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Improving conservation planning for subtidal estuarine biodiversity

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Improving conservation planning for subtidal estuarine biodiversity

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A thesis submitted for the degree of

Doctorate of Philosophy

10 April 2017

Declaration

I certify that the work presented in this thesis is, to the best of my knowledge and belief, original, except as acknowledged in the text, and that the material has not been submitted, either in whole or in part, for a degree at this or any other university.

I acknowledge that I have read and understood the University's rules, requirements, procedures and policy relating to my higher degree research award and to my thesis. I certify that I have complied with the rules, requirements, procedures and policy of the University.

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Date: 10 April 2017

Abstract

Conservation planning is used to identify areas for protection of biodiversity. In marine systems, however, such planning is often based on limited information and may therefore be conducted using conservation targets, such as arbitrary fixed percentage targets, that are unrepresentative of underlying biological assemblages, which frequently exhibit considerable spatial variability amongst areas. There is a clear need for improved methods for gathering and classifying subtidal marine biodiversity data and for setting targets in conservation planning.

Here, methods for collecting data for subtidal estuarine habitats and fish and mollusc assemblages were developed, a novel method for classifying habitats was established, and techniques for modelling surrogacy relationships between biological assemblages and abiotic variables were examined. The resulting data were used to assess the relative efficiency of different target-setting approaches in conservation planning, highlighting the benefits that accrue when conservation planning takes underlying biological diversity into consideration.

The study was based on data gathered in the Port Stephens estuary in New South Wales, Australia; part of the Port Stephens-Great Lakes Marine Park. Habitats within Port Stephens were surveyed using a combination of towed video and aerial photography over an area exceeding 50 km². A classification system for habitats was developed using surveys of benthic cover across a range of sites and depths. Relationships between habitat distributions and abiotic variables were explored using distance-based linear modelling and, for seagrass habitats, the novel application of relative environmental suitability modelling. Fish and mollusc assemblage data were gathered across habitat types, using underwater visual census, and distance-based linear modelling was again used to examine whether habitats and abiotic variables provided useful surrogates for fish and mollusc assemblages. Approaches to setting targets for conservation planning were investigated, including the potential for setting quantitative non-uniform targets based on species-area relationships.

Habitat classification identified a number of significantly different benthic habitats within Port Stephens and identified previously unknown areas of some habitats in the study area. Modelling identified strong correlations between benthic habitat distributions and abiotic variables of depth, location, substrate type, and current strength. For seagrass habitats,

wave exposure and turbidity were also shown to influence habitat distributions, and predictive modelling indicated that future sea level rises and increases in turbidity would result in substantial loss of seagrasses. Modelling demonstrated that significant differences in fish and mollusc assemblages occurred among benthic habitats and found significant relationships between these assemblages and abiotic variables. Both abiotic variables and benthic habitats were found to be useful surrogates for biodiversity in conservation planning, with combined biotic and abiotic variables providing the highest level of discrimination among assemblages. Examination of the relative efficiency of different target-setting approaches in conservation planning identified that non-uniform conservation targets for benthic habitats, based on species-area relationships, provided significant improvements in protection of species richness of fish and molluscs compared with uniform percentage targets.

In conclusion, this study demonstrated the value of assembling comprehensive biodiversity and species distributional data prior to commencing conservation planning. Where these data are available, conservation targets can be set using species-area relationships that provide increased levels of protection for species across habitat classes. Where comprehensive biodiversity data are not available, the combination of data on benthic habitats and relevant abiotic variables provides the best representation of species assemblages in conservation planning.

Acknowledgements

A PhD builds upon a mountain of other people's work and there are many people and organisations involved that need to be acknowledged. At the very top of this list is my wife Nicola who supported me throughout, was unfailing in her good humour and was the best dive buddy a researcher could ask for.

The PhD could not have been completed without the support of my principal supervisor Professor Steve Smith, and my co-supervisors Dr David Harasti and Dr Brendan Kelaher. Steve Smith was instrumental in starting the whole adventure and his encouragement and guidance allowed me to exceed my personal expectations in terms of what could be achieved in the time available. Steve also was unfailingly patient when explaining the finer points of multivariate statistical analysis and in supporting my endeavours to achieve a Thesis by Publication. David Harasti deserves special thanks for making me aware that a PhD was an option available to me. David was also pivotal in developing the initial study design, was supportive during my fieldwork, and provided insightful comments during the preparation and review of manuscripts for publication. Brendan Kelaher provided a calm voice of encouragement, especially during the numerous setbacks that occurred along the way. Brendan was highly responsive whenever feedback was needed, and provided crucial guidance on the best methods to get thesis chapters published.

I would also like to thank the numerous institutions and individuals who provided assistance along the way. My special thanks go to the Southern Cross University Marine Ecology Research Centre who provided the scholarship that funded the first year of the PhD, and to the Australian Government whose Australian Postgraduate Award funding the remainder. The New South Wales Department of Primary Industries were supportive from the outset and assisted with staff, boats, knowledge, information, and equipment. In particular I would like to thank Alan Jordan for his assistance with planning the study, Christopher Gallen and Roger Laird for assisting with towed video mapping, and Gregory West and Tim Glasby for assisting with seagrass modelling. Thanks also to the Manly Hydraulics Laboratory, and Bega Valley Shire Council who supplied data used in the study, and to the TELEMAT-MASCARET Consortium who supplied the hydrodynamic modelling software used. Finally thanks to the journal editors, and anonymous reviewers, for their valuable feedback and assistance with improving the manuscripts that make up the bulk of this thesis.

Publications included in thesis

Chapter 2: Davis T.R., Harasti D., Smith S.D.A. (2016b) Developing a habitat classification typology for subtidal habitats in a temperate estuary in New South Wales, Australia. *Marine and Freshwater Research* **67**: 1186–1195.

<http://dx.doi.org/10.1071/MF15123>

Chapter 3: Davis T.R., Harasti D., Smith S.D.A., Kelaher B.P. (2016c) Using modelling to predict impacts of sea level rise and increased turbidity on seagrass distributions in estuarine embayments. *Estuarine and Coastal Shelf Science* **181**: 294–301.

<http://dx.doi.org/10.1016/j.ecss.2016.09.005>

Chapter 4: Davis T.R., Harasti D., Kelaher B.P., Smith S.D.A. (2016a) Diversity surrogates for estuarine fish assemblages in a temperate estuary in New South Wales, Australia. *Regional Studies in Marine Science* **7**: 55–62.

<http://dx.doi.org/10.1016/j.rsma.2016.05.009>

Chapter 5: Davis T.R., Harasti D., Kelaher B.P., Smith S.D.A. (2017a) Spatial and temporal variation in subtidal molluscan diversity amongst temperate estuarine habitats. *Marine Ecology* **38**:e12428.

<http://dx.doi.org/10.1111/maec.12428>

Chapter 6: Davis T.R., Harasti D., Kelaher B.P., Smith S.D.A. (2017b) Defining conservation targets for fish and molluscs in the Port Stephens estuary, Australia using species-area relationships. *Ocean and Coastal Management* **136**: 156–164.

<http://dx.doi.org/10.1016/j.ocecoaman.2016.12.007>

Statement of contribution of others

I contributed to all components of all publications included in this thesis (Chapters 2–6) and prepared and submitted these manuscripts to the listed journals. My co-authors, Stephen Smith, Brendan Kelaher, and David Harasti assisted with study designs for these manuscripts, suggested improvements prior to submission, and assisted with addressing reviewer’s comments. Stephen Smith assisted with statistical analysis for the manuscripts contained in Chapters 2, 4 and 5. David Harasti assisted with fieldwork for the manuscript contained in Chapter 2. Brendan Kelaher provided guidance on the appropriate modelling techniques for the manuscript contained in Chapter 3.

Additional publications

During the course of this thesis, two additional peer reviewed manuscripts were published that were related to the thesis. These manuscripts are provided in full in Appendices A-B, and my contribution to each publication is listed below.

Appendix A – Davis T.R., Harasti D., Smith S.D.A. (2015c) Extension of *Dendronephthya australis* soft corals in tidal current flows. *Marine Biology* **162**: 2155–2159.

<http://dx.doi.org/10.1007/s00227-015-2732-7>

The investigations conducted in Chapter 2 led to a study examining the responses of *Dendronephthya australis* colonies to tidal current strengths (Appendix A). I designed this study, undertook all field work, assembled all data, and performed all modelling and statistical analysis. I wrote the initial draft of the manuscript, and edited the manuscript to incorporate suggestions from my co-authors. I submitted the manuscript to *Marine Biology*, and edited the manuscript to address comments from reviewers prior to acceptance.

Appendix B - Davis T.R., Smith S.D.A. (2017) Proximity effects of natural and artificial reef walls on fish assemblages. *Regional Studies in Marine Science* **9**: 17–23.

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Underwater visual censuses undertaken for Chapter 4 highlighted localised variations in fish assemblages in the vicinity of vertical walls. This observation led to a study examining variations in fish assemblages at both natural and artificial walls (Appendix B). I designed this study with assistance from my co-author, undertook all field work, assembled all data, and performed all statistical analysis. I wrote the initial draft of the manuscript, and edited the manuscript to incorporate suggestions from my co-author. I submitted the manuscript to *Regional Studies in Marine Science*, and edited the manuscript to address comments from reviewers prior to acceptance.

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Chapter 1. Introduction

The health of marine ecosystems throughout the world is in decline (Jackson 2001; Kennish 2002; Lotze *et al.* 2006), due to increasing levels of disturbance including acute and chronic anthropogenic impacts (Crain *et al.* 2009; Halpern *et al.* 2007). Threats to marine environments include habitat loss (Lotze *et al.* 2006), invasive marine species (Bax *et al.* 2003), climate change (Hoegh-Guldberg and Bruno 2010), increased nutrient flows (Nixon 1995), pollution (Long *et al.* 1995), and extractive activities (Salomon *et al.* 2008). There is global concern that these threats will lead to further degradation of marine habitats and the continued loss of marine species and biodiversity (Costello *et al.* 2010; Gray 1997; Halpern *et al.* 2008).

1.1 The need for improved conservation planning in estuaries

Estuarine systems, in particular, are in serious decline with more than 65% of the world's seagrass and wetlands habitats estimated to have been destroyed over the last 300 years (Dixon *et al.* 2016; Lotze *et al.* 2006; Unsworth *et al.* 2014). Estuaries are important centres for human populations, as they provide access to fresh water, productive and varied sources of food, and facilitate trade along sea routes and inland waterways (Erlandson 2001). The areas adjacent to estuaries represent some of the most heavily populated and industrialised regions in the world, leading to profound impacts on the health of these systems (Kennish 2002; Lotze *et al.* 2006), including eutrophication, fisheries overexploitation, chemical contamination, introduced species, habitat loss and alteration, and marine debris (Jackson 2001; Jennerjahn and Mitchell 2013; Kennish 2002). These interact, and can combine synergistically, leading to effects that are far greater than those from any one factor in isolation (Lotze *et al.* 2006). Anthropogenic impacts also interact with natural disturbances, compounding their severity, and prolonging recovery times (Jackson *et al.* 2001).

To address these impacts, effective management of estuaries must consider maintenance of ecosystem processes, protection of habitats and sustainable use of living resources (Bianchi *et al.* 2012; Gray 1997). Chronic anthropogenic impacts need to be controlled, requiring broad coastal and ocean management systems, which incorporate catchment management strategies for adjacent terrestrial areas (Cicin-Sain and Belfiore 2005). Within this framework of management strategies, marine protected areas (MPAs) are seen as a

key tool for protecting biodiversity, as they provide areas of refuge from human impacts such as over-fishing, pollution and coastal/marine developments (Agardy 1994; Mumby and Steneck 2011). The size, number, and location of MPAs contribute to their effectiveness for protecting biodiversity (Claudet *et al.* 2008). If MPAs are too small, too isolated, poorly located, or are not socially accepted, then they may not provide adequate protection (Ban *et al.* 2011). Information is therefore needed for effective MPA conservation planning to maximise biodiversity protection, including an understanding of biodiversity, the processes that maintain it, and knowledge of the extent and structure of marine habitats (Ban *et al.* 2011; Buckland *et al.* 2012).

Marine conservation planning is commonly undertaken with multiple and sometimes conflicting objectives including; conservation of biodiversity (Agardy *et al.* 2003; Leslie 2005), protecting of rare and threatened species (Leslie 2005; Powles *et al.* 2000), and meeting varied social and economic targets (Ban *et al.* 2011; Stewart and Possingham 2005). The planning process typically involves deciding where conservation actions are needed, identifying conservation objectives, and determining how these objectives should be achieved (Redford *et al.* 2003). This process is frequently facilitated by expert panels, using data on the distributions of habitats and species of interest (Leslie 2005; Powles *et al.* 2000). Marine conservation objectives are often achieved by defining limitations on particular activities in specified areas (e.g. prohibiting fishing in no-take MPAs) with the planning process typically requiring extensive public consultation before implementation (Fernandes *et al.* 2005; Leslie 2005). However, the planning process is frequently hindered by conflicting requirements amongst stakeholders, with compromises often occurring due to trade-offs arising from social, economic, and political pressures (Margules and Pressey 2000). Often these compromises hamper the ability to meet conservation objectives resulting in reduced performance of conservation areas (Agardy *et al.* 2003). Reduced performance can also occur where a lack of accurate information hinders the planning process and where conservation targets are poorly defined (Metcalf *et al.* 2013; Pressey 1994). It is, therefore, vitally important to define suitable targets and assemble accurate maps and biodiversity information if conservation planning is to successfully achieve its objectives.

1.2 Habitat classification and mapping

Maps are frequently used to record the extent and structure of marine habitats (Creese *et al.* 2009; Jordan *et al.* 2010a). Mapping requires the use of habitat classification systems to

define planning and mapping categories, with considerable variation in how habitats are classified, depending on the scale of the area being mapped (Diaz *et al.* 2004; Last *et al.* 2010). At regional scales, habitat classifications focus on variations over hundreds to thousands of kilometres and tends to reflect physical factors such as geographical location, depth, structure of the seascape, underlying geomorphology, and substrate type (Greene *et al.* 2007). Habitat maps at this scale typically contain little information on overlying biological assemblages, and even less information on the communities of mobile animals that comprise these assemblages (Diaz *et al.* 2004; Jordan *et al.* 2010b).

At local scales, marine habitats have variously been classified using physical factors (Malcolm *et al.* 2011), or a combination of physical factors and biological assemblages (Anderson *et al.* 2007; Stevens and Connolly 2005; Stolt *et al.* 2011). Ideally, habitat classification systems should incorporate both physical structures and their overlying biological assemblages (hereafter jointly referred to as “benthic habitats”) where protection of biodiversity is a primary objective (Bianchi *et al.* 2012; Last *et al.* 2010). Benthic habitat classification systems generally divide the continuum of benthic habitats into categories based on their dominant characteristics (Diaz *et al.* 2004; Last *et al.* 2010; Malcolm *et al.* 2011). Ideally, these classification systems should be exhaustive, describing all distinct benthic habitats within a region and should use categories that are easily identifiable, mutually exclusive, and which provide sufficient detail for effective management (Ball *et al.* 2006).

Marine habitat mapping can be achieved using a range of technologies including satellite imagery, aerial photography, acoustic mapping, underwater imagery, and direct sampling (Diaz *et al.* 2004). The largest coverage for habitat mapping is provided by techniques that provide information over a broad area, such as satellite imagery (Mumby and Edwards 2002) and aerial photography (Andrew and O'Neill 2000; Zharikov *et al.* 2005). However, due to limitations imposed by water depth and turbidity, these techniques cannot provide information on biological habitats that exist in deeper waters (Chust *et al.* 2010; Mumby and Edwards 2002). For shallow waters, habitat types must be inferred based on the colour or spectrum of images, and confirmed using ground truthing (Andrew and O'Neill 2000). Extensive mapping of habitats can also be conducted using acoustic mapping techniques such as multibeam sonar (Beaman *et al.* 2005; Bickers 2003) and acoustic swath mapping (Anderson *et al.* 2007; Jordan *et al.* 2010a). These techniques provide detailed information

on bottom depth, structure, and substrate type, but information on biological habitats can only be inferred from the acoustic signals (Anderson *et al.* 2009; Bickers 2003).

Currently, to obtain detailed information on biological components of subtidal habitats, as required for benthic habitat mapping, it is necessary to use either underwater imagery, or physical sampling (Diaz *et al.* 2004). Underwater imagery can be obtained using cameras operated from boats (Lefebvre *et al.* 2009; Rooper 2008; Tran 2013), mounted on remotely operated vehicles (Micallef *et al.* 2012), or carried by divers (Carleton and Done 1995). While cameras provide direct observations of sub-tidal habitats, their use in mapping is generally restricted to relatively small areas (Carleton and Done 1995), and for ground truthing habitat types for maps based on aerial photos (Andrew and O'Neill 2000), or acoustic mapping techniques (Anderson *et al.* 2009).

1.3 Biodiversity assessment and surrogacy

In addition to an understanding of benthic habitat distributions, conservation planning requires knowledge about variation in mobile species assemblages, among benthic habitats, in order to facilitate biodiversity protection. Regional biodiversity (Gamma diversity) can be divided into biodiversity within communities or habitats (Alpha diversity), and biodiversity variation among communities or habitats (Beta diversity) (Whittaker 1972). These diversity measures allow assessment of the relative importance of different habitats to overall biodiversity (Sepkoski Jr 1988), exploration of the relationships between species and habitats (Shmida and Wilson 1985), and assessment of the importance of specific habitats to threatened or protected species.

On a global scale, many projects are underway to catalogue terrestrial and marine biodiversity (e.g. EOL 2014; GBIF 2014). These projects are being driven by concern that human activities are leading to widespread extinction of species (CI 2013). Species are currently being lost at an alarming rate in terrestrial ecosystems, where areas of high diversity typically coincide with areas of high endemism (Hughes *et al.* 2002), and consequently loss of habitat has led to extinctions of multiple species (CI 2013). In marine environments, many species are less sensitive to localised habitat loss, as they have very broad distributions (Hughes *et al.* 2002). However, numerous cases of extinction of marine species still exist, primarily due to overexploitation, but with habitat loss also contributing to the extinction of species (Dulvy *et al.* 2003; Powles *et al.* 2000). It is therefore

important that improved information is available on marine biodiversity, especially for ecosystems that are exposed to multiple threats, such as those occurring within estuaries.

Assessing biodiversity in the marine environment is time consuming and requires expert taxonomic knowledge (CATAMI 2013; Last *et al.* 2010). In marine ecosystems where detailed biodiversity data are limited, surrogates are commonly used to represent overall biodiversity (Bianchi *et al.* 2012; Last *et al.* 2010). These surrogates can then be used as indicators for monitoring changes to ecosystems, and for assessing ecological impacts (Magierowski and Johnson 2006). Selection of biodiversity surrogates is generally conducted based on a number of factors including the availability of equipment, expertise for sampling, and taxonomic knowledge (Magierowski and Johnson 2006). Commonly used surrogates for biodiversity include: abiotic variables (Jordan *et al.* 2010b; Malcolm *et al.* 2011); habitats (Anderson *et al.* 2007; Dixon-Bridges *et al.* 2013); and subsets of marine phyla (e.g. molluscs (Smith 2005); and fish (Ward *et al.* 1999)). At regional or national scales, the use of abiotic variables as surrogates for biological assemblages is almost unavoidable, as the effort required to gather information on biological assemblages is prohibitive (Jordan *et al.* 2010b). At a local scale, however, benthic habitats are frequently used as surrogates for overall biodiversity in conservation planning, as these generally provide improved representation of local variations in species assemblages when compared against abiotic variables (Day *et al.* 2000; Jones and Srinivasan 2007).

Although surrogates are widely used in conservation planning, they only provide an approximate representation of overall biodiversity, with a number of studies demonstrating that surrogates perform poorly if they are not carefully selected (Dixon-Bridges *et al.* 2013; Gladstone 2002). Surrogates also have limited applicability outside the regions where they are developed, due to differences in species assemblages among regions (Grantham *et al.* 2010). As existing studies examining surrogates for temperate subtidal estuarine systems have primarily focussed on soft sediment communities (Dixon-Bridges *et al.* 2013) and seagrasses (West *et al.* 2008) there is a clear need to develop improved understanding of surrogates applicable to conservation planning in deeper areas (i.e. > 10 m) of temperate subtidal estuaries. In these areas a range of other biotic communities can exist (Smith *et al.* 2010) which are potentially not adequately represented by those surrogates generally applied in conservation planning within estuaries.

1.4 Using Port Stephens as a model for estuarine conservation planning

Conservation planning requires understanding of the complex relationships among abiotic conditions, benthic habitats, and biodiversity. The eastern bay of the Port Stephens estuary (Figure 1) was selected as a model to examine these relationships by: testing methodologies for gathering habitat and biodiversity data; investigating surrogacy among abiotic variables, benthic habitats and biodiversity; and studying methods for improving conservation planning in estuarine systems. The Port Stephens estuary was selected as it faces many of the same threats as other estuaries around the world (e.g., habitat loss, eutrophication, pollution, overfishing, and marine debris). In addition, the Port Stephens estuary is known to contain a high diversity of biota and a diversity of habitats (Carraro and Gladstone 2006; Smith *et al.* 2010) making the estuary ideally suited to exploring relationships among habitats and biological assemblages.

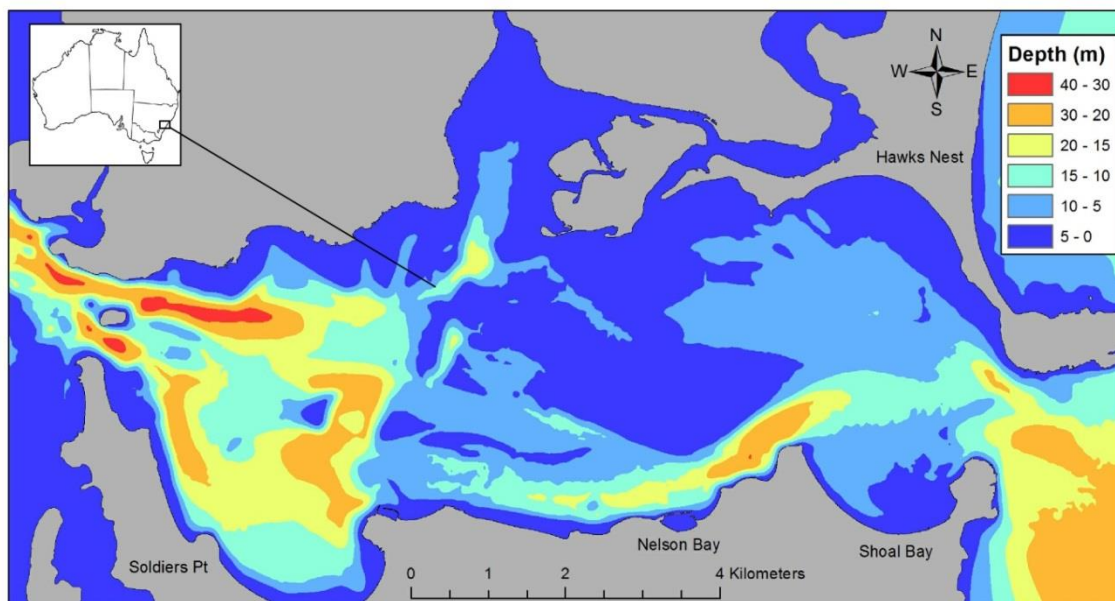


Figure 1. Eastern Port Stephens estuary. Grey areas indicate land, coloured shading indicates water depth.

1.4.1 Anthropogenic and environmental impacts in Port Stephens

The southern shoreline of the Port Stephens estuary has undergone intensive development since European colonisation (Knott *et al.* 1998). This development has resulted in loss of habitat within the estuary, through the building of marinas and breakwalls, and the reclamation of wetlands for roads and houses (Umwelt 2009). The estuary is exposed to pollution from residential, industrial, maritime, and agricultural sources (DPWS 1999;

Umwelt 2000), and to marine debris from terrestrial and marine sources (Smith and Edgar 2014). The estuary is the location for intensive farming of oysters (Nell 2001) and there is potential for introduction of pests and diseases to the estuary (Williams and Grosholz 2008). In addition, the estuary is the site of commercial and recreational fisheries, with historical records indicating a decline in the abundance of a number of targeted species within the estuary (Clarke 2011). Boating within the estuary generates impacts on marine habitats, primarily through the construction of infrastructure (e.g. marinas, boat ramps, breakwalls, jetties, and moorings) (Umwelt 2009) but also through: pollution from anti-fouling compounds, oil, waste, and debris (DPWS 1999); and damage from dredging, anchoring and poorly designed moorings (Harasti 2016), as well as propellers and associated wash (Poulos 2011; Umwelt 2009). The Port Stephens estuary is also exposed to natural disturbances with strong tidal currents causing sand movement (Austin *et al.* 2009; DPWS 1998), periods of heavy rainfall generating high fresh-water inflows from the Karuah River (DPWS 1999; NSW-DPI 2014), and waves from extreme weather events impacting shallow areas (Vila-Concejo *et al.* 2011).

1.4.2 *Conservation planning and management in Port Stephens*

Given the wide range of anthropogenic threats and natural disturbances faced by the Port Stephens estuary, it is extremely important that effective management strategies are in place, and that data on benthic habitats and marine species within the estuary are available to inform these strategies. The entire Port Stephens estuary is contained within the Port Stephens-Great Lakes Marine Park (PSGLMP) which is the largest marine park in New South Wales (NSW), covering approximately 98,000 hectares. The PSGLMP is a multiple use marine protected area (MPA) with four zoning categories that limit different activities. Approximately 17% of the park is classified as no-take (sanctuary zone) (NSW-MPA 2010a). The marine park supports important recreational and commercial fishing grounds, and aquaculture ventures, as well as areas for significant tourism and recreational activities, including whale and dolphin watching, water sports, and scuba diving (NSW-MPA 2007).

A number of plans exist to coordinate effective management of the estuary including the Port Stephens and Myall Lakes Estuary Management Plan (Umwelt 2000), the Port Stephens Foreshore Management Plan (Umwelt 2009), and the PSGLMP Operational Plan (NSW-MPA 2010a). While these plans provide a detailed framework for managing the estuary, it is generally acknowledged that there are knowledge gaps that limit the ability of

managing agencies to assess changes occurring within the estuary (DPWS 1999; Umwelt 2000). The estuary processes study, conducted by the NSW Department of Public Works and Services, notes that data on the spatial and temporal abundance and distribution of most aquatic fauna are lacking (DPWS 1999). This paucity of information presents an obstacle to management, and more quantitative data on benthic habitats and marine biodiversity is required for conservation planning, including accurate maps showing habitats types and their extent.

1.4.3 Habitat classification and mapping in Port Stephens prior to this study

In New South Wales, mapping of marine habitats is increasingly being used in the management of marine areas (NSW-DPI 2013a). For effective management, these maps need to show the extent, structure, and distribution of marine habitats (Dixon-Bridges *et al.* 2013; Jordan *et al.* 2005). The majority of habitat-mapping effort to date in NSW has focused on fully marine habitats (Jordan *et al.* 2010b; Underwood *et al.* 1991) and the existing habitat classification scheme, used extensively in NSW marine parks for fully marine areas, focuses primarily on substrate type (i.e. reef or unconsolidated substrate), and depth (Jordan *et al.* 2010b). Benthic habitats are not included in this classification system due to the difficulties associated with determining benthic habitats using swath acoustics, which has been the primary tool used for mapping (NSW-MPA 2010b). While a classification system for marine benthic habitats in south-eastern Australia has been suggested by Underwood *et al.* (1991), the applicability of this system to estuarine environments, such as in Port Stephens, had not been fully tested. Within NSW estuaries, some aquatic vegetated habitats (mangroves, seagrass and saltmarsh) have been mapped using a combination of aerial and satellite photography (Creese *et al.* 2009). Due to water turbidity, however, the type and extent of deeper benthic habitats in estuaries (i.e. at depths of more than ten metres) remained largely unquantified (Smith *et al.* 2010).

While a high diversity of biota and a diversity of benthic habitats was known to occur within the Port Stephens estuary (Carraro and Gladstone 2006; Smith *et al.* 2010), these benthic habitats had not previously been fully classified or mapped. Existing maps showed only the extent of seagrass, mangrove, and saltmarsh habitats in shallower areas (Creese *et al.* 2009) and sediment types throughout the estuary (Roy and Matthei 1996; Roy *et al.* 2001). Some effort had been invested in mapping the extent of the soft coral

Dendronephthya australis and adjacent areas of sponge habitat, on the southern shoreline of the Eastern Port (Poulos 2011). However, a large proportion of deeper areas in the remainder of the estuary had not been examined. In addition, previous habitat maps were developed over an extended period (1996–2011) and large-scale changes occurred within the estuary over this period, particularly due to the movement of sand (Austin *et al.* 2009; Vila-Concejo *et al.* 2011).

There was, therefore, a clear need to address knowledge gaps within Port Stephens about estuarine benthic habitats including: a comparison of distinct benthic habitats in Port Stephens with categories used in existing NSW habitat classification schemes; the development of a map of deeper subtidal habitats; and increasing understanding of the suitability of benthic habitats as surrogates for biodiversity within the estuary.

1.4.4 Biodiversity information and surrogacy in Port Stephens prior to this study

Data on biodiversity and distributions of most aquatic fauna in Port Stephens, across benthic habitats, was lacking prior to this study (DPWS 1999) and limited taxonomic information was available for many groups of animals that occur within the estuary (e.g. sponges, bryozoans, and cnidarians (CATAMI 2013)). Given that quantification of overall biodiversity in any system is a monumental task, studies examining surrogacy must generally focus on a subset of overall biodiversity. Ideally groups selected for representation in conservation planning should include species heavily impacted by management practices, which, for no-take areas in the PSGLMP, is primarily those species subject to intense fishing pressure. Fish and mollusc species were therefore identified as being suitable surrogates at Port Stephens, primarily due to their importance to recreational and commercial fisheries (Smith and Pollard 1996; West and Gordon 1994), and because they have proved to be good surrogates in previous studies (Gladstone 2002; Malcolm and Smith 2010; Smith 2005). These groups are also amenable to conservation planning because: detailed taxonomic information is available; they are generally abundant in NSW; and, they can be sampled using non-extractive techniques within no-take MPAs.

While some research examining diversity of fish species among habitats had previously been conducted in Port Stephens (Poulos 2011), this research did not examine all benthic habitats, and did not test whether habitats could be used as surrogates for assemblages. No research examining variation in surface-dwelling molluscs among habitats was identified

for Port Stephens, indicating a knowledge gap in this area. There was, therefore, a clear need to obtain more comprehensive information on biodiversity patterns for fish and molluscs within Port Stephens to provide data for future conservation planning, and to allow assessment of the effectiveness of using abiotic factors and benthic habitats as surrogates for fish and molluscs in conservation planning for the estuary.

1.5 Thesis Outline and Objectives

Effective conservation planning requires data on benthic habitats, knowledge of biodiversity, and development of suitable techniques for setting conservation targets and identifying conservation priorities. In this study, these needs are addressed within a temperate estuarine system for which data on benthic habitats and biodiversity was lacking. Firstly, the study examines methods for classifying and mapping subtidal benthic habitats within estuarine systems and examines the use of abiotic factors as surrogates for benthic habitats. The study then focuses on measuring the diversity of fish and mollusc species among benthic habitats and examines if abiotic factors and benthic habitats can be used as effective surrogates for this diversity. Finally, the study examines techniques to improve conservation planning to provide enhanced protection of estuarine biodiversity, using data on benthic habitats and fish and mollusc assemblages as inputs to the planning process.

Specific objectives for each chapter of the thesis are provided below:

Chapter 1 outlines the need for improved conservation planning within estuarine systems and examines previous work conducted in estuarine habitat classification, mapping, biodiversity assessment, surrogacy and conservation planning.

Chapter 2 focuses on habitat classification and mapping methods, with the objective of determining efficient and cost-effective methods to obtain benthic habitat data for conservation planning. Chapter 2 tests hypotheses about the relationships between benthic habitat distributions and abiotic variables, investigating the potential for using abiotic variables as surrogates for benthic habitats in conservation planning. Finally, this chapter provides the benthic habitat data used in the biodiversity and conservation planning studies detailed in Chapters 4–6.

Chapter 3 examines relationships between seagrass habitat distributions and abiotic variables with the objective of providing improved understanding of the general applicability of surrogacy relationships across multiple estuarine systems, and hence the

broad applicability of abiotic variables as surrogates in conservation planning. Chapter 3 also examines the potential for using species distribution models to predict the impact of threatening processes, such as climate change, on habitat distributions, with the objective of assessing how species distribution models can contribute to conservation planning for future environmental changes.

Chapter 4 examines variation in fish assemblages among the benthic habitats identified in Chapter 2, with the objective of examining the effectiveness of using benthic habitats, and abiotic variables, as surrogates for fish diversity in conservation planning. In addition, seasonal change in fish species diversity is investigated to assess the temporal stability of the benthic habitat/fish relationship. Chapter 4 also provides the data on fish assemblages and distributions which are used for conservation planning in Chapter 6.

Chapter 5 tests hypotheses about the relationships between mollusc assemblages and underlying variation in benthic habitats, physical conditions, and time with the objective of improving understanding of contributions of within habitat Alpha diversity, among habitat Beta diversity, and temporal Beta diversity, to total Gamma diversity within an estuarine system. In addition, the effectiveness of using benthic habitats, and abiotic variables, as surrogates for mollusc diversity in conservation planning is examined. The mollusc data from Chapter 5 is used for conservation planning in Chapter 6.

Chapter 6 examines differing approaches for setting targets in conservation planning, with the objectives of: assessing the relative benefits of different strategies; and assessing the importance of having comprehensive habitat and biodiversity information prior to commencing conservation planning. Comparisons are made among existing no-take zones, implemented with limited information, and alternate conservation strategies developed using comprehensive habitat and biodiversity information. The potential for implementing conservation strategies using Marxan conservation planning software (Ball *et al.* 2009) is also investigated.

Chapter 7 provides a synthesis of the significant findings of the body of work conducted for this thesis and discusses the limitations of the research, highlighting future directions for study.

Chapter 2. Developing a habitat classification typology for subtidal habitats in a temperate estuary in New South Wales, Australia

Chapter 1 describes the need for improved conservation planning and for adequate information on habitat and species distributions if planning is to provide effective protection for biodiversity. Within this framework Chapter 2 examines how habitat data can be assembled and mapped for an estuarine system and investigates the methods that can be used to develop a habitat classification system (typology) for use in conservation planning. The chapter examines relationships between habitat distributions and abiotic variables, and investigates the effectiveness of using abiotic variables as surrogates for benthic habitats in conservation planning. Chapter 2 was published in *Marine and Freshwater Research* (Davis *et al.* 2016b):

Davis, T.R., Harasti, D., and Smith, S.D.A. (2016b) Developing a habitat classification typology for subtidal habitats in a temperate estuary in New South Wales, Australia. *Marine and Freshwater Research* **67**: 1186–1195.

A more detailed discussion of the mapping component of the investigation was published as a technical report issued by the NSW DPI (Davis *et al.* 2015b). The tidal model constructed as part of Chapter 2 was also used to provide data for additional manuscripts examining; the influence of environmental variables on distributions of the soft coral *Dendronephthya australis* (Poulos *et al.* 2015), and the responses of *D. australis* colonies to tidal current strengths (Davis *et al.* 2015c) (Appendix A).

Developing a habitat classification typology for subtidal habitats in a temperate estuary in New South Wales, Australia

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2.1 Abstract

Effective estuarine management depends on adequate data about the ecology, extent and biodiversity of component habitats. However, these data are often scant, as exemplified by the Port Stephens estuary, part of the Port Stephens-Great Lakes Marine Park (NSW, Australia), for which even basic descriptions of habitat types and extent are lacking. Herein we present the results of the first quantitative assessment of sub-tidal benthic communities within the estuary, involving 130 km of towed video transects over an area exceeding 50 km². We identified previously undocumented macroalgae-dominated habitat types and found strong correlations between habitat types and depth. The soft coral *Dendronephthya australis* habitat is of particular interest because this was found to occur exclusively outside current sanctuary (no take) zones. The habitat map of Port Stephens generated during the study provides the basis for more objective representative planning in future iterations of zoning in the estuarine section of the marine park. The study also suggests that depth may be a useful proxy for estuarine habitat types where specific data are lacking. The classification methodology developed during the study was cost-effective, generated robust data and consequently has potential for wider application in other large estuarine bays.

