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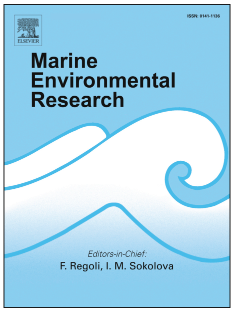

Identifying knowledge gaps in seagrass research and management: An Australian perspective

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Identifying knowledge gaps in seagrass research and management: an Australian perspective

Authors

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Contributors: PHY, TMS, RGC and SAM organized and ran the workshop and led the writing of the manuscript. RGC, SAM, RMC, ADI, ELJ, KM, JWR, CDHS, BKS and SMT facilitated discussion and coordinated the composition of questions from each field of research group. All authors attended the workshop, contributed to discussion of research questions, contributed to the writing of the manuscript and approved the final article.

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Highlights

- We provide a strategic review of research gaps for Australian seagrass ecosystems
- Priorities areas were identified at a workshop of seagrass experts
- Forty key knowledge gaps were identified across ten research fields
- This review provides a platform for a coordinated approach to seagrass research and management

Abstract

Seagrass species form important marine and estuarine habitats providing valuable ecosystem services and functions. Coastal zones that are increasingly impacted by anthropogenic development have experienced substantial declines in seagrass abundance around the world. Australia, which has some of the world's largest seagrass meadows and is home to over half of the known species, is not immune to these losses. In 1999 a review of seagrass ecosystems knowledge was conducted in Australia and strategic research priorities were developed to provide research direction for future studies and management. Subsequent rapid evolution of seagrass research and scientific methods has led to more than 70% of peer reviewed seagrass literature being produced since that time. A workshop was held as part of the Australian Marine Sciences Association conference in July 2015 in Geelong, Victoria, to update and redefine strategic priorities in seagrass research. Participants identified 40 research questions from 10 research fields (taxonomy and systematics, physiology, population biology, sediment biogeochemistry and microbiology, ecosystem function, faunal habitats, threats, rehabilitation and restoration, mapping and monitoring, management tools) as priorities for future research on Australian seagrasses. Progress in research will rely on advances in areas such as remote sensing, genomic tools, microsensors, computer modeling, and statistical analyses. A more interdisciplinary approach will be needed to facilitate greater understanding of the complex interactions among seagrasses and their environment.

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1. INTRODUCTION

Seagrasses are marine flowering plants that provide one of the most productive habitats on earth. Seagrasses support a wide array of ecosystem functions and services including nutrient cycling and particle trapping that improves water quality, stabilization of sediments, provision of food for many associated faunal species including waterfowl, dugong and turtles, the capture and storage of carbon, and the creation of habitat for animals facilitating biodiversity (Barbier et al., 2011; Costanza et al., 2014; Orth et al., 2006). The global extent of seagrass ecosystems is declining at an alarming rate, with a reduction of approximately 30% of the world's seagrass distribution post the industrial revolution (Waycott et al., 2009). Declines from anthropogenic pressures such as eutrophication, coastal and port developments are expected to continue and climate change threats are predicted to increase. Focused efforts on more effective science based conservation, monitoring, restoration and management of seagrass ecosystems are required (Kilminster et al., 2015; Orth et al., 2006; Unsworth et al., 2015).

A large portion of the planet's known seagrass meadows occur in Australian waters (Green and Short, 2003); incorporating half (37) of the world's 72 species (Kilminster et al., 2015; Short et al., 2011), and two of the five hotspots of global seagrass diversity in northern Australia (including the Great Barrier Reef) and south-western Australia (Short et al., 2007). Seagrasses in Australia face the same threats identified as major global threats, such as agricultural, urban and industrial runoff, coastal and port developments, disease and climate change (Ghorai and Sen, 2015; Grech et al., 2012; Grech et al., 2011; Short and Neckles, 1999; Sullivan et al., 2013). These threats have led to declines in Australian seagrass, with temperate systems tracking similar to global averages (Waycott et al., 2009), and recent large scale declines in tropical Queensland (e.g., McKenna et al., 2015). This has prompted actions that put Australia at the forefront of efforts to improve management and conservation outcomes (Coles et al., 2015; Kilminster et al., 2015).

Globally, seagrass research began to take off in the early 1970s, with the first review of Australian seagrass research occurring shortly after (Larkum, 1977). Since then a series of books have periodically synthesized and updated the growing knowledge on seagrass ecology both internationally (e.g., den Hartog, 1970; Hemminga and Duarte, 2000; Larkum et al., 2006) and focusing on Australia (Larkum et al., 1989). Publications on global seagrass distribution (Green and Short, 2003) and research methods (Short and Coles, 2001) have arisen from a series of biennial global seagrass workshops dating back to 1993 (Coles et al., 2014). Australia has traditionally been a large contributor to global seagrass research, producing close to one fifth of total peer reviewed literature; second to the USA (Figure 1a). While research has generally been carried out on an ad-hoc basis, a strategic review of seagrass knowledge gaps in Australia with recommendations for future research was published just before the turn of the century (Butler and Jernakoff, 1999) when approaches to seagrass ecology were still developing and were dominated by descriptive studies (Duarte, 1999). This review brought together expert working groups to focus on gaps in understanding around seagrass ecosystem function, links between seagrass habitat and fisheries, monitoring and assessment, remediation and restoration and management (Butler and Jernakoff, 1999). In the decade and a half since this review, almost 75 percent of the peer-reviewed seagrass literature globally, and 72 percent from Australia, has been published (Figure 1b).

