance limits

1. Global distributions: After eliminating duplicate records and a few obvious errors and reducing to one multiple records from closely adjacent sites, there were 379 reported records of *S. variabilis*. Records span all ocean basins, but are conspicuously absent from the North Pacific. Full data sets were available for 340 records; the datum most frequently missing was phosphate concentration.

The distribution of environmental variables for key parameters is shown in Figure 1. Globally, the environmental ranges reported or inferred from global data sets for *S. variabilis* are wide, ranging for temperature, for example, from -0.15 to +24.16° C. At least some of this range is likely to be spurious or mis-reporting. Comparisons of values measured for $\Omega_{\text{aragonite}}$ on southeast Australian reefs, for example, correlate poorly with values inferred from the GLODAP database, which is the source of saturation data for the environmental data base as a whole, and differ by as much as 0.8 from observed values (Figure 1). The relatively poor match reflects sparse data globally and hence poorly constrained distributions and point estimates in global models. As a result, absolute minimum values for any parameter derived from a global re-analysis are unlikely to be robust estimates of minimum tolerance levels.

Three lines of evidence can be derived from these data that might indicate minimum tolerance levels, however. First, absolute minima might be indicated by distributions that are skewed towards low levels. Distributions in which the numbers of reports abruptly decline below a cerain value could indicate an absolute minimum below which the species cannot persist. Second, global minima might be reflected in comparisons of distributions across regions, which are likely to have different suites of environmental parameters. A correlation between temperature and salinity, for example, in the South Pacific would confound disentangling the constraining impacts of either; however, comparisons with data from other sites where the correlation differs would help disentangle the effects. Third, stresses associated with parameter values at or below tolerance ranges for one variable, i.e., aragonite saturation state, are likely to constrain the coral's ability to withstand stressful conditions associated with other parameters, e.g., temperature. Hence a plot of two variables against each other could indicate threshold levels for one parameter below which the range of other environmental factors are limited.

Globally, the distributions of temperature and salinity are skewed towards low values, and suggest constraining values of approximately 3° C. and 34.4 psu, respectively (Figure 1). Comparisons among regions (Figure 2) are less compelling for either variable, however. Minimum reported temperatures range from about 2 to 6° C. (excluding outliers) among regions, and minimum salinities range from 34.4 to about 35.1 psu. Minimum values for dissolved oxygen and surface productivity are equally variable. In contrast, there is a tighter range of values for carbonate saturation state, with 95% confidenec interval for most regions having a minimum value of between 0.8 and 1.1. The exceptions are the Indian Ocean, which is represented by a very small sample size (three reports) and the Southern Ocean. Values of all parameters for the latter are likely to be skewed by inclusion of reported occurences of *S. variabilis* based on collections of sub-fossil samples. Live *S. variabilis* around the Drake Passage, for example, are found in a temperature range of roughly 3-5°C, which is consistent with observations elsewhere, whereas sites now occupied only by now extinct reefs have temperatures down to 1-2ºC. (R. Waller, pers. comm.).

Reported parameter values for Australia and New Zealand sites do not differ significantly for any parameter. Consequently, in order to more clearly assess potential limiting values relevant to the southern Australian region, we pooled data for the two areas and re-examined the distributions for evidence of a skew toward lower values (Figure 3). Distributions for surface productivity, salinity and dissolved oxygen are all not significantly different from normality or, in the case of surface productivity, a Poisson distribution. However, both temperature, modern (1995) and reconstructed pre-anthropogenic (1765) are negatively skewed. Implied minima are around 3ºC, and $\Omega_{aragonite}$ of 0.85 and 0.95, respectively.

Analysis of the global data base for indications of stress associated with low values are inconclusive for most parameter pairs. The exceptions are two. First, low temperaures correlate with a very restricted salinity range, and second, there is an abrupt widening of reported salinity values for saturation states > 1.0 (Figure 4). The former largely reflects the temperature/salinity relationships for the Intermediate Water Masses inhabited by *S. variabilis*. The latter, however, is consistent with narrowed environmental tolerance ranges when the taxa are under stress from low carbonate saturation states.

2. Modern distribution on SE Australian seamounts: The deepest we observed live *S. variabilis* using the ROV Jason was 1458 m (on seamount K1) (see Koslow, et al., 2001, for location information). Environmental conditions are that depth were a temperature of 2.85° C., salinity of 34.57 psu, dissolxed oxygen of 3.55 ml/l, and an $\Omega_{aragonite}$ of 0.84. The shallowest specimen we observed, at 890 m on Mongrel Seamount, was found in water that had a temperature of 6.0° C, salinity 34.43 psu, dissolved oxygen of 4.0 ml/l and a saturation state of 1.06. The *S. variabilis* reef exists in a narrower depth range, from roughly 1050 to 1275 m. The conditions at the upper and lower limits of the extensive reef were 4.75 and 3.6 C, 34.43 and 34.53 psu, 3.8 and 3.6 ml/l and $\Omega_{aragonite}$ of 1.03 and 0.91, respectively. Overall, the ranges of environmental variables at which we observed live *S. variabilis* of the Australian seamounts matches the distributions inferred from an analysis of values among sites (Figure 3).

3. Skeletal density and growth rates: Skeletal density does not correlate with carbonate ion concentration for live-caught specimens of *S. variabilis* (r = 0.10, NS, n = 13, $\Omega_{aragonite}$1.1-0.84)(Figure 5). Growth rates increase almost linearly with increasing depth/decreasing saturation state, although the relationship for Australian samples is too small to test for significance. Slow growth among shallower specimens, however, is consistent with observations made for the species in New Zealand (Neil, et al., in prep).

4. Behaviour in aquaria: Over the roughly 6 month duration of observations, temperatues in the laboratory aquaria ranged from roughly 3.5 to 7.8ºC, salinity from 28 to 38 psu, and pH from 7.68 to 8.03. Data was collected on the number of specimens with expanded oral discs for two species of solitary scleractinian corals, *Caryophyllia* cf. *diomedae* and *Desmophyllum dianthus* (data pooled), as well as *Solenosmilia variabilis*. The frequency of oral disc expansion for both the solitary species and *S. variabilis* was normally distributed with respect to salinity, with a peak value of around 34 psu for both taxa (Figure 6). However, the solitary and colonial *S. variabilis* differed with respect to apparent responses to temperature and pH. Over the observed range, there was no apparent pattern for the two solitary species, but the frequency of expanded individuals among *S. variabilis* correlated significantly and positively with both temperarture and pH.

5. Historical distributions: On the Tasmanian seamounts, *S. variabilis* reefal structure covers a total depth range of approximately 1050 to 1750 m. (Thresher, et al., submitted ms). However, the structure below approximately 1350 m, though intact, is dead (Figure 7). Radiocarbon analyses indicate the shallower reef has been present on the seamounts for at least the last 10,000 years, while the deeper, extinct reef dates from from 11,000 to 13,000 years Before Present (Figure 7).

To determine the environmental conditions coincident with the extension of *S. variabilis* into depths below its modern range, we tested for environmetal proxies in the skeletal chemistry of live-caught species. Correlations for most metal/calcium ratios were non-significant. However, suggestive correlations were found in both the solitary coral *Desmophyllum dianthus* and *S. variabilis* for depth, temperature, salinity and carbonate saturation state against barium (Ba):calcium (Ca) ratios, magnesium (Mg):Ca ratios and uranium (U):Ca ratios (Figure 8). To estimate the environmental conditions present when the deeper sub-fossil reef established, we analysed the skeletons of 5 sub-fossil specimens and compared the distribution of the proxies to those of the live-caught specimens. Ba/Ca ratios proved unusable because of extremely high values in the sub-fossil samples, apparently exogenously deposited as oxides. There was no evidence of external contamination for either Mg or U. Proxy values determined for the hisorical material in all cases fell within the ranges of modern material, suggesting temperatures and carbonate saturation levels higher at 1450-1700 m than on the modern seamounts. The lowest temperature and saturation states ($\Omega_{aragonite}$) suggested by proxies for the sub-fossil material is 3.2ºC and 0.92, both of which are within the range of the modern living reef.

