



MARINE BIODIVERSITY RESEARCH

Prediction and Management of
Australia's Marine Biodiversity

Report on application of evolutionary history to inform how species and/or communities might respond to changes in climate

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1. EXECUTIVE SUMMARY

It is common for us as scientists and managers to slip into thinking of communities, and biodiversity in general, as existing in a static state of equilibrium with fixed spatial and temporal attributes. Reality is quite different, with the biota (genes, species and communities) developing and changing continually in a dynamic competition for survival. Any record or data point is no more than a snapshot of this continuum. We're only now coming to recognise the importance of identifying, and even protecting, these evolutionary processes in the marine environment and the key areas where they occur, with the goal of maintaining the capacity of the 'system' to adapt to further change. This recognition is based on an increasingly robust marine taxonomy.

The CERF Marine Biodiversity Hub has increased our understanding of Australia's marine biota, one of the most diverse and complex of any region. We've improved and developed new continental-scale baseline datasets, and provided new analyses to support marine bioregional plans around Australia. We've shown that Australia's marine species-richness has been underestimated, especially for invertebrates. Where we can identify species, many are endemic – 27% of marine worms or polychaetes collected off Western Australian were endemic – but for some groups we do not have the taxonomic knowledge to identify to this level; only a few dozen of the over 600 species of microcrustaceans from the same area could be identified to species, so the uniqueness of this Australian fauna could not be determined. These are not isolated examples, but reflect the current state of our knowledge, especially in deeper waters.

New techniques including genetic barcoding, molecular clocks (fossil calibrated timing of evolutionary divergence) and phylogeography, were used to provide novel insights into relationships, evolutionary history and geographic distribution. We have started to identify the areas of neo-endemism and paleo-endemism – the former are important as they represent marine areas in Australia where new species have originated; the latter because they are refuges where diverse species have survived previous extreme events, including climate change.

In a changing world, and one that is increasingly influenced by anthropogenic pressures, it is important that we recognise, describe, monitor, and predict variability, from genes to species to communities, and that we understand the processes that have shaped them. Multidisciplinary research like that supported by the CERF Marine Biodiversity Hub provides the breadth of biodiversity properties that we can use to recognise change. Much of this research relies on exciting collaborations between traditional and newly-developed techniques as currently employed within the Hub. It is only with such an interpolated picture of historical change that we can understand the past, and those processes that have shaped present-day communities. Recognising where and how biodiversity is changing most rapidly is the first step in anticipating, adapting and perhaps even influencing the trajectory of change.

2. INTRODUCTION

As scientists and managers we tend to think that biodiversity has fixed attributes in space and time that can be collected on one voyage, described based on observations and collections, and predicted based on the contemporary environment. That is, we continue to follow the myths of equilibrium and stability originating with Aristotle around 330 BC. Reality is somewhat different. Speciation, range extension, range contraction and extinction are continuous processes that speed up during periods of climatic change or assisted translocation. Speciation and extinction do not occur randomly but are concentrated in time, in particular areas and in particular groups.

The marriage of traditional and developing research techniques, such as combining morphological taxonomy with phylogeography and connectivity studies, and the dating of speciation events using molecular clocks, is providing new and powerful tools for accelerating our understanding of speciation and biodiversity. At inception, the Biodiversity Program of the CERF Marine Biodiversity Hub (hereafter, “the Program”) embraced a number of these emerging techniques which are now becoming more widely accepted and utilised.

In this report we'll describe a number of these tools and synergies, and how they are revolutionising our ability to understand and manage future environmental responses to change, including global warming. We'll also outline the current state of scientific research relating to species diversity, discuss the importance of areas where new species develop (neo-endemics), the importance of areas where species have survived previous climatic extremes (paleoendemics), and the importance of those taxa that are taxonomically distinct, thus holding a higher proportion of unique genetic information. We suggest that these distinct areas of biodiversity have a high conservation value, especially in an environment that is changing rapidly.

We start first with a discussion of the state of play in the discovery and description of marine biodiversity, and the scale and importance of the task at hand, before examining how some new advances in taxonomy and genetics have enormously improved our power to recognise species and their relationships. We then discuss how this helps our understanding of evolutionary processes, and finally how we might anticipate and manage the impacts of global change on the marine biota.