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In light of this huge increase in seagrass knowledge, Australian seagrass scientists came together at the Australian Marine Sciences Association Annual Conference in Geelong, Victoria to review progress in understanding the components of seagrass systems (fields of research) and in documenting weaknesses and gaps that need to be addressed. In this paper, we revisit the work of Butler and Jernakoff (1999) to elicit an updated set of questions across a broad range of seagrass research fields that, if addressed, will increase our understanding of seagrass ecosystems and fill current knowledge gaps in seagrass research in Australia. These questions are also of great relevance to seagrass research in a global context.

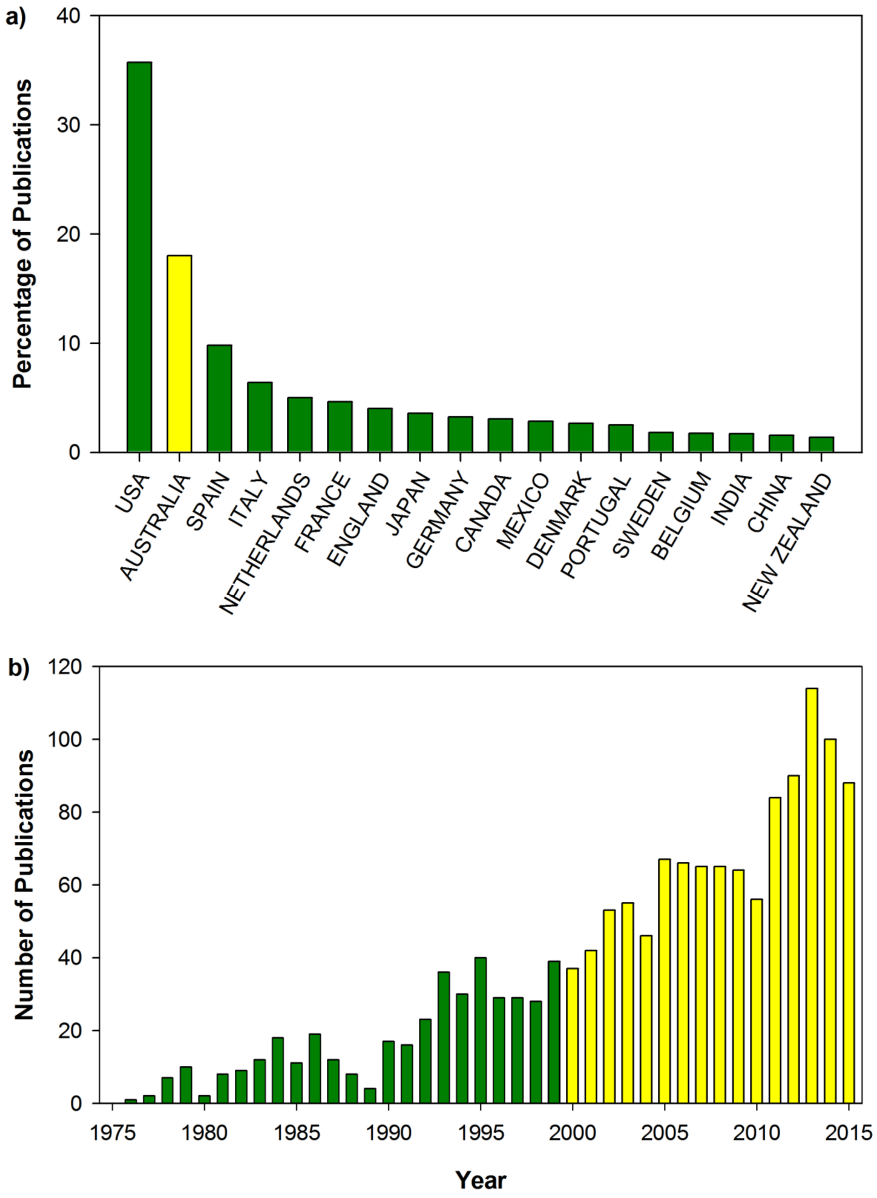

Figure 1: Summary of peer-reviewed seagrass literature showing a) percentage of publications per country of the affiliated lead institution and b) number of Australian publications per year with the yellow columns indicating publications since the last strategic review of seagrass was published in Australia in 1999. (Data sourced on 23/12/2015 from Thomson Reuters, Web of Science using the search term "seagrass" and then analysing results by "Countries/Territories". The publications affiliated with Australia were then analysed by "Publication Years").

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2. METHODS

A workshop to assemble data on gaps in seagrass research was held as part of the Australian Marine Sciences Association Annual Conference in July 2015 in Geelong, Victoria. This conference included leading marine scientists from around Australia. We followed similar protocols used previously for soliciting the opinions of experts in the fields of review (Hays et al., 2016; Sutherland et al., 2013; Wilson et al., 2010). Open invitations were sent to experts in a range of seagrass research fields targeted to be inclusive of all major seagrass research groups in Australia. Invitees who had indicated they would participate were encouraged to submit three questions in their field(s) of expert knowledge. These questions were to illicit important and feasible research questions or address management problems covering major knowledge gaps for that field.