6. Summary of tolerance data: The results of the five indirect indicators of environmental tolerances for *S. variabilis* can be summarised as follows:

- Distribition
  - global - $\Omega_{aragonite}$ probably limiting, at a value between 0.9 and 1.0
  - Australia/New Zealand distreibution - temperature and/or $\Omega_{aragonite}$ limiting, at 3.0º C and 0.85, respectively
  - Stress - *S. variabilis* stressed below $\Omega_{aragonite}$ of approximately 1.0
- Distribution on Tasmanian seamounts - Minimum temperature 2.85ºC; minimum $\Omega_{aragonite}$ of 0.84
- Growth rate/skeletal density - Not informative
- Aqarium observations: *S. variabilis* prefers higher temperatures and higher pH than solitary scleractians
- Historical distributions: Proxies suggest conditions during development of sub-fossil reef similar to those of the modern, shallower reef. Minimum temperature and carbonate saturation states indicated are 3.2ºC and 0.92, respectively.

From these data, we draw several conclusions. First, it is difficult overall to separate a lower depth distribution based on a minimum temperaure tolerance from one based on a minimum saturation state tolerance. Second, across several of the assays, minimum temperatures tend to close to 3º C. Third, across assays minimum saturation state ranges from about 0.85 to 1.0. Fourth, direct observations on Tasmanian seamounts indicate that *S. variabilis* presently survives, and appears to be growing, at a temperature of 2.85ºC and a saturation state of 0.84. However, fifth, extensive reef structure occurs only at a higher temperature (3.6º) and higher saturation state (0.91). Finally, sixth, a preference for higher temperatures and higher pH in aquaria by *S. variabilis* than two species of solitary corals is consistent with their distributions in the field (solitaries deeper and hence in cooler water and at lower saturation states than *S. variabilis*)

Spatial modeling

Results of the spatial modeling are shown in Figure 9. The model was tested for the southern Australian region by comparing the predicted distribution of habitat suitable for *S. variabilis* against those locations where it has been observed, and then tuning the miminim saturation state to optimize the fit. In brief, all sites where *S. variabilis* has been observed fall within areas identidied by the predictive map as having a suitability for *S. variabilis* of greater than 0.8 (on a scale of 0 to 1, where 1 is a perfect fit to observed environmental parameters). The fit is optimized at an assumed minimum tolerance limit of $\Omega_{\text{aragonite}}$ of 0.9.

The distribution of suitable habitat, under the same model conditions and same minimum tolerance limit, for 2099 is shown in Figure 9 bottom. The predictive model indicates that all habitats currently inhabited by *S. variabilis* will no longer fall within zones suitable for it, that no potential refugia (which are small patches mainly along the coast of South Australia) will have suitability indices greater than 0.8, and most potential sites close to the present Tasmanian seamounts, also along the coast, will have suitability values less than 0.4.

Point modeling

To refine the predictions of conditions in the Tasmanian seamount region, we used a state-of-the-art coupled ocean/atmosphere and spatially explicit model for the location and depth of the modern *S. variabilis* reef (44°20' S, 147° 17'E and 1100 m). The model assumes a "business as usual" (IPCC A2) climate change scenario, and differs from the Orr et al. (2005) model both in terms of being explicitly tuned to the modern seamount conditions and in incorporating the effects of predicted temperature changes in the water mass coincident with the *S. variabilis* reef (Antarctic intermediate Water - AAIW). The core depth of AAIW in the seamount region, defined on the basis of a salinity minimum, is about 1000 m.

Hindcast pre-industrial, modern (2010) and forecast conditions at 1100 m for the seamount location is shown in Figure 10. The model suggests pre-anthropogenic saturation conditions for the main *S. variabilis* reef was about 1.04 and current conditions of 0.96. By 2050, water temperatures at the site are predicted to rise slightly, and saturation levels to fall to about 0.91; by 2100 temperatures are predicted to have risen by a total of about 0.3°C, and saturation levels fallen to a range of between 0.83 and 0.86. The range is due primarily to uncertainties in the predicted concentrations of dissolved inorganic carbon (DIC). Variability in salinity, nutrient levels, alkalinity and pCO_2, all of which affect carbonate saturation state, are small relative to the effects of temperature and DIC. There is also model uncertainty regarding temperature changes, due to uncertain behavior of the AAIW in the face of climate change. All models predict that the AAIW will warm and most models predict it will freshen over the next century. However, the range of the temperature and salinity change predicted for the temperate South Pacific varies among models from 0.2 to 2.5° C and -0.03 to 0.01 psu, respectively (Downes, et al., 2010). Figure 10 bottom incorporates this range of uncertainty in the predictions for conditons on the Tasmanian seamounts. The range of saturation states predicted for the site of the present *S. variabilis* reef is from 0.77 to 0.92, and predicted temperature from 4.6 to 6.4° C. These values compare with the modern values of 0.96 and 4.4°, respectively.

We also used the site-specific model to explore the potential for the *S. variabilis* reef to migrate up the seamount. The shallowest seamount in the region peaks at 660 m (Koslow, et al., 2001). Forecast conditions at 660 m are compared to those at 1100m, based on highest probability changes in temperature and DIC, in Figure 11. By 2100, temperatures at 660 m are predicted to rise from the present ca. 7.8°C to just over 9°, and carbonate saturation state to fall from a present 1.4 to about 0.91.

Discussion

Concens have been raised about the impacts of shoaling aragonite saturation horizons on the viability of cold-water coral reefs globally (Guinotte, et al., 2006; Turley, et al., 2007). The magnitude of these impacts depends on a suite of factors, including the adapability of the corals, their dispersal capability and the habitat requirements for larvae. However, the immediate survival and well-being of these reefs will depend directy on two factors - their ability to tolerate low carbonate conditions and the magnitude of the fall in carbonate saturation levels. In this project, we address uncertainties associated with both in order to better define the risks posed by ocean acidification on deep-sea reefs, focussing on the *Solenosmilia variabilis* reefs on seamounts off southeasten Australia. These reefs were chosen in part as case studies, but also because they have recently been protected in Australian Commonwealth Marine Reserves due to their high conservation values. Ocean acidification poses threat to these values, as well as the reefs themselves.

Environmental tolerance linits are difficult to determine for most organisms due to the impacts of multiple stressors and logistical constraints on experimental studies. The latter is of particular significance to deepwater corals. Although several species have been maintained in coldwater aquaria, including in our laboratory, the very slow growth of most species and the potential artefacts due to chronic barotrauma for animals that normally reside at depths in excess of a kilometer dictate inferring tolerance limits from indirect sources. We use four such sources, as well as behavioural observations in aquaria. Each has limitations, such as mis-reporting and uncertain data quality for some parameters in the global analyses, but in aggregate they allow us to assess whether or not low carbonate levels constrain the distribution of *S. variabilis* and to estimate the magnitude of this limiting value. We further test this limiting value by factoring a range of values into a model predicting the modern distribution of *S. variabilis* in southern Australia, and determining the value which provides a best fit between predictions and observations. Overall, the data indicate, first, that *S. variabilis* can survive carbonate saturation levels as low as 16% under-saturation ($\Omega_{aragonite}$ = 0.84), based on our high resolution observations on the Tasmanian seamounts using an ROV. The growth rate of this specimen was the highest we have measured in modern specimens, suggesting low physiological stresses associated with the low carbonate levels. A synthesis of our observations overall, however, suggests 0.84 is probably lower than the saturation level consistently required to sustain *S. variabilis* reefs, with most assays suggesting a value closer to 0.9. In practice, this same value gave us a best fit between predicted and observed distributions of *S. variabilis* in temperate Australia.

