National Marine Science Plan White Paper Submissions for
Biodiversity Conservation and Ecosystem Health

Pelagic Ecosystems

Background

The pelagic biome is the largest, by volume, on the planet (Angel, 1993). Yet most knowledge of this biome comes from the epipelagic zone, the top 200m of the ocean, while the remainder remains virtually unexplored, including in Australian waters. The thermocline represents the last frontier of exploration of Earth's ecosystems. This white paper considers research priorities for biodiversity in the pelagic realm, comprising neritic (on the continental shelf) and oceanic (off the continental shelf) systems in Australia (Figure 1). The priorities include research on the structure, function and change in pelagic biodiversity around continental Australia, its territories and in the Southern Ocean and Antarctica (Figure 2). The dynamics of pelagic ecosystems are being impacted by the effects of global, regional and local human activities (Figure 3) but research into these effects and their management are considered in other white papers. Similarly, interactions with benthic and estuarine ecosystems may be important drivers of pelagic biodiversity in some parts of the system. While these processes and taxa are acknowledged, the attributes of the biodiversity of benthic and estuarine ecosystems are considered in other papers also. This paper focusses on the priorities for research on the biodiversity of pelagic ecosystems that will be important for underpinning the science and management of Australia's marine realm.

Pelagic biogeographic provinces have been identified for Australia (Figure 4) (Grant *et al.*, 2006; Lyne *et al.*, 2005). They fit well with the global classifications of Longhurst (Longhurst, 2007) and Spalding and co-workers (Spalding *et al.*, 2012; Spalding *et al.*, 2007). These provinces provide a general context for partitioning research into regional areas - (1) Antarctic and Subantarctic, (2) South-East Australia, (3) Great Australia Bight and South Australian gulfs, (4) South-West Australia, (5) North-West Australia, (6) Northern Australia including Gulf of Carpentaria, and (7) North-East Australia, including the Great Barrier Reef (Figure 4).

Pelagic ecosystems link coastal, neritic and oceanic biodiversity and underpin the productivity and sustainability of that biodiversity. The dynamics of pelagic marine ecosystems control delivery of nutrients and energy from (i) terrestrial and estuarine inputs, (ii) oceans external to Australia and (iii) the deep sea. In three dimensions, they determine the retention and recycling of nutrients in the epi-pelagic layer, transport/export of energy to the benthos and the transport of energy from areas of production to other areas. The spatial and temporal variability of the relative importance of all these processes gives rise to patchiness in production around Australia.

Dynamics and change of pelagic biodiversity set the context for management strategies aimed at sustaining many ecosystem services in Australia. Pelagic ecosystems are naturally dynamic, varying seasonally, annually and at longer frequencies associated with climate phenomena such as El Nino and the Pacific Decadal Oscillation. Moreover, long term trends in a number of ecosystem attributes are occurring as a result of anthropogenic influences on climate-ocean systems (Field *et al.*, 2014), with expected futures including a warming ocean, increased acidity and greater intensities of storms, along with other regionally-specific trends and perturbations.

Pelagic species will potentially respond to environmental changes by (i) tolerating the changes, although this may result in a change in performance which could alter the relative abundance of those species in the ecosystem, (ii) changing behaviours, such as occupying different depths, (iii) moving geographically to remain in the ocean conditions most conducive to their survival, and/or (iv) adapting to new conditions through changes to behaviour and physiology on evolutionary time scales.

Adaptation of industries and activities to these futures, and avoidance or mitigation of possible impacts of human activities now and in the future, requires a capability to assess

- **dynamics and trends** of pelagic ecosystems in response to variability in the marine environment over short, medium and longer time scales, including the key drivers that influence the functional components of ecosystems and whether those functions can be sustained;

- **spatial scales** of ecological processes and impacts;
- **responses** of pelagic biodiversity to future changes to the Earth system; and
- **sensitivities** of pelagic biodiversity and the ecosystem as a whole to industries/activities interacting with them.

Models of various forms representing pelagic ecosystems, informed by current state of knowledge and observations, underpin the capability to make these assessments.

Maturity

Pelagic ecosystem research in Australia has been fragmented until the 1990s with most biological research in the pelagic realm being primarily focussed on sectoral interests, such as pollution and waste management (coastal)(Fulton *et al.*, 2004), pelagic fisheries (highly migratory tunas and billfish,)(Hobday *et al.;* Young *et al.*, 2014) and how productivity in pelagic ecosystems may affect the productivity of benthic fish stocks (e.g. prawns). 'Ecosystem' research was largely focussed on the dynamics of the physical environment and its influence on primary production (biogeochemistry), a question of importance in understanding the global carbon cycle.

The advent of ecosystem-based fisheries management at the turn of the 20th Century saw more synthetic approaches to consider the effects of fishing on food webs. Such work usually targetted the effects of fishing on air-breathing vertebrates of high conservation status. Top-down effects of fishing of large pelagic predators has only become a major topic for discussion in the last decade. Over that same period, regional management to achieve sustainable multiple-use of ecosystems has increased attention on regional syntheses and modelling. This has resulted in more systematic, integrated considerations of all ecosystem components, with a realisation that, either (i) many components of ecosystems are unknown, or (ii) observations and studies of processes of the different components and their interactions with the ecosystem have not been undertaken in a systematic way, i.e. studies of particular components often do not overlap in space and time with studies of other components (e.g. predators with their prey). Consequently, the levels of uncertainty are generally high for (i) pelagic ecosystem structure, function and responses to human perturbations, and (ii) trends in key species.

Table 1 illustrates the results of an analysis of the status of knowledge on different attributes of pelagic ecosystems in 7 regions of Australia identified in Figure 4. This analysis considers four different scales at which pelagic ecosystems may be viewed - Global, Regional, Food web, Species/populations (characterised in Figure 5). It also considers progress in the development of models at each of these scales, particularly in nesting this knowledge in order to advance models that enable assessments of current and future states of habitats, species and foodwebs (Table 2, Figure 5). Progress in modelling considers the readiness of models at those scales, including both their development and skill (how well they replicate known conditions and observations). For the scales of foodwebs and species, knowledge is evaluated for each of four classes of biota - (a) microbes, (b) zooplankton and small nekton such as Antarctic krill and myctophid fish, (c) migratory fish and squid, and (d) air-breathing vertebrates.

This analysis shows good progress in placing Australian pelagic ecosystems in the global context (Matear, 2013), except for the Southern Ocean where, like in the Arctic, progress is needed to better characterise habitats, productivity and, particularly, long term variability in the region (Constable *et al.*, 2014b). For knowledge of regions, the most progress has been made for South-Eastern Australia (Everett *et al.*, 2012; Everett *et al.*, 2014; Fulton & Gorton, 2014; Hobday *et al.;* Hobday *et al.*, 2013; Hobday *et al.*, 2011; Suthers *et al.*, 2011) followed by the North-east (McKinnon *et al.*, 2014) and then the South Australian gulfs (van Ruth, 2014; van Ruth & Doubell, 2013) and the eastern part of the Great Australian Bight (Goldsworthy *et al.*, 2013; L.J. *et al.*, 2009; Rogers *et al.*, 2013). The experience in developing an Atlantis (end-to-end ecosystem plus human activities) model for south-east Australia is now being used as a foundation for model development for all other regions. The least progress on regional pelagic ecosystems is in south-west Australia and the western part of the

Great Australia Bight, with progress still not well integrated for the Southern Ocean and North-west and Northern Australia.

Decisions to mitigate impacts or to adapt to change will require more detail at the scales of foodwebs and species. Table 1 shows that, apart from South-East and North-East Australia and species that have been the foci of fisheries research, knowledge of pelagic foodwebs and species is not well integrated and mostly absent for the four classes of biota considered here, particularly for low and mid trophic levels (zooplankton and small nekton, and migratory fish and squid).

Time series of observations of biota to determine food web dynamics and phenologies, i.e. concomitant observations of predators, prey and habitats, are not common. Other than fisheries data, ships of opportunity have been used to collect protists (underway measurements), zooplankton (Continuous Plankton Recorder program), and epi- and meso-pelagic biota (acoustic data). These do not provide surveyed estimates of abundance but they are starting to be analysed to examine spatial and temporal variability of the general properties of the lower trophic levels. Some biota remain elusive and under-represented in these studies, including squid and gelatinous species.