Responses were compiled into 10 research fields covering the broad suite of research conducted on seagrass ecosystems in Australia. These were: taxonomy and systematics; physiology; population biology; sediment biogeochemistry and microbiology; ecosystem function; faunal habitats; threats; rehabilitation and restoration; mapping and monitoring, management tools. Prior to the workshop, the invitation process resulted in 172 research questions across all fields. The number of questions in each field ranged from three in seagrass sediment and microbiology to 31 in ecosystem function. The questions were used as the basis for discussion during the workshop, where participants were organized in groups representing research fields matching their expertise and each group was facilitated by a nominated coordinator. Groups discussed the status of research within their field, noting topics that were well researched and others where critical knowledge gaps remained. Using this information and the list of questions submitted for their topic they developed three to five broad research questions for their field encompassing the major knowledge gaps identified. Groups also discussed potential new technologies, methods and analytical tools that could be used to assist in answering these questions. The output of this process has not been ranked in any order of importance but has been presented in categories beginning with those relating to individual plants and species, followed by more complex ecosystem interactions and culminating in monitoring, management and restoration.

The workshop was attended by 49 participants representing all six Australian states, from government, university and private research institutions. They included representatives from all the major institutions with seagrass research laboratories (Supplementary Table 1 for attendees, affiliations and research fields). There was a broad historical background amongst participants who have studied seagrass across many geographical regions encompassing all the major seagrass groups and habitats in Australia dating back to the 1970's. The workshop included five scientists who had contributed to the 1999 review.

3. RESULTS

Questions addressing gaps and weaknesses in Australia's seagrass research knowledge

TAXONOMY AND SYSTEMATICS

1. ***How many species of seagrass grow in Australian waters?*** The Australian Plant Name Index (APNI) maintains a comprehensive list of vascular plant species in Australia (McNeil, 2015). However, there is an ongoing process of (re-)defining taxonomic concepts for species and different interpretations of available information which question the current taxonomic status of seagrass species, such as the *Zostera*/*Heterozostera* debate (see Coyer et al., 2013; Jacobs and Les, 2009; Kuo, 2005). Resolving seagrass species identification is critical for seagrass research and to ensure competent experimental design.

2. ***Do we need a better species concept for Australian seagrasses?*** Seagrasses display a high level of phenotypic plasticity (Backman, 1991; Kuo and Den Hartog, 2001), and there are several seagrass species that might be considered ‘cryptic,’ being genetically or morphologically indistinguishable (Waycott et al., 2006). With the increasing availability and decreasing costs of advanced genetic studies, there is a sense that we may be recognizing seagrass species diversity where it does not exist or missing diversity where it does exist due to the reduced morphological characters of the plants. The link between morphology, evolution, adaptation and phylogeny at different scales needs to be resolved to answer this question.

3. ***How can we increase awareness about the importance and usefulness of taxonomy for the science community and for the general population?*** Taxonomy plays an invaluable role in understanding biodiversity and conservation of plant species. Despite this there is a well-recognized lack of botanical taxonomists, creating a taxonomic bottleneck and preventing the accumulation of reliable site-specific community composition data for critical ecological studies (Callmander et al., 2005; Kim and Byrne, 2006). We need to encourage and support scientists and students who express an interest in taxonomic and systematic studies.

REPRODUCTION, DISPERSAL, RECRUITMENT AND LOCAL ADAPTATION

4. ***How do seagrass reproductive strategies vary through space and time?*** Asexual reproduction has long been considered the most important strategy for maintaining seagrass meadows. There is growing evidence that sexual reproduction may be more important in maintaining meadows than previous appreciated (e.g., Jones et al., 2008; Sinclair et al., 2014b), however, outcrossing rates have only been estimated for one Australian species to date (Sinclair et al., 2014a) so this remains a significant gap. We need to know how flowering and seed production varies across a species range and what environmental factors cause variation in annual reproductive investment. There is a need to identify triggers for floral development, pollen release and seed germination. The frequency and extent of hybridisation is not known, with speculation regarding the presence or absence of reproductive barriers (Sinclair et al., 2016).

5. ***What role do pollen, seeds and vegetative fragments play in gene flow and population connectivity?*** Knowledge of the dispersal potential of pollen, seeds, and clonal (vegetative) propagules remains poor for most species, although there has been significant progress in synthesizing current knowledge of connectivity (e.g., Kendrick et al., 2012; Sinclair et al., 2014b) and in providing the theoretical and conceptual framework for understanding movement ecology of seagrasses (McMahon et al., 2014). There is a requirement for a better understanding of patterns of connectivity and dispersal at local and regional scales for temperate and tropical species to improve marine conservation planning.