2.2 Introduction

Marine ecosystems throughout the world are being subjected to increasing levels of disturbance, are suffering from chronic anthropogenic impacts (Crain *et al.* 2009; Halpern *et al.* 2007) and are consequently in severe decline (Jackson 2001; Kennish 2002; Lotze *et al.* 2006). There is global concern that these impacts will lead to further degradation of marine habitats and the continued loss of marine species (Costello *et al.* 2010; Gray 1997; Halpern *et al.* 2008). As part of efforts to preserve biodiversity, there is a need to protect representative marine communities and the habitats in which they reside (Fernandes *et al.* 2005). Because of the difficulties associated with obtaining quantitative data on marine species, habitats are often used as surrogates for marine communities (Jordan *et al.* 2005; Rees *et al.* 2014; Shokri and Gladstone 2013; Smith 2005; Stevens and Connolly 2004), and protection of representative areas of marine habitats is frequently used as a means of protecting overall biodiversity (Gladstone 2007; Jones and Srinivasan 2007; Malcolm *et al.* 2010).

Implementing protection of representative areas of marine ecosystems requires information about the range of habitat types and their extent (Cicin-Sain and Belfiore 2005). This information-gathering process typically makes use of a Habitat Classification System (HCS) that divides the continuously varying marine environment into categories based on dominant characteristics (Diaz *et al.* 2004; Last *et al.* 2010; Malcolm *et al.* 2011). Ideally, a HCS should be exhaustive, describing all habitats within a region, and should use categories that are easily identifiable, mutually exclusive and that provide sufficient detail for effective management (Ball *et al.* 2006).

Habitat Classification Systems are strongly dependent on the size of the area being assessed and, at a local level, variation in biological assemblages over small distances becomes important, particularly when habitats contain protected or threatened species (Last *et al.* 2010). For example, the distribution of the protected sea horse species *Hippocampus whitei* within the Port Stephens estuary is closely linked to the distribution of sponge and soft coral habitats (Harasti *et al.* 2014c). The term “benthic habitat” has been defined as the place where a plant or animal is ordinarily found (Diaz *et al.* 2004), and when conservation of biodiversity is a primary objective, HCSs should ideally be based on benthic habitats, incorporating chemical properties (e.g. salinity, nutrients, pH), the physical structure of the seabed and the biological assemblages that dwell there (Bianchi *et al.* 2012; Last *et al.* 2010).

In New South Wales (NSW), Australia, the state government is currently implementing a new approach to managing the NSW coastal waters (termed the “Marine Estate”; NSW-DPI 2013a). Within NSW, a Comprehensive, Adequate, and Representative (CAR) network of multi-use marine parks was previously established with the objective of protecting biodiversity (Beeton *et al.* 2012). Under the new management approach, a CAR system of protected areas is perceived as addressing only some of the problems facing coastal waters, and threat and risk assessment are being promoted as the primary approach for ensuring the long term health of the Marine Estate (NSW-DPI 2013a). Marine habitat mapping is increasingly being used in this process to show the extent, structure and distribution of marine habitats (Dixon-Bridges *et al.* 2013). Previously, the majority of habitat-mapping effort focused on fully marine habitats (i.e. marine habitats with a low fresh water input) (Jordan *et al.* 2010b; Underwood *et al.* 1991), with the existing HCS used in NSW marine parks focussing primarily on substrate type (reef or unconsolidated substrate) and depth (Malcolm *et al.* 2011; Malcolm *et al.* 2010). Substrate type and depth were used because of the difficulties associated with determining benthic habitats using swath acoustics, which has been the primary tool for habitat mapping within NSW (Jordan *et al.* 2010b; NSW-MPA 2010b). Therefore, the existing HCS does not fully describe benthic habitats and although a broader typology (i.e. naming convention) for marine benthic habitats in NSW was developed by Underwood *et al.* (1991), its applicability is constrained to marine rocky reefs in central and southern NSW (Harriott *et al.* 1999). Within NSW estuaries, aquatic vegetated habitats (mangroves, seagrass and saltmarsh) have previously been mapped using a combination of aerial and satellite photography (Creese *et al.* 2009). In addition, work has been conducted in a number of estuaries to describe estuarine habitats in terms of sediment type and infauna (Dixon-Bridges *et al.* 2013; Hastie and Smith 2006; Jones *et al.* 1986; Lindegarth and Hoskin 2001). However, because of limitations imposed by turbidity, the type and extent of deeper benthic habitats (i.e. depths >5 m) remain largely unquantified. The Port Stephens estuary, in particular, is known to contain areas of deep water (i.e. depths of up to 40 m; DPWS 1998) and is renowned for supporting a high diversity of biota, protected species and habitats (Carraro and Gladstone 2006; Harasti *et al.* 2012; Smith *et al.* 2010). Information on aquatic vegetated habitats (Creese *et al.* 2009) and sediment types (Roy and Matthei 1996; Roy *et al.* 2001) is available for the estuary, but information on benthic habitats occurring in deeper sections of the estuary is lacking.

The Port Stephens estuary is an important location for commercial and recreational fisheries (NSW-MPA 2010a) and for marine tourism, especially dolphin watching (Allen *et al.* 2007) and scuba diving (NSW-MPA 2010a). Therefore, there is a clear need to develop an understanding of deeper benthic habitats within the estuary so they can be adequately protected within the Port Stephens-Great Lakes Marine Park (PSGLMP). Therefore, the primary aims of the present study were to: (1) develop a typology for subtidal habitats within the Port Stephens estuary; (2) examine patterns in habitat distributions with changing depth, current velocity and substrate; (3) develop a methodology that could be used for rapid visual assessment of subtidal habitat types; and (4) apply this methodology in a broad-scale assessment of habitat types in the estuary.

2.3 Materials and methods

2.3.1 Study area

The study site selected for the investigation was the Eastern Port of the Port Stephens estuary (Figure 1), a tide-dominated drowned river valley (Roy *et al.* 2001), all of which is contained within the PSGLMP. The PSGLMP is the largest marine park in NSW (98 000 ha) and has multiple zoning categories that regulate different types of activities. Approximately 17% of the park is currently classified as sanctuary zone where all extractive activities are prohibited (NSW-MPA 2010a). The Eastern Port is ~12 km long (east-west) and 5 km wide (north-south), with an area exceeding 50 km², and contains areas of deep water (i.e. depths of up to 40 m) that support a high diversity of biota (Smith *et al.* 2010). The Eastern Port is known to contain a range of habitats, some of which are considered to be uncommon in NSW (Carraro and Gladstone 2006; Poulos *et al.* 2013); however, the full extent of benthic habitats has yet to be fully classified or mapped.

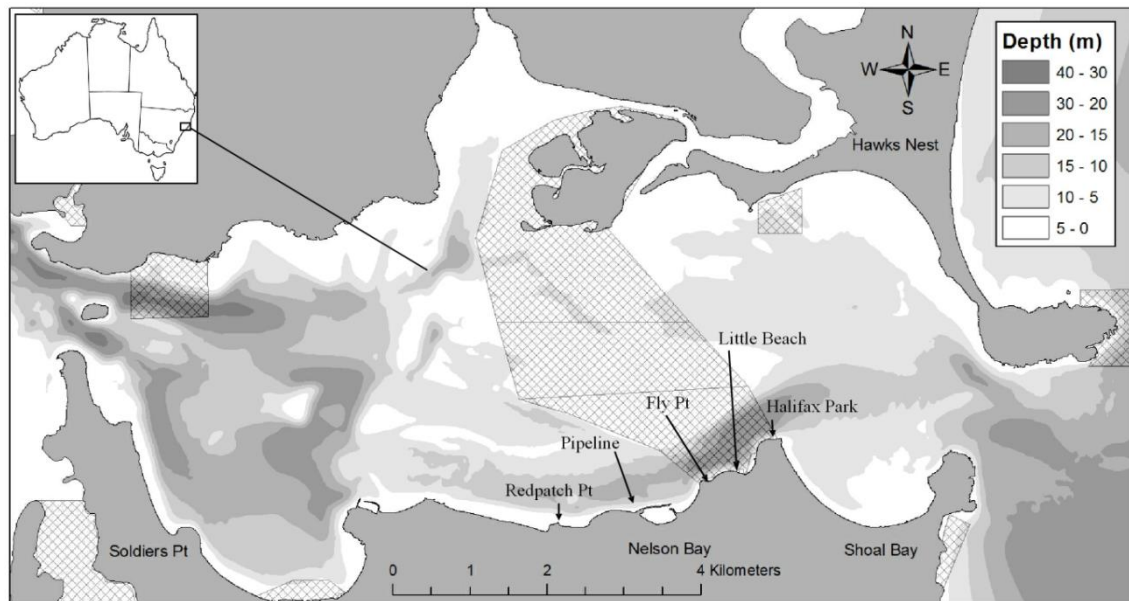


Figure 1. Eastern Port of the Port Stephens estuary. Cross-hatching indicates Sanctuary Zones.

2.3.2 Habitat classification

Within Australia, the Interim Australian National Aquatic Ecosystem (ANAE) Classification Framework was established with the objective of ensuring national consistency in classifying marine habitats (AETG 2012). The Interim ANAE Classification Framework specifies that the National Intertidal Subtidal Benthic (NISB) HCS (Mount *et al.* 2007) should be used for classifying benthic habitats based on coverage of structural macrobiota, where structural macrobiota are ‘sessile habitat-forming species that, by their presence, increase spatial complexity and alter local environmental conditions, often facilitating a diversified assemblage of organisms’ (Lilley and Schiel 2006). The ANAE and NISB are semi-hierarchical and hierarchical attribute-based classification systems using broad habitat classes subdivided by biotic and abiotic modifiers (e.g. substrate, depth, current velocity) that can be used to generate habitat typologies to meet specific management objectives (AETG 2012; Mount *et al.* 2007).

The broad structural macrobiota classes contained within the NISB (i.e. seagrass, macroalgae, filter-feeders) do not allow discrimination between some of the different seagrass and filter-feeder habitats known to occur within the Eastern Port of the Port Stephens estuary (Creese *et al.* 2009; Poulos *et al.* 2013). Thus, there was a need to determine suitable modifiers (i.e. benthic habitats types) to use within the NISB HCS. Previous studies have shown that significant variation in benthic habitats can occur across sites and between depths at a range of spatial scales (m to km; Malcolm *et al.* 2011;

Underwood *et al.* 1991). Therefore, quantitative assessments of benthic habitats were conducted, in mid-2014 at five study sites (Figure 1) at a range of depths. Because of the presence of strong tidal currents, assessments were conducted over the period of slack water (1 h either side of high tide). A broad-scale assessment of habitats throughout the Eastern Port was then conducted, between July 2014 and January 2015, using towed video transects.

2.3.3 Field methods

Quantitative assessment of sub-tidal structural macrobiota can be conducted using a variety of methods (Kingsford and Battershill 1998), including photo quadrats (Kohler and Gill 2006), line transects (Underwood *et al.* 1991) and video transects (Carleton and Done 1995; Harriot *et al.* 1994; Smith *et al.* 2008). Photo quadrats and video transects were selected for the present study because they provide an accurate method of assessment while allowing retention of a permanent record that can be re-evaluated as required (Preskitt *et al.* 2004).

For the quantitative assessment of benthic habitats, four transects, separated by at least 10 m, were established from haphazard starting points at each study site. Transects commenced at a depth of 2 m (Extreme Low Water Spring tidal level) and extended perpendicular to shore to a maximum depth of 15 m, or to the point where cover of structural macrobiota was negligible (i.e. the sand line). On each transect, five photo-quadrats (photographs) were taken along each depth contour, at 1-m depth increments (i.e. 5 photographs at 2 m, 5 photographs at 3 m, etc.). Photographs along each depth contour were separated by 1.2 m, with each photograph covering an area $\sim 0.7 \text{ m} \times 0.5 \text{ m}$. Photographs were taken perpendicular to the seabed, using a measuring rod to hold the camera a uniform 0.5 m above the substrate. In all, 1280 photographs were taken, with the number at each site varying because of differences in sand-line depth (Table 1).

Table 1: Depth of sand line and number of photo-quadrats taken at study sites

Site name	Sand line	Photo-quadrats
Fly Point	>15 m	280
Halifax	>15 m	280
Little Beach	15 m	270
Pipeline	14 m	250
Redpatch	12 m	200

Towed video transects were conducted using a DeepBlue Splashcam (<http://www.splashcam.com/>, accessed 14 May 2015) standard definition video camera, with coordinates from a Garmin GPS map 60C (<http://www.garmin.com>, accessed 14 May 2015) differential global positioning system (GPS) overlaid on each video frame. Transects were systematically located in all areas of the estuary deeper than 5 m, with lateral transects, spaced at intervals of ~500 m, used to locate areas containing structural macrobiota. Areas identified as containing structural macrobiota were then assessed using longitudinal and lateral transects spaced at intervals of 50–100 m. Approximately 130 km of towed video transects were completed in the study, at an average speed of 2.5 km h⁻¹, generating 52 h of video footage. Towed video operations were restricted to 1-2 h each day at high tide because of strong tidal currents and low visibility at other times, and a total of 44 d was required for conducting the towed video transects.

2.3.4 *Image analysis*

To obtain quantitative data from photographs, the CPCe software package (Kohler and Gill 2006) was used to analyse 20 random points in each photograph. Each point was categorised using Codes for Australian Aquatic Biota (CAAB) from the Collaborative and Automated Tools for Analysis of Marine Imagery and video (CATAMI) classification system (CATAMI 2013). CATAMI provides a standardised method for classifying substrata and marine biota, using a hierarchical system based on taxonomic classification, or on morphological characteristics where taxonomy is not easily distinguished (e.g. for macroalgae, sponges, bryozoans, cnidarians and ascidians). Data from the five photographs along each depth contour on each transect were aggregated to provide percentage cover values for CAAB classes. The four transects provided four replicates at each depth at each site, thereby incorporating spatial variation in habitats at the site scale as well as along depth gradients.

Towed video transects were assessed by playing footage back at between 1× and 2× actual speed and noting habitat types and habitat boundaries as they appeared. Habitats types were classified visually using the modified NISB HCS methodology developed in this paper. Habitat boundaries were used to generate a habitat map for the port, with interpolation used to define habitat types between towed video transects.

2.3.5 Statistical analysis

A modelling approach was used to evaluate changes in community structure across the factors of position (site), current velocity, depth and the physical habitat type (% sand). First, cover of CAAB classes were subjected to multivariate statistical analysis using the PRIMER-E and PERMANOVA+ (<http://www.primer-e.com/>, accessed 14 May 2015) software packages (Anderson *et al.* 2008; Clarke and Gorley 2006). Pairs of samples were compared using the Bray-Curtis similarity measure and the resulting similarity matrix was subjected to non-metric multidimensional scaling (nMDS), to allow visualisation of patterns in assemblage structure. Initial analyses were conducted using untransformed and square root-transformed data, and it was evident that applying a transformation to the data reduced the ability to distinguish between assemblages. This was because transformations reduce the contributions of dominant species to similarities between samples (Clarke and Gorley 2006) and abundances of dominant species and classes were the primary drivers of similarities within clusters in the assemblage data. Therefore, all subsequent analyses were conducted using untransformed data.

Cluster analyses with similarity profile (SIMPROF) permutation tests were used to assess significant structure among samples. This routine identified clusters of samples that have significantly different structure and facilitates the identification of discrete community types. Similarity percentage breakdowns (SIMPER) were subsequently used to identify the CAAB classes primarily responsible for similarities within discrete clusters. The distance-based linear model (DISTLM) routine was used to model the relationships between the patterns of benthic assemblages and the predictor variables of depth, site (as distance from the estuary mouth), broad substrate type (reef or sand; summarised as the percentage of sand) and mean current velocity for each sample (Anderson *et al.* 2008). Current velocities were extracted for each depth at each site using the existing two-dimensional (2-D) hydrodynamic model of the estuary, which incorporates the entire embayment, major tributaries and a section of adjacent offshore waters (Poulos *et al.* 2015). A step-wise procedure and the R^2 selection criterion were used to find the best model, and marginal tests determined the strength of the relationship for each predictor variable (Anderson *et al.* 2008).

2.4 Results

2.4.1 Patterns in benthic community structure

In all, 25600 random points, on 1280 photo quadrats, were examined to obtain quantitative data on benthic assemblages within the Eastern Port. Variations in assemblages with depth, and between sites, were visible in the nMDS plot for assemblages at each site at each depth (see Figure 2, which shows centroids for the four replicates at each site-depth combination). Cluster analysis using SIMPROF identified eight significantly different clusters of samples within the assemblage data (labelled A–H in Figure 2).

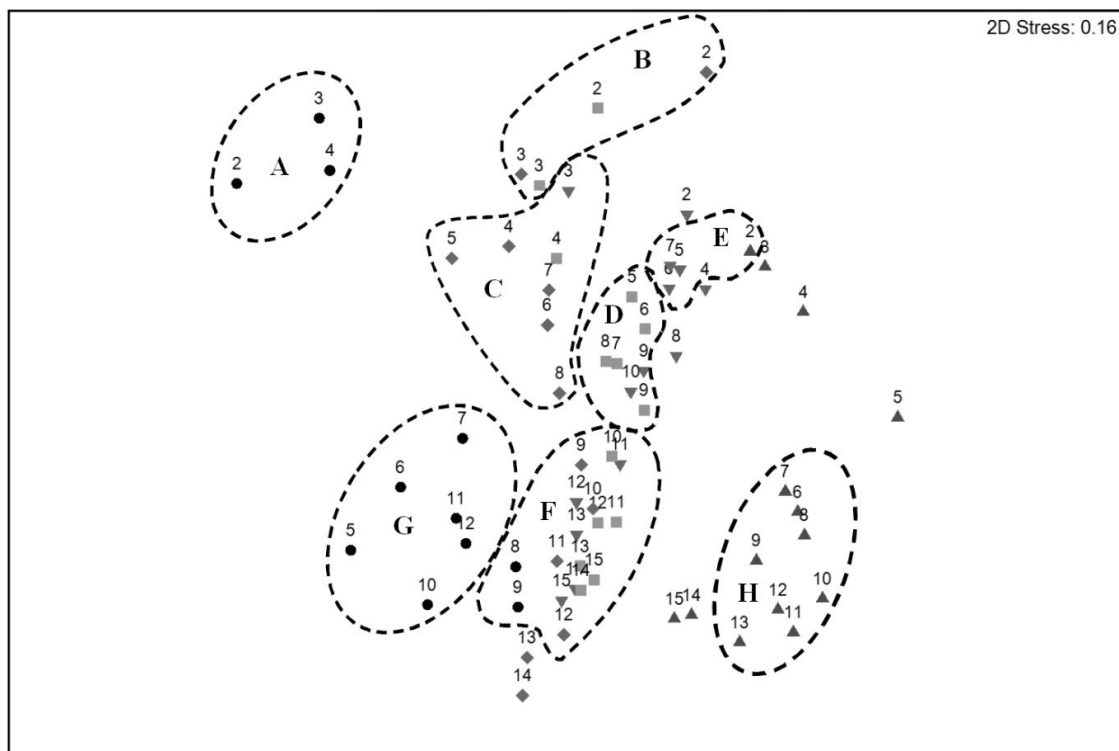


Figure 2: Non-metric multidimensional scaling (nMDS) plot of benthic community data by depth and location. Markers represent mean assemblages ($n = 4$); circle, Redpatch Point, diamond, Pipeline, square, Fly Point, inverted triangle, Little Beach, triangle, Halifax. Numbers indicate sample depths. Dashed lines and capital letters (A–H) indicate significantly different assemblages from similarity profile (SIMPROF) permutation tests (corresponding to clusters in Table 2).

SIMPER analyses identified that similarities within clusters were driven primarily by dominance of single CAAB classes (Table 2). An examination of samples lying outside clusters further identified that the majority of these samples had a strong resemblance to assemblages from one of the clusters, but with differing proportions in some CAAB classes. Where outlying samples did not resemble one of the clusters, they were generally

found to contain assemblages that were either transitional between clusters or depauperate, with <10% cover by structural macrobiota.

Table 2: Collaborative and Automated Tools for Analysis of Marine Imagery and video (CATAMI) codes for Australian Aquatic Biota (CAAB) driving >50% of the similarity between samples within significantly different clusters identified by similarity profile (SIMPROF) permutation tests. Numbers in parentheses indicate the contribution to similarities within clusters. 3-D, three-dimensional

Cluster	CAAB classes driving similarity between samples within clusters
A	CAAB 63600903 – Seagrasses: strap-like leaves (81%; i.e. <i>Posidonia australis</i>)
B	CAAB 80300902 Macroalgae: large canopy forming; brown (87%; i.e. <i>Ecklonia radiata</i>)
C	CAAB 63600903 – Seagrasses: elliptical leaves (51%; i.e. <i>Halophila ovalis</i>)
	CAAB 80300903 Macroalgae: erect coarse branching (27%)
D	CAAB 80300903 Macroalgae: erect coarse branching (43%)
	CAAB 80300902 Macroalgae: large canopy forming; brown (17%)
	CAAB 80300907 Macroalgae: erect fine branching (13%)
E	CAAB 80300903 Macroalgae: erect coarse branching (84%)
F	CAAB 10000000 Sponges (59%)
	CAAB 35000000 Ascidia (12%)
	CAAB 11001000 Cnidaria: Hydroids – (9%)
G	CAAB 11168902 Octocorals: branching (3D; 46%; i.e. <i>Dendronephthya australis</i>)
	CAAB 10000000 Sponges (18%)
	CAAB 11001000 Cnidaria: Hydroids – (8%)
H	CAAB 80300934 Macroalgae: encrusting; red: calcareous (50%)
	CAAB 25200000 Echinoderms: sea urchins (33%)

Based on these objective analyses, we propose a typology containing seven distinct subtidal benthic habitat types within the Eastern Port:

1. “*Posidonia*” habitat, dominated by the seagrass *Posidonia australis* (aligned with cluster A)
2. “*Ecklonia*” habitat, dominated by mono-specific stands of the macroalgae *Ecklonia radiata* (cluster B)
3. “*Halophila*” habitat, dominated by *Halophila ovalis* (cluster C)
4. “Branching algae” habitat, dominated by erect coarse branching algae, primarily red algal species, *Sargassum* and *Caulerpa cactoides*, with other macroalgae growth forms in lower abundance (combination of clusters D and E, because both of these were dominated by erect coarse branching algae)
5. “Filter-feeder” habitat dominated by mixed filter-feeder assemblages containing sponges in a variety of growth forms (e.g. branching, massive, encrusting), ascidians, octocorals, hydroids and bryozoans (cluster F)

6. “*Dendronephthya*” habitat dominated by mono-specific stands of the soft coral species *Dendronephthya australis*, with other filter-feeders present in lower abundance (cluster G)
7. “Barrens” habitat dominated by encrusting calcareous algae, with high abundances of the urchin *Centrostephanus rodgersii* (cluster H).

DISTLM analysis identified significant correlations between benthic communities and each of the predictor variables (i.e. depth, location, substrate type and current; $P < 0.001$ for all). The overall best model included all variables and explained 34% of the variation in community patterns ($R^2 = 0.338$). In the analysis using individual variables (i.e. marginal tests) depth ranked highest ($R^2 = 0.174$; e.g. in Figure 2, samples grade from shallow at the top of the plot to deep at the bottom), followed by current ($R^2 = 0.097$), site ($R^2 = 0.085$) and substrate ($R^2 = 0.069$). Covariance between predictor variables occurred, with depth and current increasing with distance from shore, and site and percentage sand increasing with distance from the estuary mouth.

2.4.2 Development of visual classification methodology

The habitats identified in the quantitative assessment can be distinguished from each other visually (Supplementary Figure S1) on the basis of dominant species or CAAB classes, thereby allowing the use of dominant species and CAAB classes as modifiers within the NISB HSC framework. Therefore, a visual habitat classification methodology using the NISB HCS framework and modified with additional decision rules defining habitats on the basis of dominant species and CAAB classes was developed (Figure 3). The modified methodology uses a hierarchical system with habitats initially classified by substrate coverage (i.e. covered or uncovered by structural macrobiota), with a covered habitat being one with >5% cover by seagrass or >10% benthic cover as specified in the NISB HCS (Mount *et al.* 2007). Covered habitats are then sub-divided on the basis of dominance by species or CAAB classes, with dominance defined as occurring when a species or class covers the largest proportion of the substrate (Mount *et al.* 2007).

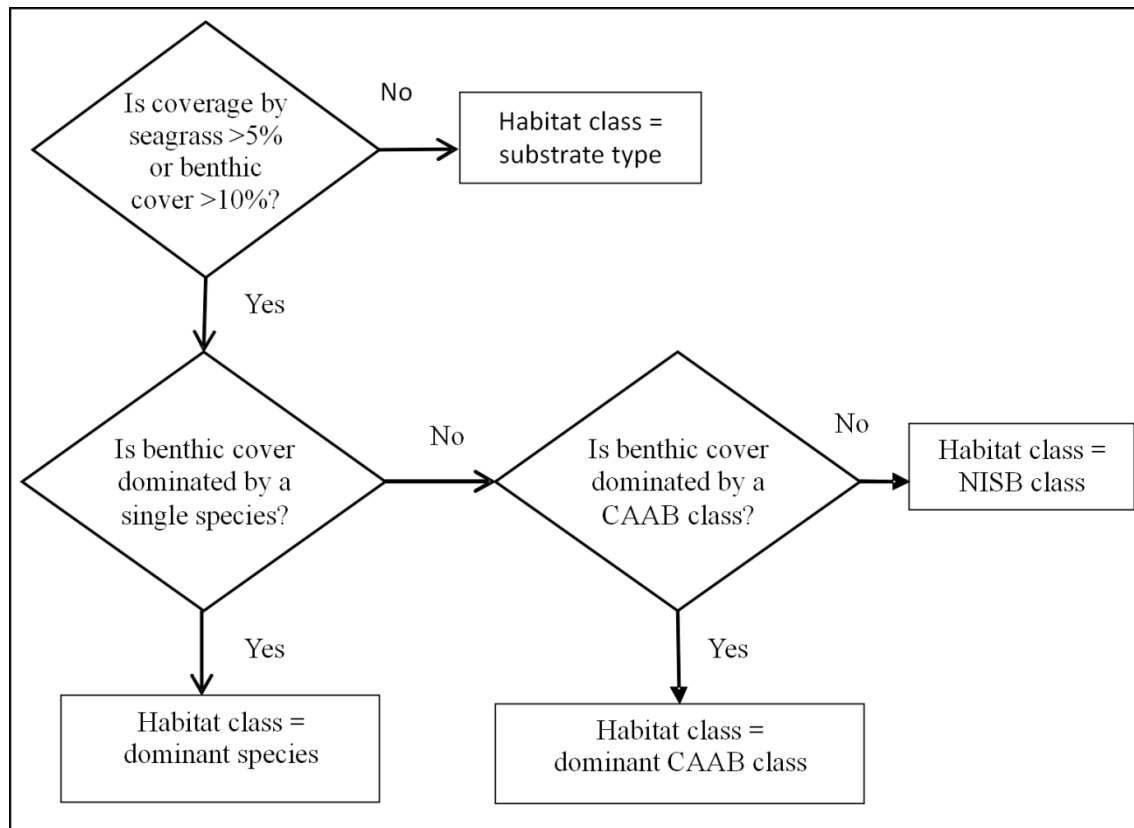


Figure 3: Visual habitat classification methodology based on the National Intertidal/Subtidal Benthic (NISB) Habitat Classification System with modifiers based on; dominance by individual species or Collaborative and Automated Tools for Analysis of Marine Imagery and video (CATAMI) codes for Australian aquatic biota (CAAB) classes.

2.4.3 Broad-scale habitat assessment

The visual habitat classification methodology (Figure 3) was further tested in a broad-scale assessment of habitat types in the Eastern Port using 130 km (52 hours) of towed video footage. This assessment located additional areas of the seven habitat types from the quantitative typology and identified three further habitat types within the Eastern Port:

1. “*Zostera*” habitat dominated by the seagrass *Zostera muelleri* subspecies *capricorni* often with *H. ovalis* present in lower abundance
2. “Sand” habitat dominated by sand with minimal benthic cover
3. “Mud” habitat consisting of bioturbated mud with numerous burrows, but with minimal benthic cover.

In total, 10 distinct subtidal habitat types were identified in the present study comprising: (1) three habitats dominated by seagrass species (*P. australis*, *H. ovalis* and *Z. muelleri*); (2) two habitats dominated by filter-feeders (a mixed filter-feeder assemblage and the soft

coral *D. australis*); (3) three habitats dominated by macroalgae (kelp – *E. radiata*, branching macroalgae and encrusting coralline algae–urchin barrens); and (4) two habitats with minimal benthic cover (sand and mud). Large areas of previously undocumented macroalgae-dominated habitat types were located and *D. australis* habitat was found to occur exclusively outside current sanctuary (no take) zones. The ten habitats identified formed a new habitat classification typology that was used to produce a habitat map for the Eastern Port (Figure 4).

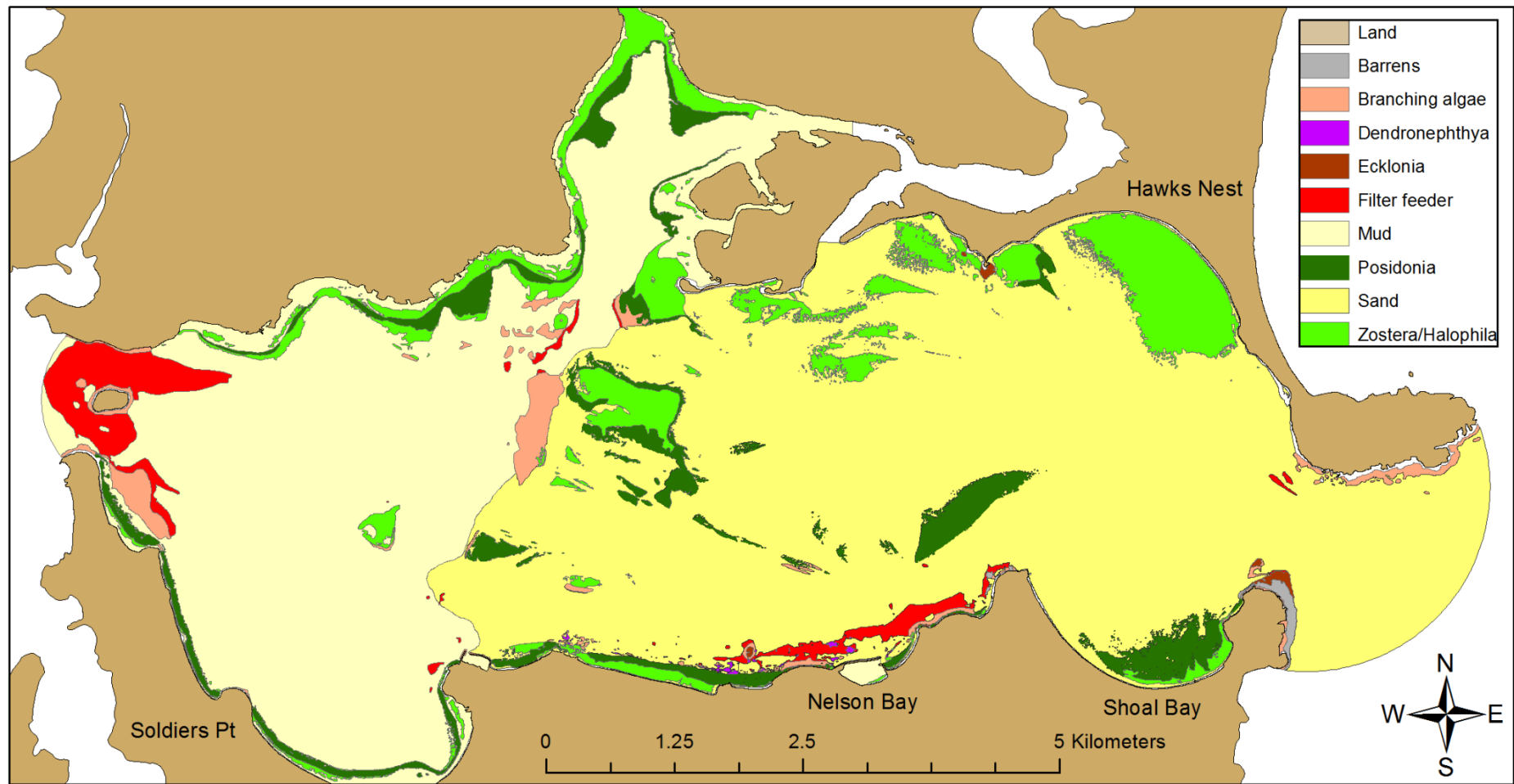


Figure 4: Habitat map for the Eastern Port showing subtidal habitat classes (sand, mud, barrens, *Ecklonia*, *Zostera/Halophila*, *Posidonia*, *Dendronephthya*, branching algae and filter-feeder).

2.5 Discussion

HCSs are used to logically partition environmental datasets so they can act as surrogates for biodiversity or ecological function, and typologies provide an extension to traditional classification systems by grouping classes for a specific purpose or management objective (AETG 2012; Ward 2014). In the present study, significantly different and visually distinguishable assemblages of structural macrobiota were used to develop a habitat classification typology for the Eastern Port of Port Stephens, with the objective of defining habitat surrogates for biodiversity. This typology provided an efficient method for visually assessing dominant marine habitats, effectively delimiting distributions of structural macrobiota. Structural macrobiota can play an important role in marine ecosystems because they create spatially complex habitats that are associated with increases in local species diversity (Lilley and Schiel 2006). Studies examining structural macrobiota within estuaries have identified that seagrasses, macroalgae and filter-feeders can harbour a range of species not found on adjacent substrata lacking biogenic structure (Ferrell and Bell 1991; Poulos *et al.* 2013).

The present study identified habitats dominated by seagrasses, macroalgae and filter-feeders, and found that many habitats within the Eastern Port were similar to marine habitats identified in other studies from central and southern NSW and Victoria (Ball *et al.* 2006; Underwood *et al.* 1991). In NSW, the typology developed for rocky reefs by Underwood *et al.* (1991) describes the *Ecklonia* and Barrens habitats identified in the present study. In addition, Underwood *et al.* (1991) identify a ‘fringe’ habitat consisting of abundant foliose algae that is equivalent to the ‘branching algae’ habitat in the present study. However, the coastal ‘fringe’ habitat occurred at very shallow depths (2-3 m) whereas the ‘branching algae’ habitat within the estuary occurred to depths of at least 8 m at some sites. Underwood *et al.* (1991) also identified a ‘deep reef’ habitat characterised by large sponges at depths > 9 m, which aligns with the ‘filter-feeder’ habitat identified in the present study. However, the coastal ‘deep reef’ habitat was associated with hard substrate (i.e. reef), whereas the estuarine ‘filter-feeder’ habitat occurred on both reef and sand. The coastal typology developed by Underwood *et al.* (1991) had no provision for seagrasses or the *Dendronephthya* habitat found in the Eastern Port. In Victoria, a HCS generated for Victoria’s Marine National Parks contained 18 classes with ‘dominant biota’, including classes matching all of the habitats identified during the present study, with the exception of the *Dendronephthya* soft coral habitat (Ball *et al.* 2006).

A comparison of habitats from the present study with similar studies in northern NSW and Queensland, identified that the Eastern Port has less in common with northern sections of the east Australian coast. A study conducted in Moreton Bay in southern Queensland identified only a single habitat that was comparable to the habitats identified in the present study (i.e. *Zostera* /*Halophila*; Stevens and Connolly 2005), with the other eight habitats identified from Moreton Bay consisting of complex assemblages with no clearly dominant taxa. This suggests that the boundaries between habitats within Moreton Bay may be less clearly defined than those within Port Stephens. Similarly, a study examining habitats on rocky reefs in northern NSW only identified habitats matching the ‘branching algae’ and ‘filter-feeder’ habitats from the present study, but found a number of coral-dominated habitats that were absent within the Eastern Port (Harriott *et al.* 1999).