Current research capacity

Research on Australia's pelagic ecosystems spans a number of Commonwealth and State agencies, coupled with universities in each region. Nodes of activity are in South-west Australia, the South Australia gulfs and eastern Great Australia Bight, Tasmania, central New South Wales and Queensland. There are no locally-based nodes of activity for North-west and Northern Australia and the Southern Ocean, although Tasmania serves as the focus for Southern Ocean research. Universities outside these nodes are participating but have far fewer resources at their disposal. Participating organisations include:

Commonwealth agencies: CSIRO, AAD, AIMS, IMOS, GA

State agencies: Australian Museum, SARDI, NSW-DPI, NSW-OEH, WA Fisheries

Universities: Flinders, UNSW, Sydney, UTS, Macquarie, Wollongong, Southern Cross, IMAS (UTas), Deakin, UWA, UQ, Griffith, Murdoch, JCU, Gold Coast

Centres: SIMS, ACE CRC

International research collaborators include those from the USA, Japan, France, and New Zealand. International programs that assist in facilitating collaborations include IMBER CLIOTOP, IMBER-ICED, ICES-WGFAST, SAHFOS (UK), IUCN.

The number of Australian research scientists supporting work on the ecology of pelagic ecosystems total less than 200. The quality of their research rates highly internationally, with many in Australia's research teams playing leadership roles in international panels and working groups, such as in the Intergovernmental Panel on Climate Change, the UN World Ocean Assessment, and in the international research programs of SCOR, SCAR, IMBER, GOOS, SOOS.

Pelagic ecosystem research is funded from core funding to the Commonwealth and State agencies, along with NCRIS, FRDC, ARC, AAS, MNF and the CRC research funding programs. This research also benefits from government programs for aid and sectoral support e.g. NERP. Increasingly, the larger integrated ecosystem programs are funded by government, industry and/or environmental NGOs to address regional marine management issues, e.g. oil/gas and fisheries.

Success of this research is indicated by the uptake internationally of Australia's approaches in ecosystem-based research and management, the application of Atlantis to other regions, and the influence of Australia in international regional management organisations such as WCPFC and CCAMLR.

Relevance

The primary end-users of research on pelagic ecosystems will be those managers, policy-makers, industry, and NGOs aiming to avoid, mitigate or limit the effects of human activities on pelagic ecosystems in order to sustain their ecosystem services. Another set of users will be those seeking to adapt human activities and societies to future conditions before problems arise. Both of these types of end-users seek advice on (i) the types of consequential ecosystem effects that might arise given various human impacts, now and in the future, and (ii) the current status and trends of habitats, species and food webs and how these might change in the future (likelihoods of future states). The relationships between different types of research and the paths to delivering to these end-users are illustrated in Figure 6.

The central role that pelagic ecosystems play in the dynamics of the marine ecosystems generally means that this research has a very high priority. An important outcome will be to provide early warning of potential shifts in ecosystem structure and function, which could be (i) rapid, (ii) surprising, and (iii) dramatic. Even for more 'open' pelagic systems where environmental change is arguably more buffered. Assessment models are need to assess risks of such changes in the future, which will be essential to adapt management systems to sustain ecosystem services, i.e. how might trophic cascades or regime shifts be detected or, indeed, predicted?

Governmental and intergovernmental end-users of this research will be Commonwealth and State government agencies responsible for sustaining marine ecosystem services in Australia and for planning for the future. As pelagic ecosystems and their biota inevitably impact on marine systems neighbouring Australia, which is in turn impacted by those systems, pelagic ecosystem research is necessary for use in international forums such as CCAMLR, CCSBT, WCPFC, IOTC, SPRFMO, SIO RFMO, IUCN, IWC, CMS, CITES and the IMO and its Convention on the Prevention of Marine Pollution (including ocean dumping and iron fertilisation). International advisory bodies on the mitigation of and adaptation to future impacts and change include the IPCC and the UN World Ocean Assessment.

Non-government end-users include industries and environmental NGOs. Industries include fisheries, aquaculture, oil and gas, tourism. Other industries that may be affecting pelagic ecosystems are those terrestrial (catchment) or coastal operators that may indirectly affect marine ecosystems through discharge or disturbance.

Increasingly, Australian researchers are being sought to contribute their expertise to international organisations and many other national research programs. International examples include contributions to IMBER, SOOS, and GOOS.

Evidence of uptake of this research occurs regularly through the establishment of ecosystem-based management measures domestically (AFMA, Environment, Agriculture) and internationally (e.g. CCAMLR, CCSBT, WCPFC, IMO). These measures include catch limits, satisfactory assessments of the ecological sustainability of fisheries (e.g. national and industry-based assessments) and conservation of species and biodiversity. Other evidence of uptake includes

- the design of monitoring programs to detect effects of industrial activity and for detecting change,
- the design of marine protected areas facilitated by knowledge of the structure and function of pelagic ecosystems,
- the international acceptance of advice from Australian researchers on future scenarios for Australian and global marine ecosystems, and
- the take-up of Australian research outputs on pelagic ecosystems, such as
    - the use of the end-to-end ecosystem modelling capability in Atlantis, and
    - approaches to observing, assessing and modelling habitats, species and food-webs.

Science needs and priorities

As described above, the capability to assess dynamics and trends, spatial scales, responses and sensitivities of pelagic biodiversity requires research on the following:

1. the functional components of pelagic ecosystems, including which species contribute to that function (the species pool),
2. the key drivers and processes that give rise to the dynamics of the functional components, or at least the key species, the spatial connectivity of the different components, and the attributes of habitats in which they live,
3. the sensitivities of biota to changes arising from human activities, and the potential for rapid change and possible regime shifts,
4. observations of variability and trends in key components of the system that satisfactorily indicate the behaviour of habitats, species, functions and food webs
5. statistical and dynamic models to undertake the assessments required by end-users.

A set of research priorities could be determined by endeavouring to fill key gaps surrounding these requirements (see Table 1). They do not need to be undertaken in sequence from Requirement 1 to Requirement 5. A further approach for determining priorities, using information currently available, is to develop models at the different scales identified in Figure 5, and then seek to evaluate their accuracy, precision and their capability for being nested within the framework of Figure 5, particularly assessing their capability for avoiding the compounding of errors that may arise when different scaled models are integrated (Evans *et al.*, 2014). The priority for the models at the different scales would be governed by the priorities for end-users. These models can then be used to evaluate hypotheses of interest to end-users. Practical short-comings of the models will be readily identifiable and signal requirements for field work. Similarly, the requirements of end-users may signal short-comings in any of the five research requirements above. The models can then be used, along with any modifications, to help design field programs to be most effective at delivering outcomes to the end-users, whether those outcomes are scientific, assessments or other end-uses. This process is illustrated in Figure 6.

The priorities for scientific research are considered here for the five requirements above along with using models to help design field programs and set priorities in the future.

1. Functional components

For ecosystems, the functional attributes of biota are those that govern the acquisition, storage and transfer of energy/nutrients. Transfer is in five dimensions – 2D geographical space, depth, time and between organisms. Size-based models reflect a simple hierarchy of energy transfer and can be useful approximations in some systems. Morphology, life history, physiology (tolerances) and behaviour may moderate such hierarchies giving rise to more definitive paths of energy transfer from lower to higher trophic levels. Similarly, some attributes of species may contribute to retaining or recycling energy/nutrients within a part of the food web e.g. the potential role of whales in recycling iron (Nicol *et al.*, 2010).

Progress has been made in developing an inventory of species in the pelagic realm. However, the characerisation of functions, particularly for lower trophic levels (protists, zooplankton, small nekton), remains incomplete, particularly for regions other than the South-East, North-East, and North (Table 1). Under-represented taxa include squid and gelatinous biota and zooplankton that are not crustaceans. Microzooplankton grazers are also poorly represented in these studies and are likely to be very important in the dynamics of lower trophic levels (Schmoker et al., 2013). A priority is to satisfactorily determine the functional groups that will give rise to different energy pathways to the higher trophic levels (Griffiths *et al.*, 2013; Irigoien *et al.*, 2014). A longer term priority is to determine the vulnerability/resilience of a functional group to future change. One aspect of that research may be to assess the genetic diversity in each functional group.

2. Key drivers, processes, connectivity, habitats

Regional distributions and dynamics of habitats and productivity are the best known attributes of pelagic biodiversity, but this is limited for the Great Australia Bight, South-West Australia and the Southern Ocean (Table 1). A noted difficulty in habitat analyses is the absence of knowledge for most pelagic species of their tolerances to different conditions of the ocean. Studies of physical and biological connectivity have been identified as a high priority in all regions and for all taxa, except perhaps in the North-East.

Generally, integrated studies of pelagic biota, including their life history, rate functions, physiology and behaviour, across the range of spatial and temporal conditions that they may experience are rare, even for key taxa. In particular, there is very little information on the possible effects that multiple simultaneous stressors may have on different functional groups. These shortcomings make it difficult to developm autecological models for different groups, and to accurately represent trophic pathways and habitat dependencies in food web and regional ecosystem models. Improved understanding of the primary factors influencing different life history stages, estimates of resource requirements, consumption rates, growth and reproductive rates and responses to different habitat variables are research priorities. Behaviours and their responses to environmental, prey and other cues need also to be characterised.