However, second, the relatively long lives and slow growth of deep-sea corals in general (Adkins, et al., 2004; Roark, et al., 2005), and *S. variabilis* in particular (Fallon, et al., ms), means that inferences derived from present day distributions and from growth rates that are inevitably averaged over decades may not reflect current environmental conditions. Recent studies suggest the early life history stages of corals may be more sensitive to low carbonate levels than fully established colonies (Dufault, et al., 2011; Albright and Langdon, 2012). If this is the case for *S. variabilis*, the critical values for its long-term viability relate less to the present conditions where colonies exist but rather those extant one or more centuries ago when the colonies first established. We can address this in three ways: by examining the global distribution of pre-anthropogenic saturation values for sites at which *S. variabilis* is present, by using the point model to estimate pre-anthropogenic values on the Tasmanian seamounts, and from the historical analysis of environmental conditions derived from proxies. With regard to the first option, estimates of pre-anthropogenic saturation levels for *S.*

variabilis sites in Australia and New Zealand show evidence of a severe constraining value at an $\Omega_{aragonite}$ of 0.9-0.94 (Figure 3). With regard to the Tasmanian seamount distribution, the point model suggests pre-anthropogenic values at *S. variabilis* depths were about 0.08 higher than they are at present (Figure 10). Applied to the present day environmental data, this shift suggests that the deepest modern day corals probably recruited into an environment with a saturation level of 0.9 - 0.92 (as oppposed to the modern value for the deepest specimen of 0.84), and that of the extant modern reef approximately 0.99. Finally, the historical analysis of the sub-fossil reef suggests a minimum value for $\Omega_{aragonite}$ of 0.92 (Figure 8). That all three analyses indicate minimum saturation values just over 0.9 suggest this is a reasonable estimate of the minimum level at which *S. variabilis* can establish and grow. The data also suggest that extensive reef formation requires saturation levels approaching 1.0, an observation consistent with both the stress analysis (Figure 4) and global analyses of cold-water reef forming corals in general (Guinotte, et al., 2006; Davies and Guinotte, 2011).

Assessing uncertainties in future environments is more difficult, in the sense that model uncertainties cannot be easily tested against data except in the very short term or via hindcasts. The main uncertainties in the current generation regional biogeochemical model we used for the point predictions on Tasmanian seamounts are (1) uncertain DIC levels in 2011, (2) uncertain behavior and characteristics of the water mass (Antarctic Intermediate Water) in which *S. variabilis* principally resides, and (3) uncertain estimates of future atmospheric CO_2. The first two we can roughly bound by means of inter-model comparisons and multiple runs using different starting conditions. Applied to the seamount environment, the boundary conditions suggest saturation levels for the site of the present *S. variabilis* reef will fall to between 0.77 and 0.92 by 2100 (Figure 10). Our highest probability estimate is 0.83-0.86. These estimates, however, assume a "business-as-usual" (IPCC A2) scenario with regard to future global CO_2 emissions. In practice, CO_2 trends are more closely tracking the most carbon-use intensive scenarios (A1F1) envisioned by the IPCC (Le Quere, et al., 2009). As a result, our predicted $\Omega_{aragonite}$ values are likely to under-estimate conditions by 2100 unless abatement programs are undertaken, and these conditions are likely to be reached sooner than predicted by our model.

The combination of a likely minimum tolerance level ($\Omega_{aragonite}$) for *S. variabilis* of approximately 0.9 and probable (under-)estimates of likely carbonate saturation levels by 2100 of 0.83-0.86 (0.77 - 0.92 including both temeprature and DIC uncertainties) are not consistent with the long-term viability of the present *S. variabilis* reefs in southern Australia. These observations largely confirm our spatial predictions as depicted in Figure 9. That individual *S. variabilis* colonies have been observed locally at saturation levels as low as 0.84, coupled with the longevity of the species, suggests that some colonies in the present reef will persist to 2100, but that recruitment is likely to be limited and the reef degrading and possibly facing local extinction. By 2100, none of the present sites of *S. variabilis* reefs are likely to have saturation levels approaching 1.0, which we estimate as the level required for continued development of extensive reef structure.

A possible biotic response to this scenario is migration of the reef into shallower areas. This could be accomplished either by migration closer to the seamount peaks, or by dispersal to and establishment of reefs on shelf edge environments. We tested the potential of the former by using the point model to forecast conditions on the shallowest peak in the seamount region, at 660 m, and comparing those conditions to the likely environmental tolerance range of *S. variabilis*. The model predicts that by 2100, temperatures at 660 m will be just over 9° C and the carbonate saturation state about 0.91. The latter is within our estimated survival range for established colonies, and marginally within the estimated tolerance limit for coral establishment. Predicted temperatures are higher than those in which the coral presently exists locally (maximum observed 6.0°) and at the upper limits of temperatures for sites at which live *S. variabilis* has been reported in Australia and New Zealand (Figure 3). Hence, we think it likely that conditions on the seamount peaks will be marginal for the continued existence of the coral in general, and for extensive reefs in particular. Sites below the peak are likely to be more conducive to coral development with respect to temperature, but move the colonies into increasingly under-saturated conditions. As above, saturation levels at the peaks are also likely to be lower than predicted by our model, due to the faster than assumed increase in global atmospheric CO_2.

Similar problems apply to the reef establishing on shelf-edge enviroments, with two further complications. First, the dispersal capability of *S. variabilis* is poorly known. Its near global distribution as a single species indicates that over evolutionary time scales there is larval dispersal among sites. However, the frequency of dispersal events is not known, and may be uncommon for such a long-lived species (see Thresher, et al., 2010). Whether the species would naturally recruit to coastal habitats over the next few decades is not clear. Second, although the spatial model predicts possible refugia along the coasts, at suitability indices up to 0.8, the model does not include substratum characteristics and hence over-estimates the abundance and extent of habitat suitable for the coral. Substratum features are important to *S. variabilis*, which appears to prefer and may be restricted to rocky habitats, but were not included in the Maxent modeling in part because of the sparsity of substratum data and in part because the minimum grid size for the model (one km^2) is large enough as to encoumpass a variety of substratum types. Nonetheless, extensive qualitative sampling along the southern Australian shelf edge suggests it is mainly soft sediment and mudstone, neither of which is likely to be condusive to settlement and growth of the coral. Although rocky habitat patches are known to occur along the coast, whether these patches are in areas likely to be suitable for the coral's survival past 2100 is not known. If environmental enevelopes suited to *S. variabilis* are available along the coast, the limitations above suggest possible management actions to maintain the reefal ecosystem locally could include assisted translocation of coral colonies and the use of artificial structures to provide suitable hard ground environments.

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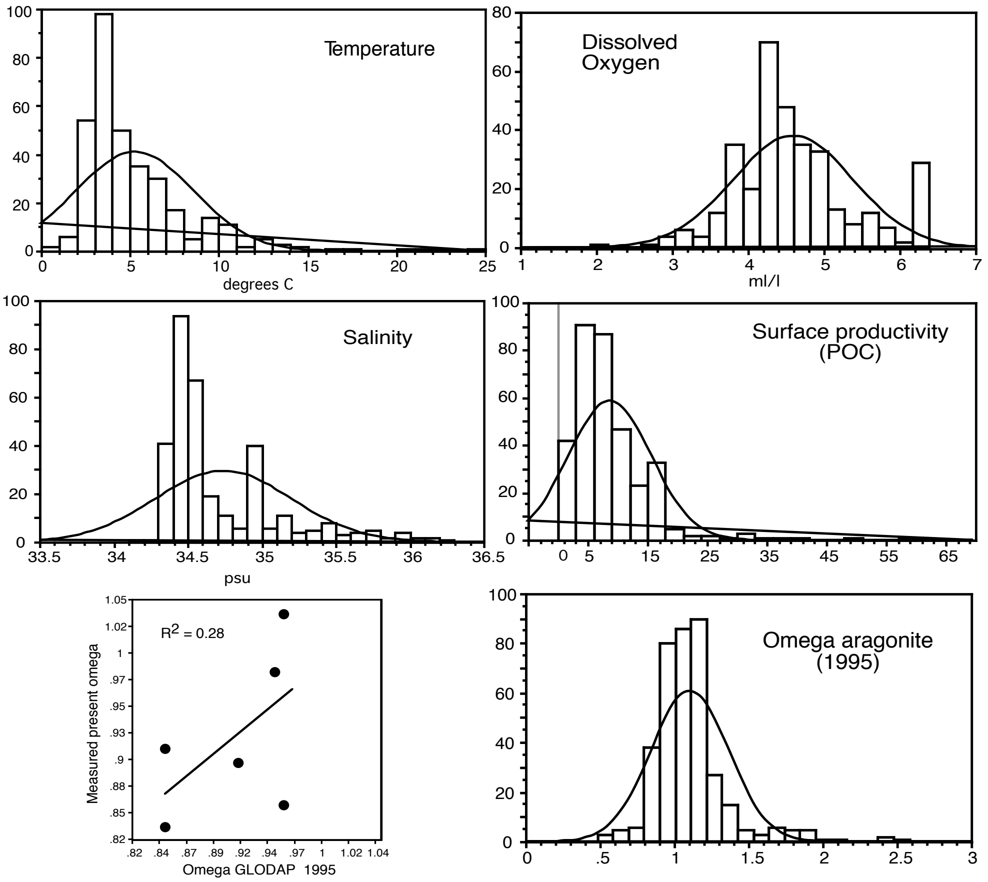