6. ***What conditions favour recruitment of sexual and asexual propagules?*** Considerable variation exists in the time vegetative fragments and seeds (dormant and non-dormant) remain

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viable and the local conditions that favour establishment are poorly understood (e.g., McMahon et al., 2014; Thomson et al., 2015). Seedling recruitment success is poorly studied in seagrasses, but generally accepted as being patchy with low long-term survival (Kendrick et al., 2012). An improved understanding of the rate of plant turnover, and the relative contribution of sexual and asexual reproduction in maintaining meadows (Macreadie et al., 2014) can be determined through temporal sampling in short-lived, annual species, but is far more difficult in long-lived perennial species.

7. *What scale does adaptation occur in seagrasses and what are the major selective forces?* The relative importance of phenotypic plasticity versus genetic adaptation in the resilience of seagrass ecosystems remains unknown but is crucial for understanding this process. Genomic and transcriptomic approaches (e.g., Golicz et al., 2015) are important tools for identifying the genes underlying adaptive traits and how they respond to climate change (Verges et al., 2014) and natural and anthropogenic stressors (Maxwell et al., 2014). Understanding the link between seagrass ecophysiology and genomics will help address how seagrass responds to stress associated with rapid change, and potentially improve conservation and restoration outcomes, which have been very poor to date (Statton et al., 2012).

PHYSIOLOGY OF SEAGRASS

8. *What are the effects of the spectral quality of light on seagrasses?* Light is essential for seagrass growth and reproduction (Lee et al., 2007; Ralph et al., 2007), however, the importance of spectral quality is less known. We need to understand the role phytochromes and specific wavelengths of light play in determining the activation and deactivation of light-dependent physiological processes (Casal, 2013) and determine whether comparable work done on marine macroalgae and terrestrial plants is useful. Altered spectral quality from leaf epiphyte cover reduces wavelengths of light available for chlorophyll absorption, thus reducing plant growth (Brodersen et al., 2015a). Variation in spectral quality, across instantaneous to seasonal time scales, is likely to elicit varied responses by seagrasses dependent on ecotype (e.g. deep vs. shallow, oceanic vs. estuarine) and should be investigated.

9. *What are the internal biochemical signaling pathways underlying plant function and reproduction?* The transfer of biochemical signals within both above-ground and below-ground seagrass biomass plays a major role in enabling seagrass responses to short- and long-term environment changes, as well as to initiate reproductive processes (e.g. germination of dormant seeds; Orth et al., 2000). We require a greater understanding of the vulnerability of this internal signaling to both natural and anthropogenic stressors.

10. *To what extent is respiration (and photorespiration) regulated in response to the environment?* Distinguishing the energetic requirements of photosynthesis, respiration and photorespiration enables us to understand the capacity of seagrasses to survive in varied light environments (Touchette and Burkholder, 2000). Future research directions could usefully address 1) the capacity for metabolic processes to respond to environmental changes (e.g. turbidity, temperature), 2) the extent that respiration is endogenously controlled, 3) the persistence of seagrasses in low light environments (and whether this is contingent on the capacity to regulate respiration), 4) the extent that energetic requirements can be modified in response to available energetic resource (light, stored compounds), and 5) whether there is an inviolable basal requirement that defines the limits of survival.

SEDIMENT BIOGEOCHEMISTRY AND MICROBIOLOGY

11. ***What is the role of microbes in seagrass resilience, function and life history?*** Although there has been some global research on the communities and functions of seagrass-associated bacteria, little work has been performed on Australian taxa, particularly endemic species. In addition to a paucity of data on the epiphytic and endophytic bacteria and eukaryotic microbes associated with Australian seagrasses, there is little information on the roles of these microbes in the seagrass lifecycle, including mediation of disease, seed germination, nutrient mobilization and sediment detoxification (Brodersen et al., 2015b; Crump and Koch, 2008; Panno et al., 2013; Sullivan et al., 2013).

12. ***How do changing environmental conditions, particularly anthropogenic pressures, influence microbial communities and how they function in seagrass meadows?*** Microbes are an important component of nutrient cycling and carbon sequestration in seagrass meadows (Hansen et al., 2000; Macreadie et al., 2015). Research on the effects of added nutrients, increased temperature, organic matter recalcitrance (resistance to decomposition), plant-derived root/rhizome exudates etc., on microbial metabolism is a priority. We also need to further elucidate the potential adverse effects of fine sediment deposits originating from terrestrial environments on seagrass health. Coastal development and run-off increase the loads of these fine sediments which may introduce harmful compounds that bind to sediment particles (e.g. diuron herbicide) and plant pathogens to the seagrass ecosystem.

13. ***What are the below-ground dynamics influencing seagrass function?*** Sediments inhabited by seagrass can vary widely in physical structure, geochemistry, microbial assemblages, and infauna composition (Di Maida et al., 2013; Moriarty et al., 1985). How do sediment attributes, both individually and in combination, influence seagrass persistence? Root and rhizome metabolism and biomass allocation influence whole-plant carbon budgets and nutrient absorption (Hemminga, 1998). How do roots and rhizomes influence seagrass response to environmental stressors? How tolerant are seagrasses to variations in pH? How is dissolved organic carbon impacted by substrate biogeochemistry?

14. ***How important are sediment characteristics for successful restoration?*** Sediment is almost always critical for seagrass growth and persistence, but excessive deposition (turbidity), accumulation (plant burial), erosion, and re-suspension can impair seagrass restoration (Irving et al., 2010; van Keulen et al., 2003). Additionally, understanding the importance of sediment quality, such as organic and nutrient content, grain size distribution, sediment source, porosity, and microbial activity may improve restoration outcomes.