The correspondence between habitats identified in the present study and marine habitats from southern NSW and Victoria is not surprising given the geographical location of the estuary (i.e. central NSW) and the large tidal flows that ensure that salinity levels are essentially marine within the Eastern Port (i.e. 35–35.5 psu; DPWS 1998). Therefore, the Eastern Port can be classified as a marine tidal delta (Roy *et al.* 2001), where subtidal communities will tend to be dominated by marine species rather than estuarine species (Attrill and Rundle 2002). These marine-dominated estuarine communities will potentially be affected by extreme weather events, which can cause reductions in salinity and increases in turbidity within the estuary (T. R. Davis, unpubl. obs.).

Benthic communities in the Eastern Port were found to be affected by depth, current, substrate type and location. Previous studies have demonstrated that depth influences the distributions of seagrasses (Abal and Dennison 1996), macroalgae (Nielsen *et al.* 2002) and sponges (Underwood *et al.* 1991), and the results from the present study concur with these findings. However, most of the variation in assemblage structure (66%) is presently unexplained. Some of the unmeasured factors that may contribute to patterns include: wave exposure, which has been shown to affect soft coral communities (Fabricius and Alderslade 2001); sedimentation, which affects both soft corals (Fabricius and Alderslade 2001) and other filter-feeders (Irving and Connell 2002); turbidity, which affects photosynthesis and therefore seagrasses, macroalgae (Nielsen *et al.* 2002) and sponges (Roberts *et al.* 2006); and substrate composition, with both sediment type (Dixon-Bridges *et al.* 2013) and reef type (Malcolm *et al.* 2010; Rees *et al.* 2014) known to influence

benthic communities. Further investigation is required to identify which, if any, of these factors affect benthic assemblages in the Eastern Port.

2.5.1 Application of study results to estuary management

This investigation has identified that the existing marine HCS for NSW (Malcolm *et al.* 2011) does not adequately describe all benthic habitats occurring in the Port Stephens estuary; this may well be the case for other similar estuaries. Although the existence and distributions of shallow benthic habitats such as seagrass and mangroves are well documented (Creese *et al.* 2009), some areas of the Port Stephens estuary have been shown to contain habitats that have not been previously mapped or adequately described. We therefore suggest that subtidal benthic habitats within the Port Stephens estuary can best be described using a new typology based on the NISB system, with modifiers to include three seagrass habitats ('*P. australis*', '*H. ovalis*' and '*Z. muelleri*'), two filter-feeder habitats ('filter-feeder' and '*Dendronephthya*'), three macroalgae habitats ('*Ecklonia*', 'barrens' and 'branching algae'), and two substrate habitats lacking biogenic cover ('sand' and 'mud'). Of particular interest is the extent of the habitat dominated by the soft coral *D. australis*, which is only known to occur in abundance within Port Stephens (Poulos *et al.* 2015; Poulos *et al.* 2013). This habitat is considered to be under threat from anthropogenic impacts (anchor damage (Harasti *et al.* 2014c), fishing line entanglement (Smith and Edgar 2014; Vegter *et al.* 2014)) and from increasing sedimentation and potentially poor water quality (Poulos *et al.* 2013). The broad-scale assessment of habitats performed during the present study revealed that the *Dendronephthya* habitat occurs entirely outside current sanctuary zones, indicating that it may not be adequately protected under the current PSGLMP zoning plan.

The results from the present study provide new and valuable insights into the range of habitats within a large NSW estuarine embayment and some of the factors that drive distribution patterns. Importantly, it also highlights discrete and important habitats that are not adequately protected within current management arrangements. The modified NISB habitat classification methodology developed during the present study is both rapid and cost-effective and has the potential to be a useful tool for ongoing monitoring of benthic habitat types and their boundaries. It also provides a framework for wider evaluation of the type and extent of habitats in other large estuarine embayments for which such data are currently lacking.

Supplementary content

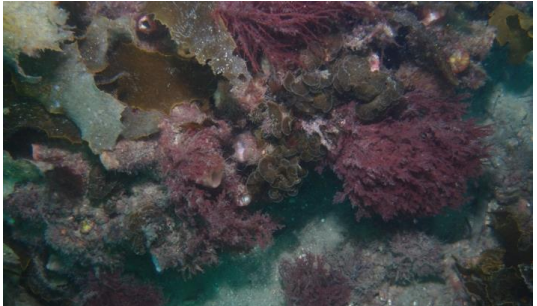
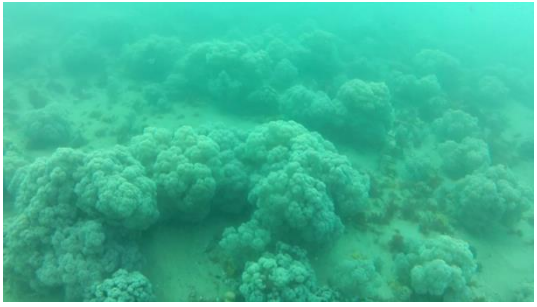
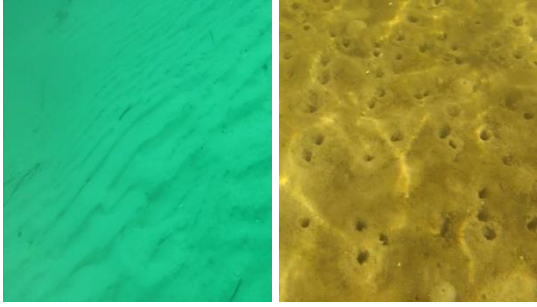
	
<i>Posidonia australis</i>	<i>Zostera muelleri</i> / <i>Halophila ovalis</i>
	
<i>Ecklonia radiata</i>	Branching algae
	
Filter-feeder	<i>Dendronephthya australis</i>
	
Barrens	Sand / Mud

Figure S1: Visually classified sub-tidal habitat types within the Port Stephens estuary. Habitat types classified by substrate type, or by dominant benthic cover if benthic cover >10%, or seagrass cover >5%.

Chapter 3. Using modelling to predict impacts of sea level rise and increased turbidity on seagrass distributions in estuarine embayments

The need for improved conservation planning described in Chapter 1 is facilitated by species distribution models that can predict species responses to anthropogenic and environmental changes over wide geographic and temporal ranges. Chapter 2 identified that the Port Stephens estuary contains a number of distinct benthic habitats, and significant correlations between habitat distributions and abiotic variables. However, the applicability of these relationships outside Port Stephens, and the impacts of changes in abiotic variables on habitat distributions were not examined.

In Chapter 3 the relationships between seagrass distributions and abiotic variables were therefore explored with the objective of developing species distribution models with broad applicability across NSW estuarine embayments. The predicted response of seagrasses to future climate change induced sea level rises and increases in turbidity were also examined, and the importance of these predicted changes for conservation planning were discussed. Chapter 3 was published in *Estuarine and Coastal Shelf Science* (Davis *et al.* 2016c):

Davis T.R., Harasti D., Smith S.D.A., Kelaher B.P. (2016c) Using modelling to predict impacts of sea level rise and increased turbidity on seagrass distributions in estuarine embayments. *Estuarine and Coastal Shelf Science* **181**: 294–301.

Using modelling to predict impacts of sea level rise and increased turbidity on seagrass distributions in estuarine embayments

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3.1 Abstract

Climate change induced sea level rise will affect shallow estuarine habitats, which are already under threat from multiple anthropogenic stressors. Here, we present the results of modelling to predict potential impacts of climate change associated processes on seagrass distributions. We use a novel application of relative environmental suitability (RES) modelling to examine relationships between variables of physiological importance to seagrasses (light availability, wave exposure, and current flow) and seagrass distributions within 5 estuarine embayments. Models were constructed separately for *Posidonia australis* and *Zostera muelleri* subsp. *capricorni* using seagrass data from Port Stephens estuary, New South Wales, Australia. Subsequent testing of models used independent datasets from 4 other estuarine embayments (Wallis Lake, Lake Illawarra, Merimbula Lake, and Pambula Lake) distributed along 570 km of the east Australian coast. Relative environmental suitability models provided adequate predictions for seagrass distributions within Port Stephens and the other estuarine embayments, indicating that they may have broad regional application. Under the predictions of RES models, both sea level rise and increased turbidity are predicted to cause substantial seagrass losses in deeper estuarine areas, resulting in a net shoreward movement of seagrass beds. Seagrass species distribution models developed in this study provide a valuable tool to predict future shifts in estuarine seagrass distributions, allowing identification of areas for protection, monitoring and rehabilitation.

3.2 Introduction

Habitat loss in marine environments has been linked to loss of biodiversity (Harasti 2016; Stuart-Smith *et al.* 2015) and species extinctions (Dulvy *et al.* 2003). Estuaries, in particular, are suffering habitat loss from anthropogenic impacts (e.g. coastal development, pollution, eutrophication), due to the concentration of human activities within and around estuarine systems (Duarte 2002; Lotze *et al.* 2006). Anthropogenic impacts are often compounded by disturbances from extreme weather events (e.g., storm waves, flooding), which are predicted to become more severe due to climate change (Emanuel 2013; Hoegh-Guldberg and Bruno 2010), and climate-induced sea level rise (Short and Neckles 1999). There is, therefore, a clear need to improve our understanding of the relationships between estuarine habitats and their environment, to inform management actions targeted at mitigating habitat loss.

Seagrass meadows are productive estuarine ecosystems that support substantial biodiversity and provide valuable ecosystem services (Barbier *et al.* 2011). While data on seagrass distributions can be obtained using a combination of aerial/satellite imagery and ground truthing (Creese *et al.* 2009; Kendrick *et al.* 2002), these data do not provide insights into how species distributions will change in response to future climate change. To address this, species distribution modelling (SDM) provides a tool that can be used to examine how species are likely to respond to future environmental changes, allowing identification of areas most likely to facilitate long-term species survival (Guisan and Thuiller 2005). Numerous techniques have been used for SDM including: presence/absence based methods such as generalised linear modelling (GLM) (Kelly *et al.* 2001), and generalised additive modelling (GAM) (Downie *et al.* 2013); and methods using presence-only data such as maximum entropy (Maxent) (Poulos *et al.* 2015), relative environmental suitability (RES) (Kaschner *et al.* 2006), and the genetic algorithm rule-set procedure (GARP) (West *et al.* 2008).

Often, seagrass SDMs are not developed to be generally applicable, but are constructed for specific objectives within localised regions, such as predicting responses to changes in turbidity (Lathrop *et al.* 2001) or identifying sites' suitability for restoration (Kelly *et al.* 2001). However, models with applicability across a range of estuarine systems are useful for developing regional management strategies (Van der Heide *et al.* 2009), and using explanatory variables with direct linkages to the ecological requirements of species is

recommended where broader applicability is an objective (Guisan and Zimmermann 2000).

Within well-mixed estuarine embayments, temperature and salinity are relatively uniform, and the dominant variables influencing seagrass distributions are light availability (Abal and Dennison 1996; Duarte *et al.* 2007), wave exposure (Fonseca *et al.* 2002; Grech and Coles 2010), current flows (Bridges *et al.* 1982; Fonseca and Bell 1998), and tidal location (Van der Heide *et al.* 2009). Seagrasses only occur where there is sufficient light for photosynthesis (Duarte *et al.* 2007), with light availability at the seabed influenced by water depth and turbidity (Anthony *et al.* 2004; Greve and Krause-Jensen 2005). Furthermore, seagrasses are influenced by tidal location with some species occurring intertidally, while others are predominantly subtidal (Van der Heide *et al.* 2009). Waves influence seagrass distributions through damaging and uprooting established plants, and preventing settlement of seeds (Carruthers *et al.* 2002), with negative effects concentrated in shallow areas where waves generate substantial forces at the seabed (Rohweder *et al.* 2012). Currents also negatively impact seagrasses (Fonseca and Bell 1998), with strong currents, driven by tidal and river flows, generating substantial forces at the seabed (Jiang *et al.* 2011).

Here, we developed RES models for large estuarine embayments in New South Wales (NSW), Australia, using variables of physiological importance to seagrasses (i.e. light availability, wave exposure, and current flow), with the objective of testing model transferability, in terms of the ability to use models created in one estuary to predict seagrass distributions for other estuaries. Models were created using data from Port Stephens and tested in four other NSW estuarine embayments, spanning over 570 km of the NSW coastline. This represents the first application of RES to prediction of estuarine seagrass distributions, with RES previously primarily used for predicting global distributions of marine species (Ready *et al.* 2010).

Although broad-scale reviews of the probable response of seagrasses to climate change have been conducted (Björk *et al.* 2008; Short and Neckles 1999), relatively few studies have examined changes in seagrass distributions at a regional scale in response to sea level rise and increased turbidity (but see Carr *et al.* 2011). It has been projected that climate change will lead to substantial sea level rise over the coming century (Church *et al.* 2013) and may also lead to regional increases in wind velocities, waves, currents, and turbidity through increased storm activity and floods (Björk *et al.* 2008). We therefore used the RES

models to calculate changes in seagrass distributions for projected climate change induced sea level rises, and for changes in turbidity. This allowed us to assess locations where seagrass loss is likely to occur, and to identify areas of high resilience where seagrasses will be relatively unaffected.

3.3 Material and methods

3.3.1 Study sites

This study examined five micro-tidal (tidal range < 2m) estuarine embayments in NSW, Australia (Table 1, Figure 1). Each estuary contained substantial areas of subtidal seagrasses (i.e. *Posidonia australis*, *Zostera muelleri* subspecies *capricorni* (hereafter *Z. muelleri*), and *Halophila ovalis*) (Creese *et al.* 2009). Separate RES models were constructed for *P. australis* and *Z. muelleri* using data from Port Stephens (Figure 1), as this embayment contained both seagrass species, and the embayment had widely varying levels of turbidity, wave exposure, and tidal currents, making it ideally suited for developing models with general applicability. A RES model for *H. ovalis* was not constructed as this species generally has sparse cover and displays seasonal changes in distribution (Stewart and Fairfull 2007). Current seagrass distributions for *P. australis* and *Z. muelleri* within Port Stephens were obtained from recent surveys (Davis *et al.* 2016b). Distribution maps were generated from high-resolution (7.5 cm GSD), geo-referenced aerial photographs from August 2014 (Nearmap 2014) which were ground-truthed using towed video (Davis *et al.* 2015b). Seagrass distributions for other estuaries were obtained from the study by Creese *et al.* (2009), with maps generated from orthorectified aerial photographs with boundary locations and species presence verified in the field.

Table 1: Study estuaries in New South Wales, Australia, with locations, water area (km²) and prevalence (% cover) of *Zostera muelleri* and *Posidonia australis*

Estuary	Location	Water area	<i>Z. muelleri</i> prevalence	<i>P. australis</i> prevalence
Wallis Lake	152.510 E, 32.174 S	93.82	31.4%	2.6%
Port Stephens	152.190 E, 32.708 S	52.04	8.1%	5.1%
Lake Illawarra	150.873 E, 34.544 S	35.81	22.3%	Nil
Merimbula Lake	149.922 E, 36.896 S	4.89	9.8%	23.5%
Pambula Lake	149.916 E, 36.948 S	3.70	9.7%	14.1%

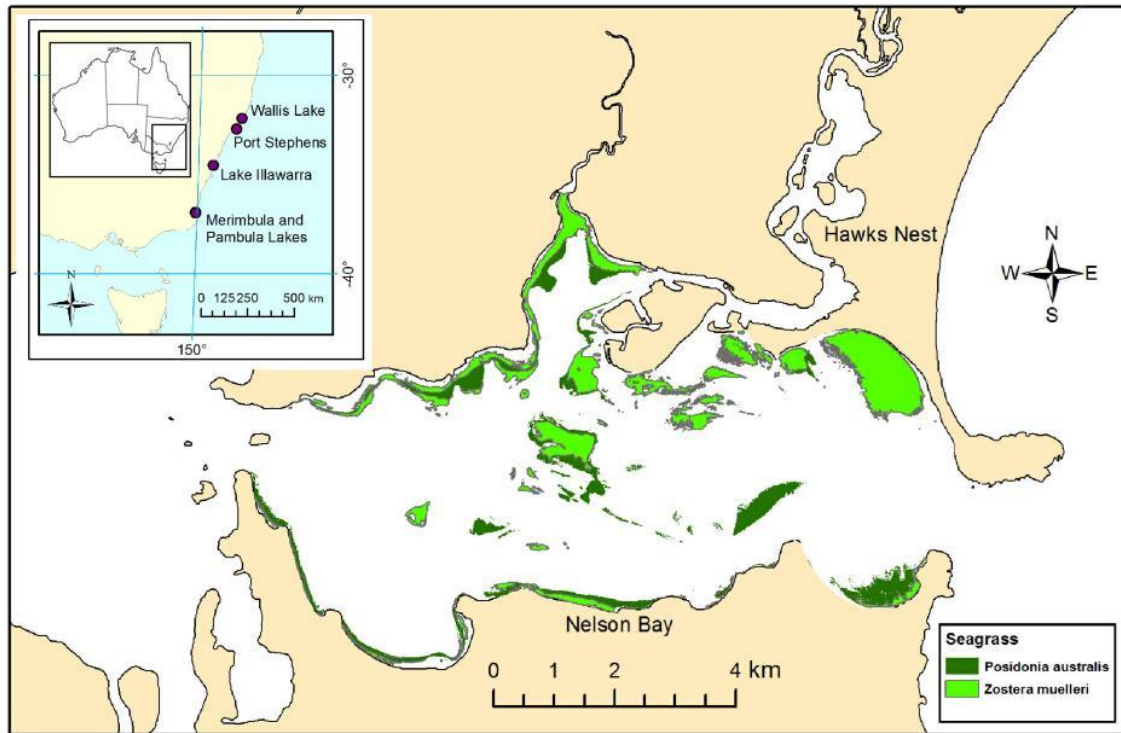


Figure 1: Maps showing the location of study estuaries (●) in New South Wales, Australia and, as an example, the spatial extent of seagrass beds from Port Stephens, which were used to develop species distribution models.

3.3.2 Calculation of explanatory variables

Light availability (*Light*), tidal velocity (*Current*), and orbital velocity at the seabed due to waves (*Waves*) were calculated for use as explanatory variables in RES models. Light availability was defined using the ratio of photosynthetically-available radiation (PAR) at the seabed (E_z) to PAR at the surface (E_0), and calculated using Beer-Lambert's law: $Light = E_z/E_0 = e^{-K_d(PAR)z}$ where; z = water depth, and $K_d(PAR)$ = irradiance attenuation coefficient. Values of $K_d(PAR)$ were calculated from measured Secchi depths (Z_{SD}) using the relationship ($K_d(PAR) = 1.4/Z_{SD}$) derived for turbid coastal waters by Holmes (1970). Secchi depth data were obtained as point measurements at multiple sites within each estuary, over extended periods (>12 months), allowing derivation of time-averaged Secchi depth distributions, with interpolation of Secchi depths between measurement sites. For Port Stephens, average Secchi depths varied from 8.8 m at the estuary entrance to 2.2 m at the western end of the embayment (pers. obs.). Secchi depths for Wallis Lakes and Lake Illawarra were obtained as point measurements from the online data repository OzCoasts (2015), with Secchi depths in Wallis Lakes varying from 2.6 m at the estuary entrance to 0.5 m in the Wallingat River, and those in Lake Illawarra varying from 2.4 m to 1.2 m. Secchi depths for Merimbula and Pambula lakes were supplied by Bega Valley Shire

Council (Elgin 2014a; Elgin 2014b), varying from 5.5 m to 4.6 m in Merimbula Lake, and from 3.1 m to 2.0 m in Pambula Lake.

Maximum tidal current velocities (*Current*) were influenced by tidal range, depth, and estuarine geometry, and were calculated for each estuary using two-dimensional hydrodynamic models constructed using TELEMAC-2D (Hervouet 2000). The accuracy of the modelling methodology was validated using measured tidal velocity data (DPWS 1998). Each tidal model included an entire estuary and a section of the coastal waters immediately adjacent to the estuary entrance, and currents were calculated for spring tides with a range of 2.0 m.

Maximum wave-induced orbital velocities at the seabed (*Waves*) were calculated by taking the maximum orbital velocity at each point for wind-driven waves and ocean swells for wave and swell directions at 45° increments from 0–360°. Orbital velocities at the seabed were calculated from wave heights using the relationships defined in Rohweder *et al.* (2012) with assumed wave breaking heights of $0.55 \times \text{depth}$ as per Nelson (1994). Wind-driven wave heights were calculated from wind speeds, fetches (the distance travelled over water by the wind), and water depths using the relationships defined in Rohweder *et al.* (2012). Wind velocities in each direction were taken as the 90th percentile wind speeds from weather stations nearest to each estuary (maximum distance 34 km) using data obtained from the Australian Bureau of Meteorology (<http://www.bom.gov.au> accessed 27 November 2015). Fetch was calculated using the Waves2012 toolbox in ArcGIS 10 (Rohweder *et al.* 2012), based on the US Army Corps of Engineers Shore Protection Manual procedure (USACE 1984). Port Stephens was the only embayment where the estuary entrance allowed substantial swell ingress, and ocean swell heights within the estuary were calculated using a two-dimensional hydrodynamic model of the estuary generated in the wave propagation simulation software ARTEMIS (Hervouet 2000). Data on storm-driven swells from 2000–2011 were obtained from the Manly Hydraulics Laboratory (<http://new.mhl.nsw.gov.au> accessed 10/12/15) and analysed to determine peak wave heights and swell periods for directions where significant swells were capable of entering the estuary (i.e. 90°, height = 3.39 m, period = 7.8–13.8 s; 135°, height = 3.68 m, period = 7.5–10.9 s), with these data applied at the ARTEMIS model offshore boundaries.

3.3.3 Relative environmental suitability model development

Relative environmental suitability models use species presence data to define ecological niches in terms of preferred and absolute presence ranges for explanatory variables (here *Light*, *Current*, *Waves*) (Kaschner *et al.* 2006). Probabilities of seagrass presence in RES models were calculated at each point using trapezoidal envelopes, which defined species-specific preferred and absolute presence ranges for explanatory variables, for data from Port Stephens using methods based on Kaschner *et al.* (2006). Probability of species presence for an explanatory variable (P_v) was defined as $P_v = 1$ for variables in the preferred range, $P_v = 0$ for values outside the absolute range, and linearly interpolating for values between preferred and absolute ranges (Figure 2). Absolute range limits were defined by the minimum and maximum values for variables where species were present in the training data. Preferred range limits were defined using species percentile occurrence levels, as per Ready *et al.* (2010), but with limits defined to maximise model precision (Kappa), rather than using fixed 10th and 90th lower and upper percentile limits (Ready *et al.* 2010). Limits to maximise Kappa were calculated for data from Port Stephens by examining all possible combinations of percentile limits (from 0–100th percentile, in 1% increments), for all explanatory variables (Supplementary Table S1). The overall probability of seagrass presence in RES models (P_{RES}) was computed by multiplying presence probabilities across all variables at each point ($P_{RES} = P_{Light} \times P_{Current} \times P_{Waves}$) with seagrass presence defined by $P_{RES} = 1.0$. Points where $0.0 < P_{RES} < 1.0$, while not used in prediction of seagrass presence, provided indications of areas where seagrasses could potentially occur under sub-optimal conditions. Models developed using training data from Port Stephens were tested by predicting seagrass presence/absence for the other four estuaries examined (external validation), with the accuracy and precision of predictions assessed using known distribution maps for seagrass species.

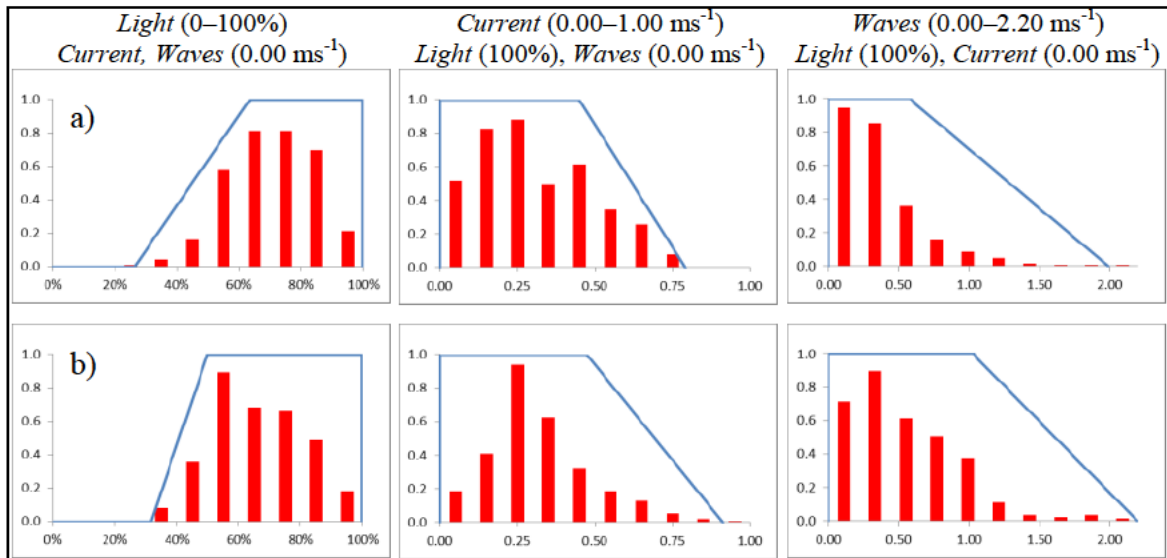


Figure 2: Relative Environmental Suitability (RES) envelopes (solid blue lines) defining probability of seagrass species presence (P_r) for explanatory variables of; % photosynthetic available radiation at the seabed (*Light*), tidal velocity (*Current*), and wave orbital velocity at seabed (*Waves*) for (a) *Posidonia australis* and (b) *Zostera muelleri*. Envelopes and curves based on presence data (red bars) from Port Stephens.

3.3.4 Modelling effects of climate change induced sea level rise and increased turbidity

The impacts of climate change induced sea level rises on seagrass distributions were simulated in study estuaries for projected rises to 2050 (0.25 m) and 2100 (0.74 m) (Intergovernmental Panel on Climate Change trajectories RCP 8.5) (Church *et al.* 2013) by increasing water depths in calculations for the explanatory variables *Light* and *Waves*. In addition, the impact on seagrass distributions of future increases in turbidity were examined by modelling nominal reductions in Secchi depth of 10–50% in each estuary, with substantial turbidity increases predicted due to increased frequency and severity of storms and floods (Björk *et al.* 2008; Waycott *et al.* 2007). For future scenarios, areas of seagrass loss were defined as those which currently support seagrass but for which future conditions preclude seagrass presence. Changes to sea levels and turbidity were considered separately as detailed projections of turbidity increases under climate change were not available for the estuaries examined. The effects of climate change on wind velocities, storm waves, and currents were not examined as the magnitude of changes to these factors could not be quantified, due to the high degree of uncertainty that currently exists in attributing global climate change effects to weather patterns at a regional scale (Bindoff *et al.* 2013).

3.4 Results

3.4.1 RES model performance

Relative environmental suitability models provided a high level of discrimination for seagrass presence/absence for the internal validation at Port Stephens, with >82% of points correctly classified and Kappa values exceeding 0.32 (Table 2). Generally, RES models accurately predicted seagrass distributions, although they over-predicted seagrass presence in northern and eastern sections of the estuary (Figure 3).

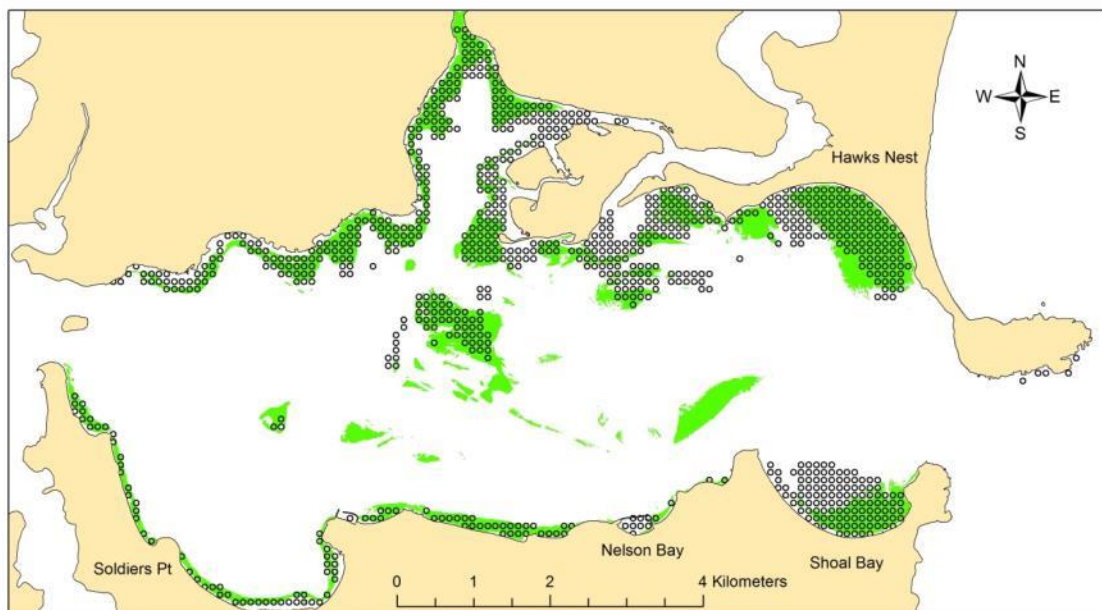


Figure 3: Distribution of seagrass in Port Stephens from aerial photography (green shading) and predicted seagrass presence (circles) for relative environmental suitability model built using training data from the Port Stephens estuary.

An average RES accuracy of $67.2 \pm 4.1\%$, and precision (Kappa) of 0.261 ± 0.082 , was achieved for estuaries outside Port Stephens (external validation) (Table 2). However, RES models tended to overestimate the extent of shallow seagrass beds (Figure 4). Precision was low for *P. australis* in Wallis Lake (Kappa = 0.05) and for *Z. muelleri* in Merimbula Lake (Kappa = 0.07), as many of the points predicted to be occupied by these species were already taken by the dominant seagrass species (i.e. *Z. muelleri* in Wallis Lake and *P. australis* in Merimbula Lake) leading to a high proportion of false presences (Table 2). An examination of RES model envelopes for *P. australis* and *Z. muelleri* found that there were considerable overlaps in the preferred ranges for these species, in terms of their light requirements and tolerances to waves and currents (Table S1). Overlaps in species

envelopes thus confounded the ability to distinguish between species in SDMs, and indicating that there is potential for competition for space between seagrass species.

Table 2: Overall model accuracy (%), model precision (Kappa statistic), true presence (%), and false presence (%) at study sites for relative environmental suitability models. (a) *Posidonia australis* presence, (b) *Zostera muelleri* subsp. *capricorni* presence

	Site	Overall accuracy	Kappa statistic	True presence	False presence
a)	Port Stephens	91.5	0.41	49.6	5.1
	Wallis Lake	67.2	0.05	62.5	32.7
	Merimbula Lake	68.6	0.19	43.8	23.8
	Pambula Lake	70.9	0.35	90.9	32.9
b)	Port Stephens	85.1	0.39	73.9	13.8
	Wallis Lake	70.0	0.41	84.8	37.7
	Lake Illawarra	85.3	0.64	94.0	17.3
	Merimbula Lake	53.0	0.07	66.7	48.6
	Pambula Lake	55.1	0.12	84.8	47.9

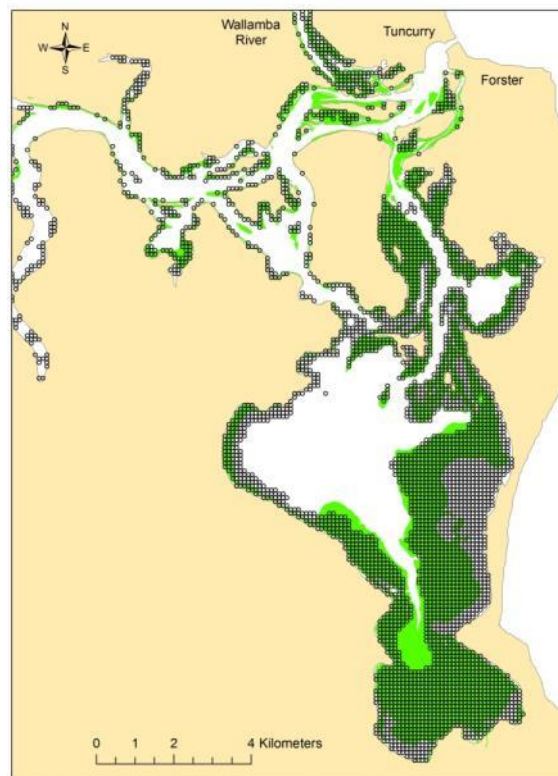


Figure 4: Distribution of seagrass in Wallis Lake from aerial photography (green shading) and predicted seagrass presence (circles) for relative environmental suitability model built using training data from the Port Stephens estuary.

3.4.2 Predicted seagrass losses due to sea level rise and increased turbidity

Substantial losses of existing seagrass cover were predicted for both sea level rise and increased turbidity, with losses varying between species and among estuaries (Table 3). Calculated losses did not account for seagrass gains from colonisation of shallow areas, due to a lack of detailed elevation data for intertidal areas and because, in many areas, it was not possible to distinguish gains from false presences in shallow areas (e.g. Figure 4). The greatest losses for sea level rise, for *P. australis* and *Z. muelleri*, were predicted to occur in Wallis Lake, with extensive shifts (~1500 m) predicted to occur by 2100 at the deeper boundary of the *Z. muelleri* beds at the southern end of the lake. Losses due to increased turbidity (i.e. 10–50% reductions in Secchi depth) were also predicted to be greatest in Wallis Lake with a 50% reduction in Secchi depth resulting in 53% loss of *P. australis* and 54% loss of *Z. muelleri* (Figure 5). Across all estuaries, it was predicted that sea level rise and increased turbidity would cause seagrass losses in deeper areas, while seagrasses were predicted to be unaffected, or have the potential to expand in shallow areas resulting in net shoreward shifts in seagrass beds (Figure 5). The greatest impacts of sea level rise and turbidity occurred in flat or gently sloping areas covered by turbid water where small increases in water depth or turbidity resulted in substantial reductions in light availability over extensive areas. In contrast, sea level rise and increased turbidity were predicted to have minimal impact on seagrasses in shallow areas with low turbidity, such as in Merimbula Lake, as these areas were predicted to receive sufficient light even when sea levels or turbidity increased. When averaged across all estuaries, seagrass losses were predicted to increase approximately linearly with increased turbidity (i.e. for 10–50% reductions in Secchi depth), with *P. australis* showing greater sensitivity to increased turbidity than *Z. muelleri* (Figure 6).