Figure 1. Distribution of key environmental predictors of the global distribution of *S. variabilis*. Curved lines indicate normal distribution. Lower right compares observed values for omega on SE Australian reefs with those predicted by GLODAP.

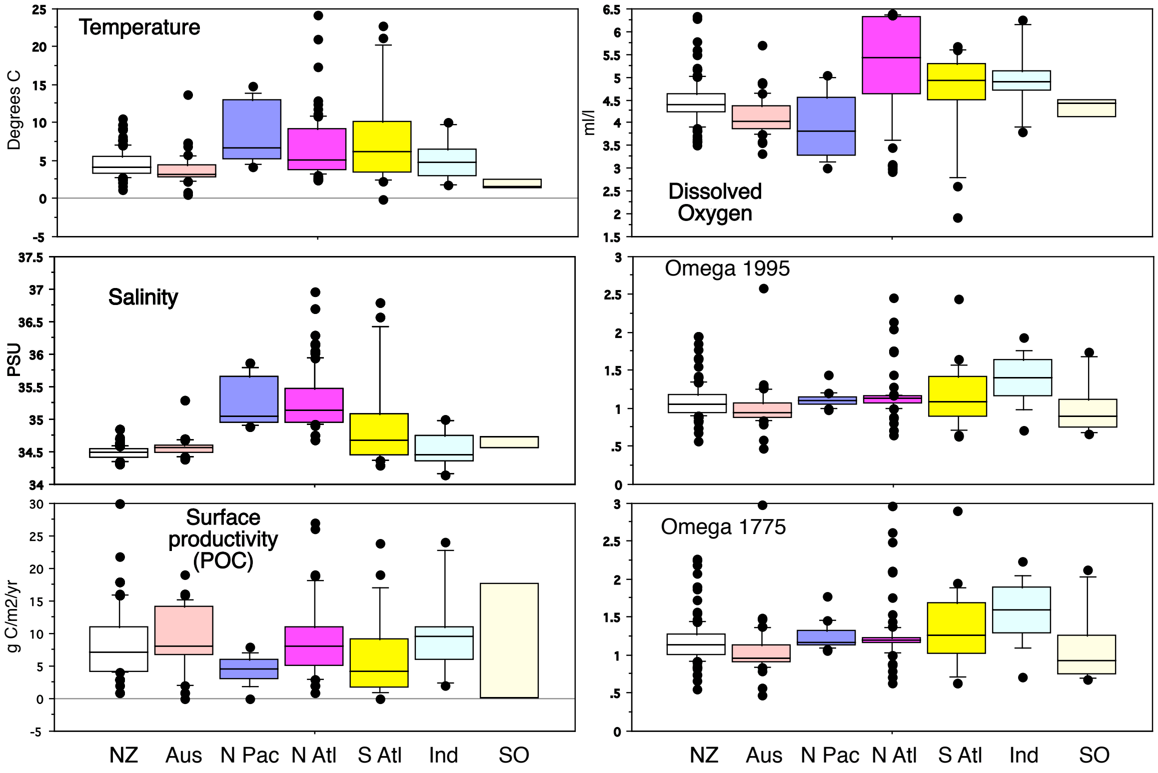

Figure 2. Regional differences in environmental parameter values for sites inhabited by *S. variabilis*

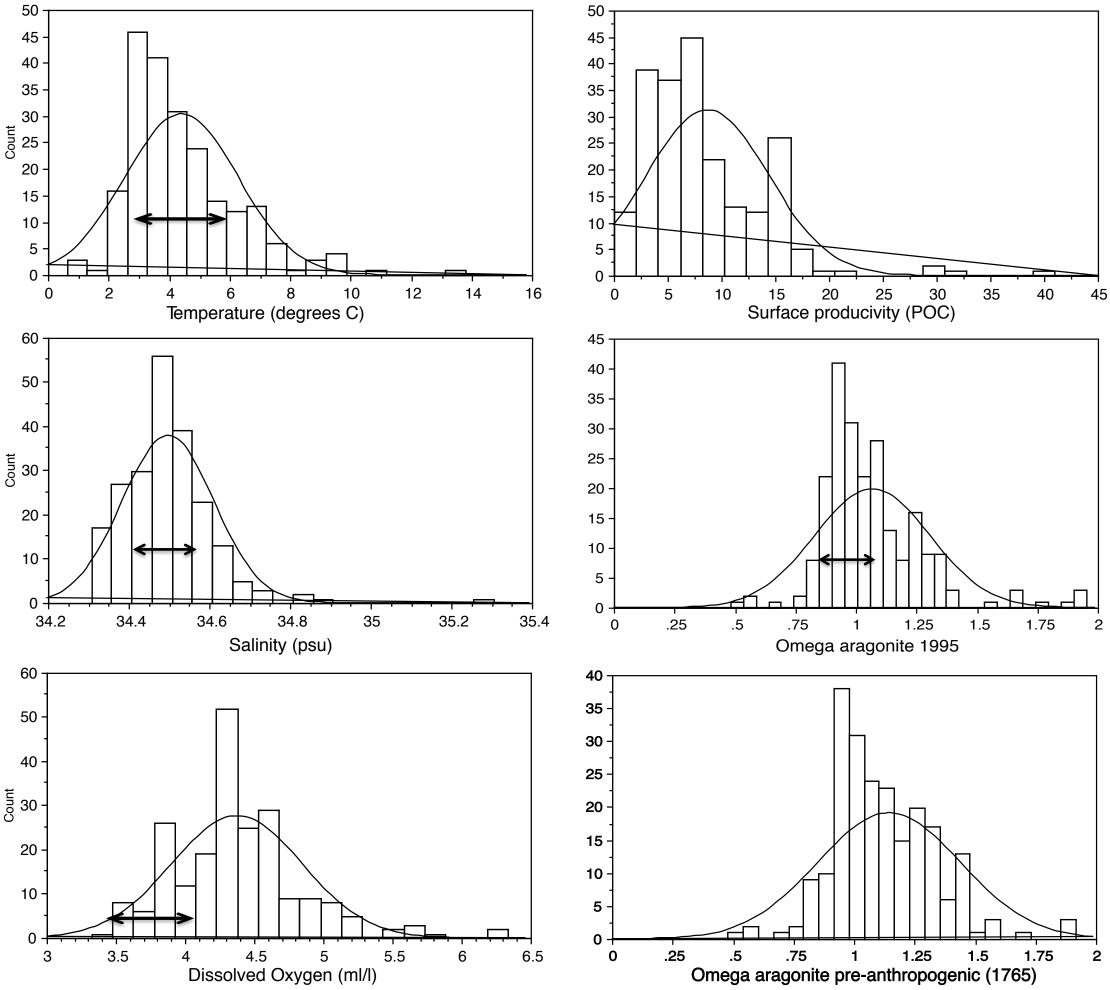

Figure 3. Distribution of key environmental predictors of the distribution of *S. variabilis* in Australia and New Zealand. Curved lines indicate normal distribution. Arrows indicate upper and lower limits of live *S. variabilis* on Tasmania reefs, as determined from ROV surveys.