3. BIODIVERSITY AND SPECIES DISCOVERY – WHERE DO WE STAND?

'Biodiversity' is a commonly applied term. Despite its broad definition¹ it is usually a summary of biological units occurring within a particular region; for the purposes of broad-scale marine conservation, these units are generally 'species'. While intra-specific diversity (including within populations) also contributes to biological diversity, delineation at least to the species level is essential for establishing a baseline of present-day biodiversity. This is especially true in the marine environment where higher level units (genera and families) are often broadly distributed across multiple ocean basins, occupy vastly different habitats, and can vary in adult body size by orders of magnitude.

Representative regional marine planning relies on a robust understanding of biodiversity and the forces driving speciation and shaping contemporary distributions. Biodiversity Program researchers contributed to a Census of Marine Life stock-take of global diversity (Butler et al. 2010) in which Australia's marine biota is recognised both as being one of the most diverse, and as having amongst the highest rates of endemism for any region (Costello et al. 2010).

It is important to note that we have nothing like a description of the marine fauna – we are still in the "discovery" phase to a spectacular extent. This is true globally, not just an Australian comment. For example, "large-scale marine biogeography is still very much in a descriptive phase. Establishing pattern is a primary objective" (Rex et al. 2005). Snelgrove (2010) begins his account of the findings of the Census of Marine Life by stressing how little we yet know. Our poor understanding of biodiversity, its evolutionary history and the processes that have shaped it, limit our ability to manage biodiversity (Hendry et al. 2010).

New collaborations between disciplines are accelerating aspects of species delineation and description beyond what was previously possible. This is both fortunate and timely; Butler et al. (2010) estimated some 33,000 Australian marine taxa are presently described, another ca. 17,000 are known and awaiting description, and over 200,000 more are awaiting discovery.

There are however, still numerous impediments to describing such a volume of new species, including the widely recognised global decline in taxonomists (Butler et al. 2010; Hendry et al. 2010) which is occurring at a time when the taxonomic questions and issues are increasing. For example the number of new species descriptions for

¹ The 1992 United Nations Earth Summit in Rio de Janeiro defined "biological diversity" as "the variability among living organisms from all sources, including, inter alia, terrestrial, marine, and other aquatic ecosystems, and the ecological complexes of which they are part: this includes diversity within species, between species and of ecosystems". This definition is used in the United Nations Convention on Biological Diversity.

Australian fishes has been consistent since the 1960's, resulting in an 83% increase over this period, despite declining numbers of employed taxonomists (Hoese et al. 2006). Lesser known groups, such as many marine invertebrates, promise even more opportunities for species discovery, leading to a re-assessment of our perception of biodiversity and levels of endemism and cryptic speciation. This was demonstrated in work undertaken in the Program in which recently collected benthic crustaceans and polychaete worms from the Western Australian continental margin were identified to species. From Albany to Ashmore Reef, temperate, subtropical and tropical faunas were sampled at some 528 stations in 100–1100 m depth. We found very high levels of endemism within these samples; about 27% of polychaete species were endemic to Western Australia, and over 39% of decapod crustacean species were endemic to southern Western Australia (Poore et al. 2008). Although many species on the Western Australian continental margin have wide latitudinal ranges, their depth distributions were narrowly defined. Describing biodiversity patterns for marine management requires an accurate taxonomy and we are only starting to achieve that in some taxa. This is evident for small infaunal species. Of over 600 species of microcrustaceans taken from mud samples all along the Western Australian continental margin, only a few dozen could be identified to species (Poore et al., unpublished results).

In addition to field surveys, work within the Program has improved, and made informative use of, existing data. We strategically compiled three continental-scale species-level datasets to complement those previously developed for fish: ophiuroids (brittle-stars), decapods (crabs, prawns, lobsters), and polychaetes (marine worms). So far, we have found that broad scale patterns of distribution of invertebrates on the Western Australian continental margin are largely consistent with those previously defined for fishes (Williams et al. 2010; McCallum et al. submitted). This lends support to Australia's existing bioregionalisation, based predominantly on the distribution of fishes, and the resulting distributional data can continue to be analysed and modelled to determine large scale patterns of biodiversity.

Existing continental-scale datasets of demersal fishes were also updated to include contemporary taxonomic and distribution data, and were analysed for bathymetric (depth related) structuring on the continental shelf (Lyne et al. 2009). Depth was shown to be an important factor in determining fish distributions at these scales, which complements earlier findings for the slope fishes (Last et al. 2005) and the results were used straight away by marine bioregional planners. We have confirmed the disjunction between shelf and slope communities and recommend that for management purposes, these continue to be treated as separate units. Endemic elements of the fish fauna were also demonstrated to be suitable surrogates for the broader fish fauna at these scales (Last et al. in press).