FAUNAL ASSEMBLAGES

15. ***How does herbivory influence the structure and function of seagrass?*** Studies in Australia are limited but suggest biogeographic differences in the relative influence of meso-, macro- and megaherbivory on seagrass (Aragones et al., 2006; Cook et al., 2011; Ebrahim et al., 2014; Verhoeven et al., 2012). A better understanding is required of how herbivory affects seagrass biomass and species composition, and how those effects interact with water and plant nutrient concentrations. It is important to know how rates of grazing of seagrass and epiphytic algae promote resilience of seagrass (Maxwell et al., 2015), whether herbivores aid seagrass

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dispersal (via direct transfer or in their faeces), and how those factors will play out under a changing climate.

16. ***What is the effect of seascape on seagrass communities?*** The spatial arrangement of seagrass patches and their relation to other habitats such as mangroves, saltmarsh, and deeper channels – termed 'seascape' – is important for structuring seagrass faunal communities (Nagelkerken et al., 2015; Smith et al., 2012). However, knowledge of the effect of seascape on the functioning of seagrass habitats and their fauna is generally lacking. Although recent work has demonstrated effects of seascape on cross habitat trophic subsidies (Davis et al., 2014), effects on processes including recruitment, bioenergetics, herbivory and the nursery role of seagrass habitats (Nagelkerken et al., 2015) remain unclear, particularly for deeper seagrass (> 15 m). We need stronger predictive capacity of seascape effects for integrated management of coastal resources.

17. ***What are the cascading effects of changes in biomass of higher order predators on faunal assemblages and seagrass structure and function?*** Changes in biomass of higher trophic levels may result from harvesting of fisheries species and/or altered distributions of prey species (Heithaus et al., 2009), and their effect on seagrass habitats and fauna are likely to vary enormously depending on the strength of interaction and number of trophic levels involved (Huijbers et al., 2015). Cascades might also affect seagrass ecosystem functions (e.g., rates of blue carbon formation, Atwood et al., 2015).

18. ***What are the effects of anthropogenic pressures on the structure and function of seagrass food webs?*** Anthropogenic pressures, including land use alterations and climate change, will alter the timing and magnitude of terrestrial nutrient delivery to seagrass ecosystems (Gillanders et al., 2011) with potentially large implications for the food webs they support. Altered nutrient delivery will likely affect primary production and nutrient content or 'food quality'; (Cebrian et al., 2009) of seagrasses and their epiphytes, with flow on effects for consumers, which are not well understood. Further knowledge is needed of the contribution of seagrass to the growth and condition of consumers relative to other basal resources and how this may alter under different land use and climate change scenarios.

SEAGRASS ECOSYSTEM FUNCTION

19. ***How do different factors (scaled from gene to landscape) influence the functional processes involved in ecosystem service delivery?*** Evidence of the ability of Australian seagrass to perform functions delivering ecosystem services is highly context-dependent (species, environment, specific spatial and temporal scales) yet these roles are applied to the seagrass group as a whole. There is a need to better understand how the delivery of ecosystem services is affected by specific factors. This information is becoming increasingly important with growing requirements for the valuation of ecosystem services (Naeem et al., 2015).

20. ***How do we incorporate structure to functional relationships across multiple spatial and organisational scales?*** Understanding complex ecological function requires a systems approach that can be supported by ecosystem modeling. Despite evidence on the role of microbial assemblages (Robertson et al., 1982) and landscape scale attributes (Bell et al., 2006), research on seagrass ecological functions has primarily focused on the habitat scale. Ecosystem

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modeling will allow the conceptualisation of complex relationships and, when coupled with observations and manipulative experiments, can identify important pathways and improve our understanding of the system as a whole.

21. ***What is the influence on the ecosystem functions as an ecosystem becomes less resilient, and how does this erode ecosystem services?*** The loss and degradation of seagrass to a point which impacts the resilience of the system is assumed to result in a similar loss of ecosystem function, yet the relationship is unlikely to be linear due to the complexities of the systems (Rist et al., 2014). Mesocosm studies could use engineered 'treatments' of altered levels of ecological function that can be subjected to different pressures to test the effect of altered function on resilience.

22. ***How do diagenetic processes and the inorganic carbon cycle influence carbon storage in seagrass meadows?*** Our knowledge of carbon cycling varies across different seagrass ecosystems (Hyndes et al., 2014). To fully comprehend and predict sequestration capability we need to better understand the diagenetic processes (chemical and physical changes to sediments) that lead to storage and the role of the inorganic carbon cycle in net carbon storage (Mazarrasa et al., 2015). The application of diagenetic biogeochemical modeling, coupled to particle transport-hydrodynamic models, will improve our understanding of carbon cycling within meadows and the fate of exported seagrass in recipient habitats.

23. ***What are the sediment budget and coastal erosion implications of seagrass loss, and do hydrodynamic conditions affect the resilience of seagrasses to other pressures?*** Waves and currents are a defining feature of the coast, yet little attention is directed at understanding how seagrasses are affected by and, in turn, affect water movement and processes associated with it (see recommendations in Koch et al., 2009). Addressing these questions requires collaboration between coastal engineers, mathematical modellers and ecologists.