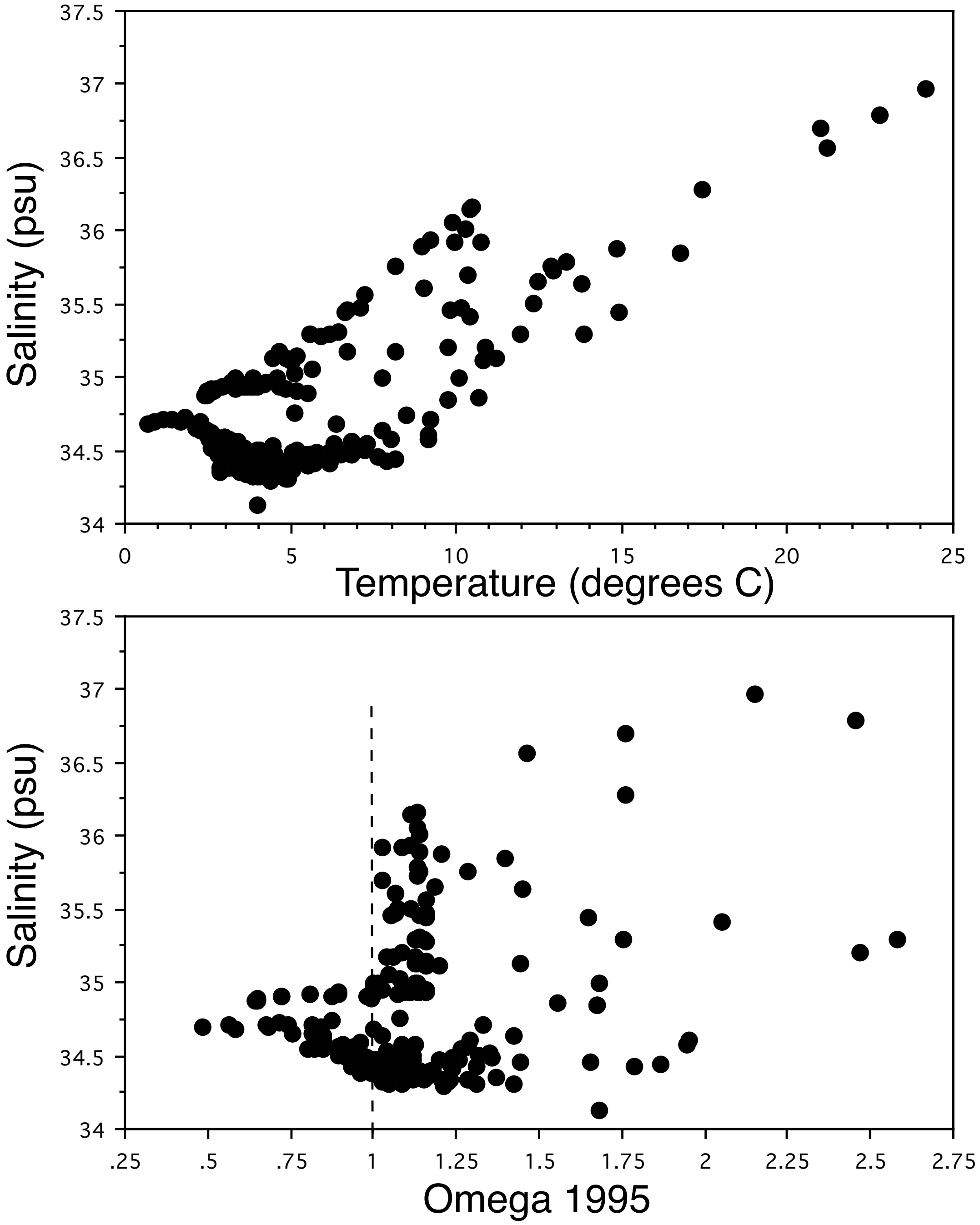

Figure 4. Global relationship between temperature and salinity and present day carbonate saturation state ($\Omega_{aragonite}$ 1995) and salinity for sites reported as inhabited by *S. variabilis*. Dashed line indicates aragonite saturation horizon.

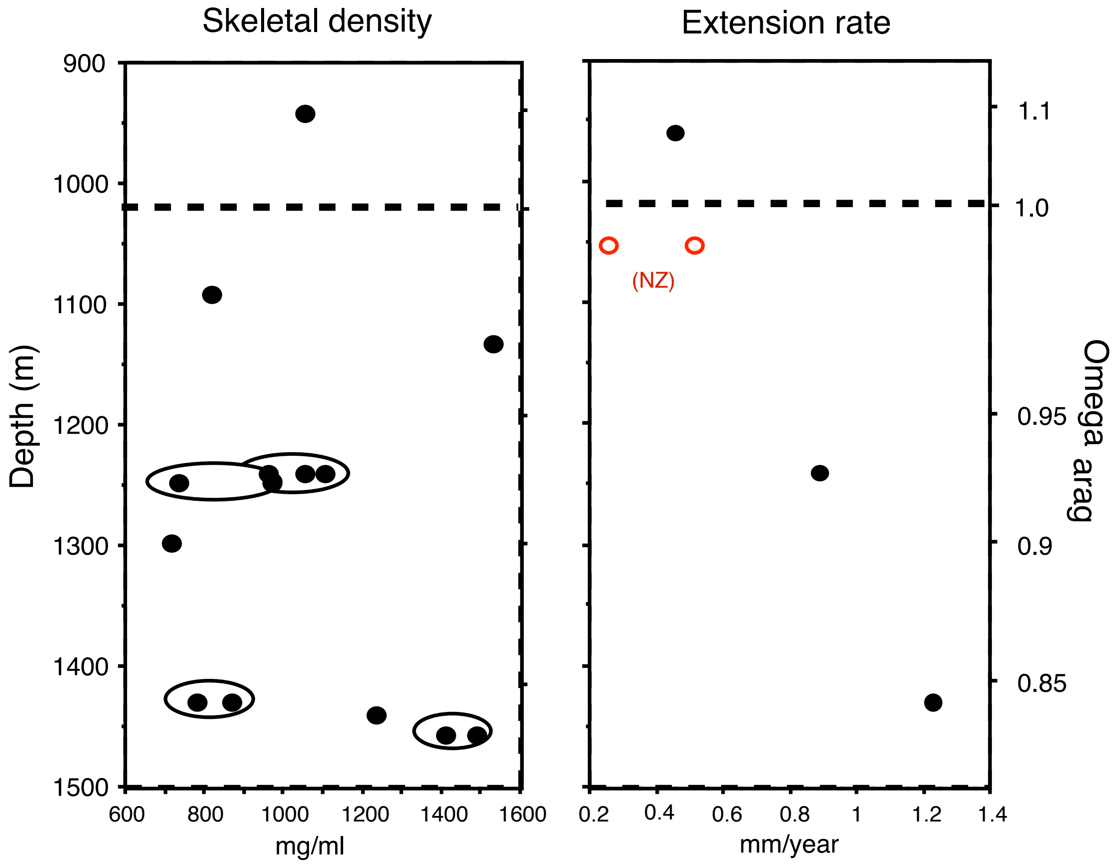

Figure 5. Skeletal density and growtrh rates of live-collected specimens of the aragonitic scleractinian *Solenomsilia variabilis*, as a function of depth/aragonite saturation level. Horizontal dashed line indicates depth of the ASH. The maximum depth at which live *S. variabilis* was seen was 1458 m. Open symbols indicate data for specimens from New Zealnd (Neil, et al., in prep), included for comparative purposes. Ovals in the skeletal density plot encircle replicate samples of the same coral, and provide an index of measurement error.