The kind of work described above can be referred to as giving us a “baseline” – a description of our present biota. Having an established baseline is a worthy goal in its own right; from there we can measure change and extrapolate this in space and time both into the future and the past. However, in this Program we have sought more; we want a better understanding of how our biota came to be. Drivers of speciation in the

marine realm are often a combination of both historical (vicariance² and dispersal) and present day processes. By understanding the processes that have influenced present-day fauna we can provide insight into those which are important for particular species, and how these species may react to present-day change.

4. CRYPTIC SPECIATION

The science of conservation biology and ecology, and natural resource management (NRM) has traditionally focused on individual species (e.g. fisheries, ecotourism). Although NRM is now moving to a more “ecosystem based” view, species are still the fundamental unit in community ecology. Scientists identify biota to species, count their abundance or measure their biomass, and use these data to detect community change over space or time. This dependence on understanding species is particularly necessary in marine environments, where many higher taxa (genera, families) are very widespread, even global, reducing their usefulness in distinguishing regional or habitat-related community differences.

Traditional taxonomic methods have relied primarily on external morphological characters, in some cases in combination with internal structures (e.g. musculature, digestive and reproductive organs, and skeletal structure and arrangement). Species definitions based on such characters typically encompass some morphological variation, allowing for individual variability, regional differentiation, or characters that respond phenotypically to environmental factors. However, since the advent of molecular sequencing, it has become obvious that these ‘species’ are often complexes of two or more cryptic species, that can’t easily be distinguished by traditional morphological techniques. Instead they can differ in reproductive behaviour, micro-anatomy, physiology and biochemistry. Cryptic species are particularly common in the sea (Knowlton 1993) and often provide insights into historical events.

A recently-described species-pair of seastars off southern Australia illustrates the point. *Tosia australis*, the common multicoloured biscuit-star easily observed around the southern coastlines, was scientifically-described in 1840. However, it wasn’t until the late 20th century that some photographs began to emerge of animals next to clusters of small juveniles. A university project investigating reproductive and genetic patterns quickly picked up that in fact there were two species, one (*T. australis*) with eggs that floated away to join the plankton and another (*T. neossia*) that sat on their negatively-buoyant eggs for a week in July, protecting them until they grew into tiny juveniles (Naughton and O’Hara 2009). The conservation needs of these species clearly differ. The brooding species forms locally-restricted populations that are vulnerable to habitat disturbance. For example, one of the 13 known populations of the Queensland seastar *Cryptasterina pentagona* was lost to cyclone Larry in 2006 (Mission Beach, Alan Dartnall, pers. comm.). Populations of the restricted intertidal seastar *Parvulastra*

² Vicariance: the subdivision of a continuously distributed biota by climatic and/or geological events.

vivipara have been relocated by hand twice by the Tasmanian Parks and Wildlife Service in 1988 and 2001 to avoid road-works. It is only through recognition that we can monitor and manage these cryptic species.

Combined genetic and morphological taxonomic investigations of squat lobsters undertaken within the Program have discovered at least six cryptic species within two genera where only two were thought to exist before (Poore and Andreakis submitted).

Genetic analyses of stony corals in the Commonwealth SE Marine Reserves, found cryptic speciation, where species previously thought to extend over a wide depth range were found to be multiple species stratified by depth (Miller et al, unpublished results). Species distribution by depth (bathomes) is a key input to marine bioregional planning.

Even some commercially important fishes, such as one deepwater snapper, have now been recognised as consisting of sub species (regional endemics). Such structuring in what were previously considered singular species has obvious, and potentially large, ramifications for managers.

Considering the increasing recognition of cryptic speciation within some common, commercially harvested fishes, it isn't difficult to realise the likely impact of this phenomenon for more poorly known biota, even in shallow waters. These few examples are just the tip of the iceberg, but illustrate how Australia's marine species-richness has been underestimated, how we're still in the discovery phase, and how such gaps in our knowledge limits our capacity to effectively manage biodiversity.

The problem for the community ecologist is to separate species from intra-specific variation. This is particularly acute for surveys of isolated habitats where you might expect some differentiation caused by genetic isolation from other populations. In these cases it is hard to detect whether the populations represent endemic species or subspecies. Speciation occurs on a time continuum, and we are studying biota that may be at any point along this progression, from a homogenous population, to readily differentiated species units. Recognising species units matters, as the listing of endemic fauna and flora will upgrade the conservation status of the surveyed habitat. The emerging fields of genomics may simplify the conservation assessment. For example, if a company wanted to mine cobalt from a remote seamount summit (an emerging prospect) then it may be easier to quantify the overall genetic differences between the seamount and other communities than establishing the endemic status of the component species.