3. Sensitivities

Tipping points (radical shifts) in the ecology and dynamics of species have been discussed as possible consequences of simultaneous multiple stressors arising from human activities and perturbations. These may be rapid. As yet, there are no assessments of risks of pelagic biodiversity experiencing tipping points in the future. Experimental manipulations of ocean conditions for lower trophic levels are needed to help identify the potential for synergistic or antagonistic effects amongst possible future stressors. Individual-based models could be used to help identify the possible consequences for higher trophic levels.

4. Observations

Most research in pelagic ecosystems relates to observing the distribution and abundance of biota and how these relate to the physical environment. Few studies have been undertaken to routinely monitor the variation of these biota over time, with even fewer studies on the covariation of these biota with their habitats, predators and prey. These data are centrally important to the development of accurate models of the dynamics of pelagic biota and of ecosystems.

The development of observing systems, globally and regionally, is urgent (IMOS, GOOS, SOOS, Tropics)(Field *et al.*, 2014). A set of essential variables (ecosystem Essential Ocean Variables; GOOS, SOOS - (Constable *et al.*, 2014a; Constable *et al.*, in prep-a)) needs to be identified that can be used to achieve the following four outcomes:

1. indicate essential dynamics of key habitats, species and the ecosystem,
2. detect change, including rapid change, in ecosystem structure and function,
3. help identify which model representations of species or foodwebs may be most plausible, or
4. test hypotheses about which scenarios for ecosystem change, including attributing causes of change, may be most plausible.

Once identified, methods for the routine collection of these data need to be established. The spatial and temporal design of the field program will need to be evaluated for its effectiveness in achieving the outcomes above while being cost-effective, following the identification of candidate eEOVs and the respective sampling methods.

5. Models

At present, modelling efforts are largely fragmented with too few practitioners (Table 2). Ideally, an ensemble of models at each scale needs to be developed to help test different ideas for representing the links between the physical environment, habitats, species and foodwebs. This approach has been the success of the modelling effort in the IPCC.

Models may vary in scale (space, depth, time, biology) and in their complexity, varying from empirical statistical models to dynamic models. These models will need to be able to utilise observations, in validation, assimilation or estimation.

Models need not wait for local data before their development. The process of building models to service end-user requirements, utilising knowledge and data from any source, can reveal the priority requirements for field or experimental research to make the outputs of the model most useful. Qualitative models (Dambacher *et al.*, 2009; Melbourne-Thomas *et al.*, 2012) exist for all Australian pelagic regions. These models could be refined further, with end user input, to explore the plausible options for model structures at different model scales and the possible range of effects of perturbations. Meta-analyses of parameters for models are becoming more widespread. These could provide a useful foundation for models in all regions, in the interim of estimating the parameters directly.

A more co-ordinated approach to linking models across scales (Figure 5) and from different research groups is needed in order that the models themselves can be shared, compared, evaluated, validated and their skill in representing true dynamics can be tested. Similar to ocean and atmospheric modelling, this requires a repository for well-documented model code, descriptions of the models and co-ordinated databases for model inputs and outputs. These requirements are increasingly achievable with the advent of the national computing facilities and cloud computing. Ideally, ensembles of models (not a single model) will be developed at each scale in order to enable comparative work and to better explore the relative importance of different factors driving food webs and ecosystems.

This co-ordinated approach will facilitate developing a fully coupled pelagic end-to-end ecosystem model encompassing Australia's marine jurisdiction, thereby facilitating the detailed exploration of biological phenomena that are not constrained to a single region.

6. Field program design

Pelagic ecosystem observations and process studies are expensive. As described above, models can be used to establish the priorities for future research most relevant to end-users. For example, the sensitivity of models to different structures, parameter estimates or time-series of data, helps identify the key areas of model uncertainty that need to be resolved.

Long-term observing systems can be designed using simulations, in the same way that management strategies for fisheries are evaluated (Smith *et al.*, 2007). A set of nested models can be used to downscale from regional dynamics to the scale of the measurements being taken. The deployment of the field equipment, voyages, gliders or some other observing platforms can be placed in the smulated region according to the proposed field design e.g. ships of opportunity. The observations (deployment methods etc) are then simulated at the correct scale in a sub-model. The biota being observed are simulated at an appropriate biological scale to properly represent the properties of the biota being measured. For example, potential eEOVs can be evaluated for their accuracy and precision in signalling change of the intended quantities in the ecosystem or in their ability to facilitate the attribution of the cause of a change (Constable *et al.*, in prep-a; Constable *et al.*, in prep-b). The analytical methods for utilising the data can also be evaluated for their ability to produce results that correctly reflect the magnitudes of quantities that would be expected from the measurements.

Specific priorities and outcomes over the next 5, 10-20 years

Within 5 years

- Inventory of ecosystem functional groups and their distinguishing attributes for each pelagic region.
- Characterisation of the attributes of habitats for pelagic biodiversity in each region, including relationships of functional groups with habitats.
- Estimation of the habitat heterogeneity of each region and future scenarios/projections for those habitats.
- Co-ordinated modelling effort for the pelagic realm, including co-ordination of code, input and output data, and methods for improving model skill.
- Initial autecological models of key taxa and functional groups, including the strengths of linkages to habitats and other taxa, to support model development and design of field programs; incorporation of relevant details into stock assessments, fisheries management and conservation of TEP species.
- Regional scale end-to-end ecosystem models for pelagic ecosystems in each region, with initial validation and evaluation of skill using available data; initial presentations of results to end-users and evaluation of their capability to address end-user needs, such as management strategy evaluation or assessing the consequences of scenarios.
- Establish risk assessment framework for assessing potential for rapid change and possible regime shifts in the future.
- Initial hindcasting and assessments of current status and trends of habitats, species and ecosystems to identify key uncertainties in model structure as well as spatial and temporal uncertainties in the assessments.
- A modelling system for evaluating eEOVs and spatial designs of biological observing systems
- Design of a pelagic biota observing system in each region
    - Identification of candidate ecosystem Essential Ocean Variables
    - Development of standard methods for measurements that underpin eEOVs
    - Analytical framework for utilising the data arising from the observing system
    - Evaluated design of the field observing system
- Co-ordinated cost-effective field program for the biological observing system in each region
- Participation in international programs on pelagic ecosystems, including
    - SOOS
    - GOOS
    - The second International Indian Ocean Expedition which is to be undertaken from 2015-2020.

Within 10-20 years

- Estimated abundances of different functional groups in each region
- Assessment of the resilience of each functional group to future change
- Estimation of the tolerances and responses of functional groups to change in habitats in each region, derived from process studies
- Estimation of the physical and biological connectivity within and across regions

- For each functional group (and key taxa), the following need to be assessed:
    - primary factors influencing the different life history stages,
    - resource requirements, consumption rates, growth and reproductive rates,
    - responses, including behaviour, to different habitat variables, prey and other cues
    - tipping points and potential for regime shifts.
- Refined autecological models of key taxa and functional groups to address key sensitivities in species and food web models and incorporating improved estimates of the influence of processes and habitats.
- Maintenance of long-term observations of eEOVs for pelagic ecosystems.
- Adaptation of observing system to new technologies.
- Fully coupled regional models to facilitate an end-to-end model of the pelagic realm encompassing Australia's marine jurisdiction, including assimilation of data from the observing system, thereby enabling consideration of cross-jurisdictional issues, assessments and management of migratory species and other biological phenomena at that scale.
- Development of assessments of status, trends and likelihood of future states of habitats, key species, and ecosystems in each region to facilitate marine planning, including
    - assessments of change in distribution, phenology and size-structure of biota, and
    - short and long-term forecasting of those states, including assessments of risk of regme shifts.
- Uncertainty estimates improved both spatially and temporally
- Identification of key gaps for assessments of ecosystem states in 2100
- Outputs used regularly to report on the state of the environment and into IPCC documentation and for underpinning regional management, including evaluation of management strategies for the regions.
- Infrastructure planning uses research outputs routinely with increasing confidence of projections and narrowed uncertainty estimates
- Sustained approach to building cooperation and collaboration of global interests in the Indian Sector, including environmentally sustainable activities with adaptation strategies for future change.