Table 3: Predicted losses for existing seagrass areas in study estuaries for projected sea level rises in 2050 (+0.25 m) and 2100 (+0.74 m), and for reductions in Secchi depth (-50%). Results for relative environmental suitability (RES) models, for *Zostera muelleri* and *Posidonia australis*, built using training data from Port Stephens

Estuary	<i>Z. muelleri</i> loss in 2050	<i>P. australis</i> loss in 2050	<i>Z. muelleri</i> loss in 2100	<i>P. australis</i> loss in 2100	<i>Z. muelleri</i> loss for Secchi (-50%)	<i>P. australis</i> loss for Secchi (-50%)
Port Stephens	-4%	-9%	-13%	-21%	-40%	-41%
Wallis Lake	-8%	-11%	-32%	-44%	-54%	-53%
Lake Illawarra	0%	n/a	-13%	n/a	-18%	n/a
Merimbula Lake	0%	0%	0%	-3%	0%	-10%
Pambula Lake	-6%	-4%	-6%	-11%	-9%	-16%

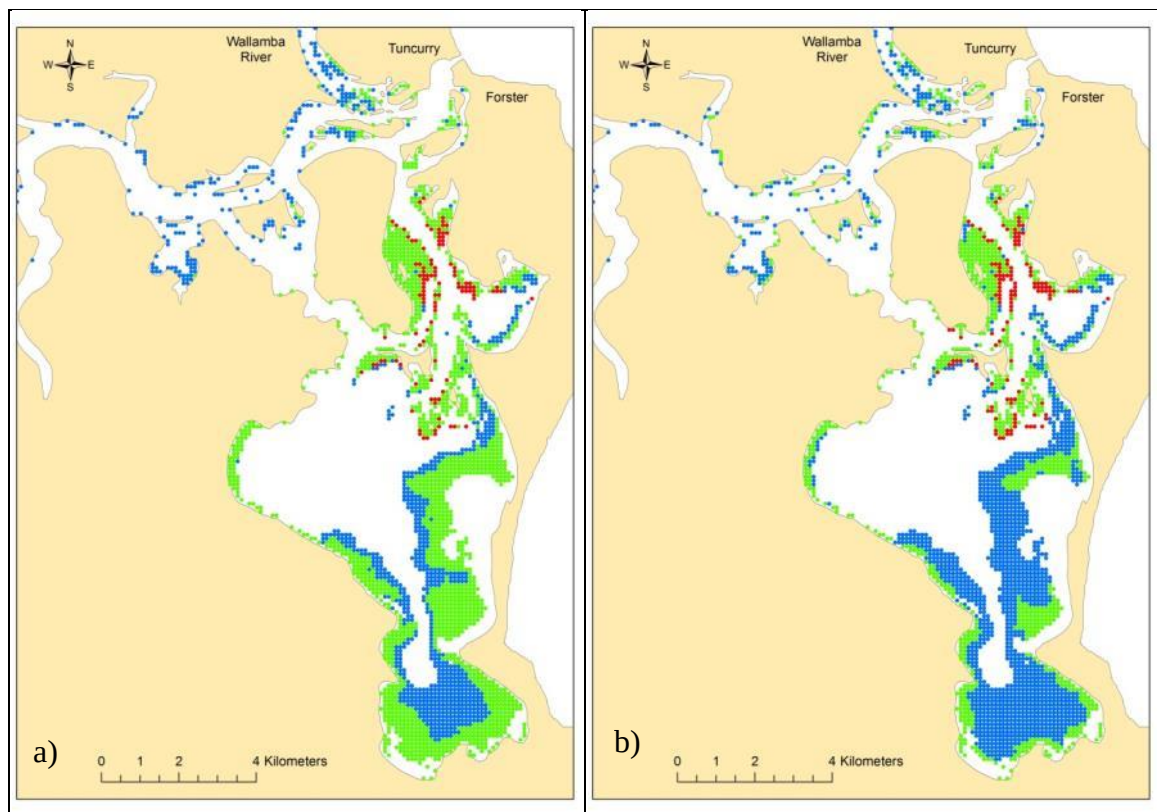


Figure 5: Predicted seagrass losses in Wallis Lake for a) a sea level rise in 2100 of 0.74 m, b) 50% reduction in Secchi depth. Results based on a relative environmental suitability model built using training data from the Port Stephens estuary. Red = *Posidonia australis* losses, blue = *Zostera muelleri* losses, green = seagrass unchanged.

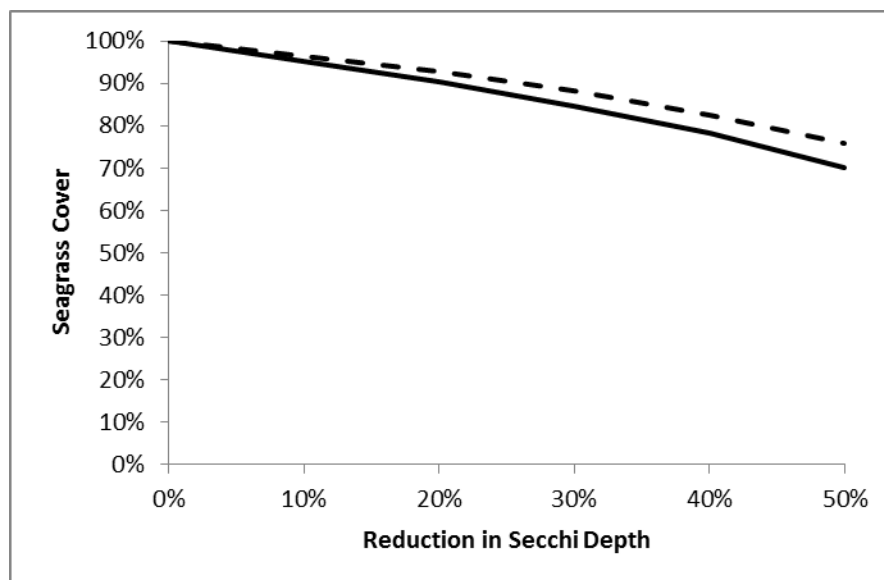


Figure 6: Predicted effect of changes in Secchi depth on seagrass distributions averaged across all study sites. Results based on relative environmental suitability models built using training data from the Port Stephens estuary. Solid Line = *Posidonia australis*, dashed line = *Zostera muelleri*.

3.5 Discussion

The main environmental variables directly influencing seagrass distributions in well mixed estuarine systems are light availability (Duarte *et al.* 2007), waves (Infantes *et al.* 2009) and, to a lesser extent, currents (Fonseca and Bell 1998). This study clearly identified that each of these variables has a significant influence on seagrass distributions in the Port Stephens estuary, and that RES models developed using these variables at this location, could be reliably applied to other estuaries over a broad section of the NSW coast.

Seagrass SDMs with broad applicability provide powerful tools for management and conservation planning. These models should be based on established relationships between seagrasses and their environment (Fonseca and Bell 1998), and allow prediction of environmental effects on seagrass distributions across a range of estuarine systems (Grech and Coles 2010). Relative environmental suitability envelopes simulate ecological niches of target species for explanatory variables (Kaschner *et al.* 2006) and we found that linkages between the preferred ranges for explanatory variables in RES models and species distributions were easily understood, supporting the contention by Ready *et al.* (2010) that RES models are easily interpretable, and are therefore useful in conservation planning.

As RES envelopes are representative of ecological niches, any overlap in envelopes among species indicates that they may compete for resources. Here we found that RES envelopes for *P. australis* and *Z. muelleri* substantially overlapped in terms of requirements for light and in their resistance to waves and currents. This indicated that *P. australis* and *Z. muelleri* may compete for space, a conclusion supported by the presence of mixed beds of *P. australis* and *Z. muelleri* in some parts of most of the estuaries examined. *Posidonia australis* was observed to dominate some mixed beds with its longer, broader leaves and dense growth (pers. obs.); however, *Z. muelleri* was found to dominate the shallow edges of beds where there was greater wave exposure and possible emersion during low spring tides. The dominance of *Z. muelleri* at the fringes of seagrass beds indicates that this species either has a higher tolerance to wave exposure than *P. australis*, or that *Z. muelleri* recovered more quickly in areas subjected to disturbances from waves. Disturbances from storms and floods occur frequently on the east Australian coast and have been linked to substantial losses of seagrass through wave damage (Preen *et al.* 1995) and increased turbidity (Campbell and McKenzie 2004). Following disturbances, many seagrass species, especially large slow-growing species such as *P. australis*, are very slow to recover, with recovery sometimes taking decades (Cambridge 1975; Kendrick *et al.* 2002). In

comparison, *Z. muelleri* often recovers relatively quickly following disturbance (Campbell and McKenzie 2004) and is therefore likely to dominate areas where seagrass beds are frequently disturbed, and is also more likely to initially colonise areas submerged by climate change induced sea level rise.

Previous studies examining anticipated distribution changes in seagrasses in response to global climate change have identified that sea level rise may cause shoreward shifts in seagrass beds (Björk *et al.* 2008; Short and Neckles 1999). Our modelling supports this conclusion, with shoreward shifts in seagrass distributions predicted in most study estuaries under the sea level rise scenarios examined. Sea level rise was found to have an effect on all of the explanatory variables examined in the study, and to influence seagrass distributions through changes to light availability and wave impacts, with both of these variables declining with increasing depth. Loss of seagrass was predicted in deeper areas due to reduced light availability, with these losses being offset by increased cover in shallow areas due to reduced wave impacts and the availability of new areas for colonisation.

The future impact of shifts in seagrass beds on overall seagrass cover depends primarily on the hypsometry of estuaries (i.e. land elevation relative to sea level), which controls the ratio of area lost to area gained by seagrasses (Carr *et al.* 2011), as well as the rate at which seagrasses can colonise newly submerged areas (Waycott *et al.* 2007). Losses can potentially be reduced where sediment accretion keeps pace with sea level rises, with seagrasses shown to increase net sediment accretion (Bos *et al.* 2007). Nonetheless, losses will be aggravated where shoreline defences are installed to prevent coastal erosion and these defences inhibit the shoreward migration of seagrass beds (Waycott *et al.* 2007). In addition, losses will be intensified in locations where climate change causes an increase in average turbidity through increased storm activity and floods, or where turbidity increases due to anthropogenic effects. In general, SDMs such as those developed in this study, provide valuable tools for managers to evaluate the complex interactions between sea level rise, turbidity, hypsometry, sediment accretion, and shoreline modifications, allowing assessment of the combined impact of these factors on the shoreward migration of seagrass beds and on total cover of seagrass species.

3.6 Conclusions

This study demonstrates the power of SDMs for predicting seagrass distributions and distributional changes. RES modelling, in particular, was able to accurately predict seagrass distributions for dominant species in the estuaries examined. SDMs can play a valuable role in predicting the future of seagrass beds under climate change, identifying locations where seagrass losses may occur as well as target areas for monitoring, and providing managers with knowledge of resilient locations, where seagrasses should withstand increases in sea levels and turbidity and where high levels of protection are warranted to ensure long-term preservation of seagrasses. In addition, models provide a tool to assist with identification of areas where conditions are suitable for seagrass rehabilitation, thereby contributing important information for restoration projects, enabling them to address the ongoing seagrass losses that are occurring within many estuarine systems.

Supplementary content

Table S1: Relative Environmental Suitability (RES) envelope limits defining probability of seagrass species presence (P_v) for explanatory variables of: % photosynthetic available radiation at the seabed (*Light*); tidal velocity (*Current*); and wave orbital velocity at seabed (*Waves*). Limits calculated from seagrass presence data from the eastern bay of Port Stephens for *Posidonia australis* and *Zostera muelleri*. Probability of seagrass presence linearly interpolated for explanatory variables between preferred and absolute ranges

Seagrass	Preferred range percentile limit	Preferred range limit for variable ($P_v = 1$)	Absolute range limit for variable ($P_v = 0$)
<i>P. australis</i>	<i>Light</i> > 29 th	<i>Light</i> > 58.1%	<i>Light</i> < 24.0%
	<i>Current</i> < 76 th	<i>Current</i> < 0.447 ms ⁻¹	<i>Current</i> > 0.790 ms ⁻¹
	<i>Waves</i> < 84 th	<i>Waves</i> < 0.580 ms ⁻¹	<i>Waves</i> > 1.992 ms ⁻¹
<i>Z. muelleri</i>	<i>Light</i> > 11 th	<i>Light</i> > 48.7%	<i>Light</i> < 31.6%
	<i>Current</i> < 85 th	<i>Current</i> < 0.472 ms ⁻¹	<i>Current</i> > 0.911 ms ⁻¹
	<i>Waves</i> < 91 st	<i>Waves</i> < 1.031 ms ⁻¹	<i>Waves</i> > 2.199 ms ⁻¹

Chapter 4. Diversity surrogates for estuarine fish assemblages in a temperate estuary in New South Wales, Australia

In Chapters 2 and 3, methods for classifying, mapping, and modelling habitat distributions were explored with the conclusion that habitat distributions in Port Stephens are strongly influenced by abiotic variables. However, while conservation planning can be conducted using habitats and abiotic variables as surrogates for biodiversity, these factors potentially do not adequately represent overlying biological assemblages.

In Chapter 4, I examine how habitats and abiotic variables perform as surrogates for fish assemblages in conservation planning, and quantify seasonal changes in fish assemblages to assess temporal stability of habitat surrogacy. Chapter 4 was published in *Regional Studies in Marine Science* (Davis *et al.* 2016a):

Davis T.R., Harasti D., Kelaher B.P., Smith S.D.A. (2016a) Diversity surrogates for estuarine fish assemblages in a temperate estuary in New South Wales, Australia. *Regional Studies in Marine Science* 7: 55-62.

Diversity surrogates for estuarine fish assemblages in a temperate estuary in New South Wales, Australia

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4.1 Abstract

The efficacy of fish diversity surrogates is central to their utility in conservation planning and management. Here we examine the linkages among a range of biotic and abiotic surrogates for estuarine fish diversity within the Port Stephens estuary in NSW, Australia. We examine the effectiveness of using biotic habitats as surrogates for diversity, and examine whether this surrogacy persists through time. The study was conducted using fish assemblage data gathered across eight *a priori* identified biotic habitat types. Significant differences in fish assemblages, species richness, and functional richness were detected among 26 out of 28 biotic habitats pairs, and these differences persisted for over 1 year within key *Dendronephthya australis* (soft coral) and filter feeder habitats, demonstrating the potential for biotic habitats to be used as surrogates for estuarine fish diversity. Significant correlations between abiotic variables (i.e. depth, location, substrate type, and substrate complexity) and fish assemblages were also established. Overall, the results demonstrate that both abiotic variables and biotic habitats can be used as surrogates for fish diversity in the study estuary, and combining both these types of predictor variables can provide a high level of discrimination among estuarine fish assemblages. The use of both abiotic variables and biotic habitats in conservation planning can, therefore, improve representation of estuarine fishes within marine protected areas.

4.2 Introduction

Understanding diversity, and relationships between diversity and habitats, is central to conservation planning (Margules and Pressey 2000; Tear *et al.* 2005), and the management of ecosystems (Grumbine 1994). Key information includes relationships between species and habitats, as well as the distributions of rare and threatened species (Margules and Pressey 2000). Regional biodiversity (Gamma diversity), is frequently partitioned into Alpha diversity, measuring the diversity of species within habitats, and Beta diversity measuring the effective number of distinct habitats occurring within regions (Whittaker 1960). This partitioning allows exploration of factors driving patterns in species assemblages both within and among habitats, and has led to the establishment of improved understanding of the relationships between habitats and their constituent species assemblages for a wide range of phyla including; vegetation (Whittaker 1960), birds (Fretwell and Calver 1969), mammals (August 1983), and fish (Malcolm *et al.* 2010; Rees *et al.* 2014; Sheaves 2016).

Assessing relationships between fish and marine habitats is particularly challenging due to the highly variable nature of fish assemblages in space and time (Birt *et al.* 2012; Willis *et al.* 2000), and habitat shifts during the ontogeny of many species, whereby individuals occupy different habitats at different points in their life cycle (Harasti *et al.* 2014a; Harasti *et al.* 2014c). To overcome problems associated with assessing fish–habitat relationships, managers of marine ecosystems often use abiotic factors (e.g. depth, substrate type) as surrogates for fish diversity (Malcolm *et al.* 2011; Mumby and Harborne 1999), as they can be measured relatively inexpensively, compared with fish assemblages, using visual and acoustic technologies (Anderson *et al.* 2009). Nonetheless, surrogates are only useful management tools if they accurately correlate with the assemblages of interest, are independent of each other, have a wide geographic range, and are amenable to survey (Smith 2005).

Studies have shown the surrogacy potential of abiotic variables (e.g. depth, location, and substrate type (Friedlander and Parrish 1998; Rees *et al.* 2014)) and biogenic habitats (Harborne *et al.* 2008; Mumby and Harborne 1999) for fully marine fish assemblages. However, relatively few studies have examined the effectiveness of such surrogates for fish diversity in estuarine ecosystems, potentially due to variability among estuarine systems (Sheaves 2016). Establishing reliable surrogates is especially important within estuaries as they contain highly diverse ecosystems that are threatened by a range of

anthropogenic stressors (Lotze *et al.* 2006). Thus, there is a clear need for a more detailed understanding of how abiotic variables and biogenic benthic habitats including sand, hereafter termed ‘biotic habitats’ perform as surrogates for fish diversity in estuarine systems.

Improved understanding of surrogates for fishes within estuaries is also needed for planning of marine protected areas (MPAs), where adequate information about species distributions is often unavailable, leading to inefficient MPA design (Ban *et al.* 2011; Malcolm *et al.* 2012). Marine protected areas are seen as key tools for protecting biodiversity (Coleman *et al.* 2013; Kelaher *et al.* 2014), as they provide areas of refuge from human impacts such as over-fishing, pollution, and coastal clearing and development (Agardy 1994; Mumby and Steneck 2011). To be effective, surrogates need to be critically evaluated (Smith 2005) and, ideally, surrogates should be assessed through time to ensure their continued effectiveness when temporal shifts in species assemblages occur (Favreau *et al.* 2006).

We investigated variation in fish diversity (measured as multivariate assemblage data, species richness, and functional richness) among distinct biotic habitats within the Port Stephens estuary in NSW, Australia, testing the primary hypothesis that fish diversity differs significantly among biotic habitats, and thereby that biotic habitats provide useful surrogates for fish diversity in the study estuary. Furthermore, temporal patterns in fish diversity within key habitats were examined, to assess the temporal stability of the surrogacy. In addition, to improve understanding of the relative importance of abiotic factors (depth, substrate type, location, and substrate complexity) as surrogates, we examined the relationships between these variables and fish assemblages, testing the secondary hypothesis that abiotic variables provide effective surrogates for fish diversity in the study estuary.

4.3 Material and methods

4.3.1 Study area

The study was conducted on the southern side of the Port Stephens estuary (Figure 1) which contains a range of temperate estuarine habitats (Davis *et al.* 2016b; Poulos *et al.* 2015) and a high diversity of biota (Poulos *et al.* 2013; Smith *et al.* 2010). The estuary is subject to strong tidal flows which ensure that salinity in the study area is essentially marine (i.e. 35 to 35.5 psu) (DPWS 1998). The entire Port Stephens estuary lies within the

98,000 Ha Port Stephens-Great Lakes Marine Park (PSGLMP), the largest MPA within the state waters of New South Wales (NSW) (NSW-MPA 2010a). Two sets of surveys were conducted. Firstly, surveys to examine the effectiveness of biotic habitats, and abiotic variables, as surrogates for fish diversity were carried out in January/February 2015 (summer 2015) within eight *a priori* defined habitat types (Davis *et al.* 2016b) (Table 1), with 6 replicate transects sampled from randomly selected starting locations ($n = 3$) within previously mapped areas ($n = 2$) for each habitat type (Davis *et al.* 2016b).

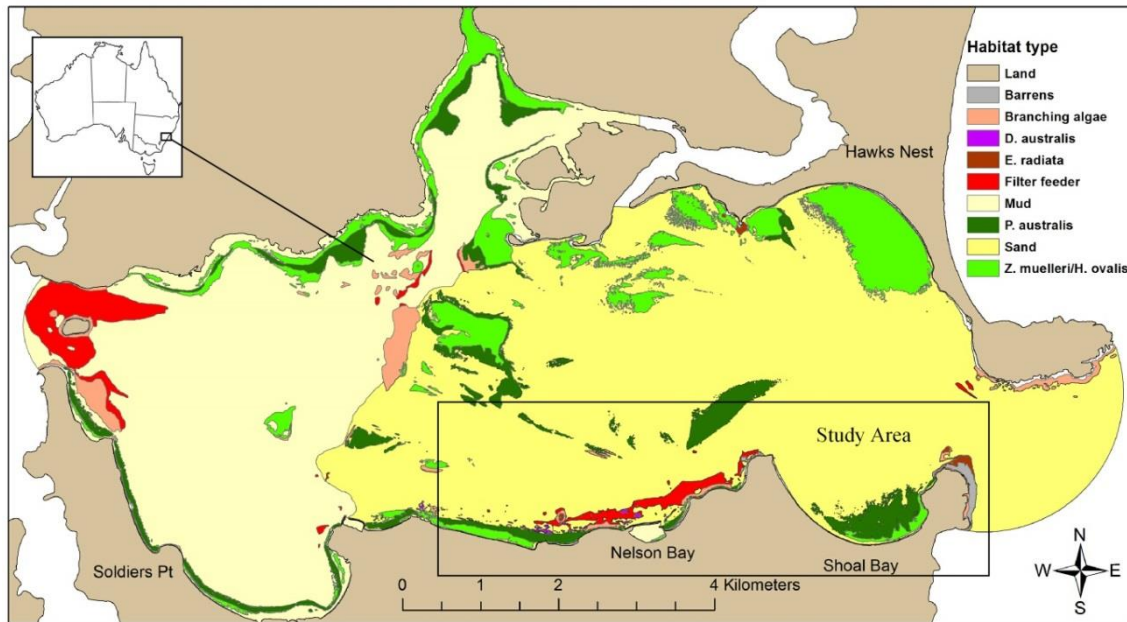


Figure 1. Study area in the Port Stephens estuary. Colours indicate habitat types.

Secondly, surveys to examine temporal stability of habitat surrogacy were undertaken for 3 month periods (hereafter periods), from June 2014 (winter 2014) to August 2015 (winter 2015), in two *a priori* selected key habitats (i.e. the soft coral *Dendronephthya australis* and filter feeder), with 12 replicate transects sampled within previously mapped areas for each habitat type. Filter-feeder and *D. australis* were selected as key biotic habitats as the presence of large areas of these habitats within an estuarine system was thought to be relatively unique; *D. australis*, in particular, was thought to be under threat from anthropogenic impacts (Harasti 2016; Poulos *et al.* 2013; Smith and Edgar 2014); and previous research indicated that these habitats contain highly diverse fish assemblages and protected species (Poulos *et al.* 2013).

Table 1: Sub-tidal habitat types within the Port Stephens estuary examined in the study of biotic habitat surrogacy for fish diversity. Habitat type classified by dominant biotic cover where biotic cover >10% or by substrate type where biotic cover <10%, as defined by Davis *et al.* (2016b)

Habitat type	Description
<i>P. australis</i>	Areas dominated by the seagrass <i>Posidonia australis</i> occurring on soft substratum
<i>Z. muelleri</i> / <i>H. ovalis</i>	Areas dominated by intermingled seagrasses <i>Zostera muelleri</i> subsp. <i>capricorni</i> and/or <i>Halophila ovalis</i> occurring on soft substratum
<i>E. radiata</i>	Areas dominated by the macroalgae <i>Ecklonia radiata</i> (i.e. kelp) occurring on hard substratum
Branching algae	Areas dominated by mixed branching and filamentous macroalgal species, with filter feeders present in lower abundance, predominantly occurring on hard substratum
Filter feeder	Areas dominated by filter feeders (i.e. sponges, ascidians, hydroids, bryozoans, and corals) with macroalgae present in lower abundance, predominantly occurring on hard substratum
<i>D. australis</i>	Areas dominated by the soft coral <i>Dendronephthya australis</i> , with other filter feeders and macroalgae present in lower abundance, predominantly occurring on soft substratum
Barrens	Areas with rocky substrate dominated by encrusting coralline algae, with high abundances of the urchin <i>Centrostephanus rodgersii</i>
Sand	Sand substrate with minimal biotic cover (i.e. <10%)

4.3.2 Survey methodology

Underwater visual census (UVC) surveys were conducted at slack water on high tide using the methodology developed by Smith *et al.* (2008). Briefly, each survey consisted of randomly positioned replicate transects within predefined areas for the specified habitat type. To ensure independence, transects were separated from each other by a distance of at least 10 m. Each transect involved counting fish in a 25 m x 5 m strip along the transect tape, to a height of 5 m above the substratum, with larger (> 50 mm) non-cryptic demersal and pelagic fish surveyed as the tape was laid, to improve counts of species that actively avoid divers (Dickens *et al.* 2011). Benthic and cryptic fish were surveyed by conducting a subsequent thorough search of the substrate to avoid biases in estimates of the abundance of cryptic species, which have been shown to occur in transect areas of this size (Brock 1982; Lincoln-Smith 1989). The benthic and cryptic fish search included searching through vegetation, as well as examining crevices and the underside of movable rocks, over a period not exceeding 30 min per transect. Vertical photo-quadrats (covering an area approximately 0.7 m x 0.5 m) were taken at five equally spaced points along each transect, and water depth and an assessment of substrate complexity were recorded for each point. From each photo-quadrat, the percentage cover of rock substratum was calculated,

providing a quantitative assessment of the proportion of hard substrate to soft sediment on each transect. Substrate complexity was qualitatively assessed in situ as the height change of the substrate within each quadrat, based on the method proposed by Gratwicke and Speight (2005), using a geometric scale (1 < 5 cm, 2 = 5–10 cm, 3 = 11–20 cm, 4 = 21–40 cm, 5 = 41–80 cm, 6 > 80 cm). Values of percentage rock substrate, depth, and substrate complexity were averaged for points on each transect and subsequently used for assessment of abiotic variable surrogacy. Water temperatures were continuously monitored at two locations spanning the study site using Onset Hobo U22-001 temperature loggers (www.onsetcomp.com accessed 18 August 2015) to provide data on temperature variations over time.

4.3.3 Statistical analysis

Data from summer 2015 was analysed to examine variation among biotic habitats for fish assemblages, species richness, and functional richness as the convex hull volume (FRic) which is calculated as the volume in functional space required to enclose the extreme values for all traits (Villéger *et al.* 2008). Functional richness was calculated using the functional diversity package ‘FD’ in R (Laliberté *et al.* 2014), with 9 functional traits obtained from Fishbase (<http://fishbase.org> accessed 10 August 2015) and from the global fishes trait database used by Stuart-Smith *et al.* (2013) (Supplementary Table S1). Non-metric multidimensional scaling (nMDS) analysis, using the PRIMER 7 software package (Clarke and Gorley 2015), was used to examine patterns in fish assemblages among biotic habitats. For all analyses similarity matrices were constructed using the Bray-Curtis index (Clarke 1993) using data that were dispersion weighted to reduce the influence of highly variable species, and then square-root transformed to reduce the influence of abundant species. Dispersion weighting down-weights species abundance counts for highly variable species (e.g. schooling fishes) that would otherwise add ‘noise’ to multivariate data (Clarke and Gorley 2015) and was found to provide similar results to removing schooling species from the data prior to applying transformations. Permutational multivariate analysis-of-variance (PERMANOVA) analyses were used to test for significant differences among biotic habitats. Pairwise PERMANOVA tests were conducted where significant differences were identified, with a significance level $P = 0.05$ used for all tests. Bonferroni corrections were not applied to account for the number of pairwise tests (28), as conclusions were not based on single pairwise test results, and the increased possibility of a Type 1 error was therefore deemed to be acceptable. Species

driving similarities within biotic habitats were identified using the SIMPER routine within the PRIMER software package (Clarke and Gorley 2015).

Temporal data spanning winter 2014 to winter 2015 were analysed in PERMANOVA to test for differences between key habitats and periods, using a 2-factor design (habitat-fixed, periods-random) with pairwise PERMANOVA analyses conducted for factors where significant differences or interactions were identified. Metric multidimensional scaling (mMDS) analysis was used to examine temporal changes in fish assemblages, displaying data as mean assemblage locations with 95% confidence intervals obtained by bootstrap averaging, with replacement ($n = 30$), across samples within each habitat/period pair (Clarke *et al.* 2014). The RELATE module in PRIMER was used to examine Spearman's rank correlations between assemblage patterns and modelled distance matrices representing: an annual cycle (cyclicality test); and a progressive change over time (seriation test) (Clarke *et al.* 2014). Species driving differences between periods were identified using the SIMPER routine, and biogeographic affinities were used to identify whether changes were driven by temperate or tropical species. Biogeographic affinities were determined from Reef Life Survey data on the thermal distribution of fish (Edgar and Stuart-Smith 2014), with species with a central tendency in thermal distributions $>23.8^{\circ}\text{C}$ (i.e. mean water temperature for Port Stephens $+2$ S.D.) deemed to be tropical immigrants. Analysis-of-variance (ANOVA) was used to test whether, proportionally, more tropical immigrants were present when water temperatures were higher (Summer/Autumn 2015), than when water temperatures were lower (Winter/Spring 2014).

The Biota and Environment matching routine (BIOENV) within the PRIMER software package was used to determine the best match between multivariate patterns in abiotic variables, with resemblance as Euclidean distance, and summer 2015 patterns in fish assemblages (Clarke 1993). Combinations of abiotic variables (comprising: depth; location (as distance from the estuary mouth); substrate type (as percentage rock substrate); substrate complexity) were tested to identify the subset that best matched fish assemblage patterns. Abiotic variables were square-root transformed to overcome skewness, standardised, and tested for co-linearity, with variables with absolute values for correlation coefficients $|r| > 0.7$ substituted as recommended by Dormann *et al.* (2013). Testing for co-linearity identified that substrate type and substrate complexity were highly correlated ($|r|=0.81$), and substrate type was therefore used to represent both variables in subsequent analyses. BIOENV was also used to test for spatial autocorrelation between summer 2015

fish assemblages and distance between transects. No significant correlation was detected ($\rho_s = 0.034$, $P = 0.267$), indicating that assemblage differences among habitats were not primarily caused by distance.

4.4 Results

4.4.1 Variations in fish diversity across habitat types

A total of 17738 fish from 175 species were identified during 156 UVC transects across habitats, and periods. Non-metric multi-dimensional scaling (nMDS) showed clustering of fish assemblages within different habitat types (Figure 2). PERMANOVA identified significant differences among assemblages, species richness, and functional richness in different biotic habitats ($P < 0.001$, all tests). Pairwise tests identified that assemblages in 26 out of 28 habitat pairs were significantly different from each other, especially where habitats had widely differing substrates and physical structures (e.g. sand and barrens) (Table 2). Differences in fish assemblages were not detected among filter feeder and branching algae habitats ($P = 0.061$), and seagrass-dominated *Z. muelleri*/*H. ovalis* and *P. australis* habitats ($P = 0.051$, Table 2) where biotic habitats were on similar substrates with similar benthic growth. Pairwise tests for species richness and functional richness also identified significant differences between some biotic habitats (Table 2) with higher species richness and functional richness generally associated with more structurally complex biotic habitats (e.g. branching algae, filter feeder) or heterogeneous reef substrates (e.g. barrens) (Table 3). SIMPER analyses identified that differences between biotic habitats were primarily driven by differing abundances of commonly occurring temperate species (Table 3).

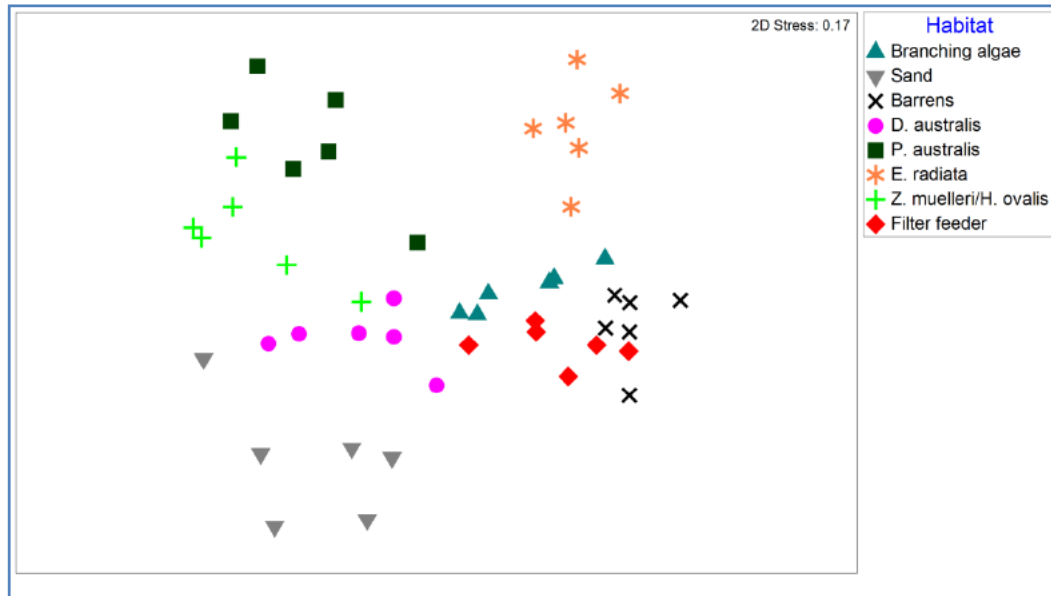


Figure 2: Non-metric Multi-Dimensional Scaling plot showing similarity of fish assemblages within biotic habitat types for the Port Stephens estuary.

Table 2: PERMANOVA pair-wise tests for differences between habitat types (*P*-values) for fish assemblages (A), fish species richness (S), and fish functional richness (F). Significant values ($P < 0.05$) in bold

		<i>D. australis</i>	Branching algae	<i>Z. muelleri</i> / <i>H. ovalis</i>	Sand	<i>P. australis</i>	Barrens	<i>E. radiata</i>
Filter feeder	A	0.005,	0.061,	0.002,	0.003,	0.003,	0.004,	0.005,
	S	0.004,	0.573,	0.009,	0.003,	0.008,	0.484,	0.271,
	F	0.007	0.180	0.026	0.004	0.004	0.395	0.087
<i>D. australis</i>	A	-	0.002,	0.005,	0.001,	0.004,	0.003,	0.002,
	S	-	0.006,	0.651,	0.005,	0.449,	0.010,	0.012,
	F	-	0.004	0.269	0.005	0.155	0.290	0.985
Branching algae	A	-	-	0.005,	0.001,	0.002,	0.001,	0.004,
	S	-	-	0.005,	0.002,	0.005,	0.222,	0.095,
	F	-	-	0.009	0.002	0.006	0.098	0.012
<i>Z. muelleri</i> / <i>H. ovalis</i>	A	-	-	-	0.008,	0.051,	0.002,	0.003,
	S	-	-	-	0.023,	0.913,	0.014,	0.023,
	F	-	-	-	0.054	0.980	0.135	0.375
Sand	A	-	-	-	-	0.001,	0.004,	0.003,
	S	-	-	-	-	0.068,	0.002,	0.005,
	F	-	-	-	-	0.051	0.001	0.004
<i>P. australis</i>	A	-	-	-	-	-	0.004,	0.001,
	S	-	-	-	-	-	0.006,	0.014,
	F	-	-	-	-	-	0.079	0.282
Barrens	A	-	-	-	-	-	-	0.004,
	S	-	-	-	-	-	-	0.586,
	F	-	-	-	-	-	-	0.440

Table 3: Species richness per transect, functional richness per transect (as convex hull volume for traits as per Table S1) (mean $\pm$ S.E., $n = 6$), and dominant species, for fish assemblages by habitat type

Habitat type	Species richness	Functional richness ($\times 10^{-3}$)	Dominant species (% contribution to assemblage similarities)
Branching algae	30.5 $\pm$ 3.5	136 $\pm$ 12	<i>Hypoplectrodes maccullochi</i> (13%) <i>Ophthalmolepis lineolatus</i> (8%)
Filter feeder	27.8 $\pm$ 3.1	112 $\pm$ 10	<i>Hypoplectrodes maccullochi</i> (18%) <i>Pseudolabrus guentheri</i> (9%)
Barrens	24.8 $\pm$ 2.3	94 $\pm$ 19	<i>Hypoplectrodes maccullochi</i> (26%) <i>Parma microlepis</i> (10%)
<i>Ecklonia radiata</i>	22.7 $\pm$ 2.6	74 $\pm$ 16	<i>Pictilabrus laticlavus</i> (15%) <i>Notolabrus gymnogenis</i> (12%)
<i>Dendronephthya australis</i>	14.3 $\pm$ 1.0	74 $\pm$ 4	<i>Upeneichthys lineatus</i> (19%) <i>Brachaluteres jacksonianus</i> (13%)
<i>Zostera muelleri</i> / <i>Halophila ovalis</i>	12.8 $\pm$ 2.4	50 $\pm$ 21	<i>Bathygobius krefftii</i> (30%) <i>Favonigobius lateralis</i> (26%)
<i>Posidonia australis</i>	12.3 $\pm$ 2.2	50 $\pm$ 14	<i>Bathygobius krefftii</i> (33%) <i>Centropogon australis</i> (19%)
Sand	8.0 $\pm$ 0.4	12 $\pm$ 2	<i>Hypoplectrodes maccullochi</i> (27%) <i>Trygonoptera testacea</i> (18%)

4.4.2 Temporal variability in fish diversity in key habitats

Metric multidimensional scaling (mMDS) for mean assemblages from each habitat in each season indicated that species assemblages changed through time (Figure 3). PERMANOVA analyses identified significant differences in assemblages, species richness, and functional richness among periods, and habitats ($P < 0.016$, all tests). Significant interactions between habitats and periods were detected for assemblages ($P = 0.020$), but were not found for species richness and functional richness ($P > 0.071$, both tests). Pairwise tests between habitats, for assemblages within periods, identified that assemblages in key habitats (i.e. filter feeder, *D. australis*) were significantly different from each other in all periods ($P < 0.001$, all pairs). Pairwise tests among periods, for assemblages within habitats, identified that assemblages in *D. australis* were significantly different from each other for all periods ($P < 0.030$, all pairs), except winter and autumn 2014 ($P = 0.390$). In the filter feeder habitat, assemblages were significantly different from each other among winter 2014 and summer/autumn/winter 2015, as well as among spring 2014 and autumn/winter 2015 ($P < 0.034$, all pairs).