5. ECOLOGY AND BARCODING

Molecular data that are useful for inferring relationships also have a practical application in identifying species. The 'barcode' concept holds that the majority of species can be identified through certain genetic sequences that tend to be similar within species but different between species (Hebert et al. 2003a). The mitochondrial

gene Cytochrome c Oxidase subunit 1 (COI) is often used for this purpose in eukaryotes (Hebert et al. 2003b). The barcode approach allows animals to be identified when the usual morphological characters cannot be assessed. Marine examples include identifying parasite life history stages in different hosts (Leung et al. 2009), identifying gut contents or prey-residues in faecal pellets (Deagle et al. 2010, King et al. 2008), and identifying larvae, including the detection of invasive larvae in ballast water (Deagle et al. 2003, Patil et al. 2006).

However, 'barcoding' has added to the work of taxonomists in interpreting the results. Genetic signatures are no different to morphological characters; there is variation along a continuum within species and between populations. Informed decisions are required to decide when variation represents speciation or purely intraspecific variability. Genetic research is not immune from errors, including transcription and labelling errors, and the retention of voucher specimens (preferably lodged with a recognised institution) is imperative for solving such problems. Incorporating genetic techniques with taxonomy is an important step, and one capable of making inferences that would not otherwise be possible (e.g. Geller et al. 2010) but it does not replace detailed, and often lengthy, taxonomic studies, especially where multiple names may have been historically attributed to a single taxon.

Phylogenetic data, often utilising multiple genes³, also improve modern ecological studies. Ecological studies can be confounded by phylogenetic bias, with shared evolutionary traits amongst species obscuring ecological trends (Telford et al. 2008). Phylogeny has also been incorporated directly into ecological analyses (Cavender-Bares et al. 2009, Leibold et al. 2010). Taxonomic distinctiveness is an index that utilises phylogeny to measure differences between communities and the impacts of anthropogenic activities (Warwick and Clarke 1995; Costa et al. 2010). Protecting phylogenetic diversity in conservation planning has been shown to be a more efficient approach to preserving diversity than protecting species richness, with the added advantage of maximising future options for evolution of a fauna in the face of global change (Forest et al. 2007)

6. PHYLOGENY AND PHYLOGEOGRAPHY

The same combination of morphological and molecular data is, of course, used not only to distinguish species but more importantly to work out the evolutionary relationships between organisms – their “family tree”. Coupled with timings estimated from the fossil record and from DNA regions functioning as a “molecular clock”, these phylogenies can be associated with approximate dates of divergence. Coupled with the geographic locations of present-day species and of fossils, they provide a “phylogeography”. A statement about relationships, evolutionary history and geographic distribution is clearly a powerful tool in working out how species came to be

³ Multiple genes are used to improve resolution in phylogenetic studies as some genes can provide detail at the tips of the evolutionary tree, while others provide detail at the base.

as they are, and where they are, and a powerful background for thinking about where they might be heading.

In this Program, phylogenies have been worked out for certain groups of squat lobsters and phylogeographies for some of them (Poore and Andreakis submitted). Preliminary molecular clock approximations suggest Western Australian populations are significantly older than those from the southwest Pacific. Further support of these results would provide robust insights into today's distribution patterns of squat lobsters, and could suggest the direction and pathway for their colonisation of the region. One of the principal events that could have resulted in geographically associated populations within species in this region was the collision between the Australian continental land mass and Indonesia approximately 25 MYA during the Miocene. These results may have significant implications for managing diversity in the demersal environment, and highlight the strength of combining more than one approach, molecular and morphological taxonomy, for recognising species, and understanding, quantifying and thereby protecting Australia's marine biota. Emphasizing areas for protection that have been demonstrated to drive speciation in previous periods may increase evolutionary options in the future.

Work within the Program using demersal fish distributions examined the affinity (relatedness) of bathomes within provinces, and with neighbouring ocean basins (Last et al. in press). This work confirmed that shelf bathomes differed markedly from those on the slope, and that latitude and depth are important at structuring distributions at these scales. Results from analyses of endemic species mirrored those utilising all species, indicating that endemics are a suitable surrogate for the broader fish fauna. While these findings may not be surprising to marine biogeographers, this is the first time the affinities of these provinces have been examined, and adds to our confidence in the bioregionalisation underlying IMCRA 4.0 (used in marine bioregional planning) as well as providing a sound basis for future discussions on IMCRA 5.0. There is also strong evidence of major differences between provinces based on latitude, reflecting tropical and temperate elements of the fauna.