Realisation

Key infrastructure and capability requirements/impediments

The development of a pelagic ecosystem observation and assessment capability to support the variety of end-users will require investment in

- an enhanced IMOS capability to support the acquisition and storage of data underpinning the ecosystem Essential Ocean Variables that will be established for each region, including
    - deployments of underway observing technologies, such as for nutrients, microbes, zooplankton (CPR), epi- and meso-pelagic biota (acoustics, cameras)
    - deployment of remote technologies (drones, gliders, moorings, or other new technologies)
    - tracking of air-breathing vertebrates

    - maintenance of data streams from satellite, air- and sea-borne technologies
    - database support
- ongoing regular access to a variety of research vessels able to sample and undertake integrated process studies throughout Australia's EEZ, including having capabilities to sample using acoustics, nets, ROVs, cameras, autonomous underwater vehicles and small boats;
- regular integrated measurements of habitats and key functional groups at sea and on land, either annually or biannually in key locations representative of each region and able to be used as reference areas (long term sites);
- laboratories for rapid processing of large numbers of samples, including investment in technologies to improve processing rates.
- aquarium facilities for life history, process and tolerance studies of microbes and zooplankton, including the ability to examine the effects of multiple stressors simultaneously.
- co-ordinated modelling capability, including code and data repositories.

Funding and coordination requirements/impediments

Investment in a modelling capability that enables researchers to work as modelling teams and able to cover the 7 regions is a high priority. Similarly, the establishment of reference areas in key locations of each region will be important for undertaking necessary process studies and for assessing status and trends in these ecosystems. Lastly, investment in in-situ sampling is needed to increase measurements and process studies in each region and to help validate a number of data types, such as from satellites, predator tracks and sensors, and acoustics. This could be achieved through increased ship time, increased deployment of remote technologies, such as gliders, developing technologies to enable rapid deployment of equipment on ships of opportunity, developing better technologies for efficient remote sampling and developing methods for more rapidly processing samples (such as molecular methods), thereby reducing staff loads. Importantly, investment in research and technical staff will be essential, including the development of students and early-career researchers.

The development of nodes of activity in pelagic ecosystem research has greatly enhanced research outputs. Continuation and expansion of existing nodes is desirable. New nodes in regions without a local node of researchers should be developed to enhance the development of local research teams as well as providing local end-users with access to the relevant research team.

IMOS has been a very successful integrator and developer of pelagic marine observing in Australia. Expansion of its capability is necessary to facilitate the increased requirement of observations in pelagic ecosystems.

A great impediment to pelagic ecosystem research is the ability to attract required budgets to sustain an integrated program in distant water locations, such as in Australia's EEZ. At present, no funding agency is able to provide a single grant to support such integrated studies for the duration required. There are no mechanisms for submitting such a program of work and securing funding under one umbrella. This is impeded also by the different rules governing applications from government agencies and universities, particularly when grants for post-doctoral fellows and students are being requested.

Contributors

Andrew Constable	Australian Antarctic Division
Beth Fulton	CSIRO Oceans & Atmosphere Flagship
Neville Barrett	Institute of Marine and Antarctic Studies
Stephanie Brodie	University of New South Wales
Colin Creighton	
Karen Evans	CSIRO Oceans & Atmosphere Flagship
Jason Everett	University of New South Wales
Al Gabric	Griffith University
Gustaaf Hallegraeff	Institute of Marine and Antarctic Studies
Nick Hardman-Mountford	CSIRO Oceans & Atmosphere Flagship
Michelle Heupel	Australian Institute of Marine Science
Alistair Hobday	CSIRO Oceans & Atmosphere Flagship
Rudy Kloser	CSIRO Oceans & Atmosphere Flagship
Sophie Letern	Flinders University
David McKinnon	Australian Institute of Marine Science
Jessica Meeuwig	University of Western Australia
Jessica Melbourne-Thomas	Australian Antarctic Division
Clive McMahon	Sydney Institute of Marine Science, University of New South Wales
Moninya Roughan	Sydney Institute of Marine Science, University of New South Wales
Marcus Sheaves	James Cook University
Colin Simpfendorfer	James Cook University
Iain Suthers	Sydney Institute of Marine Science, University of New South Wales
Kerrie Swadling	Antarctic Climate and Ecosystems Cooperative Research Centre; Institute of Marine and Antarctic Studies
Paul van Ruth	South Australian Research and Development Institute - Aquatic Sciences
Tim Ward	South Australian Research and Development Institute - Aquatic Sciences
Dirk Welsford	Australian Antarctic Division

Table 1. Progress in states of knowledge of different attributes of pelagic ecosystems in 7 regions of Australia (Figure 4). Progress is considered for 4 scales of research - Global, Regional, Food web, Species/populations (Figure 5). 'Models' = readiness of models at those scales, including development and skill (how well they replicate known conditions and observations). 'Relative productivity' = productivity of the region in the global context e.g. primary production. 'Interannual/interdecadal' = variability and trends over years and decades, which are important for assessing change. 'Habitats' = different pelagic habitats and their relationships within regions. 'Physical connectivity' = connectivity (3-D) within regions, via movement of ocean or sea ice. 'Productivity' = patchiness of productivity within a region. 'Functional attributes' = degree to ecosystem functions are known (e.g. aggregation of species into functional groups). 'Temporal variability' = observations indicating intra- and inter-annual variability in different components, particularly relating to phenology and the degree to which the abundances of different taxa/functional groups are correlated. 'Biological connectivity' = connectivity (3-D) within regions arising from the behaviours of species. 'Key processes/drivers' = relative importance of different physical and biological interactions that influence the ecology of species (e.g. responses to single and multiple stressors). Knowledge of foodwebs and species are considered for each of M = Microbes, S = zooplankton and small nekton, L = migratory fish and squid, A = air-breathing vertebrates. Colours indicate progress: red = very limited, orange = limited, yellow = some elements have progressed, light green = coverage of many priority areas, dark green = coverage of most areas.

	1. Southern Ocean	2. South-east	3. GAB & SA gulfs	4. South-west	5. North-west	6. North & Gulf	7. North-east & GBR
Global context Models							
Relative productivity							
Interannual/interdecadal							
Regional context Models							
Habitats							
Physical connectivity							
Productivity							
Food web context	M S L A	M S L A	M S L A	M S L A	M S L A	M S L A	M S L A
Functional attributes							
Temporal variability							
Biological connectivity							
Models							
Species/populations	M S L A	M S L A	M S L A	M S L A	M S L A	M S L A	M S L A
Key processes/drivers							
Models							

Table 2. Summary review of the status of pelagic ecosystem models in 7 regions of Australia (Figure 4).

1. Antarctic and Subantarctic	Conceptual models on ecosystem structure (Melbourne-Thomas *et al.*, 2013), a partial model of biogeochemistry and production for for Kerguelen region as well as whole of Southern Ocean; simple predator-krill models are available but driven by knowledge from Antarctic Peninsula and Atlantic sector; a NetLogo and Atlantis models almost ready for trials (rudimentary heading for mature; Bedford pers comm UTAS, Fulton pers com CSIRO).
2. South-East Australia	Conceptual models exist (e.g. (Hosack & Dambacher, 2012), mature Ecopath with Ecosim (EwE) models exist for small sections of this region (Bulman *et al.*, 2006), mature Atlantis model (Atlantis-SPF; Fulton) also exists (other Atlantis models exist for the region too but more demersally focused; (Fulton EA, 2014)).
3. Great Australia Bight and SA Gulfs	Conceptual models exist (Hayes *et al.*, 2012), mature BGC model exists for Spencer Gulf (Doubell et al), mature EwE model exists (Goldsworthy *et al.*, 2013), an Atlantis model is being currently calibrated (rudimentary heading for mature; (Fulton & Gorton, 2014)
4. South-West Australia	Conceptual models exist (Hayes *et al.*, 2012), a couple of small scale rudimentary EwE models (mainly for demersal species; (Lozano-Montes *et al.*, 2011) exists and Atlantis model is under calibration (pers com Lozano-Montes CSIRO)
5. North-West Australia	Conceptual models exist (Hosack *et al.*, 2012), rudimentary-mature models exist for Gascoyne and Pilbara both InVitro (Fulton *et al.*, 2011; Gray, 2006) and EwE (Bulman, 2006; Fulton *et al.*, 2011), but in terms of pelagic components more rudimentary and simplified than for demersal stocks and habitats.
6. Northern Australia including Gulf of Carpentaria	Conceptual models exist (Hosack *et al.*, 2012), Gulf of Carpentaria has a mature EwE model (Dichmont *et al.*, 2013; Okey, 2006), again more demersally focused, plus MICE models (focused on commercial crustaceans, (Plagányi *et al.*, 2014; Plaganyi *et al.*, 2011) and numerous multispecies models. Biggest gap in dynamic models is across NT.
7. North-East Australia (incl GBR)	Conceptual models exist (Dambacher *et al.*, 2012), mature Atlantis model exists for the Coral Sea (pers com Hutton CSIRO) and offshore waters down the east coast, MICE and EwE models exists for ETBF region (Griffiths et al 2010, pers. com. Hillary CSIRO). Mature EwE models also complete for GBR ((Gehrke, 2007; Gribble, 2009), Atlantis models under development (pers com. Fulton CSIRO).
	eReefs – coupled physical and biogeochemical model of the Great Barrier Reef
Whole of Australia (Earth System, biogeochemistry)	Partial models exist (e.g. biogeochemical plankton models, (Matear, 2013)) with project proposals in place for an Australia wide for a size-based model to be developed.