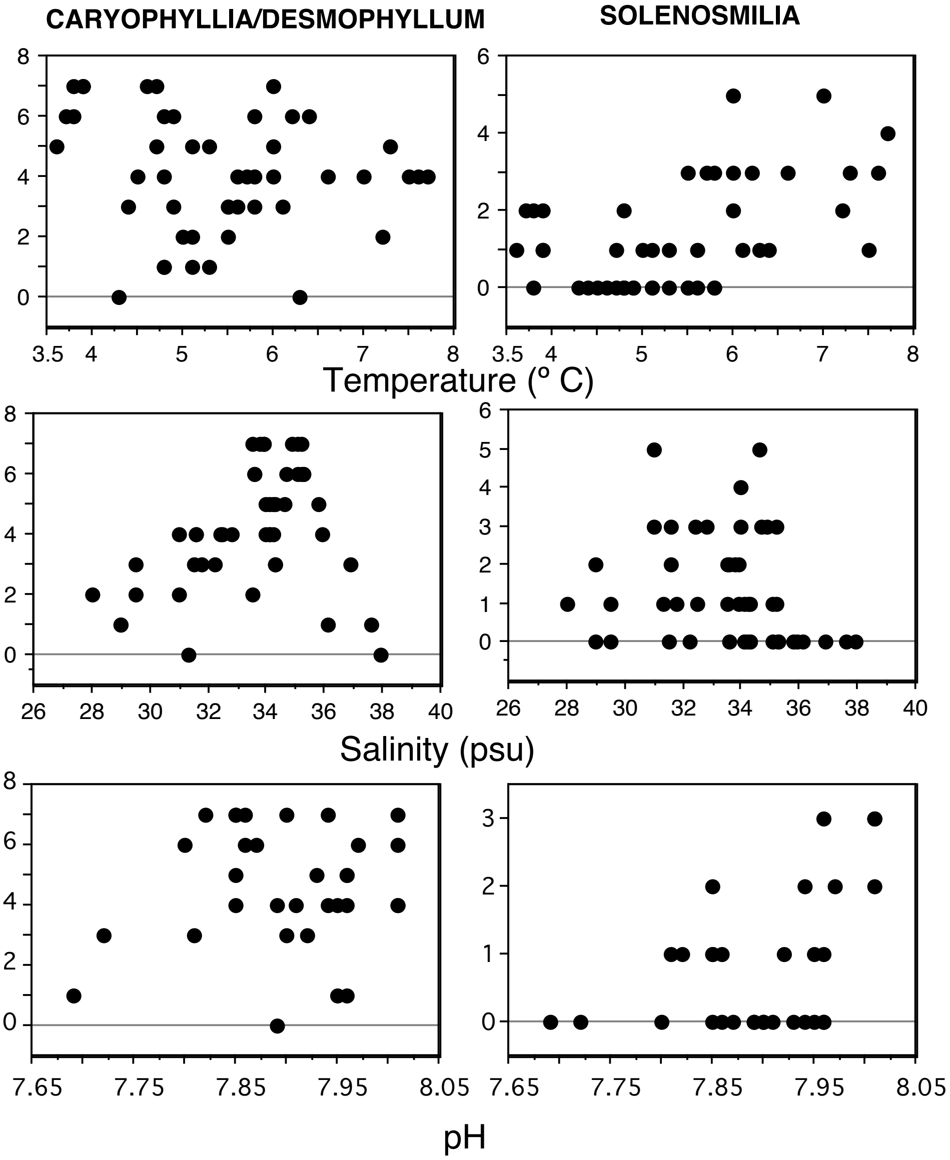

Figure 6. Number of open (oral disc expanded) individuals of two solitary corals (*Caryophyllia* cf. *diomedae* and *Desmophyllum dianthus*) pooled and *Solenosmilia variabilis*, as a function of measured temperature, salinity and pH in laboratory aquaria.

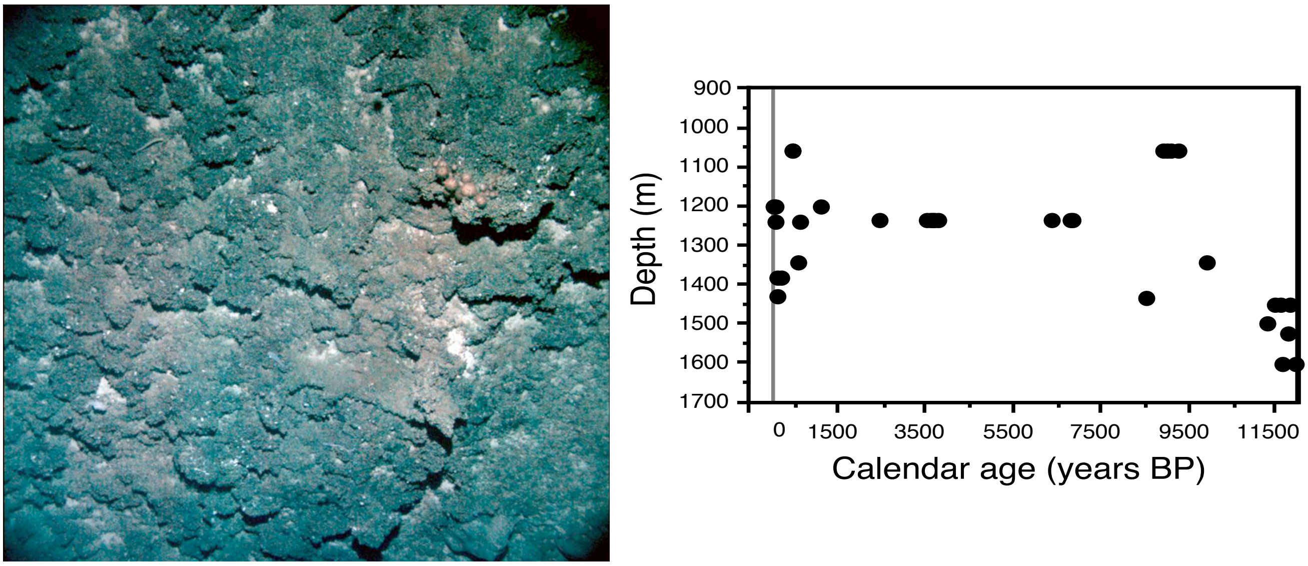

Figure 7. Left. Dead sub-fossil *S. variabilis* reef at 1425 m on Mongrel Seamount. The area of the image is approximately 3 m X 3 m. Right. Depth/age distribution of sub-fossil *S. variabilis*.