7. PHYLOGENETIC ENDEMISM AND THE IDENTIFICATION OF REFUGES

It is increasingly recognised that we require more than a simple measure of species richness in order to prioritize areas for biodiversity conservation. We know that hot spots of species richness, endemism and anthropogenic threat do not necessarily coincide, on land (Orme et al. 2005) or in the sea (Tittensor et al. 2010) and that phylogenetic diversity may be a more efficient basis for terrestrial reserve planning than simple species richness (Forest et al. 2007).

The taxonomic distinctness of the component species is an additional feature of biodiversity that we explicitly or implicitly value when making conservation choices (Vane-Wright et al. 1991). It is often considered reasonable to put more resources into

conserving species with no living relatives than one member of a species complex. The rationale is that this will provide greater adaptive capacity for the fauna to respond to future change (climate, invasive species, etc.). Moreover, conservation of rare lineages is likely to conserve rare genes and associated bioactive compounds, one of the objectives behind biodiversity conservation. Such considerations require incorporating phylogenetic information (some measure of how related species are) into conservation planning, in addition to data on species distributions. An indirect approach is to use phylogenetic diversity instead of species diversity. However, more quantitative measures of phylogenetic endemism are beginning to emerge that directly identify concentrations of spatially restricted evolutionary diversity (Rosauer et al. 2009). These measures combine phylogenetic trees generated from molecular data with fine-resolution maps of species endemism. The work of this Program is giving us, for the first time, data enabling us to use these kinds of methods for marine species in conservation planning.

Narrowly ranging species with few living relatives are more likely to be palaeoendemics, ancient species with a remnant distribution, rather than neoendemics that have speciated more recently with identifiable sister taxa. Understanding the spatial distribution of palaeoendemics is likely to identify long-term refugia, areas with comparatively stable climatic regimes that have persisted through various climatic cycles. Protecting these areas is a conservation priority as they have contributed to the maintenance of biodiversity over time, although we need to better understand their potential role for contemporary communities. Protecting areas that are the centre of neo-endemism is also a conservation priority on evolutionary timescales if there are reasons to suggest that future speciation will develop from the same areas (see next section).

Glacial refuges have not been systematically identified for the Australian marine environment. However, the South Australian Gulfs region is likely to retain its ecological structure (low wave energy, relatively warm temperatures) at different sea-water levels across climatic cycles (Barrows et al. 1996; O'Hara unpublished data). Other warm-water thermal refuges are likely to exist along the east and west coasts of Australia, and interglacial refuges (for cold water species) may have occurred around southern Tasmania. Deep coral reefs have been inferred to be a refuge from warming events and other disturbances, at least for species that tolerate a wide range of depths (Bongaerts et al. 2010). These areas should be given special consideration in conservation planning.

8. CONNECTIVITY, BARRIERS AND THE MAINTENANCE OF EVOLUTIONARY PROCESSES

Over the long term it is also important to protect evolutionary processes in order to promote the persistence and future generation of biodiversity (Klein et al. 2009). The distribution of neoendemics or sister species can assist in identifying areas of active

speciation. These 'evolutionary fronts' can include habitat mosaics or ecological gradients that generate species through allopatry or ecological specialisation respectively (Schneider et al. 1999).

In the Australian marine environment, both Bass Strait and Torres Strait have been identified as potential 'species pumps' (Uthicke and Benzie 2003; Waters 2008). The lowering of sea-levels during glacial climatic cycles creates land-bridges that separate marine populations. The disjunct populations become reproductively isolated through genetic drift and can develop into separate species that remain distinct on secondary contact during inter-glacial cycles when the land-bridge is re-flooded. It is still unclear how important the recent climatic cycles are in this regard, as most sister species that are distributed across Bass Strait have been dated to greater than one million years using molecular clocks (Waters and Roy 2003; Williams et al. 2003; BurrIDGE and Smolenski 2004; Waters et al. 2004; Naughton and O'Hara 2009). However, modern ecological processes can also generate semi-permeable barriers to gene flow, resulting in distinct populations on either side of the barrier which can be detected by their molecular signature (Dawson 2005; Waters 2008).