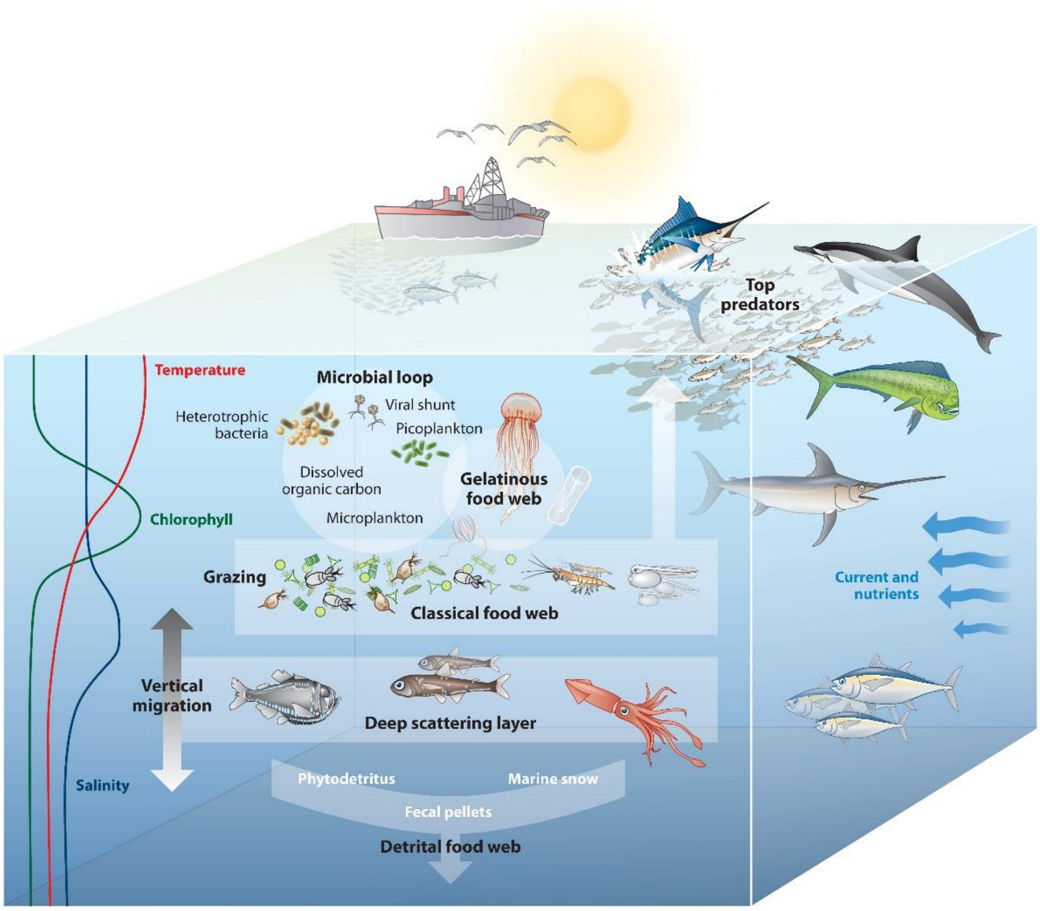


Figure 1 Biodiversity assets and ecosystem processes of pelagic biomes in tropical marginal seas. (Figure 5 from (McKinnon *et al.*, 2014))

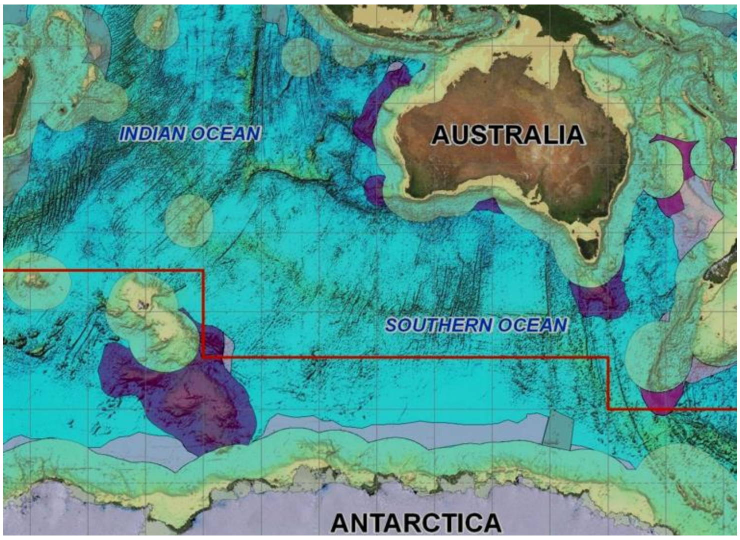


Figure 2 Map showing Australia's maritime jurisdiction, including external territories. (Red line shows the boundary to the area of the Convention on the Conservation of Antarctic Marine Living Resources). Note that this is not an equal area projection. (Geoscience Australia, 2010)

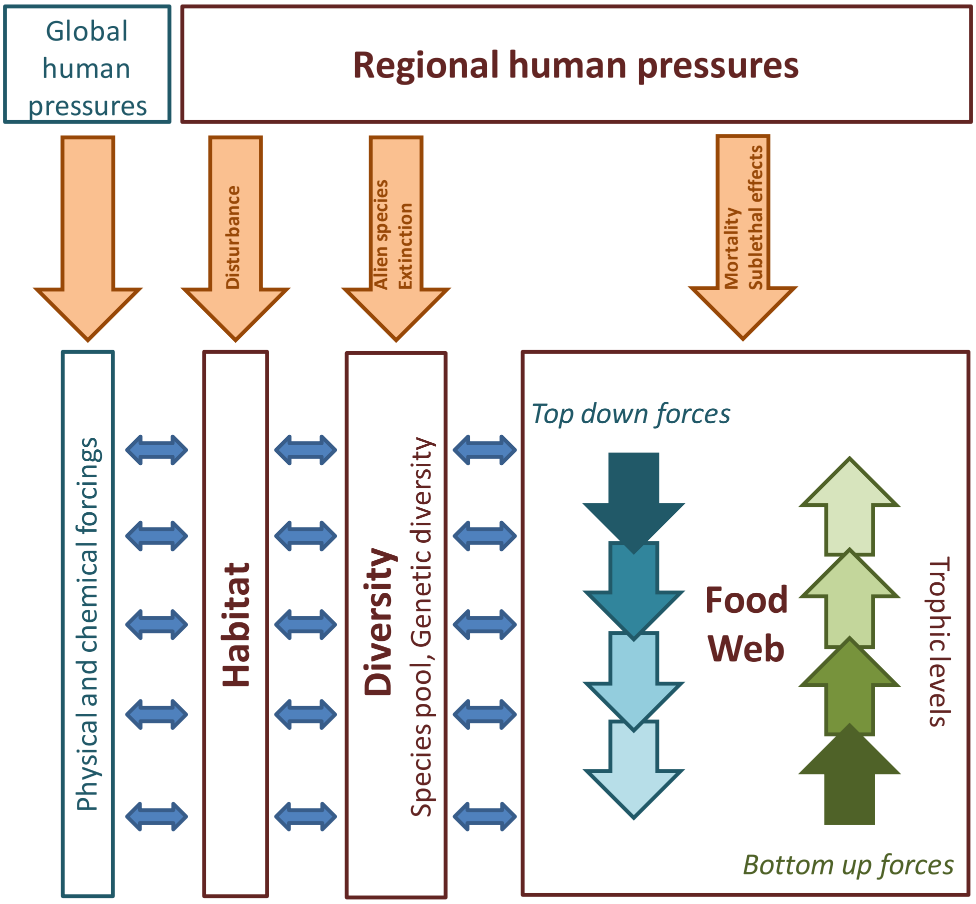
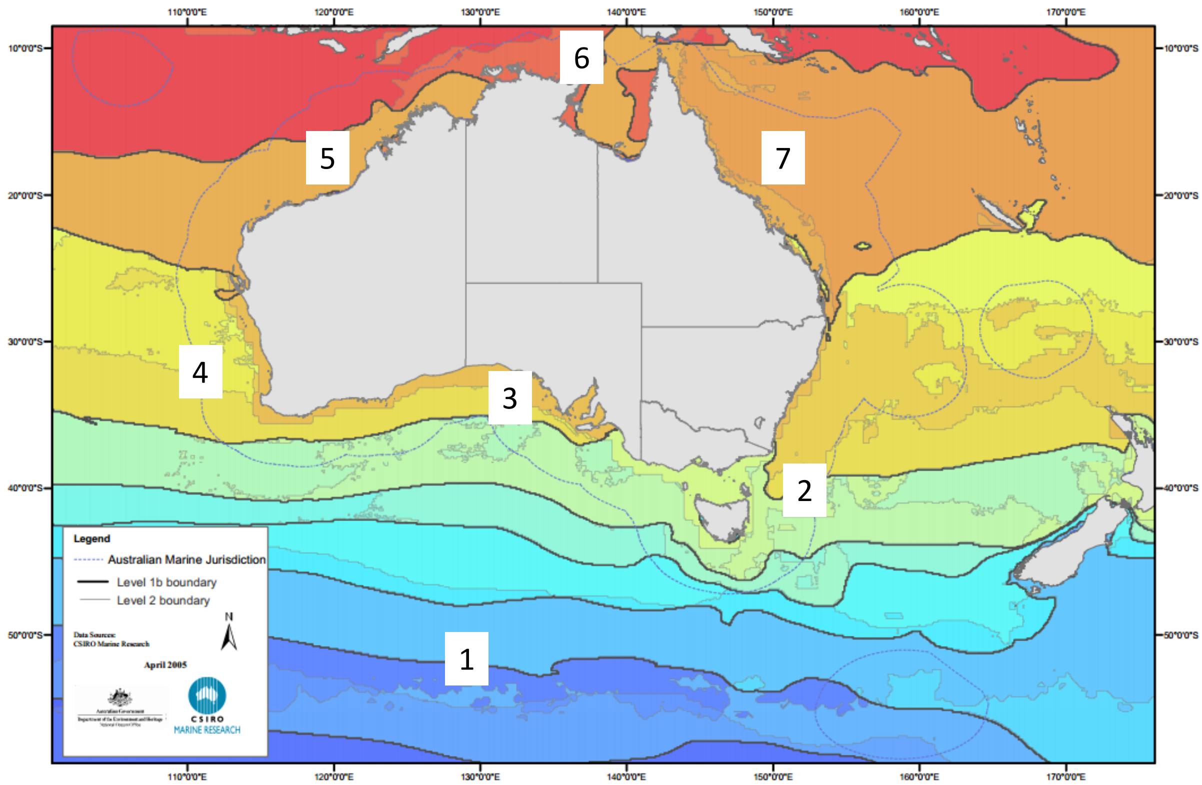