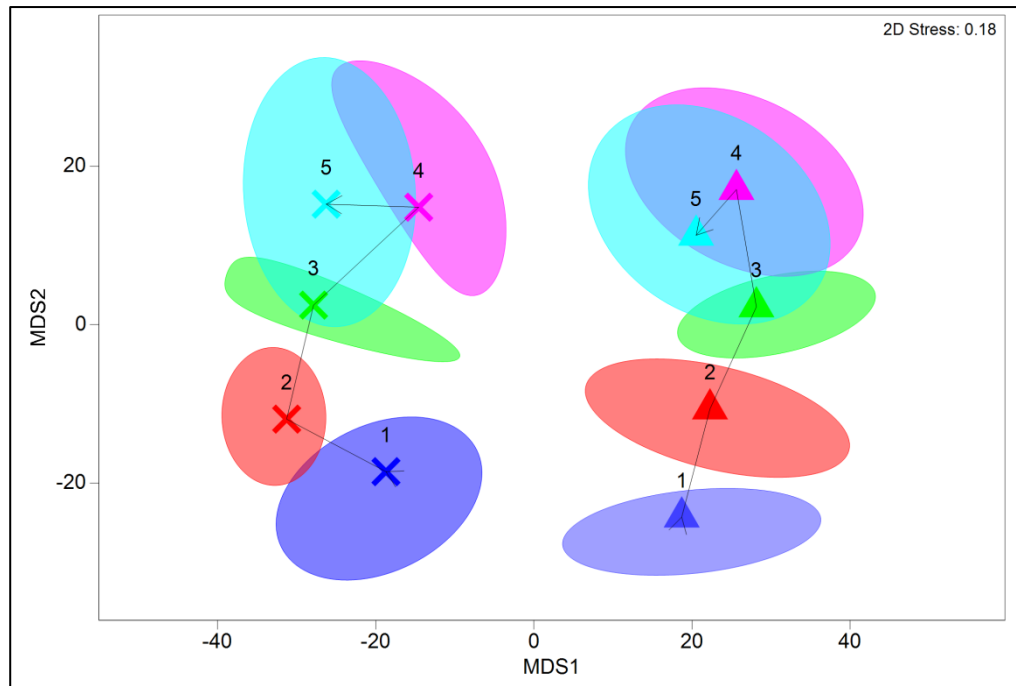


Figure 3: Metric multi-dimensional scaling plot showing similarity of mean fish assemblages within habitat types across time in the Port Stephens estuary. (Triangles = filter feeder habitat, Crosses = *D. australis* habitat, 1 = winter 2014, 2 = spring 2014, 3 = summer 2015, 4 = autumn 2015, and 5 = winter 2015). Ellipses show approximate 95% confidence boundaries for mean position calculated by bootstrap averaging across transects with replacement. Lines with arrows indicate progression in assemblages from winter 2014 to winter 2015.

SIMPER analyses identified that differences in species assemblages between periods were driven by changes across a wide range of predominantly temperate species, with no single species contributing > 5% to differences among periods for the filter-feeder habitat, or > 8% to differences for *D. australis* habitat. No significant annual cycle in fish assemblages was detected in either filter-feeder habitat ($P = 0.213$, $\rho = 0.020$), or *D. australis* habitat ($P = 0.196$, $\rho = 0.025$). Testing for a progressive change in assemblages (i.e. seriation) identified a significant, albeit relatively weak (i.e. low ρ -value), relationship between changes to fish assemblages and elapsed time in both filter-feeder habitat ($P < 0.001$, $\rho = 0.145$), and *D. australis* habitat ($P < 0.001$, $\rho = 0.186$).

Significant differences among key habitats for species richness and functional richness were driven by higher species richness and functional richness in the filter-feeder habitat compared to the *D. australis*, across all periods (Table 4). Significant differences in species richness and functional richness between periods were influenced by higher richness in both habitats during summer/autumn 2015 when water temperatures were highest (Table 4). SIMPER analyses identified that assemblage changes over time were

predominantly driven by temperate fish species. Tropical species were not highly abundant, but a significantly greater proportion ($P = 0.016$) was present during summer/autumn 2015 ($3.8 \pm 0.6\%$, mean $\pm$ S.E.) than during winter/spring 2014 ($1.8 \pm 0.5\%$).

Table 4: Seasonal Alpha diversity in key habitat types (Filter feeder, *Dendronphthya australis*) calculated as species richness per transect and functional richness per 25 m x 5 m transect (mean $\pm$ S.E., $n = 12$). Seasonal water temperature averaged across days and sites (mean $\pm$ S.E., $n = 90-92$)

Season	Species richness (Filter feeder)	Species richness (<i>D. australis</i>)	Functional richness (Filter feeder) ($\times 10^{-3}$)	Functional richness (<i>D. australis</i>) ($\times 10^{-3}$)	Seasonal water temperature ($^{\circ}\text{C}$)
Winter 2014	20.1 ± 1.7	11.1 ± 1.1	69 ± 11	51 ± 11	16.90 ± 0.09
Spring 2014	18.7 ± 1.7	11.8 ± 1.0	72 ± 9	58 ± 10	20.14 ± 0.15
Summer 2015	26.6 ± 1.7	14.3 ± 1.1	114 ± 9	72 ± 8	22.74 ± 0.20
Autumn 2015	27.6 ± 2.6	14.6 ± 1.6	116 ± 11	54 ± 10	20.39 ± 0.13
Winter 2015	21.4 ± 1.9	11.2 ± 0.8	88 ± 16	34 ± 4	16.94 ± 0.07

4.4.3 Relationships between abiotic variables and fish assemblages

BIOENV analyses identified significant Spearman rank correlations (ρ_s) between all abiotic variables examined and summer 2015 fish assemblages ($P < 0.010$), with the highest correlation occurring for substrate type ($\rho_s = 0.614$), then substrate complexity ($\rho_s = 0.494$), then depth ($\rho_s = 0.273$), and the lowest correlation occurring for location ($\rho_s = 0.069$). Testing correlations between combinations of abiotic variables and fish assemblages identified that the greatest explanatory power was provided by a combination of substrate type and depth ($\rho_s = 0.693$), while explanatory power was reduced when substrate type, depth, and location were combined ($\rho_s = 0.614$).

4.5 Discussion

Abiotic and biotic surrogates are frequently used to represent differences in fish diversity among areas in conservation planning (Malcolm *et al.* 2012; Mumby and Harborne 1999; Rees *et al.* 2014), with these surrogates needing to be easy to measure, and representative of species of interest, if they are to be effective (Smith 2005). Where significant relationships can be established between habitats and species assemblages these provide an indication that habitats can provide highly cost-effective surrogates for biological assemblages in marine conservation planning (Ward *et al.* 1999). In this study, we identified significant differences in fish diversity between biotic habitats within an

estuarine system, and showed that these differences persisted through time within two key habitats, thereby, demonstrating significant relationships between biotic habitats and fish diversity within the Port Stephens estuary, and indicating the potential utility of biotic habitats as surrogates for fishes in conservation planning in the estuary.

Differences in biological assemblages among biotic habitats have been linked to variations in resources, or other limiting factors (Guisan and Thuiller 2005), with increased habitat complexity linked to higher fish diversity through the provision of more diverse food resources (Ross 1986), and more varied options for sheltering from predators and environmental extremes (Anderson *et al.* 1989; Charbonnel *et al.* 2002; Friedlander *et al.* 2003). We found significant differences in fish assemblages among the majority of the benthic habitats examined, predominantly among habitats on differing substrates with differing levels of complexity in terms of either biotic growth or structure. In addition, both species richness and functional richness tended to be greatest in biotic habitats containing diverse benthic growth (e.g. branching algae and filter feeder) or heterogeneous reef substrates (e.g. barrens) while simpler habitats (e.g. sand and *Z. muelleri*/*H. ovalis*) had lower species and functional richness. Of particular note was the key *D. australis* habitat, which had fish assemblages that were significantly different to all other habitats examined, supporting previous work identifying *D. australis* as a unique habitat of particular importance to fish species (Poulos *et al.* 2013).

In contrast, differences in fish assemblages were not detected where biotic habitats were on similar substrates with similar benthic growth (e.g. filter feeder and branching algae), with the inability to detect significant differences between some habitat types indicating that they could possibly be grouped in future local conservation planning, where protection of fish diversity is the primary objective. This could potentially simplify planning and management, especially where the spatial distributions of these habitats are contiguous. It should be noted however that differences in fish assemblages between seagrass-dominated *Z. muelleri*/*H. ovalis* and *P. australis* habitats, that were not detected in our study, were found by Middleton *et al.* (1984) using a combination of methods (i.e. poisoning, beam trawling, and gill netting), suggesting that increased replication within habitats in the study period may have improved the ability to detect differences among fish assemblages in some habitats in our study.

Another factor contributing to differences in fish assemblages among habitats was temporal variation, which has been shown to occur in many regions due to fluctuations in

water temperatures and seasonal breeding cycles (Booth *et al.* 2007), as well as seasonal changes in food availability (Edgar and Shaw 1995). It was, therefore, anticipated that fish assemblages in this study would exhibit annual cyclic variations, and that species richness and functional richness would be higher when average water temperatures were at their greatest, due to the recruitment of tropical larvae (Booth *et al.* 2007). Species richness and functional richness were found to be greatest in the warmer months and, as anticipated, the proportion of tropical species was also greater during warmer months. However, despite the observed increased prevalence of tropical species over summer/autumn, the anticipated annual cycle in fish assemblages was not detected, with fish assemblages in winter 2014 and winter 2015 strongly differing in both habitats. Instead, fish assemblages exhibited a temporal drift in composition, with an inter-annual change in assemblages greater than any change between adjacent periods. This long-term shift in assemblages resulted from changes in abundances of large numbers of predominantly temperate species over time, outweighing the impact of immigrant tropical species. The lack of an apparent seasonal effect on fish assemblages was not entirely unexpected because there are often no clear seasonal changes in demersal fish assemblages along the NSW coast (Gray and Otway 1994). Despite this, there were significant differences in fish diversity among the key biotic habitats across all periods of sampling, indicating that temporal shifts in fish assemblages do not dilute the surrogacy value of habitat types for the key habitats in this study. Results from previous research indicates that temporal differences also persist between fish assemblages in *Z. muelleri* and *P. australis* (Middleton *et al.* 1984) and between *Z. muelleri* and sand (Gray *et al.* 1996), indicating that temporal persistence in fish assemblage patterns also occurs among other habitats. However, further work is required to determine whether differences detected in this study persist for all habitats within the study locality.

Examination of correlations between fish assemblages and abiotic variables highlighted that variations in fish assemblages were closely correlated with substrate type and substrate complexity, moderately correlated with depth, and weakly associated with location. Substrate type and substrate complexity were found to be strongly correlated with each other, with substrate complexity increasing with the percentage of rocky substrate: these variables were therefore assessed as being interchangeable in their ability to act as surrogates for fish assemblages. However, substrate type would be the logical choice to use as a surrogate given the relative ease with which it can be measured using modern

acoustics techniques (Jordan *et al.* 2010b) and the importance of substrate type in determining the structure of fish assemblages (Malcolm *et al.* 2012; Morton and Gladstone 2014). The ability of abiotic variables to act as surrogates for fish assemblages was further improved when depth was considered, supporting the secondary hypothesis that abiotic variables can provide effective surrogates for fish assemblages. It should be noted however that using abiotic surrogates increases the risk of errors associated with distinguishing between sites which have similar abiotic conditions but dissimilar habitats (false homogeneity), and sites with dissimilar abiotic conditions but similar habitats (false heterogeneity - Stevens and Connolly (2004)). In the study area, abiotic surrogates would not provide an effective mechanism for distinguishing between barrens and filter feeder or branching algae habitats, a false homogeneity error, with these habitats all occurring on hard substratum at similar depths. In addition abiotic surrogates would not adequately distinguish between sand, *P. australis*, and *Z. muelleri* with these habitats occurring on soft sediment at similar depths.

The results of this study demonstrate that both biotic habitats and abiotic variables are effective surrogates for fish diversity, a conclusion that is supported by previous work in Western Australian estuaries, where fish community structure is correlated with the type of substrate and benthic vegetation (Valesini *et al.* 2014), and in central NSW where combining abiotic and biotic factors was shown to provide improved effectiveness in conservation planning for temperate reefs (Lindsay *et al.* 2008; Malcolm *et al.* 2012). Identifying the relative importance of the biotic and abiotic surrogates for fishes was complicated by relationships that exist between these surrogates within the estuary (Davis *et al.* 2016b). It should be noted, however, that assessment of biotic habitats currently requires costly visual surveys, due to limitations in the ability of acoustic survey techniques to distinguish between different types of biogenic habitats (Jordan *et al.* 2010b). It could therefore be argued that abiotic variables provide a more cost-effective surrogate for fish diversity, especially in situations where resources are constrained, as abiotic variables (e.g. depth, location, substrate type) are amenable to measurement using acoustic techniques (Jordan *et al.* 2010b), however care is required to address false homogeneity and false heterogeneity where abiotic surrogates are used in isolation (Stevens and Connolly 2004). Where data for both abiotic variables and biotic habitats are available, our study results suggest that combining these data will provide a higher level of discrimination between distinct fish assemblages, than using either type of surrogate in

isolation, thereby ensuring improved representation of fish species distributions in conservation planning and fisheries management. Additionally, it was demonstrated that diverse biotic habitats warrant increased levels of protection in conservation planning, as these habitats generally contain functionally diverse fish assemblages with a correspondingly high importance to ecosystem function (Farré *et al.* 2015; Poulos *et al.* 2013).

With estuaries facing an increased range of anthropogenic threats it is essential that effective conservation strategies are in place (Lotze *et al.* 2006). Conservation planning for marine ecosystems is challenging, especially when knowledge about the distribution of species is lacking, and suitable diversity surrogates have not been established. Our study demonstrates that both biotic habitats and abiotic variables have the potential to act as effective surrogates for temperate estuarine fish diversity in Port Stephens. The use of these surrogates in conservation planning will allow efficient and cost-effective determination of MPA boundaries where protection of fish diversity is a primary objective.

Supplementary content

Table S1: Functional traits used in calculation of functional richness, sourced from Fishbase (<http://fishbase.org> accessed 10 August 2015)* and the trait database from Stuart-Smith et al. (2013)^

Functional trait	Description
Maximum Length*	Numeric value: Maximum body size for species (cm)
Trophic Level*	Continuous index: 1 + mean trophic level of food items, calculated as the weighted mean based on diet composition, and trophic level of food items, with primary producers and detritus having a trophic level of 1
Trophic Group^	Factor: Benthic invertivore, browsing herbivore, scraping herbivore, higher carnivore, or planktivore
Water Column Position^	Factor: Benthic, demersal, site attached pelagic, or roaming pelagic
Diel activity period^	Factor: Diurnal, nocturnal
Preferred substrate^	Factor: Hard substrate or soft sediment
Complexity preference^	Factor: Associated with habitats of low, medium, or high complexity
Grouping tendency^	Ordered factor: 1 = solitary, 2 = found in pairs, 3 = sometimes aggregating or schooling
Vulnerability*	Continuous index: 0-100 indicating vulnerability to fishing (Cheung <i>et al.</i> 2005)

Chapter 5. Spatial and temporal variation in subtidal molluscan diversity amongst temperate estuarine habitats

Chapter 4 describes the effectiveness of using benthic habitats and abiotic variables as surrogates for fish. However, the broader applicability of benthic habitat and abiotic variable surrogacy across other phyla was not assessed, and drivers for differences in assemblages amongst benthic habitats were not fully explored.

The ability to use habitats and abiotic variables as surrogates for a second marine phylum (i.e. molluscs) was therefore examined in Chapter 5, and drivers behind differences in mollusc assemblages amongst benthic habitats were explored and discussed. Chapter 5 has been accepted for publication by Marine Ecology (Davis *et al.* 2017a):

Davis T.R., Harasti D., Kelaher B.P., Smith S.D.A. (2017a) Spatial and temporal variation in subtidal molluscan diversity amongst temperate estuarine habitats. *Marine Ecology* **38**:e12428.

Spatial and temporal variation in subtidal molluscan diversity amongst temperate estuarine habitats

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5.1 Abstract

Effective management of marine ecosystems is enhanced when detailed information on biodiversity is available. Key information to underpin management actions and conservation planning includes relationships between species assemblages and environmental gradients, and information on species distributions. We conducted a subtidal biodiversity assessment of surface-dwelling sub-tidal molluscs in eight *a priori* defined habitat types using underwater visual censuses to quantitatively explore relationships between molluscan assemblages, and their correlation with benthic habitats and abiotic variables. In addition, variations in diversity were examined for two key habitat types (areas dominated by *Dendronephthya australis* and by filter feeders) over a period of 15 months to examine temporal change. We found that molluscs form distinct assemblages within subtidal habitats, but that assemblages within key habitats show inherent temporal variability. Regional (Gamma) diversity of molluscs was found to result from a combination of: (a) within habitat Alpha diversity, which increased with habitat complexity; (b) between habitat Beta diversity, with significant differences in molluscan assemblages amongst habitats with differing benthic growth, substrate type, and depth; and (c) temporal Beta diversity, with significant changes detected in molluscan assemblages over time. The results demonstrate how habitats and abiotic variables (principally depth, and substrate type) combine to contribute to molluscan biodiversity in temperate estuaries, and illustrate the value of these factors as surrogates for surface-dwelling sub-tidal molluscs in conservation planning.

5.2 Introduction

Detailed biodiversity data facilitates effective management of marine ecosystems by providing insights into species distributions, including those of rare, threatened, and endangered species (Margules and Pressey 2000), and improving understanding of relationships between species assemblages and their environment (Whittaker 1960). Species assemblage information at the regional level (Gamma diversity) can be partitioned into diversity of species within habitats (Alpha diversity), and the degree of differentiation amongst habitats (Beta diversity) (Whittaker 1972). This partitioning facilitates understanding of relationships amongst species diversity, habitats, and environmental gradients, and has led to improved knowledge of associations between habitats and overlying species assemblages for a wide range of taxa including vegetation (Whittaker 1960), fish (Malcolm *et al.* 2010) and molluscs (Harrison and Smith 2012).

Molluscs are the most diverse marine phylum, with an estimated 43600–51700 described species (Appeltans *et al.* 2012). Molluscan assemblages have been used as a means of rapidly assessing biodiversity for a wider range of taxa (Smith 2005) and as metrics for assessing environmental impacts (Terlizzi *et al.* 2005). In addition, studies of molluscan death assemblages (Smith 2008; Warwick and Turk 2002), and fossil records (Kidwell 2001), have provided mechanisms for assessment of diversity patterns over wide geographical and temporal scales (e.g. Kelaher *et al.* 2004). Molluscs are therefore important in marine conservation for their ability to act as indicators of change in marine ecosystems. However, the use of molluscs for these purposes requires baseline data on molluscan assemblages, and improved understanding of relationships between molluscan diversity and regional environmental gradients.

Molluscs have been shown to form distinct assemblages within different habitats in coral reefs (Sanvicente-Añorve *et al.* 2012), temperate reefs (Harrison and Smith 2012; Kelaher *et al.* 2007a), rocky shores (Smith 2005), and soft-sediment environments (Absalão *et al.* 2006). Molluscan assemblages are also influenced by physical gradients, particularly depth (Martins *et al.* 2014; Olabarria 2006), location (Harrison and Smith 2012; Kelaher *et al.* 2007b), and substrate type (Absalão *et al.* 2006). However, relatively few studies have examined patterns in subtidal molluscan diversity within temperate estuarine systems, with those that have focussing mainly on soft-sediment communities (Mendes *et al.* 2007; Skilleter and Warren 2000; Troncoso *et al.* 2005).

Here, we assess living surface-dwelling subtidal molluscan assemblages in an estuarine system to evaluate relationships with underlying variations in benthic habitats, physical conditions, and time. Data were examined with the objectives of improving understanding of contributions of within habitat Alpha diversity (Alpha_h), amongst habitat Beta diversity (Beta_h), and temporal Beta diversity (Beta_p), to total regional gamma diversity (Gamma_r) within an estuarine system, thereby facilitating the use of molluscs as environmental indicators in marine ecosystem management. In addition, the relationships between abiotic variables and molluscan assemblages were examined for factors of location, depth, habitat height, and substrate type in order to establish the suitability of these potential predictors as surrogates for surface-dwelling molluscan biodiversity in conservation planning. In order to be useful as surrogates, predictor variables must be distinct, representative of the species of interest, and be amenable to survey (Smith 2005). Where strong linkages can be established, the best suite of predictors can be used as surrogates in management and conservation planning, providing a mechanism for protecting molluscan biodiversity without the need for exhaustive biodiversity surveys in all areas.

5.3 Material and Methods

5.3.1 Study area

The study was conducted on the southern side of the Port Stephens estuary (Figure 1), which contains a range of temperate coastal and estuarine habitats (Davis *et al.* 2016b; Poulos *et al.* 2015) and a high diversity of biota (Poulos *et al.* 2013; Smith *et al.* 2010). The entire Port Stephens estuary lies within the Port Stephens-Great Lakes Marine Park (PSGLMP), the largest Marine Protected Area (MPA) in New South Wales (NSW) (NSW-MPA 2010a). Two sets of surveys were conducted. Firstly, surveys to examine variation in mollusc diversity across benthic habitats were carried out within eight *a priori* defined habitat types (Table 1). Two haphazardly selected sites, separated by at least 200 m, were sampled within each habitat type. These surveys were conducted during summer (2015) when water temperatures on the east Australian coastline are generally at their highest (Booth *et al.* 2007), and mollusc biodiversity is also at its highest (pers. obs.). Secondly, surveys to examine temporal variation in molluscan diversity (temporal Beta diversity) were conducted every 3 months over a period of 15 months from June 2014 to August 2015, in two *a priori* selected key habitats (i.e. soft coral *Dendronephthya australis* and filter feeders), with four haphazardly selected sites sampled within each habitat type (Table

1). Filter feeder and *D. australis* habitats were selected for this study as previous research indicated that these habitats contained diverse invertebrate assemblages (Poulos *et al.* 2013), and *D. australis*, in particular, was thought to be under threat from anthropogenic impacts (Harasti 2016; Smith and Edgar 2014).

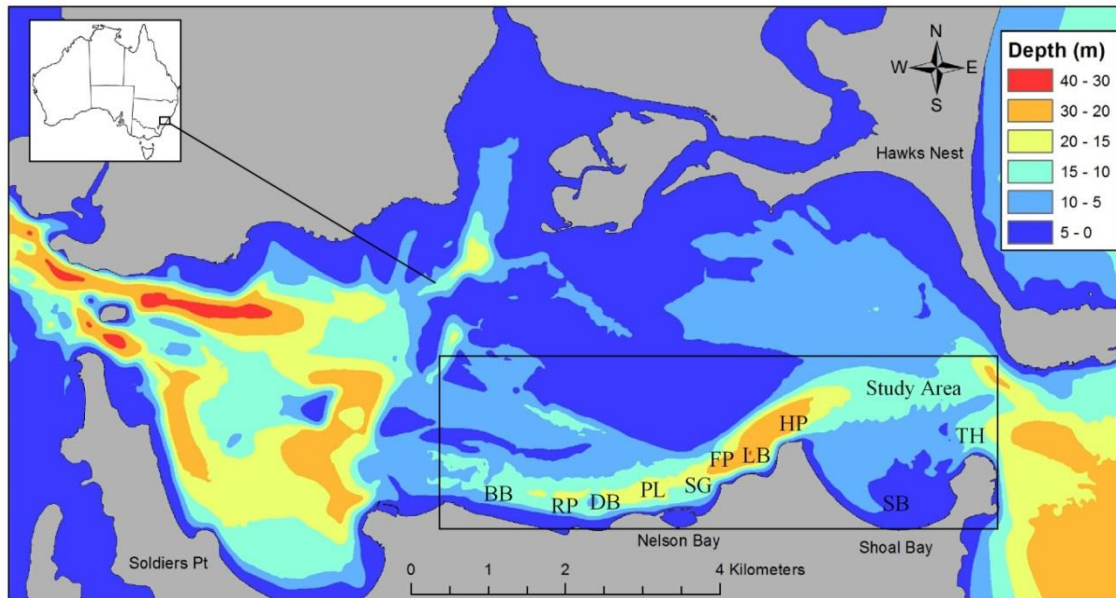


Figure 1. Study area in the Port Stephens estuary on the East Coast of Australia. Colours indicate the average water depth. Labels denote sites as per Table 1 (BB = Bagnalls Beach, RP = Redpatch Point, DB = Dutchies Beach, PL = Pipeline, SG = Seahorse Gardens, FP = Fly Point, LB = Little Beach, HP = Halifax Point, SB = Shoal Bay, TH = Tomaree Head).

Table 1: Sub-tidal habitat types within the Port Stephens estuary as defined by Davis *et al.* (2016b) with habitat descriptions, associated sites examined to quantify molluscan diversity with location (km from estuary entrance), habitat complexity class (low-high), average depth (m), average substrate type (% rock), and average habitat height class (1-6).

Habitat type	Description	Study sites, location (km)	Habitat complexity, depth, (m), substrate type (% rock), height class (1-6)
Filter feeders	Areas dominated by filter feeders (i.e. sponges, ascidians, hydroids, bryozoans, and corals) with macroalgae present in lower abundance	Fly Point (3.7), Seahorse Gardens (3.9) *Little Beach (3.2) *Pipeline (4.7)	Complexity = High Depth = 11.3 ± 0.6 Substrate = 51.2 ± 10.3 Height class = 3.9 ± 0.2
<i>D. australis</i>	Areas dominated by the soft coral <i>Dendronephthya australis</i> , with other filter feeders and macroalgae present in lower abundance	Pipeline (4.7), Bagnalls Beach (6.6) *Dutchies Beach (5.3) *Redpatch Point (5.6)	Complexity = Medium Depth = 8.8 ± 0.4 Substrate = 28.3 ± 3.3 Height class = 3.4 ± 0.2
Branching algae	Areas dominated by mixed branching and filamentous macroalgal species, with filter feeders present in lower abundance	Fly Point (3.7), Pipeline (4.7)	Complexity = High Depth = 7.2 ± 0.3 Substrate = 50.9 ± 3.7 Height class = 4.4 ± 0.2
<i>E. radiata</i>	Areas dominated by the macroalgae <i>Ecklonia radiata</i> (i.e. kelp)	Fly Point (3.7), Pipeline (4.7)	Complexity = Medium Depth = 2.6 ± 0.2 Substrate = 93.8 ± 3.7 Height class = 5.0 ± 0.0
Barrens	Areas with rocky substrate dominated by encrusting coralline algae, with high abundances of the urchin <i>Centrostephanus rodgersii</i>	Tomaree Head (0.0), Halifax Point (2.5)	Complexity = Medium Depth = 8.0 ± 1.4 Substrate = 84.0 ± 4.7 Height class = 5.3 ± 0.2
<i>P. australis</i>	Areas dominated by the seagrass <i>Posidonia australis</i>	Shoal Bay (1.6), Little Beach (3.2)	Complexity = Medium Depth = 3.3 ± 0.2 Substrate = 1.5 ± 1.1 Height class = 3.7 ± 0.1
<i>Z. muelleri</i> / <i>H. ovalis</i>	Areas dominated by intermingled seagrasses <i>Zostera muelleri</i> subsp. <i>capricorni</i> and/or <i>Halophila ovalis</i> .	Little Beach (3.2), Seahorse Gardens (3.9)	Complexity = Low Depth = 3.5 ± 0.5 Substrate = 3.3 ± 1.7 Height class = 2.1 ± 0.1
Sand	Sand substrate with minimal biotic cover (i.e. <10%)	Little Beach (3.2), Seahorse Gardens (3.9)	Complexity = Low Depth = 8.5 ± 0.7 Substrate = 0.0 ± 0.0 Height class = 1.1 ± 0.1

* indicates additional sites assessed in temporal study

5.3.2 Survey methodology

The Port Stephens estuary contains large areas designated as sanctuary zones, where extraction of living biota is prohibited (NSW-MPA 2007). It was therefore appropriate to limit biodiversity sampling to an observational method, and underwater visual census (UVC) was selected, using methodology developed by Smith *et al.* (2008), as UVC has been shown to provide reliable quantitative data on epibenthic molluscan assemblages (Harrison and Smith 2012). Briefly, each survey consisted of three randomly positioned replicate transects within the specified habitat type. To ensure independence, transects were separated from each other by a distance of at least 10 m. Each transect survey involved counting large surface-dwelling molluscs (i.e. ≥ 5 mm in length) in a 25 m x 5 m strip along the transect tape, using the World Register of Marine Species (WoRMS) as the naming standard for species classification (WoRMS Editorial Board 2015). Transects comprised a thorough search, including searching through vegetation, and examining crevices and the underside of movable rocks, over a period not exceeding 30 min.

Values for substrate type, depth, habitat height, and location were used in assessment of abiotic variable surrogacy for mollusc assemblages (Table 1). Salinity was not used as the study area in the Port Stephens estuary is well mixed, with salinity levels that are similar to near shore coastal waters (~ 35 psu) throughout most of the year (DPWS 1998). Substrate type was quantitatively assessed as percentage cover of rock substratum using vertical photo-quadrats (covering an area approximately 0.7 m x 0.5 m) taken at five equally spaced points along each transect. For each quadrat, the depth and an assessment of habitat height was also recorded, with habitat height qualitatively assessed as the average height change within each quadrat, based on the method proposed by Gratwicke and Speight (2005) with a geometric scale for height classes (1 < 5 cm, 2 = 5–10 cm, 3 = 11–20 cm, 4 = 21–40 cm, 5 = 41–80 cm, 6 > 80 cm). Location (measured as distance from the estuary entrance) was calculated using a geographic information system, with location used to represent gradients of reduced wave exposure (Jiang *et al.* 2013) and increased turbidity (pers. obs.) with distance from the estuary entrance. Water temperatures were continuously monitored at two sites spanning the study site using Onset Hobo U22-001 temperature loggers (www.onsetcomp.com accessed 18 August 2015) and used to examine temporal relationships between mollusc assemblages and average seasonal temperatures.

5.3.3 Statistical analysis

Gamma diversity for summer (2015) (Gamma_s) was calculated as total species richness across all 8 habitat types, and partitioned using $\text{Gamma}_s = \text{Alpha}_s \times \text{Beta}_s$, with Alpha_s calculated as the average across all habitats of species richness in each habitat, and Beta_s providing a measure of full changes in species composition amongst habitats in the study region (Whittaker 1972). Gamma_s from summer (2015) was compared with total regional Gamma diversity (Gamma_t) estimated by extrapolation of the species accumulation curve across all sites, habitats, and time periods, with extrapolation conducted using the EstimateS software package (<http://purl.oclc.org/estimates>) (Colwell 2013). Upper and lower 95% confidence intervals for Gamma_t were calculated using the non-parametric, individual-based, species richness estimation technique (Chao 1) developed by Chao (1984) (Colwell and Coddington 1994).

Data from summer (2015) were used to calculate within habitat (Alpha_h) diversity as species richness in each habitat. Pielou's evenness (J') was calculated to provide a measure of variability in species abundances within habitats. Beta diversity between habitat pairs (Beta_h) was assessed using Jaccard distance (1 - Jaccard index) (Jaccard 1912) and Bray-Curtis dissimilarity (Bray and Curtis 1957). An abundance-based measure such as Bray-Curtis dissimilarity is recommended where exploration of relationships between Beta diversity and spatial and environmental factors is a primary objective (Anderson *et al.* 2011). The Biota and Environment matching routine (BIOENV) within the PRIMER 7 software package (Clarke *et al.* 2014) was used to determine the best match between multivariate molluscan diversity patterns and abiotic variables (substrate type, depth, habitat height, and location). Abiotic variables were square-root transformed to overcome skewness, standardised to a common scale, and tested for co-linearity, with variables with co-linearity $|r| > 0.7$ combined as recommended by Dormann *et al.* (2013).

Non-metric multidimensional scaling (nMDS) analysis using PRIMER was conducted to examine patterns in molluscan assemblages amongst habitats, with similarity matrices constructed using the Bray-Curtis index (Clarke 1993) using data that were dispersion weighted to reduce the influence of highly variable species within habitats, and then square-root transformed to reduce the influence of abundant species. Permutational multivariate analysis of variance (PERMANOVAs) were used to test for significant differences in assemblages amongst habitats using a two-way nested design with habitats (fixed factor) and sites nested within habitats (random factor). Species driving similarities

within habitats, and dissimilarities amongst habitats, were identified using the similarity percentage breakdowns (SIMPER) routine within the PRIMER software package (Clarke and Gorley 2015). PERMANOVA analyses were used to test for differences in species richness per transect amongst habitats with differing levels of complexity, with habitat complexity qualitatively classified as: high complexity where habitats contained both complex benthic assemblages (varied benthic species assemblages) and complex physical structures (varied sizes and shapes of bottom structures); medium complexity where habitats contained either complex benthic assemblages or complex physical structures; and low complexity where habitats containing only simple benthic assemblages and structures (Table 1).

Temporal data spanning June 2014 to August 2015 were analysed to examine variations in species richness amongst 3-month time periods in each key habitat. Temporal Beta diversity between periods (Beta_p) was assessed as Jaccard distance and Bray-Curtis dissimilarity. PERMANOVA was used to test for differences in species richness per period amongst habitats and to test for differences in molluscan assemblages amongst key habitats and time periods, using a 3-factor design (habitat: fixed factor; sites nested within habitats: random factor; times: random factor). Metric multidimensional scaling (mMDS) analysis was used to display the relative positions of the assemblage means within each habitat within each time period. Bootstrap averaging was used to display approximate 95% confidence intervals for these means by averaging, with replacement, across samples within each habitat/period pair, and calculating the intervals within which 95% of the bootstrap averages fell (Clarke *et al.* 2014). The RELATE module in PRIMER was used to test for cyclical temporal variation using Spearman's rank correlations between Bray-Curtis similarities for transects within each habitat, and modelled distance matrices representing separations amongst transects over an annual cycle (cyclicity test) (Clarke *et al.* 2014).

5.4 Results

5.4.1 Molluscan Gamma diversity in the study region

A total of 6739 individuals from 143 species was identified during 156 UVC transects across all sites, habitats, and time periods. Abundance of molluscs was generally low (0.35 individuals per m^2) due to a lack of dense mussel and oyster beds. Molluscan diversity was dominated by heterobranch sea slugs (76 species) and shelled gastropods (40 species), with

lower diversity of bivalves (14 species), cephalopods (9 species) and chitons (4 species). Estimated Γ_{t} diversity for the study area, obtained by extrapolation of the species accumulation curve across habitats and times, was 159–242 species (Chao 1 95% confidence intervals) (Figure 2). New species were still being encountered at a rate of 1 every 4 transects after 15 months of surveys covering an area exceeding 1.9 hectares, indicating that many molluscan species within the study region were rare in both time and space.