Incorporating phylogeographies with the timing of evolutionary events (through gene drift, or molecular clocks calibrated against fossil records) links speciation events with historical processes, for example the emergence of the Bass Strait in recent times, or the breakup of Gondwana some 165 MYA. Some of those palaeo-phylo-geographic studies do tell us things about the limits of the movement of some groups. Those limits might be physiological – e.g. temperature – or some kind of interaction with other species that we haven't studied – we're not likely to know which. But we will sometimes have a general picture of the movements, and limits to movement, of some groups. This information could be used to bound predicted changes under climate change from climatic envelope models that experience suggests are unlikely to capture species distributions very well.

Work within the Program combined fossil-calibrated 'molecular clocks' with traditional taxonomy and biogeography to examine the congruence of speciation processes in southern Australia among selected genera within three families (the wrasses, leatherjackets and stingarees) (Andreakis et al. in prep.).

There is evidence for parallel micro- and macro-evolutionary events for fishes over a number of geological periods, ie. the repeated cycles of warming and cooling in southern Australia, combined with the subsequent repeated emergence and flooding of the Bass Strait land bridge (discussed above). These combined with a long period of relative isolation created high levels of endemism in southern Australia. Further work by hub researchers is examining the role of sister species in paired demersal provinces on the northeastern and northwestern coasts. The study is examining the role and function of sister species in similar bathomic units on each coast, much as a census will compare demographic patterns between cities or populations. Of particular interest is whether the relative nutrient loads have influenced the demographics of each bathome, and whether sister species pairs are filling similar functional roles in the two

areas. This may provide insights into the adaptability and potential role of sister species following translocation and adaptation, and therefore whether we need to be concerned about ecosystem units or ecosystem processes containing few sister species or little functional redundancy.

Our knowledge about speciation processes in the deep sea is still largely speculative (Wilson and Hessler 1987; Raupach and Wägele 2006; Samadi et al. 2006; Macpherson et al. 2010; Menot et al. 2010). There are examples of sister species being separated at oceanic scales suggesting isolation by distance (e.g. Duncan et al. 2006; Imron et al. 2007). Other deep-sea groups have numerous sympatric species suggesting that speciation has resulted from adaptive radiation (Machordom and Macpherson 2004). Sister species distributed in adjacent depth strata have been identified on continental slopes and seamounts (McClain and Hardy 2010; England et al. in prep., A & B; O'Hara et al. in prep.), suggesting that depth-related environmental gradients or habitat differences may promote adaptive radiation.

Work by Program researchers (Miller et al. 2010; England et al. in prep., A & B; O'Hara et al. in prep.) has highlighted the complexity of seamount ecosystems. Reproductive life history appears to explain differences in population structure at continental scales between some organisms, those species with long-lived pelagic larvae proving to be more connected than those with short-lived larvae or no larval period. Genetic exchange between seamounts occurs for at least some species over thousands of kilometres. These findings challenge widely held paradigms regarding seamount isolation (Miller et al. 2010; O'Hara and Tittensor 2010; Rowden et al. 2010), but we stress that seamount communities are composed of a multitude of species with varying life history strategies, and consequently varying levels of connectivity. A more robust understanding of connectivity between populations can better inform the size, location and spatial arrangement of MPA's, and management measures required for areas that are inherently difficult to study, such as the continental slope, abyss and seamounts.

The study of molecular phylogeographies and connectivity in the oceans is still in its early stages. Despite increasing scientific knowledge, the translation to conservation management in the oceans is not as straightforward as on land. Partly this is due to terrestrial connectivity often focussing on iconic megafauna, whereas CAR principles (Comprehensiveness, Adequacy and Representativeness) for marine reserve networks necessitate a more general approach that accounts for animals with very different evolutionary pathways, life history strategies and dispersal strategies. This uncertainty is illuminating however, in that it starts to define what science can and cannot provide to support network design or to measure to what extent a marine reserve network is providing greater conservation value than the sum of its constituent reserves. These early results and the areas of uncertainty that they have highlighted would have a role in designing on- and off-reserve management options that are robust to this uncertainty. For example, the deepwater dogfish *Centrophorus harrissoni* has been recorded along the eastern seaboard and on remote seamounts in the Tasman Sea. It is unclear whether individuals at these locations represent different populations, or different species. This uncertainty continues to hamper development of management

and conservation arrangements for a shark that is of high conservation concern (Graham and Daley in press).