Figure 3 A framework for considering dynamics and change in pelagic marine ecosystems, including drivers of change in habitats, species and food webs. Horizontal blue arrows indicate connections, including feedbacks, between different ecosystem components at different trophic levels (effects of climate change and ocean acidification may not just be on the lowest trophic levels). Downward orange arrows show effects of global and regional human pressures. Each trophic level of the food web may be impacted by both bottom-up and top-down forces as a result of human pressures in different parts of the food web (from (Constable *et al.*, 2014a))

(a)



(b)

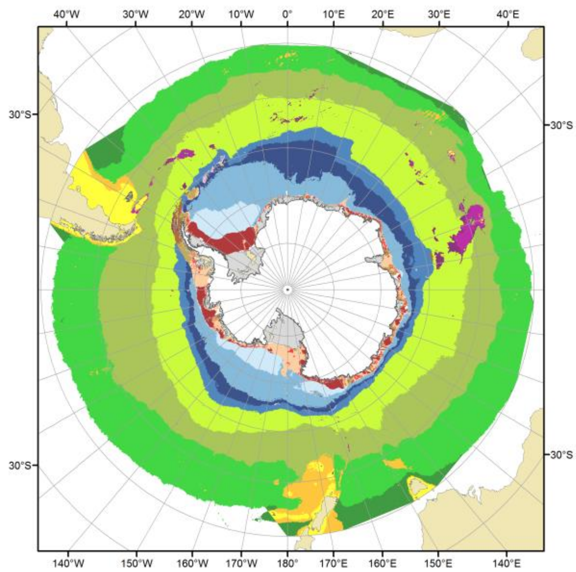


Figure 4 Marine regionalisation showing the major pelagic regions of interest to Australia. (a) Level 2 classification of pelagic regions (Figure 5-4 from (Lyne *et al.*, 2005)). Exclusive Economic Zone is shown as a thin blue line. Numbers relate to the regions in the text: **(**1) Antarctic and Subantarctic, (2) South-East Australia, (3) Great Australia Bight and South Australia gulfs, (4) South-West Australia, (5) North-West Australia, (6) Northern Australia including Gulf of Carpentaria, (7) North-East Australia, incl Great Barrier Reef. **(b) Pelagic regionalisation for the Southern Ocean (Figure 18, (Grant *et al.*, 2006)).**

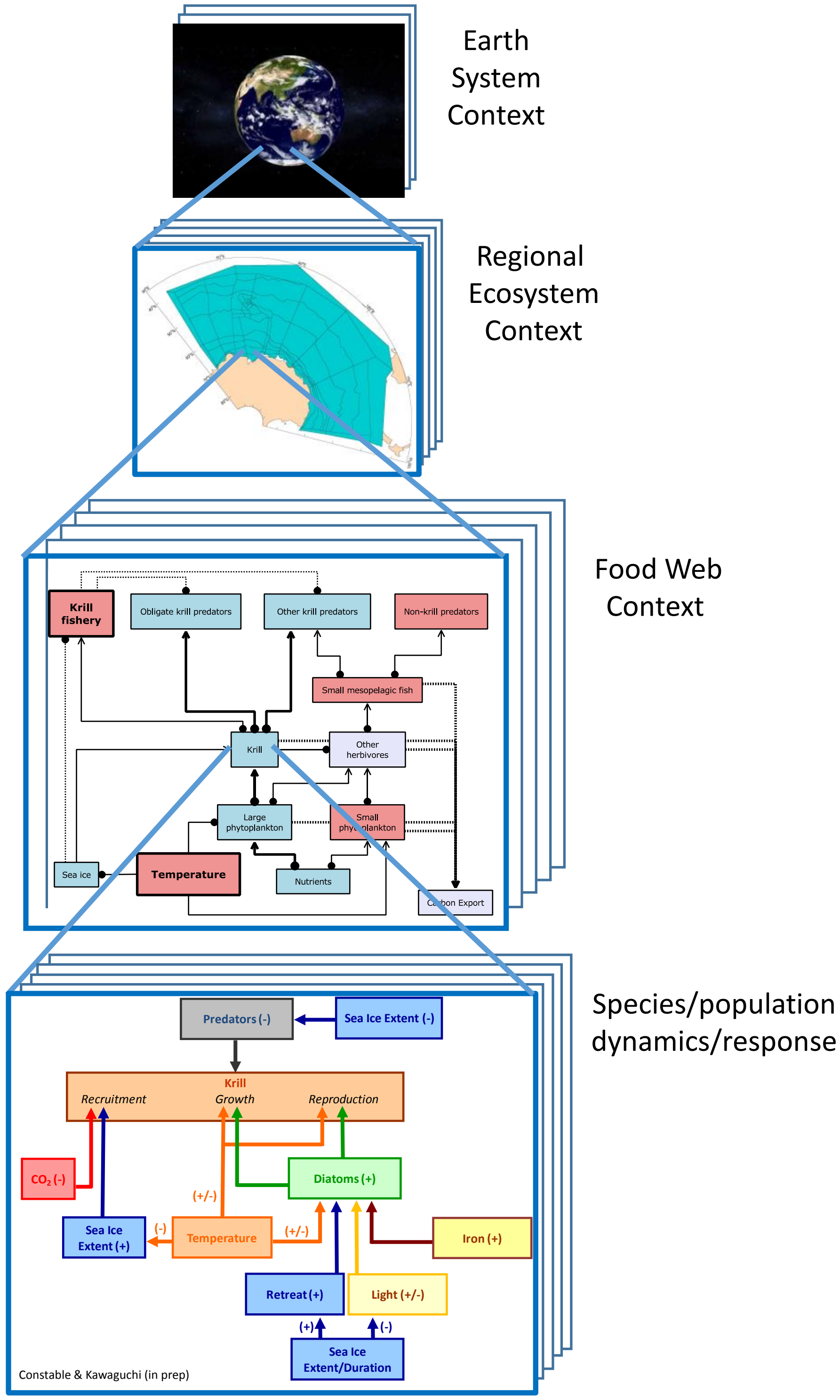


Figure 5 Nested approaches to considering priorities for pelagic ecosystem science. The relationship between different scales of models is shown, ranging from the Earth System context, the end-to-end ecosystem models required for regional ecosystem contexts, the development of MICE models (Models of Intermediate Complexity for Ecosystem assessments) for establishing the food web context for decisions, through to species/population models for stock assessments and impacts of changing habitats on important species. Shadow boxes represent ensemble models characterising different processes or structures. Example is for the Indian Sector of the Southern Ocean (Constable *et al.*, in prep-b), showing an individual based model for Antarctic krill, nested within a simplified Antarctic food web model, nested within an Atlantis model for the region, which in turn is bounded by an Earth System model.