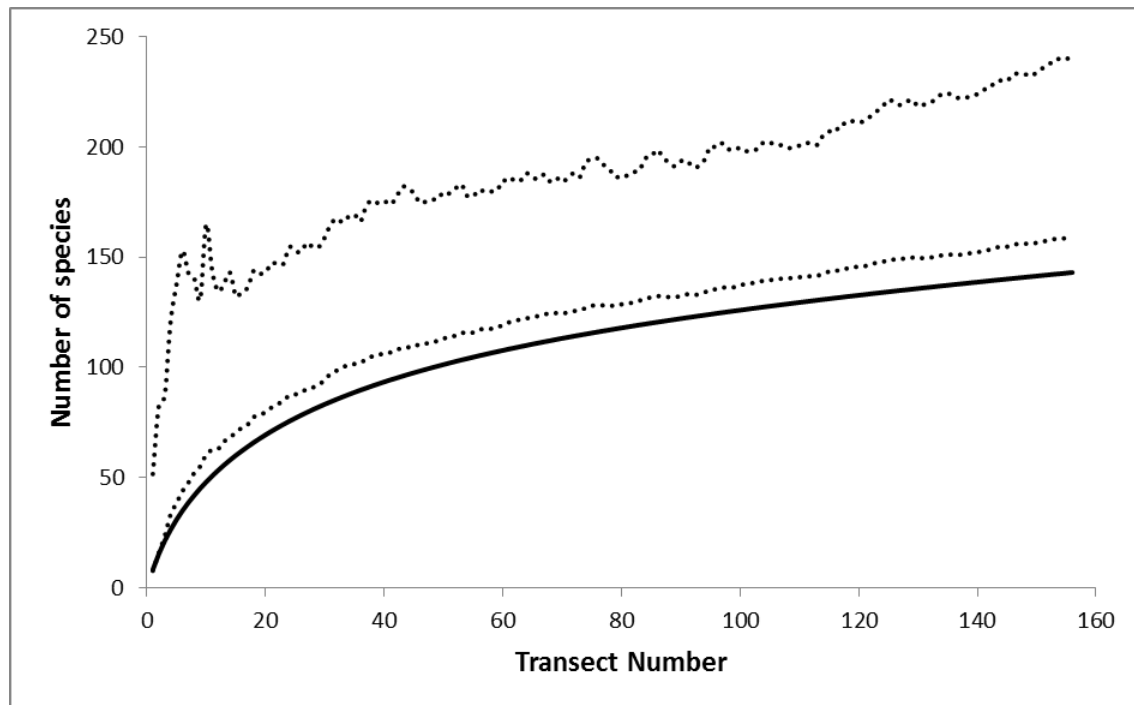


Figure 2: Species accumulation curve for surface dwelling molluscs (25 m x 5 m belt transects) across sites, habitat types, and 3-month periods spanning June 2014 to August 2015, in the Port Stephens study area (solid line) and Chao 1 95% confidence intervals for estimated total species richness (dotted lines). Calculated in EstimateS (Colwell 2013) by averaging across 100 randomisations of transect order.

For summer (2015) data, Γ_{s} diversity was 93 species, α_{s} diversity was on average 25.8 species per habitat, and β_{s} diversity was 3.6 full changes in species composition amongst habitats in the study region, with both α_{s} and β_{s} making major contributions to summer regional Γ_{s} diversity. A total of 44 species were found only within a single habitat, and no species were found in all 8 habitats. The aeolid nudibranch *Pteraeolia ianthina* was the most abundant species with 180 individuals found across 5 habitats (not found in sand, *Posidonia australis*, and *Dendronephthya australis*), and the cephalopod *Octopus tetricus* was the most widespread species, with 54 individuals occurring across 7 habitats (excluding *Zostera muelleri* / *Halophila ovalis*).

5.4.2 Molluscan Alpha_h diversity within habitats

Highest Alpha_h diversities (40 species) occurred in *Ecklonia radiata*, filter feeder, and branching algae habitats, while the lowest Alpha_h diversity (8 species) occurred in sand (Table 2, supplementary Figure S1). A significant relationship was identified between average species richness per transect within habitats and habitat complexity ($P < 0.001$) with significantly higher species richness per transect ($P < 0.018$) occurring in high complexity habitats (14.2 ± 1.1) than in medium (8.2 ± 1.0) and low complexity habitats (4.0 ± 1.0), and significantly higher species richness per transect in medium complexity habitats ($P = 0.004$) than in low complexity habitats. The highest number of habitat-specific species (12) occurred within *E. radiata*, while sand was found to contain no habitat specific species (Table 2). Molluscan assemblages across all habitats displayed high Pielou's evenness (0.64–0.82, Table 2), indicating that species assemblages were not dominated by highly abundant species. SIMPER analyses identified that different habitat types were generally dominated by differing classes of molluscs, with high complexity habitats (i.e. branching algae, filter feeders) dominated by heterobranch gastropods (e.g. *Aphelodoris varia*, *Pteraeolidia ianthina*), habitats with profuse algal or seagrass foliage (i.e. *E. radiata* and *P. australis*) dominated by shelled gastropods (e.g. *Agnewia tritoniformis*, *Calthalotia fragum*), and low complexity habitats with sparse or negligible benthic cover (i.e. *Z. muelleri* / *H. ovalis*, and sand) dominated by cephalopods (e.g. *Octopus tetricus*, *Sepia plangon*) (supplementary Table S1).

Table 2: Alpha_h diversity of molluscs in habitat types (as species richness), habitat Pielou's evenness (J'), and species unique to each habitat. Results for pooled data across 6 transects in each habitat from summer (2015)

Habitat type	Habitat Alpha_h diversity	Habitat Pielou's evenness	Habitat unique species
Filter feeder	40	0.82	6
<i>D. australis</i>	22	0.73	7
Branching algae	40	0.68	8
<i>E. radiata</i>	40	0.73	12
Barrens	26	0.64	2
<i>P. australis</i>	12	0.81	4
<i>Z. muelleri</i> / <i>H. ovalis</i>	18	0.76	5
Sand	8	0.82	0

5.4.3 Molluscan $Beta_h$ diversity amongst habitats

Examination of $Beta_h$ diversity (calculated as Jaccard distance and Bray-Curtis dissimilarity) indicated that $Beta_h$ diversity was generally higher between habitats with differing levels of complexity, with the highest $Beta_h$ diversity occurring between sand and barrens habitats (Jaccard distance = 0.97, Bray-Curtis dissimilarity = 0.99) (Table 3). Two-way nested PERMANOVA analyses for summer (2015) data identified significant differences amongst habitat types for molluscan assemblages ($P < 0.001$), and significant differences amongst sites within habitats ($P = 0.003$). Non-metric multi-dimensional scaling (nMDS) showed clusters of assemblages by habitat type indicating that the differences amongst sites within habitats were small compared to differences amongst habitats (Figure 3). Pairwise tests identified that assemblages amongst habitat types were generally significantly different for habitats with differing complexities (e.g. sand and filter feeders, Table 3).

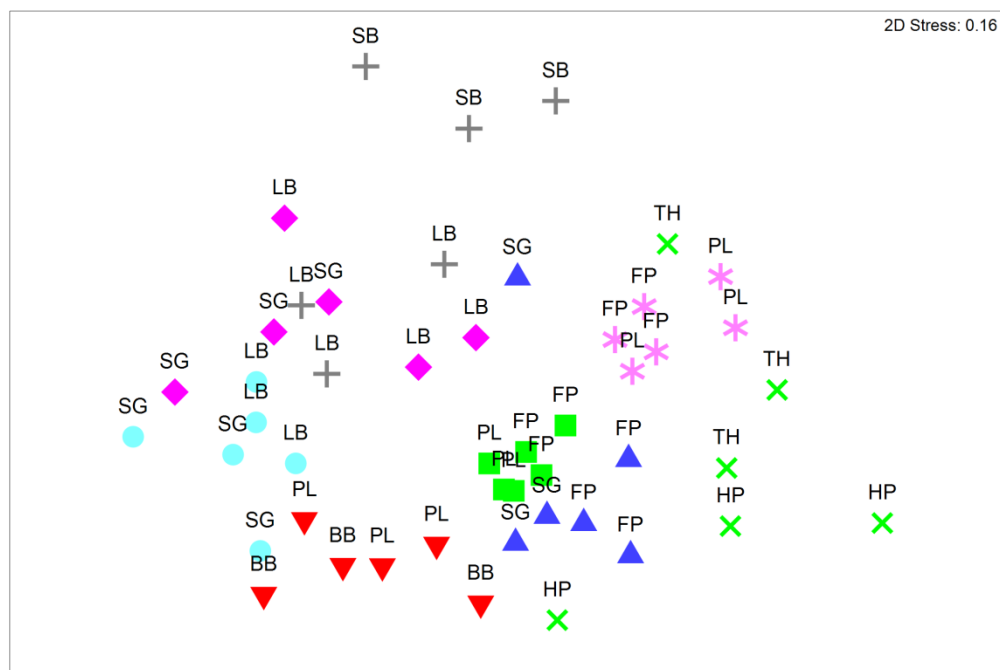


Figure 3: non-metric Multi-Dimensional Scaling plots for summer (2015) molluscan assemblages within *a priori* identified habitat types in the Port Stephens estuary. Symbols denote habitat types (blue triangle = filter feeder, red inverted triangle = *D. australis*, green square = branching algae, pink asterisk = *E. radiata*, green cross = barrens, grey plus = *P. australis*, pink diamond = *Z. muelleri/ H. ovalis*, cyan circle = sand). Labels denote sites as per Table 1 (LB = Little Beach, SB = Shoal Bay, SG = Seahorse Gardens, FP = Fly Point, PL = Pipeline, BB = Bagnalls Beach, HP = Halifax Park, TH = Tomaree Head).

Table 3: Amongst habitat beta diversity between habitat types (as Jaccard distance and Bray-Curtis dissimilarity), shared species between habitats, and PERMANOVA pair-wise tests for differences in mollusc assemblages between habitats (*P*-values) significant values in bold

Habitat 1	Habitat 2	Jaccard distance	Bray-Curtis dissimilarity	Shared species	Pair-wise (<i>P</i>)
Filter feeder	<i>D. australis</i>	0.78	0.88	11	0.023
	Branching algae	0.57	0.65	24	0.158
	<i>E. radiata</i>	0.69	0.86	19	0.028
	Barrens	0.63	0.90	18	0.068
	<i>P. australis</i>	0.92	0.96	4	0.093
	<i>Z. muelleri</i> / <i>H. ovalis</i>	0.82	0.86	9	0.031
	Sand	0.91	0.96	4	0.005
<i>D. australis</i>	Branching algae	0.78	0.84	11	0.026
	<i>E. radiata</i>	0.87	0.95	7	0.020
	Barrens	0.80	0.92	8	0.037
	<i>P. australis</i>	0.90	0.70	3	0.106
	<i>Z. muelleri</i> / <i>H. ovalis</i>	0.92	0.68	3	0.033
	Sand	0.75	0.77	6	0.024
Branching algae	<i>E. radiata</i>	0.77	0.88	15	0.039
	Barrens	0.73	0.94	14	0.036
	<i>P. australis</i>	0.87	0.90	6	0.080
	<i>Z. muelleri</i> / <i>H. ovalis</i>	0.79	0.84	10	0.020
	Sand	0.86	0.93	6	0.004
<i>E. radiata</i>	Barrens	0.65	0.78	17	0.165
	<i>P. australis</i>	0.89	0.86	5	0.112
	<i>Z. muelleri</i> / <i>H. ovalis</i>	0.86	0.86	7	0.029
	Sand	0.96	0.99	2	0.007
Barrens	<i>P. australis</i>	0.91	0.98	3	0.155
	<i>Z. muelleri</i> / <i>H. ovalis</i>	0.84	0.96	6	0.023
	Sand	0.97	0.99	1	0.006
<i>P. australis</i>	<i>Z. muelleri</i> / <i>H. ovalis</i>	0.80	0.44	5	0.636
	Sand	0.82	0.77	3	0.117
<i>Z. muelleri</i> / <i>H. ovalis</i>	Sand	0.92	0.72	2	0.130

Results for pooled data across 6 transects in each habitat from summer (2015).

5.4.4 Abiotic variable surrogacy for molluscan assemblages

BIOENV analyses identified significant Spearman rank correlations (ρ_s) between all abiotic variables examined and molluscan assemblages ($P < 0.01$) indicating that variations in molluscan assemblages correlated with variations in abiotic variables, and therefore abiotic variables could potentially be used as surrogates for molluscan assemblages in conservation planning. The highest correlation was for substrate type ($\rho_s =$

0.523), followed by habitat height ($\rho_s = 0.354$), depth ($\rho_s = 0.230$), and location ($\rho_s = 0.225$). Testing for co-linearity identified that substrate type and habitat height were highly co-linear ($|r| = 0.81$), and substrate type was therefore used to represent both variables in subsequent analyses. Testing correlations between all possible combinations of the remaining abiotic variables and molluscan assemblages identified that the greatest explanatory power for assemblage patterns was provided by the combination of substrate type and depth ($\rho_s = 0.565$). Explanatory power reduced slightly when location was added to substrate type and depth ($\rho_s = 0.554$), indicating that relationships between molluscan assemblages and location were not consistent over the relatively short distances that separated study sites.

5.4.5 Temporal changes in diversity within key habitats

PERMANOVA analyses identified significant differences amongst 3-month periods, habitats, and sites within habitats ($P < 0.001$, all tests) for molluscan assemblages in key filter feeder and *D. australis* habitats. Interactions between habitats and periods were detected ($P = 0.002$), and pairwise tests between habitats identified that habitats were significantly different from each other in all periods ($P < 0.006$, all pairs), with significantly higher species richness per period (averaged across 5 periods, $P = 0.015$) in filter-feeder habitat (46.6 ± 3.4), than in *D. australis* habitat (34.6 ± 1.9). Pairwise tests between periods identified that all periods were significantly different from each other in both key habitats with the exception of Winter (2014) and Winter (2015) in *D. australis* (Table 4). Temporal Beta_p diversity between periods (as Jaccard distance and Bray-Curtis dissimilarity) was generally higher for non-adjacent periods for both key habitat types (Table 4) indicating that differences between mollusc assemblages increased with temporal separation. Metric multidimensional scaling (mMDS) for average molluscan assemblages within each habitat across seasonal time periods indicated that assemblages shifted with time (Figure 4), and a significant cyclical pattern in molluscan assemblages was detected in both filter feeder ($\rho = 0.169$, $P < 0.001$), and *D. australis* ($\rho = 0.219$, $P < 0.001$) habitats.

Table 4: Mollusc species for periods, temporal Beta_p diversity between periods (as Jaccard distance and Bray-Curtis dissimilarity), shared species between periods, and PERMANOVA pairwise tests for differences in mollusc assemblages between periods (*P*-values) significant values in bold.

Period 1 (species)	Period 2 (species)	Jaccard distance	Bray-Curtis dissimilarity	Shared species	Pairwise (<i>P</i>)
(i) Filter feeders					
Winter 2014 (46)	Spring 2014 (52)	0.58	0.50	29	0.024
Winter 2014 (46)	Summer 2015 (55)	0.58	0.63	30	0.001
Winter 2014 (46)	Autumn 2015 (45)	0.46	0.52	32	0.016
Winter 2014 (46)	Winter 2015 (35)	0.53	0.51	26	0.004
Spring 2014 (52)	Summer 2015 (55)	0.51	0.60	35	0.001
Spring 2014 (52)	Autumn 2015 (45)	0.61	0.61	27	0.001
Spring 2014 (52)	Winter 2015 (35)	0.62	0.43	24	0.005
Summer 2015 (55)	Autumn 2015 (45)	0.53	0.54	32	0.043
Summer 2015 (55)	Winter 2015 (35)	0.64	0.61	24	0.001
Autumn 2015 (45)	Winter 2015 (35)	0.52	0.52	26	0.006
(ii) <i>Dendronphthya australis</i>					
Winter 2014 (30)	Spring 2014 (40)	0.57	0.29	21	0.039
Winter 2014 (30)	Summer 2015 (31)	0.61	0.89	17	0.001
Winter 2014 (30)	Autumn 2015 (35)	0.59	0.85	19	0.002
Winter 2014 (30)	Winter 2015 (37)	0.60	0.41	19	0.066
Spring 2014 (40)	Summer 2015 (31)	0.55	0.84	22	0.001
Spring 2014 (40)	Autumn 2015 (35)	0.68	0.82	18	0.001
Spring 2014 (40)	Winter 2015 (37)	0.65	0.21	20	0.001
Summer 2015 (31)	Autumn 2015 (35)	0.65	0.59	17	0.001
Summer 2015 (31)	Winter 2015 (37)	0.61	0.76	19	0.001
Autumn 2015 (35)	Winter 2015 (37)	0.74	0.76	15	0.003

Results for (i) filter feeder and (ii) *Dendronphthya australis* habitats for pooled data from 12 transects in each habitat in each 3-months period.

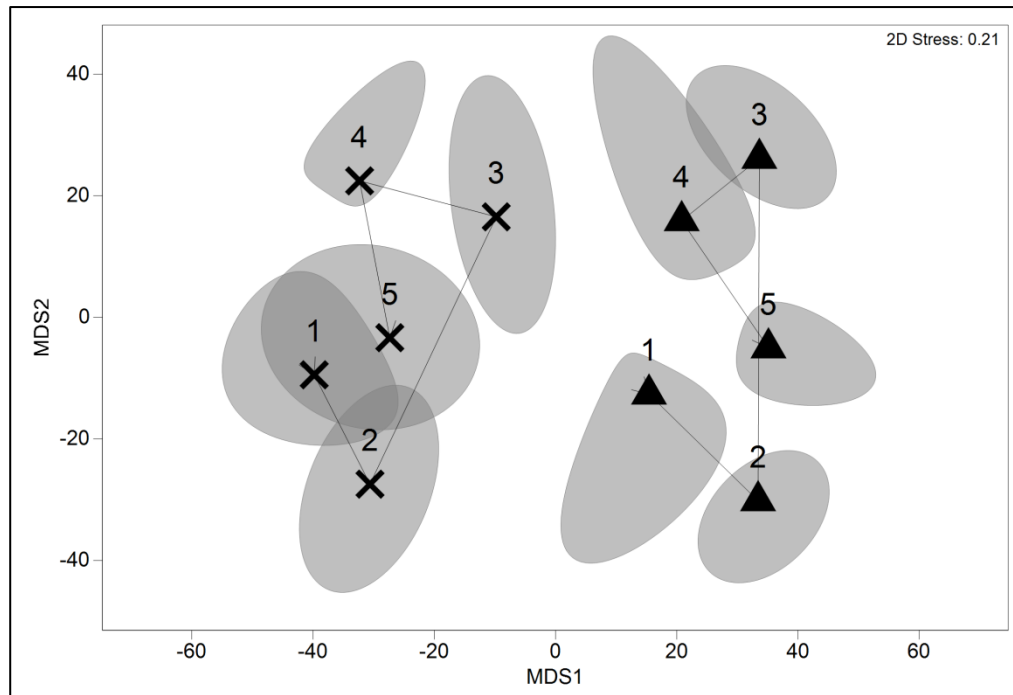


Figure 4: Metric Multi-Dimensional Scaling plot showing similarity of mean molluscan assemblages based on 12 transects within each habitat types in each time period. Numbers denote time periods (1 = winter 2014, 2= spring 2014, 3 = summer 2015, 4 = autumn 2015, and 5 = winter 2015). Crosses denote *Dendronephthya australis* habitat and triangles denote filter-feeder habitat. Ellipses show approximate 95% confidence boundaries for mean assemblage position, calculated by bootstrap averaging across transects with replacement. Lines indicate progression in molluscan assemblages from winter 2014 to winter 2015.

SIMPER analyses identified that temporal variations were primarily driven by changes in the dominant molluscan species and classes within each habitat. Filter feeder habitat was generally dominated by heterobranch species (except in mid-2014 i.e. winter), with the dominant species changing from *Flabellina rubrolineata* in mid-2014, to *Polycera capensis* in late 2014, to *Aphelodoris varia* in early 2015, and finally to *Pteraeolidia ianthina* in mid 2015. In contrast, assemblages in *D. australis* habitat were dominated by a mixture of molluscan classes (i.e. cephalopods, heterobranchs, and shelled gastropods), with both the dominant species and the dominant class changing between periods. The heterobranchs *Dermatobranchus* sp. and *Tularia bractea* and the shelled gastropod *Globovula cavanaghi* dominated from mid–late 2014, the cephalopods *Octopus tetricus* and *Sepia plangon* dominated in early 2015, and the heterobranch *Dermatobranchus* sp. dominated mid 2015 (supplementary Table S2).

5.5 Discussion

Molluscs have been shown to form diverse assemblages across a wide range of ecosystems, including coral reefs (Bouchet *et al.* 2002), temperate reefs (Harrison and Smith 2012; Kelaher *et al.* 2007a; Smith *et al.* 2008), and on the continental shelf (Martins *et al.* 2014). Our study of a temperate estuarine system has demonstrated that estuaries can also harbour diverse molluscan assemblages, with 143 subtidal surface-dwelling species identified. Regional Gamma_t diversity of surface-dwelling molluscs was generated by a combination of: within habitat Alpha_h diversity, which increased with complexity of habitat benthic growth and structure; between habitat Beta_h diversity, which was greatest where there were distinct differences between habitats in terms of benthic growth, substrate type, or depth; and, between period temporal Beta_p diversity resulting from significant changes in molluscan assemblages over time.

5.5.1 Within habitat variation in molluscan assemblages

Molluscan assemblages have been shown to vary within habitats at spatial scales spanning from metres, to thousands of kilometres (Kelaher *et al.* 2004). We found significant differences in assemblages amongst the 8 habitats types examined, and between sites within habitats. Higher within habitat Alpha_h diversity (measured as species richness) was linked to habitat complexity (i.e. varied benthic assemblages, and sizes and shapes of bottom structures) with higher diversity, especially of heterobranch sea slugs, occurring in habitats containing complex benthic assemblages (e.g. filter feeders, branching algae). The high proportion of heterobranch species occurring within Port Stephens has been attributed to varied oceanographic conditions, topography and benthic assemblages (Nimbs *et al.* 2016). Many mollusc species are known to consume filter-feeding organisms or algae (McDonald and Nybakken 1997), and complex benthic assemblages provide niches for numerous molluscs that have specialised dietary requirements (e.g. Smith 2011), thereby promoting increased diversity. Structural complexity has been linked to increased species richness for both fish (Walker *et al.* 2009) and molluscs (Kelaher *et al.* 2007b), with complexity providing shelter from predation, leading to higher survival rates for juvenile recruits and adults (Chemello and Milazzo 2002). In contrast to the more complex habitats, we found Alpha_h diversity to be lower in those habitats with both limited complexity of benthic assemblages, and limited structural complexity (i.e. sand, *Z. muelleri* / *H. ovalis*), reinforcing the conclusion that molluscan diversity was strongly

enhanced in habitats that provided multiple feeding niches and/or places to shelter from predation.

5.5.2 *Variation in molluscan assemblages amongst habitats*

Estuaries are influenced by multiple overlapping environmental gradients including salinity, turbidity, sedimentation, depth, water flow, and substrate type. These gradients have been linked to the presence of complex arrays of benthic habitats (Davis *et al.* 2016b), and habitat complexity has in turn been linked to greater diversity of vertebrate (Harborne *et al.* 2008) and invertebrate (Wells 1998) species. In general, high between habitat Beta_h diversity occurs amongst habitats that have substantial separations along environmental gradients, generating conditions where there is little or no overlap in available ecological niches, and therefore negligible overlap in species assemblages (Whittaker 1972). Our study supports this with significant differences detected in molluscan assemblages amongst the 8 *a priori* defined habitat types investigated, with the greatest dissimilarity occurring for those habitats that differed most in terms of complexity.

Previous research has demonstrated correlations between molluscan assemblages and variations in substrate type (Absalão *et al.* 2006), depth (Martins *et al.* 2014; Rule and Smith 2007), location (Harrison and Smith 2012; Smith *et al.* 2008), and structural complexity (Kelaher *et al.* 2007b). We identified close correlations between molluscan assemblages and substrate type and habitat height, moderate correlations with depth, and a weak association with location. The weak association with location highlighted the relative importance of habitat height, depth, and substrate in structuring molluscan assemblages at a local scale. Substrate type and habitat height were found to be strongly correlated with each other, indicating that these variables were interchangeable in their ability to predict mollusc distributions, and the overall ability of abiotic variables to match patterns in molluscan assemblages was found to strengthen when variables were combined. The greatest explanatory power for predicting mollusc distributions was provided by a combination of substrate type and depth, indicating that these two variables may provide useful surrogates for mollusc diversity when detailed information is lacking.

5.5.3 *Temporal variation in molluscan assemblages*

Previous studies of molluscan diversity have shown that many molluscan species are rare in time and space (Aldea *et al.* 2009; Bouchet *et al.* 2002; Wells 1998). The results from our study concur with these findings with new species still being identified after an

intensive 15-month survey program with a search area of more than 1.9 hectares. We detected significant changes in molluscan assemblages within habitats over time, with both abundances and dominant species changing through time. Temporal variations in molluscan assemblages have been linked to variations in food availability, with abundances of species changing in synchrony with availability of prey species (Williams 1993). Our study results indicate that although food availability may have driven some of the observed changes, it does not explain variations across all species, with *Dermatobranchus* sp., which preys on *D. australis*, showing marked variations in abundance, despite the continued presence of *D. australis* over the entire study duration. Both water temperatures (Hall Jr 1964) and larval recruitment (Schultz *et al.* 2011) have also been linked to changes in mollusc abundances, and these factors may have played a role in the observed cyclic variations observed in molluscan assemblages. The highest species richness in the filter feeder habitat coincided with the summer/autumn periods when water was warmest, and when the East Australian Current has been shown to transport tropical larvae southward (Booth *et al.* 2007). However, in the *D. australis* habitat, no discernible pattern in species richness was observed between periods. The temporal variability in molluscan assemblages demonstrated by our results indicates that capturing a true understanding of regional molluscan diversity would require an assessment covering all habitats, over an extended period, in order to record the presence of rare and ephemeral species.

5.6 Summary

Globally, the health of estuarine systems is declining (Lotze *et al.* 2006) with estuaries threatened by habitat loss, eutrophication, fisheries overexploitation, chemical contamination, introduced species and marine debris (Jackson 2001; Kennish 2002; Smith and Edgar 2014). Certainly, the significant relationship identified between benthic habitat types and surface-dwelling molluscan assemblages in this study demonstrates the critical role that preventing habitat degradation or loss can play in preserving molluscan biodiversity within estuarine systems. The associations identified between molluscan assemblages and habitat type, substrate type, and depth, show that these variables provide useful surrogates for molluscan biodiversity. Our study results indicate that combining these data would provide a high level of discrimination for surface-dwelling molluscan species distributions in conservation planning, with surrogates providing a means of identifying key areas for conservation, without the need for exhaustive biodiversity

surveys in all areas. Biodiversity surveys will still be required in conservation management for monitoring species of concern, and for detection of invasive species. However, the information assembled here can inform effective management actions, by improving understanding of how habitats and abiotic variables combine to contribute to molluscan biodiversity in temperate estuaries, and by illustrating the value of these factors as surrogates for predicting molluscan diversity in conservation planning.

Supplementary content

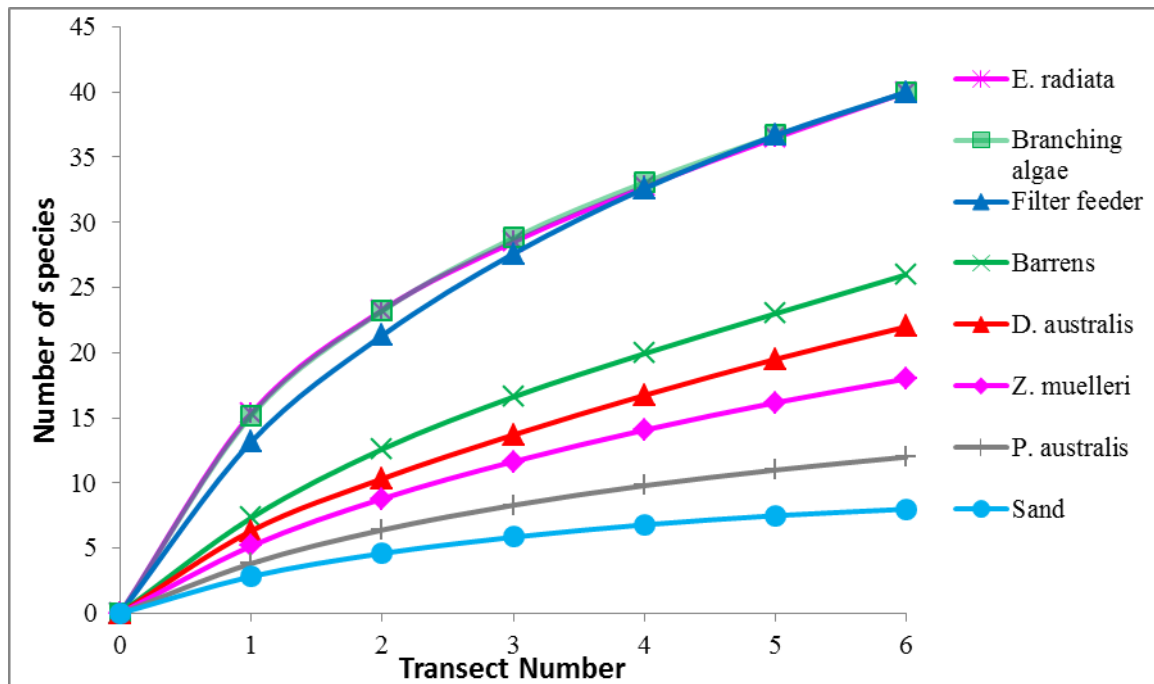


Figure S1: Species accumulation curves for surface dwelling molluscs amongst habitat types in Port Stephens (25 m x 5 m belt transects, summer 2015). Calculated in EstimateS (Colwell 2013) by averaging across 100 randomisations of transect order.

Table S1: Percentage contribution of principle species driving similarities amongst transects within habitats types calculated in SIMPER (% similarity). Results for pooled data across 6 transects in each habitat from summer (2015)

Habitat type	Species driving similarities within habitats
Filter feeder	Polycera capensis 27% Pteraeolidia ianthina 15% Aphelodoris varia 11%
D. australis	Octopus tetricus 64% Sepia plangon 20%
Branching algae	Aphelodoris varia 24% Pteraeolidia ianthina 23% Ceratosoma amoenum 12%
E. radiata	Agnewia tritoniformis 12% Cabestana spengleri 12% Cronia aurantiaca 10%
Barrens	Doriprismatica atromarginata 27% Ostrea angasi 19% Agnewia tritoniformis 15%
P. australis	Calthalotia fragum 41% Eurytrochus strangei 31%
Z. muelleri / H. ovalis	Sepia plangon 46% Idiosepius notoides 32%
Sand	Sepia plangon 59% Idiosepius notoides 20%

Table S2: Principle species driving similarities amongst transects in key habitats (filter feeder, *Dendronephthya australis*) within 3-month periods (Winter 2014-Winter 2015) calculated in SIMPER (% similarity). Results for pooled data from 12 transects in each habitat in each period

Period	Principle species driving similarities (Filter feeder)	Principle species driving similarities (D. australis)
Winter 2014	Octopus tetricus 18% (cephalopod)	Dermatobranchus sp. 32% (heterobranch)
	Flabellina rubrolineata 15% (heterobranch)	Globovula cavanaghi 26% (shelled gastropod)
Spring 2014	Flabellina rubrolineata 23% (heterobranch)	Tularia bractea 29% (heterobranch)
	Ceratosoma amoenum 16% (heterobranch)	Globovula cavanaghi 19% (shelled gastropod)
Summer 2015	Polycera capensis 30% (heterobranch)	Octopus tetricus 47% (cephalopod)
	Aphelodoris varia 11% (heterobranch)	Sepia plangon 16% (cephalopod)
Autumn 2015	Aphelodoris varia 20% (heterobranch)	Sepia plangon 43% (cephalopod)
	Pteraeolidia ianthina 15% (heterobranch)	Globovula cavanaghi 28% (shelled gastropod)
Winter 2015	Pteraeolidia ianthina 29% (heterobranch)	Dermatobranchus sp. 30% (heterobranch)
	Flabellina rubrolineata 17% (heterobranch)	Sepia plangon 21% (cephalopod)

Chapter 6. Defining conservation targets for marine biodiversity using species-area relationships

Chapter 6 examines conservation planning methods to maximise biodiversity protection in Port Stephens, using habitat data from Chapter 2, and data on fish and mollusc assemblages from Chapters 4–5. The assessment examines protection provided by existing no-take zones, uniform percentage targets for benthic habitats, and variable targets generated using species-area relationships for fish and molluscs. The benefits to conservation planning of having improved information on habitat and species distributions are discussed. Chapter 6 was published in *Ocean and Coastal Management* (Davis *et al.* 2017b):

Davis T.R., Harasti D., Kelaher B., Smith S.D.A. (2017b) Defining conservation targets for fish and molluscs in the Port Stephens estuary, Australia using species-area relationships. *Ocean and Coastal Management* **136**: 156–164.

Defining conservation targets for fish and molluscs in the Port Stephens estuary, Australia using species-area relationships

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6.1 Abstract

Effective planning for marine protected areas should be based on conservation targets that are representative of underlying habitats and species distributions. Here, we present the results of an investigation into using species-area relationships (SARs) to define habitat conservation targets for two dominant taxonomic groups (fish and molluscs) using data from the Port Stephens estuary in New South Wales, Australia. Results demonstrated that planning conducted using variable habitat targets, based on SARs, provided significant improvements in representation of habitats and species, compared to planning using uniform (fixed percentage) habitat targets. Planning based on SARs was also found to provide significant improvements in species protection for fish and molluscs when compared with planning implemented without the benefit of detailed biodiversity information. However, SAR targets were found to be sensitive to the function type chosen to represent species distributions (i.e. power-law and exponential), and to the method used for estimation of species richness. Therefore, where SARs are used to set targets in conservation planning, it is important to ensure that they are representative of underlying species distributions. Overall, the improved performance of conservation planning based on SARs indicates the potential for broader application of this technique in planning marine protected areas.

6.2 Introduction

Effective conservation planning in marine protected areas (MPAs) involves systematic scientific investigations and consultation with stakeholders (Airamé *et al.* 2003; Fernandes *et al.* 2005). Given important MPA features are not readily apparent from the surface, planning for MPAs therefore needs to be based on accurate information, and robust methodology (Fernandes *et al.* 2005; Stewart *et al.* 2003). Despite this, MPA planning decisions are often made on an *ad hoc* basis, or with incomplete information, leading to inefficient, or inadequate design (Pressey 1994; Stewart *et al.* 2003).

Marine conservation planning is implemented to accomplish a range of objectives including achieving social and economic goals (Ban *et al.* 2011; Stewart and Possingham 2005), protecting rare and threatened species (Leslie 2005; Powles *et al.* 2000) and conservation of biodiversity (Agardy *et al.* 2003; Leslie 2005). Within this broader management framework, planning to protect biodiversity is frequently conducted using uniform conservation targets for habitats or regions, with a 10% target specified for marine areas in Convention on Biological Diversity Aichi Target 11, and 20% targets widely applied in marine protected area planning (Fernandes *et al.* 2005; Green *et al.* 2009). The use of uniform targets has, however, been criticised because they imply that all regions or habitats are adequately protected by the same criteria, which ignores biological variations across regions and habitats (Agardy *et al.* 2003; Pressey *et al.* 2003). Alternatives to uniform targets are therefore needed (Pressey *et al.* 2007; Svancara *et al.* 2005) and conservation targets based on species-area relationships (SARs) are increasingly being used for this purpose in marine conservation planning (Ashworth *et al.* 2010; Foster *et al.* 2013; Metcalfe *et al.* 2013).

The species-area relationship is one of the most widely recognised patterns in ecology (Connor and McCoy 1979), with the number of species in a taxonomic group increasing with total area (Arrhenius 1921). It therefore follows that the number of species protected will rise as the size of an effective protected area increases, and that SARs can therefore be used to calculate targets aimed at protecting a specified proportion of local species richness (Desmet and Cowling 2004). This conservation approach provides a scientific basis for quantitatively setting non-uniform targets for habitats to protect the species they shelter (Metcalfe *et al.* 2013), and has been identified as being especially useful where protection of a broad range of species is required (Neigel 2003).