9. EVOLUTIONARY RESPONSE TO CLIMATE CHANGE: ENHANCING CAPABILITY FOR PREDICTION

The marine fossil record along the SE Australian coast indicates the possible effects of past climate change. During the last interglacial (isotope stage 5e, 123k ago), sea-surface temperatures were 1–2° warmer than today. Fossils from this period of the subtropical gastropod *Turbo torquatus*, currently restricted to NSW, SA and SW Australia, can be found commonly along the western and central coasts of Victoria (Sherwood et al. 1994; O'Hara 2001). The bivalve *Anadara trapezia*, illustrates the complex interaction between range, available habitat and temperature (Kendrick et al. 1991; Murray-Wallace et al. 2000). *Anadara trapezia* is currently restricted to estuaries in eastern Australia, from Port Phillip Bay in Victoria to central Queensland (19°S), and is also found in one small population at Albany in Western Australia. It tolerates a wide range of temperatures and has a high dispersal capability and yet does not occur today in the South Australian Gulfs or in estuaries on the western coast. Nevertheless it was ubiquitous across southern Australia during the last two interglacials (isotope stages 5e and 7) even reaching New Zealand. It was common 6,500 year ago in the Tamar estuary in northern Tasmania but is absent today (Goede et al. 1993). However, it is surprising that there are so few examples of marine invasions in the recent fossil record, suggesting that the effects of climate change will be very complex, and the ecological interactions not easy to predict. It is well understood that we cannot expect the wholesale movement of entire communities or ecosystems. There will be winners and losers in the ongoing poleward redistribution of taxa, and as yet undefined opportunities for directing evolution of the new communities or ecosystems.

Current approaches to prediction are generally broad-scale and imprecise and therefore have varying value in precisely predicting shorter-term processes of extinction and/or range shift in response to global change (climate change, ocean acidity, etc.). These may be refined by the insights from the large-scale, long-time studies – and it is valuable to have that sort of envelope around what's possible – but the details of the responses of the biota to changes will be very complex. Predictions will not be of the form “a certain isotherm will move south by 1 degree latitude, therefore all the species will move south by 1 degree” – some species will move more than others, and species interactions will therefore change. Importantly, range shifts may create opportunities for speciation – extinction of a competitor, the possibility of a new food supply, opportunities for new mutualistic interactions. An example is the collision of the Australian Plate with southeast Asia, resulting in many new shallow water, tropical habitats and consequent explosive speciation (e.g. Williams and Duda 2008). Thus, it will not be possible to predict new communities in detail with even the most sophisticated modelling tools we have available.

And even as our already-powerful modelling tools improve, we will remain limited by the detailed biological data with which to parameterize them. At the individual-species level, of course there is (and needs to be) continuing research on their physiological limits, and on specialised aspects such as stress/adaptation genes (Hoffman and Weeks 2007; Johnson et al. 2009; Kellermann et al. 2009) which enable us to predict vulnerability to anthropogenic activities, to identify traits that enable adaptation to climatic stress, and to understand the genetic basis of these traits. We know that there are species that appear to be good colonisers, and others that historically haven't been (e.g. handfish, once widespread including Europe, but now greatly restricted (Last and Gledhill 2009)). But all invasions, historical and present, are a battle between invaders and prior occupants. This highlights the complexity of predicting species movements; we will see colonisers/invaders and prior occupants competing and preying on one another, the complexity increases exponentially. All of this will reshape communities and promote evolutionary change.

Nevertheless, we can assume some southward migration with changing isotherms as widely reported globally (e.g. Hoegh-Guldberg and Bruno 2010) and more recently, Program scientists have demonstrated this for fishes in southeastern Australia (Last et al. 2010). These distributional changes potentially will have a leading (invasive) and trailing (retreating) edge (Davis and Shaw 2001). O'Hara and Poore (2000) found that the southern (invasive) edge of marine species distributions tended to be congruent between invertebrate species while the trailing edge is more stochastic.