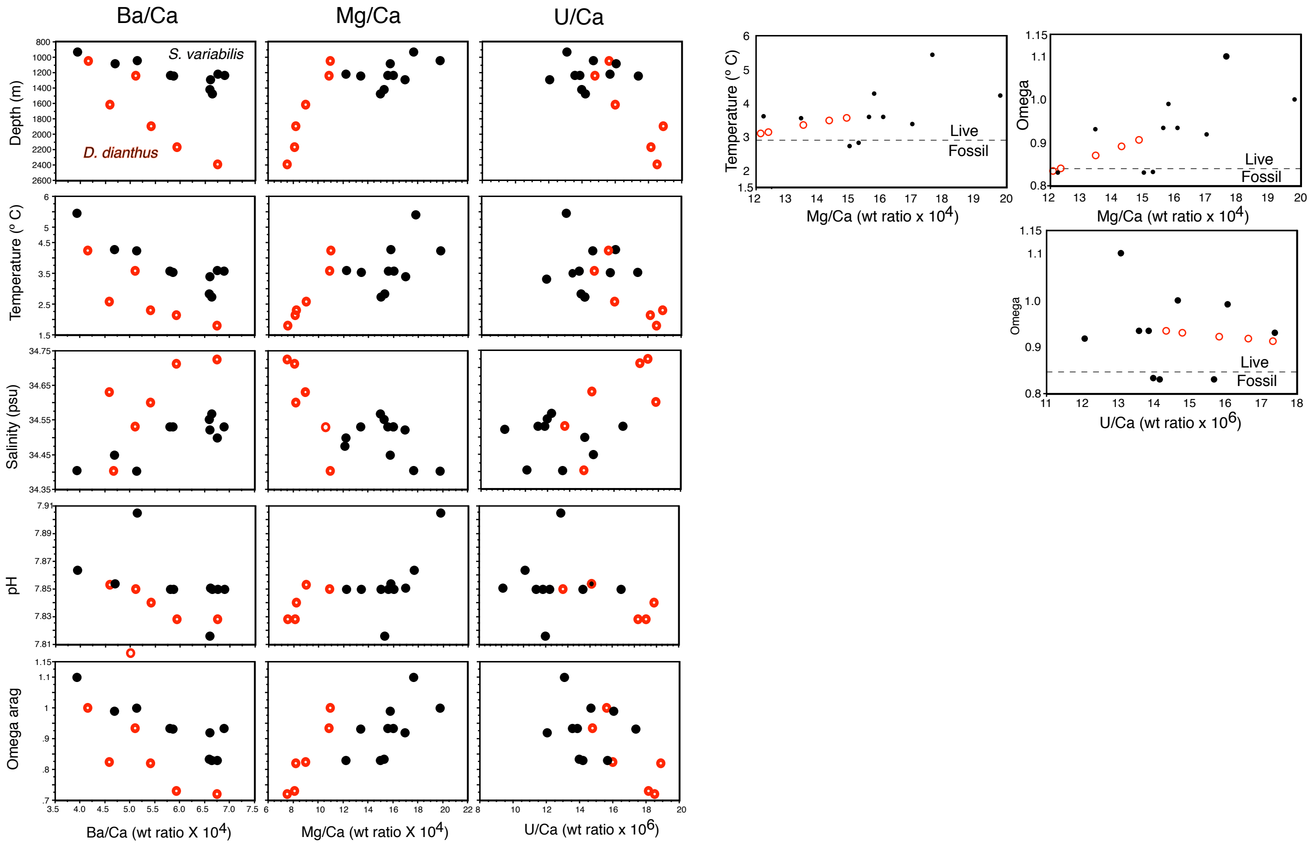

Figure 8. Left: Correlations between five environmental variables and Ba/Ca, Mg/Ca and U/Ca ratios in live-caught *S. variabilis* (solid black symbols) and *D. dianthus* (solid red symbols). Right: Range of proxy values for sub-fossil *S. variabilis* (open red symbols) compared to data from live caught specimens. Dashed lines indicate the depth that divides the modern live reef from the deeper sub-fossil reef.

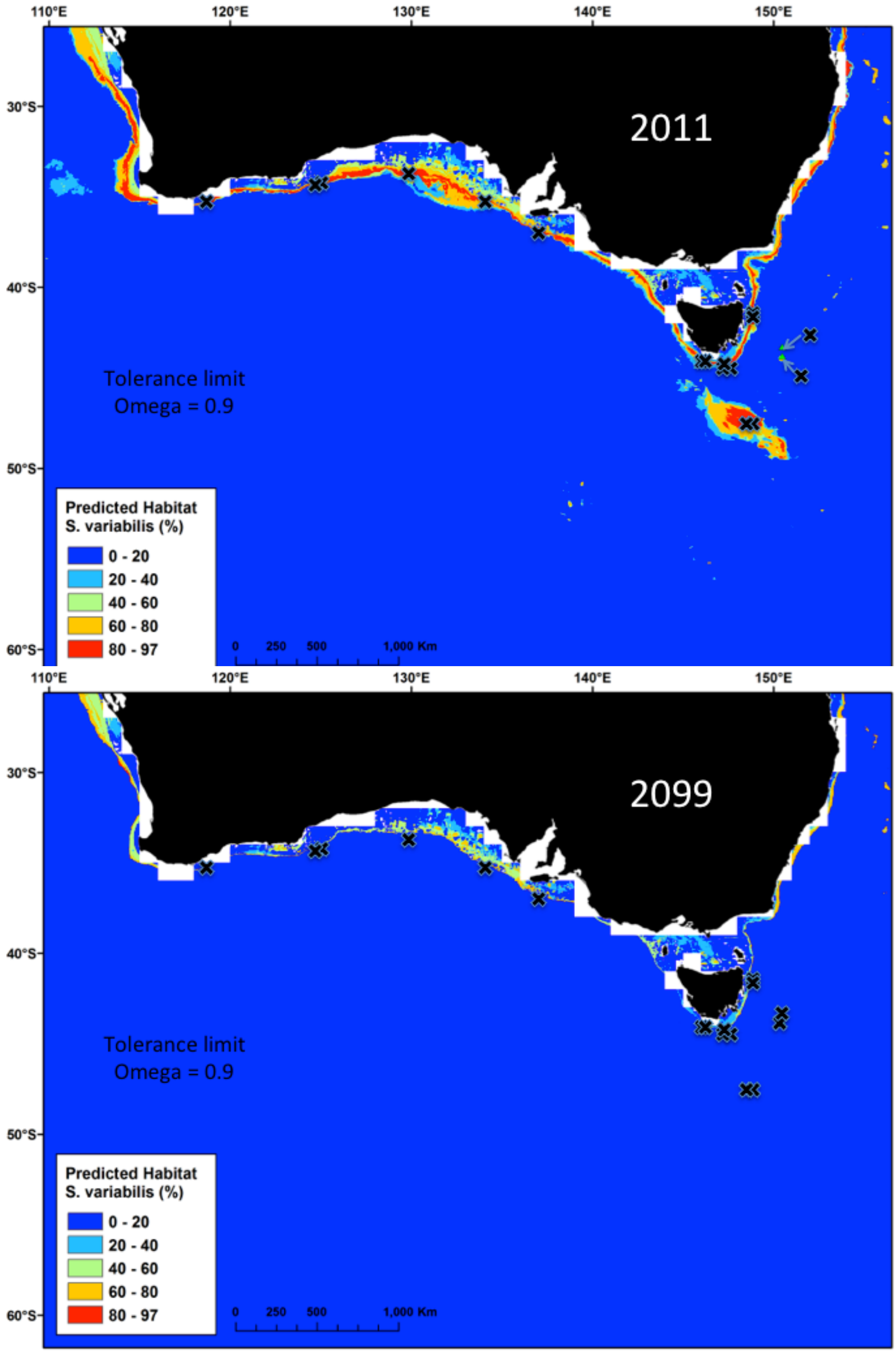

Figure 9. Top: Habitat suitability map for southern Australia at present based on procedures in Davies and Guinotte (2011), a carbonate saturation state distribution at depth derived from Orr et al (2005), and an assumed minimum carbonate tolerance limit for *S. variabilis* of 0.9. Colors indicate predicted degree of habitat suitability (red = highest). X's indicate sites where live S. *variabilis* has been found. Bottom: The predicted distribution of suitable habitat in 2099.