Habitat targets for species protection defined based on SARs (SAR habitat targets) depend on the taxonomic group (Holt *et al.* 1999), the type of SAR function (Connor and McCoy 1979), and the methodology used to derive functions from measured species data (Metcalf *et al.* 2013). Multiple functions are available to represent SARs (Connor and McCoy 1979), with power-law functions generally having the broadest applicability (Connor and McCoy 1979; Williamson *et al.* 2001). However exponential functions are also widely applicable (Tittensor *et al.* 2007; Williamson *et al.* 2001) and other types of functions have been derived (Smith 2010; Tjørve 2003). Previous studies examining the use of SARs to set conservation targets for MPAs have generally been based on benthic fauna (Foster *et al.* 2013; Metcalf *et al.* 2013; Rondinini 2011), and have often selected power-law functions *a priori* to represent SARs (Metcalf *et al.* 2013; Rondinini 2011). However, the influence of taxonomic group and type of SAR function on SAR habitat targets has not been fully examined.

Given the complexity associated with defining SAR habitat targets, it is important to demonstrate that this methodology offers benefits, in terms of species protection, compared with using simpler uniform habitat targets, or conservation planning without detailed biodiversity data. Here, we investigate using SARs to set habitat conservation targets for two taxonomic groups (fish and molluscs) for the Port Stephens estuary, New South Wales, Australia, using data gathered over a 15 month period (Davis *et al.* 2016a). We further examine the impact on SAR derived conservation targets for habitats (SAR habitat targets) of using different SAR functions (power-law and exponential), and different algorithms for estimating species richness, with the objective of determining the sensitivity of targets to SAR modelling assumptions. We test the hypothesis that SAR habitat targets provide improved protection for fish and mollusc species, compared to uniform habitat targets. Finally given the Port Stephens estuary is within a large multi-use marine park, we examine the potential for implementing SAR habitat targets within the estuary using Marxan conservation planning software (Ball *et al.* 2009). The study aims to provide marine park management agencies with new approaches to use in conservation planning for protection of sub-tidal estuarine habitats and species.

6.3 Material and methods

6.3.1 Study site

The study was conducted using data from the Port Stephens estuary (Figure 1) which lies within the existing Port Stephens-Great Lakes Marine Park (PSGLMP), managed by the New South Wales (NSW) Marine Estate Management Authority. The PSGLMP is the largest marine park in NSW and was zoned into NSW protection-level categories, including no-take marine sanctuaries, in 2007 (NSW-MPA 2007). The Port Stephens estuary is a tide-dominated drowned river valley (Roy *et al.* 2001), which contains a diverse range of estuarine and marine habitats (Davis *et al.* 2016b). The estuary is of importance in NSW as it contains extensive areas of the threatened seagrass *Posidonia australis* (Creese *et al.* 2009), is the only known location where the soft coral *Dendronephthya australis* occurs in abundance (Poulos *et al.* 2013) and is important for threatened and protected species (Harasti *et al.* 2014b; Wiszniewski *et al.* 2009).

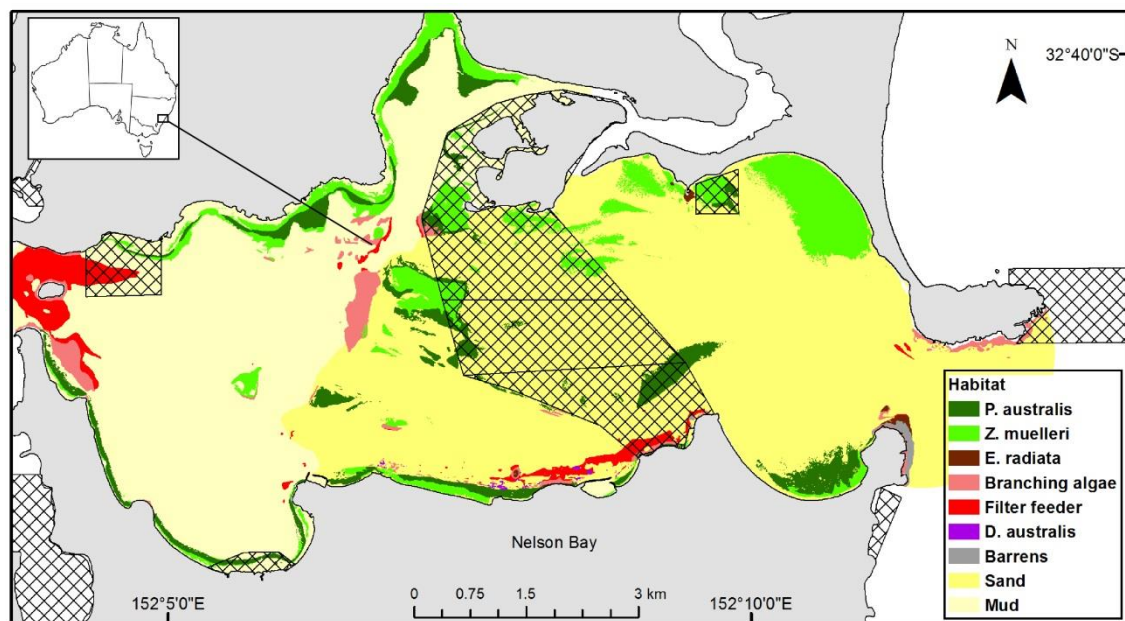


Figure 1: The Port Stephens estuary, New South Wales, Australia with existing no-take areas (hatched areas), and habitat types as described in Table 1.

6.3.2 Assessment of biological assemblages

Within the Port Stephen estuary, habitats were classified into eight major categories (Table 1) by Davis *et al.* (2016b) using the Australian CATAMI system for classifying underwater imagery (CATAMI 2013). Biodiversity data were gathered in each habitat type, every three months from June 2014–August 2015, for fish (Davis *et al.* 2016a) and molluscs, giving twelve randomly situated replicate underwater visual census (UVC) belt

transects (25×5 m) in each habitat, with methods adapted from Smith *et al.* (2008). These taxonomic groups were selected as they have been shown to provide useful surrogates for other phyla in marine assemblages (fish (Ward *et al.* 1999), and molluscs (Smith 2005)). As biodiversity measures for habitats should be based on resident species, and exclude accidental or temporary immigrants, non-resident species (e.g. tropical and pelagic species) were excluded from all calculations. Tropical species typically occur in the study area only for brief periods (Booth *et al.* 2007), and pelagic species are highly variable at small spatial scales (McClanahan *et al.* 2007).

Table 1: Sub-tidal habitat types in the Port Stephens estuary. Habitat types classified by dominant biotic cover as defined by (Davis *et al.* 2016b)

Habitat type	Description
Barrens	Areas of rocky boulders dominated by encrusting coralline algae, with high abundances of the urchin <i>Centrostephanus rodgersii</i>
Branching algae	Areas dominated by mixed branching and filamentous macroalgal species, with filter feeders present in lower abundance
<i>D. australis</i>	Areas dominated by the soft coral <i>Dendronephthya australis</i> , with other filter feeders and macroalgae present in lower abundance
<i>E. radiata</i>	Areas dominated by the macroalgae <i>Ecklonia radiata</i> (i.e. kelp)
Filter feeder	Areas dominated by filter feeders (i.e. sponges, ascidians, hydroids, bryozoans, and corals) with macroalgae present in lower abundance
<i>P. australis</i>	Areas dominated by the seagrass <i>Posidonia australis</i>
Sand/Mud	Sand or mud substrate with minimal biotic cover (i.e. <10%)
<i>Z. mulleri</i>	Areas dominated by intermingled seagrasses <i>Zostera muelleri</i> ssp. <i>capricorni</i> and/or <i>Halophila ovalis</i>

The ability of power-law functions (Eq. 1) and exponential functions (Eq. 2) to represent fish and mollusc SARs was evaluated by fitting both types of functions to species accumulation curves generated for fish and mollusc data (Figure 2),

$$S = c A^z \quad (1)$$

$$S = d + e \log(A) \quad (2)$$

(S = species, A = area, z = slope in log-log space, e = slope in log-linear space, c , d = constants dependent on function and region)

Species accumulation curves were generated by averaging across 100 random transect sequences, using EstimateS (Colwell 2013), for the 96 transects conducted (i.e. twelve replicate transects in eight habitats). The accuracy of SAR function fit to measured species

accumulation curves was assessed for both power-law and exponential functions using least-squares error estimates. Exponential functions (fish, $R^2 = 0.998$ and molluscs, $R^2 = 0.982$) provided a superior fit to observed distributions, compared with power-law functions (fish, $R^2 = 0.928$ and molluscs $R^2 = 0.963$, Figure 2), indicating that exponential functions provide more accurate representation of SARs for fish and molluscs within the study area.

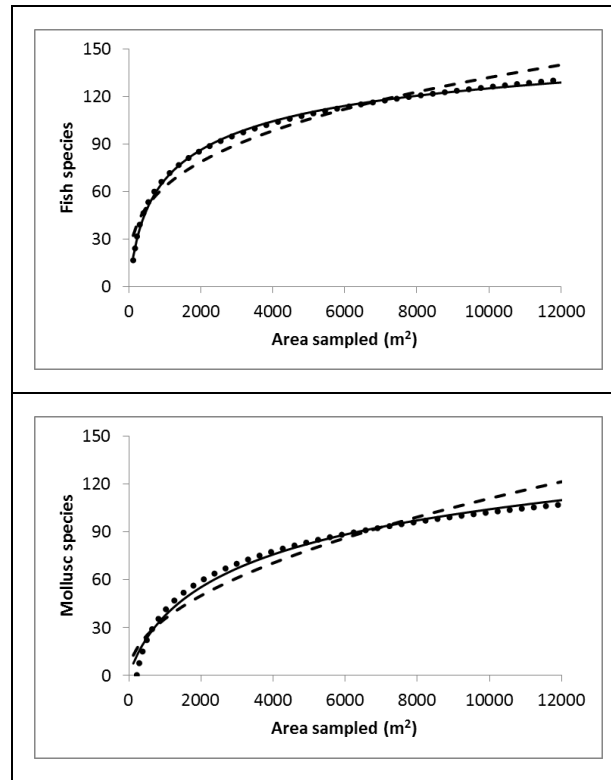


Figure 2: Species accumulation curves (solid lines) across all subtidal habitats in the Port Stephens estuary for fish and molluscs, and species-area relationship curves for exponential functions (dotted lines), and power-law functions (dashed lines).

6.3.3 Evaluation of conservation target sensitivity to SAR modelling assumptions

To evaluate sensitivity of SAR habitat targets to SAR modelling assumptions, targets were calculated for two taxonomic groups (fish and molluscs), for two different SAR function types (power-law and exponential), and two different algorithms for estimating species richness (Bootstrap and Jackknife 2). SAR habitat targets were calculated to protect 80% of the selected taxonomic group within each habitat, with the species protection level set at 80% as recommended by the Joint Nature Conservation Committee for conservation of marine species (Ashworth *et al.* 2010). Comparisons among SAR habitat targets for alternate methods were conducted using two-tailed paired Student's *t*-tests.

Species-area relationships were derived for each habitat, taxonomic group, function type, and species richness estimation technique, using the methodology proposed by Desmet and Cowling (2004), with functions fitted through (S_h, A_h) , where S_h = the average species richness per transect in habitat-h, and A_h = habitat transect area (0.015 ha), and (S_{Th}, A_{Th}) , where S_{Th} = the estimated total species richness in habitat-h, and A_{Th} = total area of habitat-h in the study region. From these, the slope (z) of the power-law function in log-log space (Eq. 3), and the slope (e) of the exponential function in log-linear space (Eq. 4) were calculated. Species-area relationship habitat targets (A') were then calculated to provide specified species protection levels (S') using equations derived for power-law functions (Eq. 5), and logarithmic functions (Eq. 6, ref. supplementary Appendix S1 for derivations).

$$z = (\log(S_{Th}) - \log(S_h)) / (\log(A_{Th}) - \log(A_h)) \quad (3)$$

$$e = (S_{Th} - S_h) / (\log(A_{Th}) - \log(A_h)) \quad (4)$$

$$A' = \sqrt[z]{S'} \quad (5)$$

$$A' = 10^{((S'-1)S_{Th}/e)} \quad (6)$$

Values for S_h and A_h were obtained from sampling data for each taxonomic group, values for A_{Th} were calculated using ArcMap (<http://www.esri.com/>, accessed 17 April 2015) using habitat maps of the Port Stephens estuary (Davis *et al.* 2015b), and values for S_{Th} were estimated for each taxonomic group using either Bootstrap or Jackknife 2 species richness estimation techniques in EstimateS (Colwell 2013). Estimated values for S_{Th} were calculated based on 100 random sampling sequences for each taxonomic group, across 12 transects in each habitat. The adequacy of sampling for calculation of S_{Th} was assessed by examining standard deviations between the final two estimates for S_{Th} (i.e. S_{Th} obtained from data for 11 and 12 transects), and ensuring that these were <5% of S_{Th} , as recommended by Desmet and Cowling (2004). Maximum deviations between estimates for S_{Th} , calculated from 11 and 12 transects, were 3.7% for fish and 4.3% for molluscs. Bootstrap species richness estimates were selected as these generally provided the lowest species richness estimates from the alternative options available in EstimateS (i.e. ACE, Bootstrap, Chao 1, Chao 2, ICE, Jackknife 1, Jackknife 2) and were used in the study conducted by Desmet and Cowling (2004). Jackknife 2 estimates were selected as these were generally among the highest species richness estimates for the study data, and Jackknife 2 has been shown to provide accurate estimates for species richness for small numbers of samples, as was the case for this study (Colwell and Coddington 1994).

6.3.4 Conservation strategy evaluation

Protection levels for fish and mollusc species were compared among four alternate conservation strategies: (1) existing no-take areas; (2) uniform habitat targets for each habitat type; (3) SAR habitat targets for fish; and (4) SAR habitat targets for molluscs. Comparisons were conducted for the same total protected area (i.e. the area of existing no-take areas, 960 ha) determined from habitat maps of the Port Stephens estuary (Davis *et al.* 2015b) using ArcMap . Uniform habitat targets (18.5%) were calculated from the ratio of total target area (960 ha) to total study site area (5181 ha). Habitat targets based on SARs were calculated to provide equal protection in each habitat for the selected taxonomic group. Comparisons were conducted using one-tailed, paired Student's *t*-tests for differences in average species protection among strategies, examining the hypothesis that species protection for conservation based on SAR habitat targets would be higher than for uniform habitat targets, and existing no-take areas.

For each conservation strategy, protection levels for fish and molluscs were calculated using SARs for each taxonomic group based on exponential functions and Jackknife 2 estimates for total species richness. Exponential functions were selected as they provided the most accurate representation of SARs for the study region (Figure 2), and Jackknife 2 estimates were used as these provided the most conservative (i.e. highest) estimates for total species richness.

6.3.5 Application of conservation targets in the Port Stephens estuary using Marxan

Marxan analyses were conducted using SAR habitat targets for fish and molluscs in the Port Stephens estuary, with a total target protected area of 960 ha. One hundred Marxan solutions were generated for each set of targets, using 614 hexagonal planning units (PUs), each with area ≤ 10 ha. Hexagonal PUs were selected as these provide more efficient solutions than square PUs (Nhancale and Smith 2011). Ten-hectare PUs were used as they provide sufficient spatial resolution to distinguish among habitats across the study area, with smaller PUs shown to provide more efficient solutions in conservation planning (Pressey and Logan 1998). A boundary length modifier (BLM) was applied to Marxan solutions to encourage compactness in conservation zones, with the BLM adding a cost penalty to solutions proportional to the free-edge length of selected PUs in solutions (Ardron *et al.* 2008). The magnitude of the BLM (0.02) was selected so that average

values for BLM cost penalties had the same order of magnitude as PU costs, as recommended by Ardron *et al.* (2008). Calibrations were conducted to examine the effect of differing values for the BLM, with the selected value providing a good compromise between solution compactness and efficiency.

6.4 Results

6.4.1 Fish and mollusc species richness

Observations of fish and mollusc species across habitats identified 178 species of fish and 111 species of molluscs. Species richness in the study region was found to generally be higher for habitats with complex biotic assemblages and/or physical structures, with average species richness increasing from 6.6 ± 0.5 fish/transect and 2.3 ± 0.4 molluscs/transect in sand/mud, to 26.3 ± 1.8 fish/transect and 12.4 ± 1.1 molluscs/transect in branching algae (Table 2). Estimates of total species richness, from Bootstrap and Jackknife 2 extrapolation of species accumulation curves, also varied among habitats from 25–91 for fish, and from 10–87 for molluscs (Table 2). Jackknife 2 species richness estimates were significantly higher than Bootstrap estimates across habitats for both fish and molluscs ($P < 0.001$, both *t*-tests).

Table 2: Average species richness per 25×5 m transect (mean $\pm$ S.E, n=12) and Bootstrap / Jackknife 2 estimates of total species richness for fish and mollusc species in the Port Stephens estuary by habitat type (as per Table 1)

Habitat type	Average species / transect (Fish)	Bootstrap species richness (Fish)	Jackknife 2 species richness (Fish)	Average species / transect (Molluscs)	Bootstrap species richness (Molluscs)	Jackknife 2 species richness (Molluscs)
Barrens	22.2 ± 1.2	61	79	5.2 ± 0.6	27	40
Branching algae	26.3 ± 1.8	76	91	12.4 ± 1.1	58	87
<i>D. australis</i>	12.2 ± 0.8	38	52	5.9 ± 0.6	33	50
<i>E. radiata</i>	19.3 ± 1.3	55	60	11.4 ± 1.0	50	68
Filter feeder	26.1 ± 2.6	73	86	10.3 ± 1.3	56	76
<i>P. australis</i>	11.3 ± 1.1	43	49	3.0 ± 0.5	14	19
Sand/Mud	6.6 ± 0.5	25	33	2.3 ± 0.4	10	14
<i>Z. mulleri</i>	12.3 ± 1.1	38	47	3.5 ± 0.7	21	31

6.4.2 Influence of species-area relationships on conservation targets

Habitat targets based on SARs, to preserve 80% of species, were found to vary substantially among habitats, were highest for habitats with lowest spatial extents, and were significantly influenced by factors used to define SARs (Table 3). Average SAR

habitat targets were significantly higher for molluscs ($23.5 \pm 2.3\%$, mean $\pm$ S.E.) than for fish ($16.0 \pm 1.7\%$, $P < 0.001$), primarily due to most molluscs being rarer and more variable than fish (Table 2). Habitat targets were also significantly influenced by the choice of SAR function, with average SAR habitat targets based on power-law functions (Table 3 (1)-(2)) significantly higher than those for exponential functions (Table 3 (3)-(4), $P < 0.001$). This difference resulted from SARs based on power-law functions predicting lower levels of species protection than exponential functions, for the same SAR habitat target. Therefore a greater proportion of each habitat was required in no-take areas to protect 80% of species for SARs based on power-law functions (e.g. Figure 3). Similarly, SAR habitat targets for Jackknife 2 species richness estimates (Table 3) were significantly higher than those for Bootstrap estimates ($17.6 \pm 1.9\%$, Table 3, $P < 0.001$) (e.g. Figure 3).

Table 3: Habitat areas and species-area relationship habitat targets (%) required to protect 80% of species (fish / mollusc) in habitats in the Port Stephens estuary for species-area relationships based on: (1) Power-law function with Bootstrap estimate of species richness; (2) Power-law function with Jackknife 2 estimate; (3) Exponential function with Bootstrap estimate; and (4) Exponential function with Jackknife 2 estimate

Habitat type	Area (ha)	(1) Power-law and Bootstrap (fish / mollusc)	(2) Power-law and Jackknife 2 (fish / mollusc)	(3) Exponential and Bootstrap (fish / mollusc)	(4) Exponential and Jackknife 2 (fish / mollusc)
Barrens	9.8	23.2 / 40.9	31.1 / 48.3	12.4 / 19.3	15.7 / 21.6
Branching algae	96.6	15.3 / 27.5	20.0 / 35.9	6.5 / 10.3	8.1 / 12.4
<i>D. australis</i>	3.6	32.7 / 35.4	42.1 / 45.9	18.8 / 20.0	22.9 / 24.4
<i>E. radiata</i>	6.4	26.4 / 38.9	29.4 / 45.9	14.6 / 19.8	15.9 / 22.4
Filter feeder	132.8	13.4 / 29.3	17.7 / 35.5	5.6 / 10.3	7.0 / 11.7
<i>P. australis</i>	264.4	18.7 / 23.7	22.1 / 30.2	6.6 / 7.9	7.5 / 9.4
Sand/Mud	4247.7	12.1 / 13.9	17.1 / 21.4	3.2 / 3.6	4.1 / 4.9
<i>Z. mulleri</i>	419.5	13.1 / 27.3	17.6 / 34.7	4.7 / 8.2	5.9 / 9.6

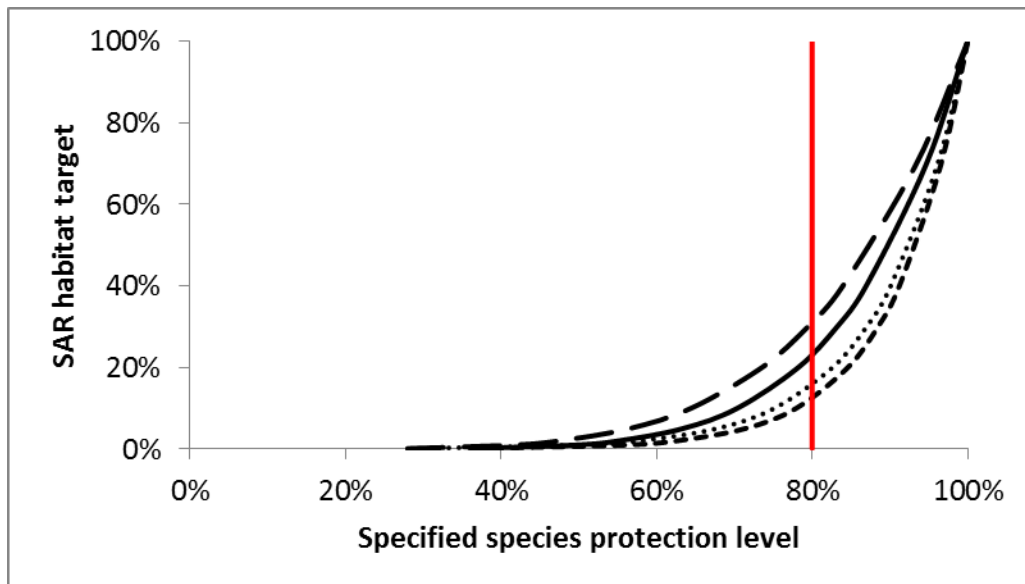


Figure 3: Species-area relationship (SAR) habitat targets, for barrens habitat, to provide specified species protection levels for fish in the Port Stephens estuary. Curves based on: Power-law function with Jackknife 2 estimate (long dashes); Power-law function with Bootstrap species richness estimate (solid line); Exponential function with Jackknife 2 estimate (dotted line); Exponential function with Bootstrap estimate (short dashes). 80% species protection target shown as vertical red line.

Overall, the greatest influence on SAR habitat targets resulted from the choice of function used to represent SARs, with choice of taxonomic group having a lesser effect, and choice of species richness estimator having the lowest effect on targets. The most conservative (i.e. highest) SAR habitat targets occurred for habitats with limited spatial extents, where SARs were generated using power-law functions, based on molluscs, with Jackknife 2 species richness estimates (Table 3).

6.4.3 Habitat and species protection levels for alternate conservation strategies

Comparisons among MPA conservation strategies showed substantial differences in protection levels for habitats, fish, and molluscs for alternate strategies (Table 4). Within existing no-take areas, protection for habitats varied from 0.0% for the soft-coral habitat *D. australis*, to 25.4% for the seagrass habitat *P. australis*, for fish species from 0.0–89.4%, and for mollusc species from 0.0–88.8%. The high variability in protection levels in existing no-take areas suggests that a lack of detailed biodiversity information prior to implementation in 2007, handicapped selection of representative habitat areas, especially for the least extensive habitats in the study area (i.e. barrens, *D. australis*, and *E. radiata*).

Applying uniform 18.5% habitat targets across habitats provided substantial improvement in protection levels for habitats and species, compared to existing no-take areas, with the same total protected area (960 ha, Table 4). Uniform habitat targets provided protection for equal proportions of all habitats (18.5%), and average protection levels for species across habitats were significantly higher for uniform targets ($83.7 \pm 1.1\%$) than for the existing no-take areas ($71.6 \pm 7.2\%$, $P = 0.040$, Table 4). Using uniform habitat targets also reduced variability in protection levels for species across habitats, with standard deviations in protection levels of 1.1% for uniform targets, compared to 7.2% for existing no-take areas.

Simulated implementation of SAR habitat targets provided further improvements in species protection levels, compared to uniform habitat targets, with significant increases in average protection levels for species ($P < 0.001$, both tests) for SARs based on fish ($88.3 \pm 0.3\%$) and molluscs ($89.0 \pm 0.2\%$, Table 4). These improvements were achieved through increased protection for less extensive habitats, and for habitats with higher species richness, generating increased protection for species for the same total protected area (960 ha).

Table 4: Habitat protection levels (%) and species protection levels (%) for fish and molluscs for alternate conservation strategies in the Port Stephens estuary (total protected area 960 ha); 1) Existing no-take areas; 2) conservation targets based on uniform protection for habitat; 3) species-area relationship (SAR) habitat targets for fish data; 4) SAR habitat targets for mollusc data. Species protection levels calculated using species area relationships with exponential functions and Jackknife 2 estimates of total species richness

Habitat type	1) Existing no-take areas			2) Uniform habitat targets			3) SAR habitat targets-fish			4) SAR habitat targets-molluscs		
	Habitat	Fish	Molluscs	Habitat	Fish	Molluscs	Habitat	Fish	Molluscs	Habitat	Fish	Molluscs
Barrens	10.5	75.6	70.5	18.5	81.8	77.9	36.3	89.1	87.1	40.6	90.2	88.2
Branching algae	9.3	81.1	77.2	18.5	86.6	83.8	25.2	89.1	86.6	29.2	90.4	88.2
<i>D. australis</i>	0.0	0.0	0.0	18.5	77.1	76.2	44.6	89.1	89.5	43.6	89.2	88.2
<i>E. radiata</i>	8.0	72.6	66.3	18.5	81.6	77.5	36.6	89.1	86.3	41.4	90.2	88.2
Filter feeder	19.7	87.8	84.9	18.5	87.3	84.3	23.3	89.1	86.4	28.3	90.2	88.2
<i>P. australis</i>	25.4	89.4	88.4	18.5	86.9	85.7	24.3	89.1	87.9	24.9	89.0	88.2
Sand/Mud	18.2	89.3	88.8	18.5	89.4	88.8	17.5	89.1	88.5	16.8	88.9	88.2
<i>Z. mulleri</i>	19.4	88.4	86.0	18.5	88.1	85.6	21.3	89.1	87.0	25.1	90.0	88.2
Average		73.0±10.7	70.3±10.5		84.8±1.5	82.5±1.7		89.1±0.0	87.4±0.4		89.8±0.2	88.2±0.0

6.4.4 Implementation of conservation strategies in the Port Stephens estuary

Marxan analyses to implement SAR habitat targets for fish and molluscs identified that multiple efficient solutions were possible for both taxonomic groups (Figure 4). Examination of the drivers behind frequently selected planning units (PUs) in Marxan solutions found that selection frequencies for PUs in localised regions were primarily driven by targets for specific habitat types (Figure 4a). Thus, targets for *E. radiata* and barrens drove selection frequency for PUs at the entrance to the estuary (region “A”, Figure 4a), and targets for *D. australis* and filter-feeder habitats drove selection frequencies along the southern shoreline of the central section of the estuary (region “B”, Figure 4a). Finally, selection frequencies in the entrance to the Myall Lakes (region “C”, Figure 4a) were to meet targets for seagrasses and branching algae, while PUs at the western end of the estuary (region “D”, Figure 4a) were selected to meet targets for filter feeders and branching algae.

Comparisons between locations of frequently selected PUs from Marxan solutions, and existing no-take areas, identified that existing no-take areas did not incorporate most of the PUs with high selection frequencies (Figure 4). The lack of overlap between existing no-take areas, and frequently selected PUs in Marxan solutions based on SARs indicates that existing no-take areas require substantial modification to improve levels of protection to those obtained in analyses using SARs.

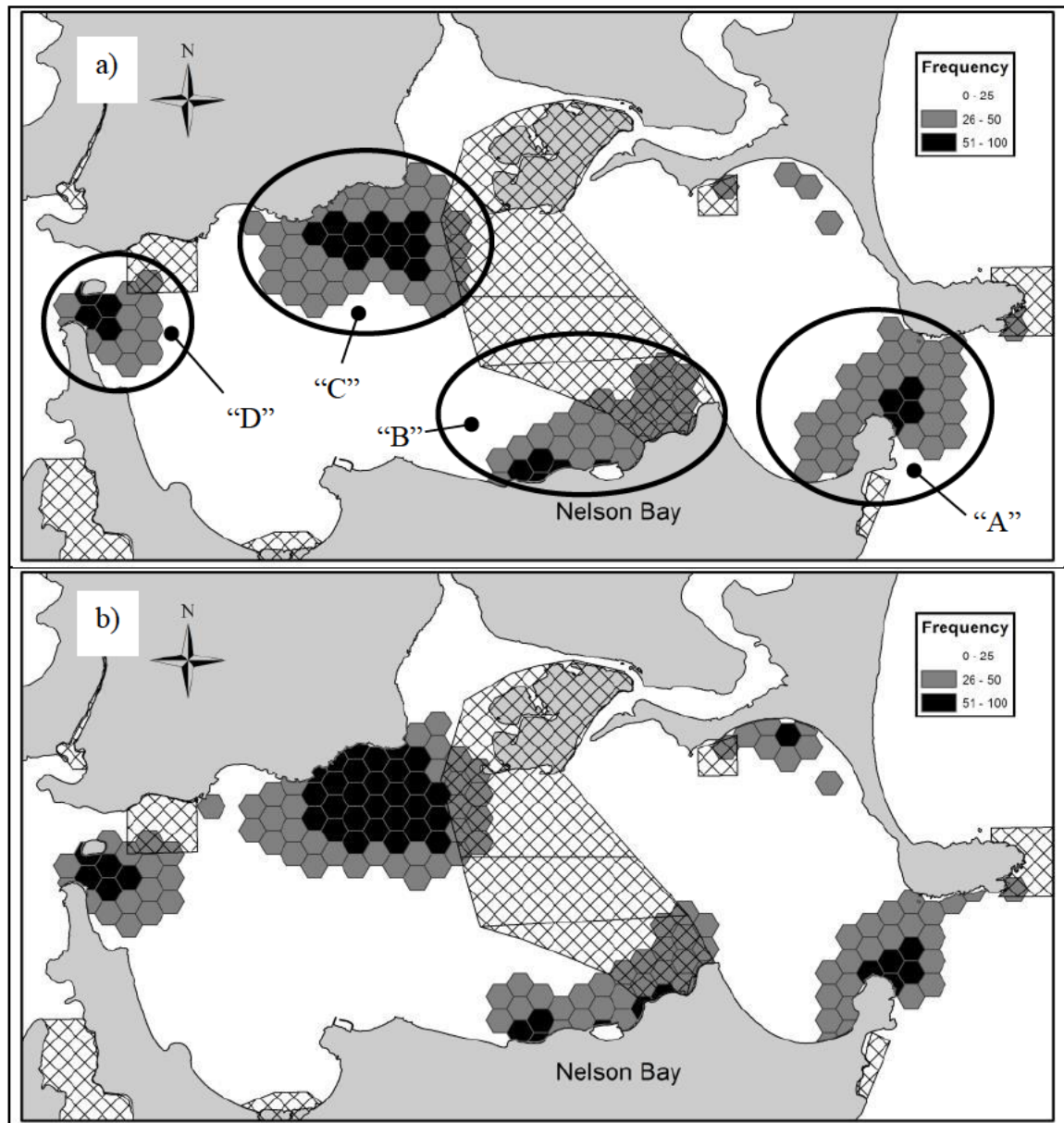


Figure 4: Marxan planning unit selection frequencies for protection of a) fish and b) molluscs in the Port Stephens estuary. Frequencies based on 100 solutions with targets for species-area relationships based on exponential functions with Jackknife 2 species richness estimates. Port-Stephens-Great Lakes Marine Park existing no-take areas shown as hatched areas. Circled regions (“A”-“D”) indicate areas where planning unit selection frequency was driven by targets for specific habitat types as discussed in the main text.

6.5 Discussion

Achieving efficient protection of species in conservation planning requires information on habitat and species distributions, and the use of appropriate methods for setting conservation targets (Margules and Pressey 2000). Here, we demonstrate that significant

improvements in species protection can be achieved using variable conservation targets for habitats based on SARs, compared to uniform targets. However SAR habitat targets were found to be significantly influenced by the taxonomic group used in their derivation, the type of SAR function selected, and the species richness estimates used to derive SARs. Therefore, although SAR habitat targets can provide theoretical improvements in conservation efficiency, it is important that the methodology used to define SARs is appropriate and adequately represents underlying species distributions (Connor and McCoy 1979).

Species-area relationships often vary between taxonomic groups (Holt *et al.* 1999) and our results indicate that significant differences occur in targets for habitats derived using SARs from different taxonomic groups, with lower targets calculated for fish than for molluscs. These differences were primarily driven by greater spatial variability in mollusc populations among transects, necessitating protection of a larger proportion of their habitats in order to achieve the same level of protection as fish. These results indicate that the applicability of targets based on SARs across different taxonomic groups is limited, and careful consideration should be given to these limitations when SARs are used to set targets for the conservation of biodiversity across multiple taxonomic groups. Ideally, where data is available, habitat targets should be calculated across all taxonomic groups and the most conservative habitat targets used in conservation planning.

It is also important that functions used to represent SARs are only selected *a priori* where evidence exists to support use of the chosen function. If this evidence is not available, then functions need to be tested against observations, and the most appropriate function selected (Connor and McCoy 1979; He and Legendre 1996). We found that choice of different SAR functions resulted in significant differences in calculated conservation targets. Therefore, inappropriate *a priori* selection of a SAR function can strongly affect predicted protection levels for species, and the habitat conservation targets required to achieve these. Power-law functions, despite being widely applied (Williamson *et al.* 2001), are not the only type of curve that can, or should, be used to represent SARs (Connor and McCoy 1979). Here, we identified that exponential functions more accurately represented species distributions for both fish and molluscs, with exponential functions recommended for studies where sampling occurs over small areas, as is the case in this study (He and Legendre 1996).

Inaccuracies in habitat targets resulting from use of inappropriate SAR functions could potentially be exacerbated by poor selection of algorithms for estimation of species richness. For example, Metcalfe *et al.* (2013) found that choice of algorithms influenced targets based on SARs. In our study there were also significant differences between habitat targets calculated using species richness from different species richness estimation algorithms. We found that the most conservative habitat targets were provided by using the algorithm predicting the highest species richness (Jackknife 2), but importantly we found that algorithm choice had a lower effect on habitat targets than choice of SAR function and taxonomic group.

6.5.1 Comparison of conservation strategy performances

Although uniform targets have been widely applied in marine conservation planning (Fernandes *et al.* 2005; Green *et al.* 2009), they are no longer seen as an ideal approach due to their lack of connection to underlying biodiversity and ecological processes (Agardy *et al.* 2003; Pressey *et al.* 2003). Indeed, we found that conservation targets for habitats, based on SARs, provided significant improvements in species protection levels for fish and molluscs when compared with uniform habitat targets. Therefore, our results support the study hypothesis that habitat targets based on SARs outperform uniform habitat targets, in terms of protection for fish and molluscs species.

Within the Port Stephens estuary, planning for existing no-take areas was conducted without the detailed biodiversity information on distributions of habitats and fish and molluscs species that is now available (Davis *et al.* 2016a; Davis *et al.* 2016b). Studies in both terrestrial (Grand *et al.* 2007) and marine environments (Stewart *et al.* 2003) have identified that planning using inadequate data leads to inefficient design of terrestrial reserves and marine no-take areas. In our study, the existing no-take areas provided inadequate protection for some habitats, and the species they contain, especially *D. australis*, and *E. radiata*. These results clearly highlight the importance of having adequate biodiversity information prior to conducting systematic conservation planning.