THREATS TO SEAGRASS ECOSYSTEMS

24. ***How do seagrasses respond to multiple threats and stressors?*** Seagrasses live in coastal environments where they are exposed to multiple threats and stressors (Jackson et al., 2001), and in marine systems the interactive effects of stressors are generally more severe than the cumulative effects (Crain et al., 2008). However, most of our predictions of response to threats are based on responses to single stressors (e.g., Ralph et al., 2007). We need to improve our understanding of how multiple threats interact in effecting seagrass response, including threats associated with climate change (e.g., Short and Neckles, 1999). This information can help to prioritize management actions for particular threats or combination of threats and provide insight into the capacity for acclimation to a changing environment.

25. ***What are the threats and implications from changes in the ecosystem for seagrass habitat?*** Threats to seagrasses may arise due to changes in other components of the ecosystem; For example, range shifts (Mazaris et al., 2013), species introductions (Williams, 2007), or species loss (de Fouw et al., 2016; Jackson et al., 2001) and changes in the behaviour of resident species can threaten seagrass habitat through changes in interactions such as through increased

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grazing rates (Verges et al., 2014). We need to improve our understanding of interactions in seagrass ecosystems.

26. ***What are the mechanisms and thresholds for sub lethal and lethal effects, and the spatial and temporal scales over which they occur?*** Seagrass resilience is driven by the ability to resist pressures and recover from impacts (Kilminster et al., 2015). Our ability to predict vulnerability to threats is limited by our understanding of these factors (thresholds) and their mechanisms.

27. ***What is the significance of historical changes in stressors to seagrasses over geological timescales, the most recent Anthropocene, and with projected climate change?*** Seagrasses evolved ~ 100 mya and have survived over a range of environmental conditions (Orth et al., 2006). Since the 1950's significant global declines have occurred due to human activities (Waycott et al., 2009) and some aspects of climate change are predicted to threaten seagrasses into the future. Understanding the scale of historical, current, and future pressures can give insight into the evolutionary capacity of seagrasses to adapt to change.

MAPPING AND MONITORING

28. ***How can we standardise methods used to map and monitor seagrass communities in Australia?*** Seagrass mapping and monitoring methods are diverse, ranging from broad scale (e.g. remote sensing from satellites) to fine scale (e.g. assessments of shoot counts). Approaches depend on the objectives of the program and resource availability. With at least 54 monitoring programmes in Australia (Kilminster et al., 2015), there is a need to standardise the seagrass metrics (distribution, biomass, seed banks, etc.) measured, and the mapping and monitoring approaches. Could classifications such as species life history, meadow form and habitat type (Kilminster et al., 2015) be a starting point to a national set of mapping and monitoring guidelines?

29. ***Should monitoring environmental conditions (abiotic and biotic) be a component of seagrass monitoring programs?*** Threats to seagrasses and the services they provide are well documented (Brown et al., 2014; Grech et al., 2012; Grech et al., 2011). These threats potentially reduce the resistance and recovery of seagrasses, and their resilience from pressures associated with climate change. Mapping and monitoring seagrass change and performance is a key priority in many coastal monitoring programs, but understanding the environmental factors that underpin the causes of change are also critical. There should be more emphasis on monitoring a suite of abiotic and biotic environmental conditions.

30. ***Which bio-indicators give early warning signs of loss and should they be incorporated into monitoring programs?*** A suite of 'early warning' bio-indicators at appropriate temporal and spatial scales should be incorporated into monitoring programs via a pre-determined set of criteria or thresholds, which if exceeded are capable of triggering a management response. Monitoring seagrass health/performance (e.g., carbohydrate stores, metabolomics, C: N: P ratios, level of metals) have the potential to provide early warning signs of seagrass stress. Although there is still much work to be done on identifying robust bio-indicators (McMahon et al., 2013), an initial suite of indicators could be trialled amongst existing monitoring programs for effectiveness and reliability.

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31. ***Is optical remote sensing an effective tool in seagrass mapping and monitoring?*** Interdisciplinary work between remote sensing and seagrass ecological research is now being coordinated. Remote sensing has successfully been used in clear relatively shallow water where seagrasses can be differentiated from each other or from other substrate types to determine seagrass presence/absence, seagrass metrics (species composition, horizontal projected percentage cover, biomass), maps of shallow meadow boundaries, and to provide information over large spatial (100s km^2) and temporal (seasons - years) scales (Roelfsema et al., 2013; Roelfsema et al., 2014). Water quality information derived from remote sensing has also been successful in interpreting ecological changes in seagrass (Petus et al., 2014). Further research is required to understand the theoretical and methodological aspects of remote sensing as a tool for mapping and monitoring seagrass, and to integrate optical remote sensing techniques with field based mapping and monitoring techniques.