Emerging research combining spatial modelling with ecological niche modelling aims to better predict both historic and future invasion events, and likelihood of invasion of specific habitats (Steiner et al. 2008). These predictions have obvious application to climate change work, but do have limitations, namely the need for robust baseline data of species habitat requirement. Further, such predictions are only dealing with a single species at a time. Therefore, it will be necessary to *monitor changes* in marine communities, and engage in an iterative process of monitoring, interpreting changes, making best-guess limited predictions, monitoring further, and so on. Papers like that of Last et al. (in press) are early parts of this process – measure from the baseline. However, note that we are *not* advocating blind, uninformed (and therefore very expensive and possibly uninformative) monitoring. We advocate targeting the monitoring as well as possible, by being as informed as possible about what is *likely* to happen. Long-term studies like the ones undertaken in the Marine Biodiversity Hub provide a reasonable boundary to the sorts of changes we might expect, and hence what to monitor. The developing Commonwealth marine reserve network provides an opportunity to set aside scientific reference areas that can be used for robust monitoring over the coming decades. Linking management objectives and actions to monitoring (eg. through the Common Assessment and Reporting Framework developed by the States and Commonwealth under the Marine and Coastal Committee), will then provide the opportunity for scientific knowledge and management opportunities to advance in synchrony.

10. CONCLUSION

The world is changing. Environmental professionals (like DSEWPC staff) have known for a generation the anthropogenic causes of this (pollution, over-exploitation, habitat loss, ...) and sought to manage them. In addition, we are now increasingly concerned about climate change. It was true before, but is now conspicuously true, that we cannot manage with the aim of restoring a system to some former state – rather, we are managing a system on a trajectory, and the best we can hope for is to influence its trajectory. Our capacity to predict that trajectory is limited.

Biodiversity research can help. Research, now with sophisticated multidisciplinary combinations of techniques as utilised within the Program, some only recently available, can tell us how the fauna came to be the way it is, including how it responded to past changes. This not only gives us a general framework for how it is likely to respond to future changes, but also gives some specific tools including:

- Rapid identification of known species (barcoding).
- Identification of cryptic species.
- Identification of refuges where species have survived earlier environmental changes.
- Understanding of capacities for dispersal and connectedness, and of the scale of range shifts, with immediate application, e.g. to the design of MPA networks.
- The concepts of phylogenetic endemism and of taxonomic distinctness, which can bring some of the most advanced ecological thinking to bear on conservation planning and management.
- Understanding of major biogeographic discontinuities and their stability, again with application to conservation planning.

None of this reduces the need for the work of taxonomists, nor does it reduce the complexity of ecological prediction. We can predict the kinds of processes that will occur, but prediction at a detailed level will be almost impossible. Therefore:

We need to hedge our bets in management. From a management viewpoint, our research will help to set bounds on likely possibilities, and suggest what to look out for, monitor, guard against, and focus on. It is likely that predictions (as opposed to scenarios) will only be attempted when it really matters (a key pest species that might have wide effects, a key industry, etc.); they will have to be quite detailed, system- and taxon-specific, dependent on *targeted* research, and expensive. In general, the climate models are not yet very helpful regarding the sort of fine oceanographic detail we need for this exercise, although there can be exceptions. However, it will be possible to give some advice concerning likely possibilities with more limited information. For example, regarding climate change:

- We expect warm temperatures further south, especially in the SE corner, and current research already tells us the sorts of biotic changes to expect.
- We expect shallowing of the aragonite saturation depth, with broadly predictable consequences for calcareous organisms.

- strengthening easterlies and diminishing westerlies along Australia's southern coast may alter the timing and strength of upwellings.
- sea-level will rise, reducing some coastal habitats and increasing the isolation of those that remain.
- we expect southward shifts in some distributions but others may not be able to shift, and this will generate novel communities and ecosystems.
- a comment on provincial boundaries here – at present we can only speculate as to why certain provincial boundaries are apparently stable and the same for diverse fauna – perhaps these features will not shift with climate change.

Beyond that, we will have to remember that species interact; we must expect many ecological changes, much more subtle than mere shifts of distribution, and consequent evolutionary changes. Our management regimes will need to anticipate the most reasonably likely of these, monitor for them, and continually adjust both our understandings, and our monitoring and management regimes, as the reality unfolds.

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APPENDIX A

Publications contributing to this milestone from Marine Biodiversity Hub and associated projects.

Andreakis, N., Ahyong, S. and Poore, G. (in prep.). Taxonomy, phylogeny, comparative phylogeography and origins of the squat lobster family Galatheididae in the Indo-Pacific.

Andreakis, N., Ahyong, S. and Taylor, J. (in prep.). Systematics, Phylogenetics, morphological evolution and phylogeographic patterns in *Munidopsis*.

Andreakis, N., Gledhill, D.C., Rowe, D.L., Puckridge, M., Innes, B.H., White, W., Butler, A., van Oppen, M.J.H. and Last, P.R. (in prep.). Signatures of speciation, and the origins of Australian Labrids, Monacanthids and Urolophids.

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