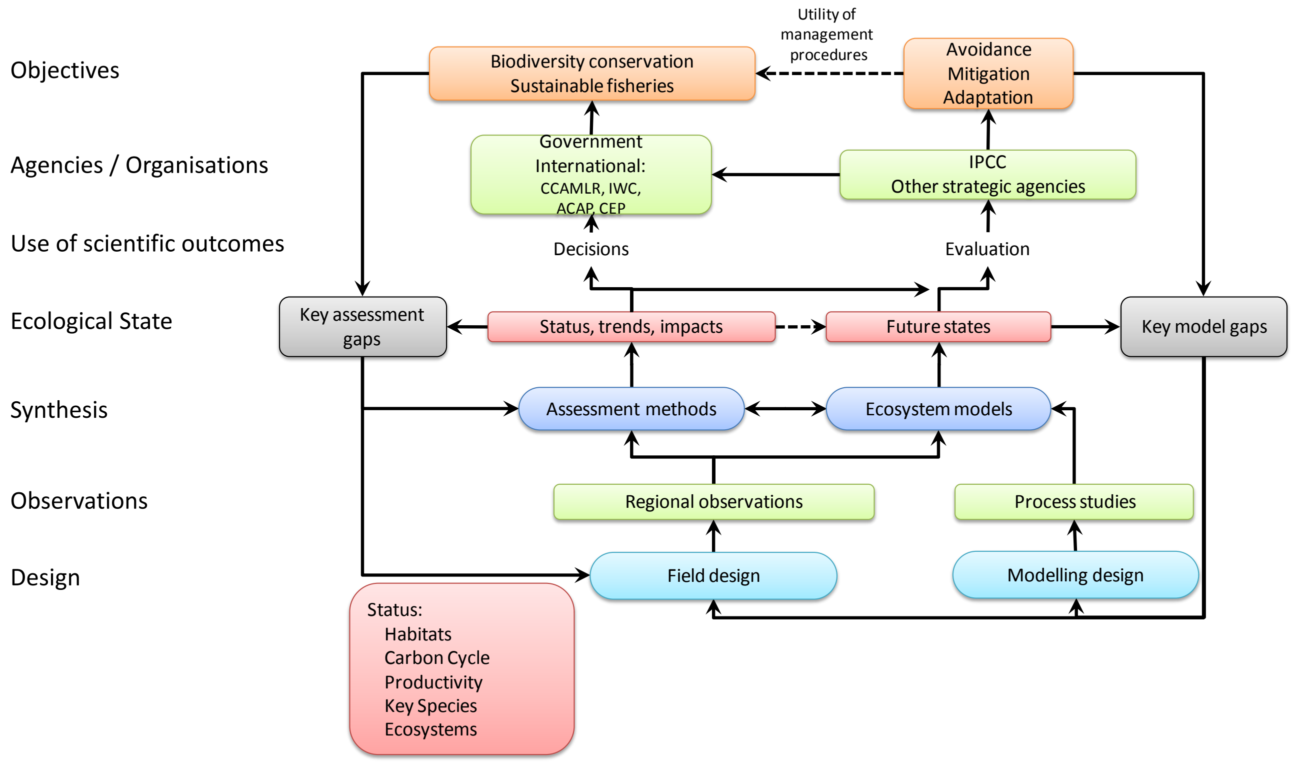


Figure 6 Relationships between science, policy and management, particularly the agencies, their objectives, their use of scientific outputs often relating to ecological states, the process of synthesising results to produce the outputs, the collection of observations and the process for designing the requirements for observations. Examples in the polygons are for the Southern Ocean where the objectives primarily relate to conservation and sustainable fisheries. Science priorities may be determined by difficulties encountered by agencies to achieve their objectives or difficulties in delivering robust estimates of ecological status. (after (Constable *et al.*, in prep-b))

References

Angel MV (1993) Biodiversity of the Pelagic Ocean. *Conservation Biology,* **7**, 760-772.

Bulman C (2006) Trophic webs and modelling of Australia's North West Shelf. North West Shelf Joint Environmental Management Study Technical Report – Vol 9. Hobart, CSIRO.

Bulman C, Condie S, Furlani D, Cahill M, Klaer N, Goldsworthy S, Knuckey I (2006) *Trophic dynamics of the eastern shelf and slope of the South East Fishery: impacts of and on the fishery,* Hobart, CSIRO.

Constable AJ, Costa DP, Schofield O, Ballerini T, Urban E (2014a) Outcomes and context for future work from the Workshop on ecosystem Essential Ocean Variables (eEOVs) for the Southern Ocean. Rutgers University, New Brunswick, USA, 18-21 March 2014. pp 31 pp., in prep., Rutgers University.

Constable AJ, Costa DP, Schofield O, Ballerini T, Urban E (in prep-a) A framework for identifying essential variables to monitor change in marine ecosystems: ecosystem Essential Ocean Variables (eEOVs). pp 31 pp., in prep.

Constable AJ, Melbourne-Thomas J, Corney SP *et al.* (2014b) Climate change and Southern Ocean ecosystems I: how changes in physical habitats directly affect marine biota. *Global Change Biology,* 10.1111/gcb.12623, n/a-n/a.

Constable AJ, Melbourne-Thomas J, Press AJ, Haward M (in prep-b) Climate change impacts on Southern Ocean ecosystems: the roles for the Southern Ocean Observing System and the Southern Ocean Sentinel programs. in prep.

Dambacher JM, Gaughan DJ, Rochet M-J, Rossignol PA, Trenkel VM (2009) Qualitative modelling and indicators of exploited ecosystems. *Fish and Fisheries,* **10**, 305-322.

Dambacher JM, Hosack GR, Rochester WA (2012) Ecological Indicators for the Exclusive Economic Zone of Australia's East Marine Region. A report prepared for the Australian Government Department of Sustainability, Environment, Water, Population and Communities. Hobart, CSIRO Wealth from Oceans Flagship.

Dichmont CM, Ellis N, Bustamante RH *et al.* (2013) Evaluating marine spatial closures with conflicting fisheries and conservation objectives. *Journal of Applied Ecology,* **50**, 1060-1070.

Evans K, Brown JN, Sen Gupta A, Nicol SJ, Hoyle S, Matear R, Arrizabalaga H (2014) When 1+1 can be >2: Uncertainties compound when simulating climate, fisheries and marine ecosystems. *Deep Sea Research Part II: Topical Studies in Oceanography,* **in press**, 11 pp.

Everett J, Baird M, Oke P, Suthers.I.M. (2012) An Avenue of Eddies: Quantifying the biophysical properties of mesoscale eddies in the Tasman Sea. *Geophysical Research Letters,* **39**.

Everett JD, Baird ME, Roughan M, Suthers IM, Doblin.M.A. (2014) Relative impact of seasonal and oceanographic drivers on surface chlorophyll a along a Western Boundary Current. *Progress in Oceanography,* **120**, 340-351.

Field CB, Barros RB, *Al*. *E* (2014) Summary for Policy Makers. In: *Climate Change 2014: Impacts, Adaptation, and Vulnerability. Report of Working Group II.* (eds Field CB, Barros RB) pp 44 pp. San Francisco, Intergovernmental Panel on Climate Change.

Fulton EA, Gorton R (2014) Adaptive Futures for SE Australian Fisheries & Aquaculture: Climate Adaptation Simulations. Australia, CSIRO.

Fulton EA, Gray R, Sporcic M *et al.* (2011) Ningaloo Collaboration Cluster: Adaptive Futures for Ningaloo. Ningaloo Collaboration Cluster Final Report No. 5.3. Hobart, CSIRO.