SEAGRASS MANAGEMENT

32***. Is there a need for a national approach to seagrass management in Australia?*** Seagrass meadows extend around the Australian continent occurring in all states and territories; however there is no nationwide approach to seagrass management (Butler and Jernakoff, 1999; Coles and Fortes, 2001). The piecemeal and inconsistent approach to management extends to data collection, making any scientific evaluation of protection approaches, the number of permits issued, level of compliance, success of protected area approaches etc. almost impossible (Sheaves et al., 2016). Marine sanctuary zones in Australia poorly represent the extent and variability of seagrass habitat. We cannot be sure at the moment if any of Australia's approaches to seagrass protection are actually effective.

33. ***Are there some "must protect" seagrass meadows that we can identify?*** There is a role for seagrass scientists to identify some key strategic meadows for special protection. This could include meadows that support populations of iconic protected species such as green sea turtles (*Chelonia mydas*) or dugong (*Dugong dugon*); provide ecosystem services such as removing nutrients from eutrophic systems or supporting fisheries populations. There is also a need for the establishment of national seagrass reference sites in areas of low human impact. Meadows could be prioritized for protection based on the relative ecological importance.

34. ***In other jurisdictions such as fisheries there are clearly defined links between changes in target populations and management instruments – can similar tools be applied for seagrass management?*** If a fish population declines there is a well-established set of tools available to fisheries managers, such as establishing quotas and spatial closures. Could a similar management framework be developed to protect seagrass assets? Models are available which link catchment/watershed management and farm management to water quality and sediment runoff. Good quality catchment models with strong links between model outcomes and land management could empower natural resource managers to make decisions resulting in better outcomes for seagrass.

35. ***Would a more rigorous economic analysis of seagrass ecosystem values support stronger seagrass management and protection****?* General figures are available (see Costanza et al., 2014) but site-specific economic evaluations of seagrass ecosystem services are few. Detailed economic studies and economic modeling of the costs of damage to seagrass meadows at the estuary scale, such as used in the United States (National Marine Sanctuaries Act 2000,

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National Oceanic and Atmospheric Administration, 2013), would provide a useful tool to support better seagrass asset protection and quantify the costs of restoration in the event of their loss.

36. ***How can scientists best communicate with policy makers and managers?*** Seagrass scientists must find innovative and concise ways to communicate their science to environmental decision makers who are often overloaded with information from competing stakeholders. Report card and "traffic light" summaries are an increasingly popular means to provide a concise visual summary of often complex environmental information and this may be an applicable technique for communicating seagrass status on a national scale. A national approach to reporting ecosystem condition will require the development of standardized and comparable indicators.

SEAGRASS RESTORATION AND REHABILITATION

37. ***Can we effectively integrate environmental variation with multiple scales of biological organization (genes to metapopulations) to improve and better predict restoration success?*** Local environments influence seagrass gene expression, seed germination, growth rate, and reproductive output, as well as meadow structure, connectivity, extinction, and recolonization (Dattolo et al., 2013; Kilminster et al., 2015). Understanding these interactions within the context of the species targeted for restoration is critical for developing guiding principles regarding site selection, timing, methodology, and defining success.

38. ***How do we reliably and cost-effectively scale-up restoration from local experimental scales (i.e., metres) to larger scales (i.e., hundreds of metres or more)?*** Persistent restored meadows are becoming more common in small-scale experimental trials (Tanner et al., 2014), but this success appears difficult to translate to larger scales that meaningfully address seagrass loss. Do the factors limiting seagrass establishment through restoration fundamentally change from small to large scales, or does large scale restoration just require greater effort and resources (Irving et al., 2011)?

39. ***Is the restoration of seagrass functions implicit in physical restoration, or is additional intervention required?*** Many questions remain concerning the functionality, and by extension, 'success' of restored seagrass meadows. Data describing seagrass physiology (e.g. photosynthetic rates), population dynamics (e.g. meadow expansion, reproductive output), and ecosystem functions (e.g. carbon capture, nutrient cycling, sediment stabilization, habitat, and food for fauna) would demonstrate contributions of restored seagrass to local ecosystems, and aid the development of indicator-based assessments of success for restoration projects.

40. ***How do we build resilience in restored seagrass meadows?*** Traits such as meadow age, size, connectivity, genetic diversity, and inhabiting fauna may help build and maintain resilience (Olds et al., 2012), but data are lacking. Perhaps, where shifting environmental or climate conditions prevent like for like replacement, restoring a species that is naturally more resilient than what has been lost, even if that species wasn't originally present, is more effective long-term (i.e. building novel ecosystems with species more tolerant of disturbance). Crucially, the factors that allow us to 'future-proof' restored seagrasses warrant substantial consideration to ensure contemporary restoration efforts aren't eroded under future conditions.