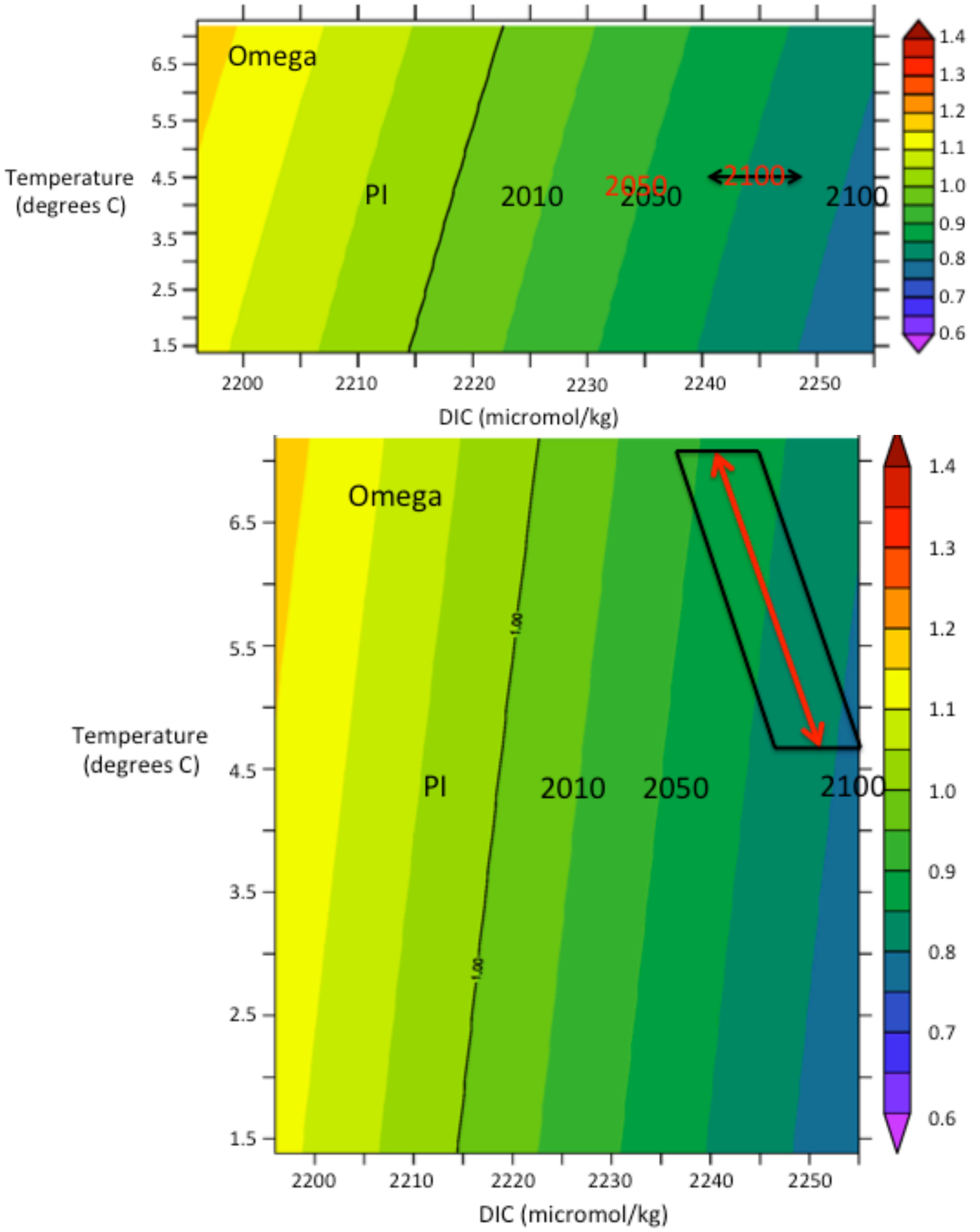

Figure 10. Hindcast (pre-industrial = PI), modern and predicted carbonate saturation conditions ($\Omega_{\text{aragonite}}$) in 2050 and 2100 for the Tasmanian seamount region (44°20' S, 147° 17'E) at the mean depth of the modern *S. variabilis* reef (1100 m), assuming a "business as usual" (A2) climate change scenario. The black numbers indicate predictions ingoring impacts of temperature changes at depth, and are similar to those predicted by Orr, et al. (2005). Top: mean conditions as predicted by the model. Horizontal line through 2100 indicates the range of uncertainty due to forecast ranges of DIC (dissolved inorganic carbon) in 2100. Bottom: Range of uncertainty for 2100 incorporating both ucertainty in DIC values (horizontal lines) and temperature change at ca. 1100 m (red double-ended arrow). The parallelogram indicates the range of possible saturation states for the Tasmanian seamount region. Color code for $\Omega_{\text{aragonite}}$ is the same in both plots, and shown on the right.

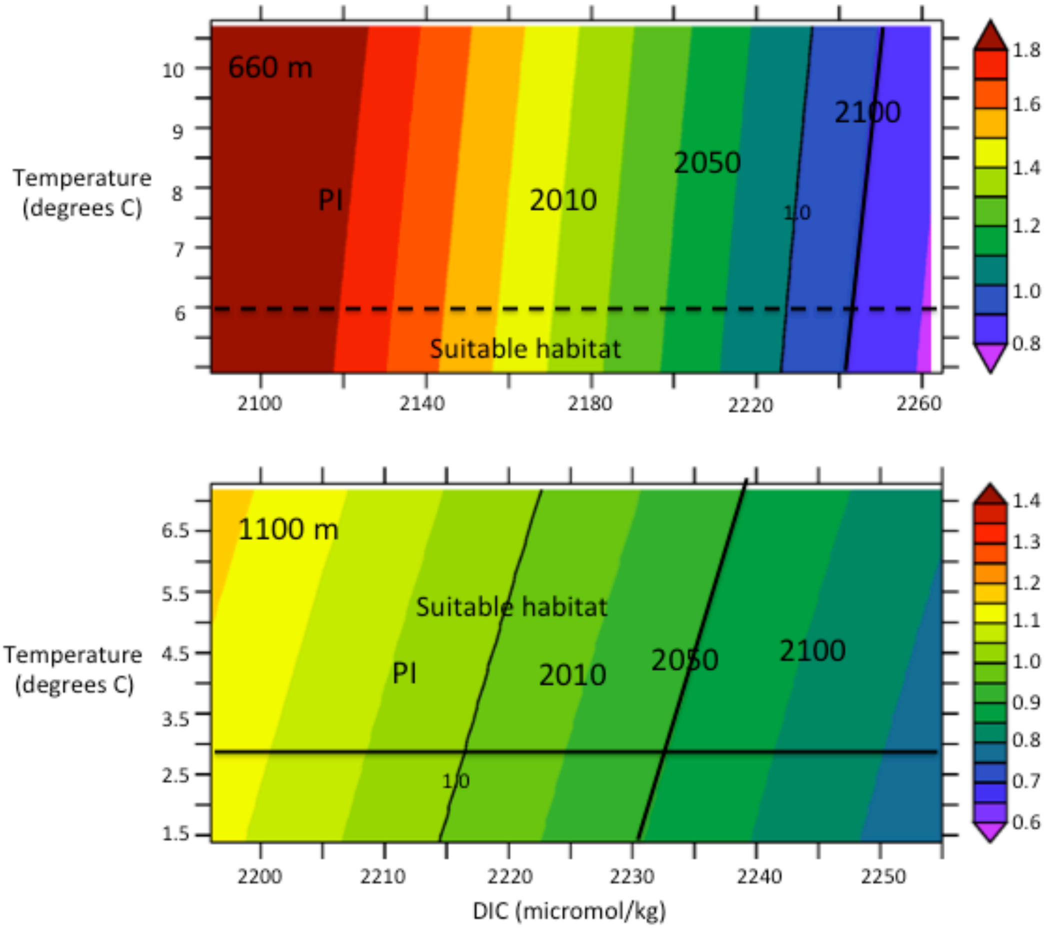

Figure 11. Forecast saturation conditions for the top of the shallowest seamount in the Tasmanian region (660 m depth) in 2050 and 2100 (top), as compared with conditions at 1100 (bottom), based on highest probability estimates of local changes in temperature and DIC. Black diagonal lines indicate the estimated tolerance limit of *S. variabilis* to low carbonate saturation levels (0.9). Horizontal line in the bottom figure indicates apparent minimum temperature tolerance (2.85° C). Suitable habitat for the coral is therefore defined by the upper right hand area bounded by the intersection of the two lines. The same approach is used in the 660 m analysis, but dashed line indicates roughly estimated long-term temperature maxima for *S. variabilis* (ca. 6° C), with suitable habitat in the lower right area bounded by the intersection of the two lines.

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