Fulton Ea SA, Smith Dc, Johnson P (2014) An Integrated Approach Is Needed for Ecosystem Based Fisheries Management: Insights from Ecosystem-Level Management Strategy Evaluation. *PLoS ONE,* **9**, e84242.

Fulton EA, Smith ADM, Johnson CR (2004) Biogeochemical marine ecosystem models I: IGBEM - a model of marine bay ecosystems. *Ecological Modelling,* **174**, 267-307.

Gehrke PC (2007) A comparative analysis of coastal fishery food webs in the Great Barrier Reef region. CSIRO: Water for a Healthy Country National Research Flagship.

Goldsworthy SD, Page B, Rogers PJ *et al.* (2013) Trophodynamics of the eastern Great Australian Bight ecosystem: Ecological change associated with the growth of Australia's largest fishery. *Ecological Modelling,* **255**, 38-57.

Grant S, Constable A, Raymond B, Doust S (2006) Bioregionalisation of the Southern Ocean: Report of Experts Workshop, WWF- Australia and ACE CRC. Hobart, September 2006.

Gray R, Fulton, E.A., Little, L.R. And Scott, R. (2006) Operating Model Specification Within an Agent Based Framework. North West Shelf Joint Environmental Management Study Technical Report - Vol 16. pp 127 pp, Hobart, CSIRO.

Gribble NA (2009) Testing the robustness of a linked-ecosystem trophic model of the Great Barrier Reef, World Heritage Area. 18th World IMACS / MODSIM Congress, Cairns, Australia 13-17 July 2009. http://mssanz.org.au/modsim09.

Griffiths S, Olson R, Watters G (2013) Complex wasp-waist regulation of pelagic ecosystems in the Pacific Ocean. *Reviews in Fish Biology and Fisheries,* **23**, 459-475.

Hayes KR, Dambacher JM, Lyne V, Sharples R, Rochester WA, Dutra LXC, Smith R (2012) Ecological Indicators for Australia's Exclusive Economic Zone: Rationale and Approach with Application to the South West Marine Region. A report prepared for the Australian Government Department of Sustainability, Environment, Water, Population and Communities. Hobart, CSIRO Wealth from Oceans Flagship.

Hobday AJ, Bell JD, Cook TR, Gasalla MA, Weng KC Reconciling conflicts in pelagic fisheries under climate change. *Deep Sea Research Part II: Topical Studies in Oceanography,* http://dx.doi.org/10.1016/j.dsr2.2014.10.024.

Hobday AJ, Young JW, Abe O *et al.* (2013) Climate impacts and oceanic top predators: moving from impacts to adaptation in oceanic systems. *Rev Fish Biol Fisheries,* 10.1007/s11160-013-9311-0, 10.

Hobday AJ, Young JW, Moeseneder C, Dambacher JM (2011) Defining dynamic pelagic habitats in oceanic waters off eastern Australia. *Deep Sea Research Part II: Topical Studies in Oceanography,* **58**, 734-745.

Hosack GR, Dambacher JM (2012) Ecological Indicators for the Exclusive Economic Zone of Australia's South East Marine Region. A report prepared for the Australian Government Department of Sustainability, Environment, Water, Population and Communities. Hobart, CSIRO Wealth from Oceans Flagship.

Hosack GR, Dambacher JM, Rochester WA, Dutra LXC (2012) Ecological Indicators for the Exclusive Economic Zone of Australia's North and North West Marine Regions. A report prepared for the Australian Government Department of Sustainability, Environment, Water, Population and Communities. Hobart, CSIRO Wealth from Oceans Flagship.

Irigoien X, Klevjer TA, Rostad A *et al.* (2014) Large mesopelagic fishes biomass and trophic efficiency in the open ocean. *Nature Communications,* **5**.

L.J. M, Page BC, Goldsworthy SD, Ward TM, Paton D, Waterman M, Murray MD (2009) Demographic and morphological responses to prey depletion in a crested tern (*Sterna bergii*) population: can fish mortality events highlight performance indicators for fisheries management? *ICES Journal of Marine Science,* **66**, 237-247.

Longhurst AR (2007) *Ecological geography of the sea,* London, UK, Academic Press.

Lozano-Montes HM, Loneragan NR, Babcock RC, Jackson K (2011) Using trophic flows and ecosystem structure to model the effects of fishing in the Jurien Bay Marine Park, temperate Western Australia *Marine and Freshwater Research,* **62**, 421 – 431.

Lyne V, Hayes D, Mcdonald D *et al.* (2005) National Marine Bioregionalisation of Australia. pp 169, Canberra, Australia, Department of the Environment and Heritage and CSIRO.

Matear RJ, M. A. Chamberlain, C. Sun, and M. Feng (2013) Climate change projection of the Tasman Sea from an Eddy resolving Ocean Model. *J. Geophys. Res. Oceans,* **118**, 2961–2976.

Mckinnon AD, Williams A, Young J *et al.* (2014) Tropical Marginal Seas: Priority Regions for Managing Marine Biodiversity and Ecosystem Function. *Annu. Rev. Mar. Sci.,* **6**, 17.11–17.23.

Melbourne-Thomas J, Constable A, Wotherspoon S, Raymond B (2013) Testing paradigms of ecosystem change under climate warming in Antarctica. *PLoS ONE,* **8**, e55093.

Melbourne-Thomas J, Wotherspoon S, Raymond B, Constable A (2012) Comprehensive evaluation of model uncertainty in qualitative network analyses. *Ecological Monographs,* **82**, 505-519.

Nicol S, Bowie A, Jarman S, Lannuzel D, Meiners KM, Van Der Merwe P (2010) Southern Ocean iron fertilization by baleen whales and Antarctic krill. *Fish and Fisheries,* **11**, 203–209. doi: 210.1111/j.1467-2979.2010.00356.x.

Okey TA (ed) (2006) *A trophodynamic model of Albatross Bay, Gulf of Carpentaria: revealing a plausible fishing explanation for prawn catch declines. ,* Cleveland, Australia, CSIRO Marine and Atmospheric Research.
Plagányi É, Punt A, Hillary R *et al.* (2014) Multi-species fisheries management and conservation: tactical applications using models of intermediate complexity. *Fish and Fisheries,* **15**, 1-22.
Plaganyi EE, Weeks SJ, Skewes TD *et al.* (2011) Assessing the adequacy of current fisheries management under changing climate: a southern synopsis. *ICES Journal of Marine Science,* **68**, 1305-1317.
Rogers PJ, Ward TM, Van Ruth PD *et al.* (2013) Physical processess, biodiversity and ecology of the great Australian Bight region: a literature review. *CSIRO Australia*.
Schmoker C, Hernández-León S, Calbet A (2013) Microzooplankton grazing in the oceans: impacts, data variability, knowledge gaps and future directions. *Journal of Plankton Research,* **35**, 691-706.
Smith ADM, Fulton EA, Hobday AJ, Smith DC, Shoulder P (2007) Scientific tools to support the practical implementation of ecosystem-based fisheries management. *ICES Journal of Marine Science,* **64**, 633-639.
Spalding MD, Agostini VN, Rice J, Grant SM (2012) Pelagic provinces of the world: A biogeographic classification of the world’s surface pelagic waters. *Ocean & Coastal Management,* **60**, 19-30.
Spalding MD, Fox HE, Allen GR *et al.* (2007) Marine Ecoregions of the World: A Bioregionalization of Coastal and Shelf Areas. *BioScience,* **57**, 573-583.
Suthers IM, Young JW, Baird ME *et al.* (2011) The strengthening East Australian Current, its eddies and biological effects—An introduction and overview. *Deep Sea Research Part II: Topical Studies in Oceanography,* **58**, 538-546.
Van Ruth PD (2014) Plankton in Spencer Gulf. In: *Natural History of Spencer Gulf.* (eds Shepherd SA, Madigan S, Gillanders B, Murray-Jones S, Wiltshire D) pp 171–180. Adelaide, Royal Society of South Australia.
Van Ruth PD, Doubell MJ (2013) Spatial and temporal variation in primary and secondary productivity and lower trophic ecosystem function in Spencer Gulf, South Australia. In: *PIRSA Initiative II: carrying capacity of Spencer Gulf: hydrodynamic and biogeochemical measurement, modelling and performance monitoring. FRDC Project No. 2009/046. SARDI Publication No. F2013/000311-1. SARDI Research Report Series No. 705.* (ed Middleton JF) pp 97 pp. Adelaide, South Australian Research and Development Institute (Aquatic Sciences).
Young JW, Hunt BPV, Cook TR *et al.* (2014) The trophodynamics of marine top predators: Current knowledge, recent advances and challenges. *Deep Sea Research Part II: Topical Studies in Oceanography,* **in press**, 18 pp.