4. DISCUSSION

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Seagrass research in Australia and globally has progressed markedly since the last systematic review and research and development plan (Butler and Jernakoff, 1999). The fact that over 70% of seagrass peer reviewed literature has been generated since the previous review serves to emphasize how quickly the methods and application of seagrass science have advanced. Four general trends have been observed in seagrass research since the turn of the century. Firstly, progression from studies of individual plants or meadows, to studies that incorporate linkages and connections between meadows on regional scales (e.g., Ruiz-Montoya et al., 2015) and among other habitats within the seascape including saltmarsh, mangroves and coral reefs (e.g., Nagelkerken et al., 2015). Secondly, increased importance of the below-ground biosphere to seagrass resilience is becoming more apparent (Suykerbuyk et al., 2015) including the interaction between seagrass roots and rhizomes, microbial communities and sediment chemistry (e.g., Brodersen et al., 2014; Trevathan-Tackett et al., 2014). Increased focus on knowledge gaps in this area is expected in the future. Thirdly, the study of the interactive effects of multiple stressors on plant function is replacing studies of individual environmental variables (e.g., Collier et al., 2011; York et al., 2013). This is increasingly important with the realization of the complexity of problems like climate change. Finally, from a management perspective there has been a shift from a paradigm of assessment, monitoring and explanation, to one of investigation and understanding involving experimental manipulation, with more emphasis on ecological values and the outcomes of management intervention (Coles et al., 2015; Kilminster et al., 2015).

Entire concepts and research fields have also developed since the previous review, particularly around the issues of global climate change. The concept of ‘Blue Carbon’ has seen considerable research effort focus on quantifying the carbon stocks in Australian seagrasses and valuing their ecosystem service (Lavery et al., 2013). Understanding how seagrasses react to changing ocean temperatures, acidification and sea level rise are also new aspects to global change research that have emerged in the last decade.

This evolution in seagrass research builds on earlier studies, and is driven by rapid advances in technology and conceptual approaches which are sure to continue. Modern techniques of remote sensing using satellite imagery, unmanned underwater vehicles and drones equipped with sophisticated camera technology and global positioning systems, and satellite tagging and acoustic telemetry for tracking animals, are transforming the rapid assessment, mapping and monitoring fields. Developments in microelectrodes and optical sensors, microscopy, flow cytometry and stable isotope tracers have advanced understanding in plant physiology, biogeochemistry and trophodynamics (e.g., Brodersen et al., 2015b; Connolly and Waltham, 2015; Koren et al., 2015; Trevathan-Tackett et al., 2014). Advances in molecular techniques are improving our understanding of seagrasses from the molecular level through transcriptomic, proteomic, genomic and metabolomic analyses, (e.g., Mazzuca et al., 2013) to the population level with next generation DNA sequencing techniques such as microsatellite markers and single-nucleotide polymorphisms (SNPs) improving our ability to measure genetic diversity, connectivity, resilience, and plant adaptation (e.g., Oetjen et al., 2010). Genetic sequencing is also being used to characterize microbial communities associated with seagrasses (Sun et al., 2015) and advances in environmental sampling (eDNA) are making this possible in larger faunal communities through metabarcoding techniques (Cowart et al., 2015). Increases in computing power has allowed for advances in statistical and spatial analyses and modeling, and have led to the new field of bioinformatics that enables the exploration of very large datasets

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produced by new technologies (Lucas et al., 2012; Procaccini et al., 2007). The synthesis of the large volumes of environmental and experimental data into models of habitat suitability, threat assessments, growth dynamics in relation to environment and climate, trophodynamics, and hydrodynamics will lead to greater predictive power of how seagrasses will respond to future scenarios of change and perturbation (e.g., Grech and Coles, 2010; Maxwell et al., 2015; Petus et al., 2014; Saunders et al., 2013; York et al., 2012). Understanding the complexities of the interactions affecting seagrass ecosystem and the growing human pressures that are impacting them will also require an interdisciplinary approach to investigation bringing together researchers from many different fields.

Gaps remain however, as our present review has emphasized. We do not have a national approach to seagrass management and research, with federal, state, territory and local jurisdictions having differing rules, approaches, and emphases. Large gaps remain in our knowledge of even the extent of seagrass meadows along the northern Australian coastline and in deeper (> 15m) waters. Taxonomic and systematic progress has been slow, and controversy over species classifications still exists despite improved molecular techniques for determining phylogeny. The lack of new seagrass researchers trained in recognising the taxonomic features of seagrass families that compliment new molecular toolkits has restricted progress in these areas. Without a clear picture of species and their history other research approaches are compromised.

Restoration of seagrass in Australia has gained renewed attention and is a fast growing area for research; however the questions proposed in this review start with basic knowledge of scale and reproductive output, seedling germination and success. To date, most efforts in Australia have been small-scale and have had a high degree of failure; successful and cost-effective restoration at larger spatial scales seems a long way off (van Katwijk et al., 2015). A greater understanding of restoration success will come from a synthesis of the growing knowledge base from other areas of research including reproduction and seed ecology, sediment chemistry and microbial activity, genetic diversity, natural resilience, connectivity, and the use of the latest technologies (Williams et al., 2014).

The Australian research community has advanced our knowledge of seagrass ecosystems enormously over the previous four decades. This review has identified gaps in our understanding of seagrass systems based on Australian experience that is relevant to the broader global research community. We cover a wide range of research fields and incorporate a divergence of views as to what are the top priorities but common themes, synergies, and overlaps can be seen in the priorities outlined by various groups. While it is not possible to predict all future discoveries related to seagrass ecology as evidenced from the previous review (Butler and Jernakoff, 1999), we provide a platform for a more coordinated approach. The challenge now is to build on our current knowledge - to understand the complex interactions between seagrasses and their environment, to provide advice for best management practice, and to protect the important habitats and the ecological systems dependent on them.

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