The absence of adequate protection within existing no-take areas for the soft coral *D. australis*, is of particular concern. The Port Stephens estuary is the only location where this species is known to occur in abundance (Poulos *et al.* 2015), and there is evidence that the habitat is under threat (Harasti 2016; Smith and Edgar 2014). *D. australis* shelters a number of protected and endemic species, especially syngnathids (seahorses and pipefish,

Harasti *et al.* 2014c), and loss of *D. australis* habitat has been linked to declines in populations of the protected seahorse *Hippocampus whitei* (Harasti 2016). Species with limited geographic ranges are at higher risk of extinction, especially if they are subjected to disturbances (Purvis *et al.* 2000) and estuarine systems, such as Port Stephens, are subjected to high levels of disturbance due to their proximity to centres of human habitation (Kennish 2002). Achieving adequate levels of protection for *D. australis* is therefore vital to prevent local extinction of this species, and the species it shelters. While increased representation of *D. australis* within no-take areas will address some of the threats faced by this habitat (i.e. those related to fishing), the habitat also faces a number of threats that are not addressed by no-take zones (e.g. entanglement by marine debris (Smith and Edgar 2014) and mooring damage (Harasti 2016)). An integrated management approach, addressing all threats faced by *D. australis*, is therefore required to provide adequate protection for this habitat.

In contrast, *E. radiata* (kelp) is a broad-ranging habitat-forming species, occurring throughout NSW (Coleman *et al.* 2011; Underwood *et al.* 1991) and more generally across temperate areas of the southern hemisphere (Wernberg *et al.* 2003). The current low level of protection for this habitat within the Port Stephens estuary should therefore be compensated for, to some extent, by protection of other areas of the habitat within marine sanctuaries across its range.

Ideally, conservation targets should be influenced by the spatial extent of habitats, and by species distributions, with increased protection for rarer and more diverse habitats, as these are at increased risk of significant species losses and extinctions (Purvis *et al.* 2000; Sala *et al.* 2002). Examination of the outcomes of using SARs to set conservation targets found that this methodology achieved these objectives, with elevated protection levels for rarer habitats, and habitats with higher species richness.

6.5.2 *Application of conservation strategies using Marxan*

Setting habitat targets is only one stage in the conservation planning process and meeting conservation objectives also requires that these theoretical targets can be achieved in practice within the areas of interest (Margules and Pressey 2000). Here, we identified that habitat targets generated using SARs for fish and molluscs could be applied in the Port Stephens estuary, with multiple efficient solutions obtainable using Marxan. Implementation of these solutions would, however, require substantial modification of

existing no-take areas to incorporate additional areas of some habitats. This could be achieved with no net increase in total conserved area by allowing small reductions in the protected area for more extensive habitats (e.g. sand or mud). The Marxan solutions provide guidance on areas that could be incorporated into existing no-take areas to achieve improvements in protection for habitats and species, and those which could be removed from existing no-take areas to offset the costs associated with the improvements, and to improve the overall efficiency of conservation planning.

While planning using conservation targets for habitats from SARs has been shown to provide efficient solutions for species protection, these solutions have substantial limitations. Habitat targets from SARs are set to protect a specified level of local species richness, based on a limited temporal snapshot of species diversity, but do not ensure that viable populations are protected (Smith 2010), and do not provide insight into which species are protected and which are not (Desmet and Cowling 2004; Metcalfe *et al.* 2013). Additional consideration therefore needs to be given in conservation planning to protecting areas that are of importance to threatened species. Conservation planning also needs to account for threats to habitats, and the risk levels associated with those threats, incorporating habitat vulnerability as an additional criterion to rank conservation need, with increased levels of protection indicated for habitats which are at high risk from serious threats (Green *et al.* 2009). Habitats also need additional protections where threats are not addressed by no-take areas, such as those from pollution, climate change, coastal development, invasive marine species and increased nutrient flows (Crain *et al.* 2009). Finally, it should be noted that achieving conservation outcomes is only one facet of systematic conservation planning, with social and economic objectives equally important if conservation plans are to be successfully implemented and adopted by the wider community (Green *et al.* 2009; Stewart and Possingham 2005).

6.6 Conclusions

Using SARs to systematically define conservation targets for habitats can provide significant improvements in representation of habitats and species in conservation planning. Habitat targets based on SARs were found to provide significant improvements in protection for fish and mollusc species, compared to uniform habitat targets, for the Port Stephens estuary. The methodology developed in this study, therefore, provides management agencies with the basis for more objective planning of zoning iterations for the estuarine section of the PSGLMP. The improved performance of habitat targets based

on SARs, compared to uniform habitat targets, indicates potential for broader application of this technique in planning marine reserve networks where detailed biodiversity information is available. The use of SARs for these purposes, however, needs to be based on appropriate methods, with careful consideration given to choice of SAR function type, taxonomic group, and species richness estimation technique. In addition, overall planning should consider social and economic objectives, in combination with these environmental targets, and should incorporate broader assessments that examine risks and threats to habitat and species viability.

Supplementary content

Appendix S1: Derivation of equations relating conservation targets to species protection levels for species-area relationship functions.

Power law function

The power-law function (Eq. A1) relates the number of species observed (S) to the area sampled (A), where slope (z) defines an assumed linear relationship between $\log(S)$ and $\log(A)$, and c is a constant.

$$S = c A^z \quad (\text{A1})$$

From (Eq. A1), for a region with total area (A_T), the total species within the area (S_T) is given by:

$$S_T = c A_T^z \quad (\text{A2})$$

Rearranging (Eq. A2) gives:

$$c = S_T / A_T^z \quad (\text{A3})$$

Substituting (Eq. A3) into (Eq. A1) gives:

$$S = S_T A^z / A_T^z \quad (\text{A4})$$

Rearranging (Eq. A4) gives:

$$\begin{aligned} S/S_T &= A^z / A_T^z \\ &= (A/A_T)^z \end{aligned} \quad (\text{A5})$$

Defining the species protection level (S') = S/S_T and the conservation target (A') = A/A_T and substituting into (Eq. A5) gives:

$$S' = (A')^z \quad (\text{A6})$$

Finally taking the z th root of both sides of (Eq. A6) gives the relationship between the conservation target (A') and the species protection level (S') for the power-law function:

$$A' = \sqrt[z]{S'} \quad (\text{A7})$$

Exponential function

The exponential function (Eq. B1) relates the number of species observed (S) to the area sampled (A), where slope (e) defines an assumed linear relationship between S and $\log(A)$, and d is a constant.

$$S = d + e \log(A) \quad (\text{B1})$$

From (Eq. B1), for a region with total area (A_T), the total species within the area (S_T) is given by:

$$S_T = d + e \log(A_T) \quad (B2)$$

Rearranging (Eq. B2) gives:

$$d = S_T - e \log(A_T) \quad (B3)$$

Substituting (Eq. B3) into (Eq. B1) gives:

$$\begin{aligned} S &= S_T - e \log(A_T) + e \log(A) \\ &= S_T + e \log(A/A_T) \end{aligned} \quad (B4)$$

Defining the species protection level (S') = S/S_T and the conservation target (A') = A/A_T and substituting into (Eq. B4) gives:

$$\begin{aligned} S' &= S/S_T \\ &= (S_T + e \log(A'))/S_T \end{aligned} \quad (B5)$$

Rearranging (Eq. B5) gives:

$$\begin{aligned} e \log(A') &= S' \cdot S_T - S_T \\ &= (S' - 1) \cdot S_T \end{aligned} \quad (B6)$$

Dividing both sides of (Eq. B6) by e gives:

$$\log(A') = (S' - 1) \cdot S_T / e \quad (B7)$$

Finally raising 10 to the power of both sides of (Eq. B7) gives the relationship between the conservation target (A') and the species protection level (S') for the exponential function:

$$A' = 10^{((S' - 1)S_T / e)} \quad (B8)$$

Chapter 7. Synthesis

This thesis aimed to improve methods to improve conservation planning for estuarine biodiversity, examining both deeper habitats (>10 m depth) where knowledge gaps existed about benthic habitats and species assemblages (DPWS 1999; Umwelt 2000), and shallow subtidal habitats where previous research had predominantly been focussed (Creese *et al.* 2009).

7.1 Contribution to understanding of subtidal estuarine biodiversity

Prior to this study, limited information was available about distributions of benthic habitats, fish and molluscs species within Port Stephens (DPWS 1999; Umwelt 2000). The quantitative assessments conducted as part of this study, therefore, provide a substantial new body of data about benthic habitats (Chapter 2), fish assemblages (Chapter 4) and molluscan assemblages (Chapter 5) within the estuary. New and valuable insights were obtained, with extensive areas of previously undocumented habitats identified, while some habitats, particularly *Dendronephthya australis*, were found to be inadequately represented within current no-take marine protected areas (MPAs) (Chapter 2). It was identified that existing NSW Habitat Classification Systems, for fully marine (Malcolm *et al.* 2010; Underwood *et al.* 1991) and estuarine ecosystems (Creese *et al.* 2009), did not adequately describe all habitats occurring within Port Stephens. A new habitat classification typology was developed to address this deficiency (Chapter 2), with the methodology used to develop this typology providing a potential approach for classifying habitats in other estuaries where data are currently lacking. The habitat typology and habitat maps developed as part of this study, therefore, provide the basis for more objective representation of estuarine habitats in Port Stephens in future planning and are being used by NSW DPI (marine parks) in regards to management of the Port Stephens estuary.

Prior to this study, knowledge about variation in fish assemblages among subtidal benthic habitats was also lacking for Port Stephens. While some effort had previously been invested in examining differences in fish assemblages among habitats (Poulos *et al.* 2013), data were not available for all habitat types, and data on temporal variations in assemblages were limited. These knowledge gaps were addressed through a quantitative assessment of fish assemblages across all identified habitat types, with an additional assessment of temporal changes for two habitats of ecological importance (filter feeders

and *D. australis*, Chapter 4). Analysis of quantitative survey data identified significant variation in fish assemblages among benthic habitats, with greater fish diversity in habitats with diverse benthic growth and heterogeneous reef structures. Overall diversity of fish species within Port Stephens was primarily driven by the richness of habitats occurring within the estuary. Examination of temporal shifts in assemblages showed that they changed within each habitat over time, while remaining significantly different among habitats (Chapter 4).

For molluscs, no quantitative data were available detailing variation in assemblages among habitats in Port Stephens prior to this study. As a consequence, it was not previously possible to develop conservation strategies aimed directly at protection of subtidal molluscan diversity. To address this limitation, a quantitative assessment of molluscan assemblages was conducted across all subtidal habitat types, with an assessment of temporal changes conducted in two habitats (filter feeders and *D. australis*, Chapter 5). An important outcome from this study was improved understanding of the drivers behind the high regional (Gamma) diversity of molluscs in Port Stephens. High Gamma diversity was found to result from a combination of: high diversity of species within some habitats (Alpha diversity); significant differences in species assemblages among habitats (Beta diversity); and differences in assemblages occurring over time (temporal Beta diversity). Alpha diversity was found to increase with habitat complexity, with higher diversity occurring in habitats with varied biotic composition and heterogeneous reef structures. Beta diversity increased with differences in benthic growth among habitats, substrate type and depth, while temporal Beta diversity increased with time and seasonal separation, with significant variation in assemblages occurring among seasons and among years (Chapter 5).

Assemblage data gathered for fish and molluscs provides valuable baseline information for future planning in Port Stephens and for ongoing monitoring to detect changes to assemblages within the estuary. In addition, these data allow comparison of assemblages in Port Stephens with other estuarine and coastal ecosystems, thereby facilitating exploration of larger ecological patterns in diversity of fish and molluscs. The strong links established among habitats and fish and molluscs assemblages indicates that preventing habitat loss has a key role to play in averting loss of biodiversity within Port Stephens, supporting findings that halting habitat loss is crucial to stopping loss of biodiversity in estuarine ecosystems (Kennish 2002; Lotze *et al.* 2006). In addition, strong correlations between

habitat types and fish and mollusc assemblages indicate the potential to use habitats as surrogates for these assemblages in planning for protection of estuarine biodiversity.

7.2 Contribution to improved conservation planning

Effective conservation planning for protection of biodiversity requires either detailed information on species distributions, or, where these data are not available, reliable surrogates for species distributions. Where surrogates are used in planning, these need to be representative of species of interest, widely applicable, and amenable to survey (Smith 2005). In this study, the use of surrogates for subtidal marine biodiversity was explored by examining the use of abiotic variables as surrogates for benthic habitats (Chapter 2) and the use of abiotic variables and benthic habitats as surrogates for fish (Chapter 4) and molluscs (Chapter 5). Initially the potential for using abiotic variables (depth, substrate type, distance from estuary entrance and current velocity) as surrogates for benthic habitats was examined using data from Port Stephens (Chapter 2). This study identified strong correlations between habitat distributions and abiotic variables, with a key finding being that abiotic variables, especially depth, provides a useful surrogate for benthic habitats in planning where data on habitats is lacking.

The use of abiotic variables as surrogates for habitats was further explored by examining the use of light availability, current flows and wave exposure in species distribution models (SDMs) for seagrasses (Chapter 3). Models based on these variables accurately predicted seagrass distributions within Port Stephens and, when tested in four other estuarine embayments, were found to provide a high level of accuracy in predicting dominant seagrass distributions within other estuaries. These results indicate that SDMs, based on abiotic variable surrogates, can have broad applicability across multiple estuarine systems, especially where the selected variables have a direct physiological relationship to the species of interest. The potential for using seagrass SDMs to predict the effects of threatening processes, such as climate change, was also explored, examining the impact of sea level rise and increased turbidity on seagrass distributions in five estuarine embayments (Chapter 3). This analysis demonstrated that SDMs can contribute valuable information to management on potential impacts of future environmental changes, predicting that both sea level rise and increased turbidity would cause losses of seagrass in deeper estuarine areas. Overall, SDMs were found to provide useful tools for identification of areas for protection, monitoring and rehabilitation of seagrasses, contributing important

information to help combat the worldwide loss of seagrasses in estuarine systems (Lotze *et al.* 2006).

Surrogates are also frequently used in the planning for no-take MPAs, especially where a detailed understanding of species distributions is lacking. In NSW, fish and molluscs represent the majority of commercially and recreationally fished species (NSW-DPI 2008; NSW-DPI 2013b), making these groups of primary importance in planning no-take MPAs. However, prior to this study, knowledge about effective surrogates, that could be used to represent fish and mollusc assemblages in planning for NSW estuaries, was poorly developed. To address this shortfall, surrogacy for fish (Chapter 4) and molluscs (Chapter 5) was examined using data from Port Stephens. Significant correlations were found among fish and mollusc assemblages, benthic habitats and the abiotic variables; water depth, location, substrate type, and habitat height. This demonstrated the potential to use both abiotic variables and benthic habitats as surrogates for fish and mollusc assemblages, with the combination of abiotic variables and benthic habitats shown to provide the greatest level of discrimination among assemblages. This key finding has important management implications, demonstrating the potential for using surrogates for fish and mollusc assemblages in conservation planning within Port Stephens, and indicating the potential for wider application of surrogates in planning within NSW estuaries. The information assembled here informs management by improving our understanding of surrogacy for fish and molluscs while demonstrating that surrogacy provides a means of identifying key areas for conservation, without the need for exhaustive biodiversity surveys.

Planning in MPAs also requires setting conservation targets for species, or targets for the surrogates used to represent these species in planning (Agardy *et al.* 2003). Within NSW estuaries, this has generally been conducted by using habitats as surrogates representing overall biodiversity, with uniform percentage targets considered for habitat classes in initial planning (Breen *et al.* 2004), and final no-take MPA boundaries established following extensive public consultation (NSW-MPA 2010a). However, detailed information on distributions of deeper habitats within estuaries has generally been lacking in NSW, as shown by the study of habitats in Port Stephens (Chapter 2). This paucity of information potentially leads to poor representation of deeper estuarine habitats in no-take MPAs in NSW. In addition, the application of uniform percentage targets across widely

differing habitat types has been criticised (Agardy *et al.* 2003; Pressey *et al.* 2003) and further investigation of the consequences of using this approach was warranted.

To address these concerns about the effectiveness of existing conservation planning methods, the performance of alternative conservation strategies was examined using data from Port Stephens (Chapter 6). Comparisons were conducted among: existing no-take zones; theoretical no-take zones planned with detailed habitat data with uniform conservation targets for habitats; and theoretical no-take zones planned with detailed habitat, fish and mollusc data with conservation targets based on species-area relationships (SARs). Performance of these alternative conservation strategies was assessed by comparing the protection levels achieved for habitats, and fish and molluscs species across the study area. The investigation identified that existing no-take zones in Port Stephens do not adequately protect all habitats and the fish and mollusc assemblages they contain, with protection levels significantly lower than those theoretically obtained by the other conservation strategies examined. Furthermore, conservation planning using uniform targets for habitats performed poorly, in terms of protection of fish and mollusc diversity, when compared against planning using non-uniform targets for habitats based on SARs (Chapter 6). Overall, biodiversity protection within no-take zones was found to improve as the quality of habitat and species assemblage data improved and also improved when conservation targets considered SARs. The improved performance of planning with targets based on SARs indicates the potential for broader application of this technique in implementing no-take MPAs, where detailed biodiversity information is available, and where protection of biodiversity is a primary objective.

7.3 Research limitations and future research directions

The main limitation for the majority of the investigations conducted in this thesis was the limited geographical extent of the studies, with most research focussed on ecological patterns occurring within the Port Stephens estuary. The localised focus of the research, therefore, limits the ability to apply the study's findings across other estuarine embayments in NSW, and further work is required to achieve this. Detailed mapping of deeper areas within other estuarine embayments in NSW would allow testing of the general applicability of the habitat classification typology developed, and would allow determination of whether deeper habitats in Port Stephens are representative of those in other systems. Further research into improved methods for mapping deeper habitats would also be beneficial, as substantial effort is currently required to map these habitats in turbid

estuarine conditions. Further studies of variation in fish and molluscs among habitats in other estuaries would increase understanding of potential surrogates for representing fish and molluscs in other NSW estuarine ecosystems and allow identification of the most appropriate surrogates for use in regional estuarine conservation planning.

While the effectiveness of using habitats as surrogates for fish and mollusc assemblages was evaluated, using Marxan in a hypothetical planning scenario in the Port Stephens estuary, a similar examination of the use of abiotic surrogates in conservation planning was not conducted in this thesis. A beneficial extension to the work in this thesis would, therefore, be to examine how both habitats and abiotic surrogates perform in conservation planning across multiple NSW estuaries. Testing, conducted using hypothetical planning scenarios, would provide improved understanding of the broader applicability of these surrogates and identify their roles in conservation planning to preserve subtidal estuarine biodiversity in NSW.

An additional limitation of the examination of surrogates was the focus on planning for no-take MPAs (sanctuary zones), with the role of Habitat Protection Zones (HPZs) in management of NSW MPAs not examined in detail. Sanctuary Zones provide the highest level of protection for both habitats and the species assemblages in NSW MPAs, however additional conservation benefits are provided by HPZs, which protect habitats through limitations on activities such as commercial trawling and netting, while still permitting other extractive activities, such as recreational fishing and collecting (NSW-MPA 2007). Study findings could be extended through consideration of the contributions that HPZs make to conservation objectives in the study area. In addition hypothetical conservation planning scenarios, considering both no-take MPAs and HPZs, would provide valuable information about the adequacy of existing zoning.

The focus on fish and molluscs in this thesis was an additional research limitation, with the applicability of surrogacy relationships not tested for other major phyla (e.g. meiobenthos, crustaceans, polychaetes). These other taxa constitute part of overall regional biodiversity and play important roles in trophic pathways and ecosystem functions that ultimately support fish and molluscs. Some work examining variation in polychaete assemblages among habitats in Port Stephens has been conducted (Dixon-Bridges *et al.* 2013), indicating that there are limitations in the effectiveness of using habitats as surrogates for polychaetes. Further work is therefore required to establish whether surrogates for fish and mollusc assemblages also adequately represent a broader range of phyla. However, given

the majority of commercially and recreationally fished species in NSW are fish and molluscs (NSW-DPI 2008; NSW-DPI 2013b), additional work examining surrogacy for other phyla may not be warranted. In addition molluscs have been shown to provide reliable indicators for other phyla on rocky shores (Gladstone 2002; Smith 2005) indicating that the surrogates for molluscs identified here may also provide useful surrogates for other phyla in planning. It should be noted that the study of molluscs conducted in this thesis focussed on large surface dwelling subtidal molluscs (≥ 5 mm in length) and did not examine smaller molluscs (i.e. < 5 mm) or molluscs living within unconsolidated substrates. Further examination of differences in small and in-faunal molluscs among habitats would extend the research contained here, allowing further testing of surrogacy across a wider range of mollusc species.

A major outcome from this study was the finding that SDMs can be used to model impacts of environmental changes on seagrasses across multiple estuarine systems. This result indicates that there may also be potential to use SDMs to simulate the responses of other estuarine habitats to environmental changes. In addition the predictive power of the SDMs developed here could be further enhanced by using ongoing monitoring to calibrate models against longer-term observations. This would allow refinement of the models to improve correlations between model predictions and actual species distributional changes. An obvious extension of the research detailed here would be to improve the SDM developed for *D. australis* (Poulos *et al.* 2015) to investigate causes for its decline within Port Stephens since 2011 (Davis *et al.* 2015b; Harasti 2016). Application of SDMs to modelling responses of habitats to environmental change provides a powerful tool for conservation planning, allowing the development of conservation plans aimed at mitigation of future habitat losses.

7.4 Conclusions

The research from this thesis substantially improves understanding of subtidal ecosystems occurring within Port Stephens and within NSW estuarine embayments more generally. Significant correlations were established among abiotic variables, benthic habitats and fish and mollusc assemblages, indicating the potential for using abiotic variables and benthic habitats as surrogates for fish and mollusc biodiversity in conservation planning. The thesis demonstrates that effectiveness of conservation planning is reduced where planning is conducted using inadequate data, suggesting that a lack of information may have contributed to poor representation of benthic habitats and fish and molluscs assemblages in

existing no-take zones within the Port Stephens-Great Lakes Marine Park. Development of SDMs, based on abiotic variables, highlighted the potential for using SDMs in prediction of benthic habitat distributions in estuaries and demonstrated that models provide powerful tools for predicting the response of estuarine communities to environmental change. Importantly, representation of biodiversity within no-take MPAs in Port Stephens could be improved by conducting conservation planning using the data gathered and methods developed in this study.

7.5 Recommendations

Where possible, it is recommended that detailed biodiversity data are assembled for critical areas of the marine estate, to improve conservation planning, and facilitate the use of threat and risk assessment in management. This study has demonstrated that limited information on biodiversity can hinder effective conservation planning and biodiversity data provide invaluable knowledge about the presence of threatened and endangered species. These data allow assessment of potential threats to species, and provide information to improve our understanding of the level of risk associated with these threats.

This study also provides a range of surrogacy approaches that could be used to represent estuarine biodiversity in conservation planning. The actual approach selected depends on the level of information available to planners and it is recommended that a hierarchal structure is used to determine the most appropriate methodology. At the lowest level, where only abiotic data (e.g. depth, substrate type) are available, these data can be applied as surrogates for habitats, provided adequate surrogacy relationships have been established (Chapter 2). Planning can then be conducted using uniform targets for the specified ranges of the abiotic variables (e.g. depth ranges) as has previously been applied for planning in NSW marine protected areas (Malcolm *et al.* 2011). Where more detailed data on habitat distributions are available, planning can be conducted at a finer spatial scale using habitats as surrogates for wider biodiversity (Chapters 4 and 5), with conservation targets specified as a proportion of each habitat type. Finally, where detailed data on biodiversity within habitats are available, conservation targets can be defined using SARs, with conservation targets set to protect a proportion of the species within each habitat, thereby providing increased protection in rarer and more biodiverse habitats (Chapter 6).

References

- Abal, E., and Dennison, W. (1996) Seagrass depth range and water quality in southern Moreton Bay, Queensland, Australia. *Marine and Freshwater Research* **47**: 763-771.
- Absalão, R.S., Moreira, J., and Troncoso, J.S. (2006) Common environmental descriptors of two benthic amphi-atlantic mollusc assemblages. *Brazilian Journal of Oceanography* **54**: 65-73.
- AETG (2012) Aquatic ecosystems toolkit. Module 2. Interim Australian national aquatic ecosystem classification framework. Aquatic Ecosystems Task Group, E Australian Government Department of Sustainability, Water, Population and Communities, Canberra.
- Agardy, T. (1994) Advances in marine conservation: the role of marine protected areas. *Trends in Ecology & Evolution* **9**: 267-270.
- Agardy, T., Bridgewater, P., Crosby, M.P., Day, J., Dayton, P.K., *et al.* (2003) Dangerous targets? Unresolved issues and ideological clashes around marine protected areas. *Aquatic Conservation: Marine and Freshwater Ecosystems* **13**: 353-367.
- Airamé, S., Dugan, J.E., Lafferty, K.D., Leslie, H., McArdle, D.A., *et al.* (2003) Applying ecological criteria to marine reserve design: a case study from the California Channel Islands. *Ecological applications* **13**: 170-184.
- Aldea, C., Olabarria, C., and Troncoso, J.S. (2009) Spatial patterns of benthic diversity in molluscs from West Antarctica. *Antarctic Science* **21**: 341-353.
- Allen, S., Smith, H., Waples, K., and Harcourt, R. (2007) The voluntary code of conduct for dolphin watching in Port Stephens, Australia: is self-regulation an effective management tool? *Journal of Cetacean Research and Management* **9**: 159-166.
- Anderson, M., Gorley, R., and Clarke, K. (2008) PERMANOVA+ for PRIMER: Guide to software and statistical methods. PRIMER-E Ltd., Plymouth, UK.
- Anderson, M.J., Crist, T.O., Chase, J.M., Vellend, M., Inouye, B.D., *et al.* (2011) Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist. *Ecology letters* **14**: 19-28.
- Anderson, M.J., and Millar, R.B. (2004) Spatial variation and effects of habitat on temperate reef fish assemblages in northeastern New Zealand. *Journal of Experimental Marine Biology and Ecology* **305**: 191-221.
- Anderson, T., Brooke, B., Radke, L., McArthur, M., and Hughes, M. (2009) Mapping and characterising soft-sediment habitats, and evaluating physical variables as surrogates of biodiversity in Jervis Bay, NSW: Jervis Bay post-survey report: December 2007-November 2008. Geoscience Australia, Canberra.

- Anderson, T.J., Cochrane, G.R., Roberts, D.A., Chezar, H., and Hatcher, G. (2007) A rapid method to characterize seabed habitats and associated macro-organisms. *Geological Association of Canada* **47**: 71-79.
- Anderson, T.W., DeMartini, E.E., and Roberts, D.A. (1989) The relationship between habitat structure, body size and distribution of fishes at a temperate artificial reef. *Bulletin of Marine Science* **44**: 681-697.
- Andrew, N.L., and O'Neill, A.L. (2000) Large-scale patterns in habitat structure on subtidal rocky reefs in New South Wales. *Marine and Freshwater Research* **51**: 255-263.
- Anthony, K., Ridd, P.V., Orpin, A.R., Larcombe, P., and Lough, J. (2004) Temporal variation of light availability in coastal benthic habitats: Effects of clouds, turbidity, and tides. *Limnology and Oceanography* **49**: 2201-2211.
- Appeltans, W., Ahyong, S.T., Anderson, G., Angel, M.V., Artois, T., *et al.* (2012) The magnitude of global marine species diversity. *Current Biology* **22**: 2189-2202.
- Ardron, J.A., Possingham, H.P., and Klein, C.J. (2008) Marxan good practices handbook. Pacific Marine Analysis and Research Association, Vancouver.
- Arrhenius, O. (1921) Species and area. *Journal of Ecology* **9**: 95-99.
- Ashworth, J., Aish, A., and Stoker, B. (2010) The marine conservation zone project: Ecological network guidance. NEatJNC Committee, Sheffield and Peterborough, UK.
- Attrill, M., and Rundle, S. (2002) Ecotone or ecocline: ecological boundaries in estuaries. *Estuarine, Coastal and Shelf Science* **55**: 929-936.
- August, P.V. (1983) The role of habitat complexity and heterogeneity in structuring tropical mammal communities. *Ecology* **64**: 1495-1507.
- Austin, T., Short, A., Hughes, M., Vila-Concejo, A., and Ranasinghe, R. (2009) Tidal hydrodynamics of a micro-tidal, wave dominated flood-tide delta: Port Stephens, Australia. *Journal of Coastal Research* **56**: 693-697.
- Baine, M. (2001) Artificial reefs: a review of their design, application, management and performance. *Ocean & Coastal Management* **44**: 241-259.
- Ball, D., Blake, S., Plummer, A., and Victoria, P. (2006) Review of marine habitat classification systems. Parks Victoria, Melbourne, Australia.
- Ball, I.R., Possingham, H.P., and Watts, M. (2009) Marxan and relatives: software for spatial conservation prioritisation. In 'Spatial conservation prioritisation: quantitative methods and computational tools'. pp. 185-195. Oxford University Press, Oxford, UK.

- Ban, N.C., Adams, V.M., Almany, G.R., Ban, S., Cinner, J.E., *et al.* (2011) Designing, implementing and managing marine protected areas: Emerging trends and opportunities for coral reef nations. *Journal of Experimental Marine Biology and Ecology* **408**: 21-31.
- Barbier, E.B., Hacker, S.D., Kennedy, C., Koch, E.W., Stier, A.C., *et al.* (2011) The value of estuarine and coastal ecosystem services. *Ecological Monographs* **81**: 169-193.
- Bax, N., Williamson, A., Aguero, M., Gonzalez, E., and Geeves, W. (2003) Marine invasive alien species: a threat to global biodiversity. *Marine Policy* **27**: 313-323.
- Beaman, R.J., Daniell, J.J., and Harris, P.T. (2005) Geology–benthos relationships on a temperate rocky bank, eastern Bass Strait, Australia. *Marine and Freshwater Research* **56**: 943-958.
- Beeton, R., Buxton, C., Cutbush, G., Fairweather, P., Johnston, E., *et al.* (2012) Report of the Independent Scientific Audit of Marine Parks in New South Wales. NSW Department of Primary Industries and Office of Environment and Heritage, NDoPIaOoEa Heritage, New South Wales.
- Bianchi, C.N., Parravicini, V., Montefalcone, M., Rovere, A., and Morri, C. (2012) The challenge of managing marine biodiversity: A practical toolkit for a cartographic, territorial approach. *Diversity* **4**: 419-452.
- Bickers, A.N. (2003) Cost effective marine habitat mapping from small vessels using GIS, sidescan sonar and video. In 'Coastal GIS', Wollongong. (Eds. DCD Woodroffe and RA Furness), pp. 553-572.
- Bindoff, N.L., Stott, P.A., AchutaRao, M., Allen, M.R., Gillett, N., *et al.* (2013) Detection and attribution of climate change: from global to regional. In 'Climate change 2013 the physical science basis: Working group I contribution to the fifth assessment report of the Intergovernmental Panel on Climate Change'. pp. 867-952. IPCC, Cambridge, UK.
- Birt, M.J., Harvey, E.S., and Langlois, T.J. (2012) Within and between day variability in temperate reef fish assemblages: learned response to baited video. *Journal of Experimental Marine Biology and Ecology* **416**: 92-100.
- Björk, M., Short, F., Mcleod, E., and Beer, S. (2008) Managing seagrasses for resilience to climate change. IUCN, Gland, Switzerland.
- Bohnsack, J., and Bannerot, S.P. (1986) A stationary visual census technique for quantitatively assessing community structure of coral reef fishes. National Oceanic and Atmospheric Administration, USDo Commerce, Springfield, US.
- Bohnsack, J.A. (1989) Are high densities of fishes at artificial reefs the result of habitat limitation or behavioral preference? *Bulletin of Marine Science* **44**: 631-645.
- Bohnsack, J.A., Harper, D.E., McClellan, D.B., and Hulsbeck, M. (1994) Effects of reef size on colonization and assemblage structure of fishes at artificial reefs off southeastern Florida, USA. *Bulletin of Marine Science* **55**: 796-823.

- Booth, D.J., Figueira, W.F., Gregson, M.A., Brown, L., and Beretta, G. (2007) Occurrence of tropical fishes in temperate southeastern Australia: Role of the East Australian Current. *Estuarine Coastal and Shelf Science* **72**: 102-114.
- Bos, A.R., Bouma, T.J., de Kort, G.L., and van Katwijk, M.M. (2007) Ecosystem engineering by annual intertidal seagrass beds: sediment accretion and modification. *Estuarine, Coastal and Shelf Science* **74**: 344-348.
- Bouchet, P., Lozouet, P., Maestrati, P., and Heros, V. (2002) Assessing the magnitude of species richness in tropical marine environments: exceptionally high numbers of molluscs at a New Caledonia site. *Biological Journal of the Linnean Society* **75**: 421-436.
- Bray, J.R., and Curtis, J.T. (1957) An ordination of the upland forest communities of southern Wisconsin. *Ecological monographs* **27**: 325-349.
- Breen, D., Avery, R., and Otway, N. (2004) Broad-scale biodiversity assessment of the Manning Shelf Marine Bioregion. NSW Marine Parks Authority, NSW, Australia.
- Bridges, K., Phillips, R., and Young, P. (1982) Patterns of some seagrass distribution in the Torres Strait, Queensland. *Marine and Freshwater Research* **33**: 273-283.
- Brock, R.E. (1982) A critique of the visual census method for assessing coral reef fish populations. *Bulletin of Marine Science* **32**: 269-276.
- Buckland, S.T., Baillie, S.R., Dick, J.M., Elston, D.A., Magurran, A.E., *et al.* (2012) How should regional biodiversity be monitored? *Environmental and Ecological Statistics* **19**: 601-626.
- Burchmore, J., Pollard, D., Bell, J., Middleton, M., Pease, B., *et al.* (1985) An ecological comparison of artificial and natural rocky reef fish communities in Botany Bay, New South Wales, Australia. *Bulletin of Marine Science* **37**: 70-85.
- Cambridge, M. (1975) Seagrasses of south-western Australia with special reference to the ecology of *Posidonia australis* Hook F. in a polluted environment. *Aquatic Botany* **1**: 149-161.
- Campbell, S.J., and McKenzie, L.J. (2004) Flood related loss and recovery of intertidal seagrass meadows in southern Queensland, Australia. *Estuarine, Coastal and Shelf Science* **60**: 477-490.
- Carleton, J., and Done, T. (1995) Quantitative video sampling of coral reef benthos: large-scale application. *Coral Reefs* **14**: 35-46.
- Carr, J.A., D'Odorico, P., McGlathery, K.J., and Wiberg, P.L. (2011) Modeling the effects of climate change on eelgrass stability and resilience: future scenarios and leading indicators of collapse. *Marine Ecology Progress Series* **448**: 289-301.
- Carr, M.H., and Hixon, M.A. (1997) Artificial reefs: the importance of comparisons with natural reefs. *Fisheries* **22**: 28-33.

- Carraro, R., and Gladstone, W. (2006) Habitat preferences and site fidelity of the Ornate Wobbegong Shark (*Orectolobus ornatus*) on rocky reefs of New South Wales. *Pacific Science* **60**: 207-223.
- Carruthers, T., Dennison, W., Longstaff, B., Waycott, M., Abal, E., *et al.* (2002) Seagrass habitats of northeast Australia: models of key processes and controls. *Bulletin of Marine Science* **71**: 1153-1169.
- CATAMI (2013) CATAMI classification scheme for scoring marine biota and substrata in underwater imagery Version 1.3: December 2013. CATAMI, CTW Group, Canberra, Australia.
- Chao, A. (1984) Nonparametric estimation of the number of classes in a population. *Scandinavian Journal of Statistics* **11**: 265-270.
- Charbonnel, E., Serre, C., Ruitton, S., Harmelin, J.-G., and Jensen, A. (2002) Effects of increased habitat complexity on fish assemblages associated with large artificial reef units (French Mediterranean coast). *ICES Journal of Marine Science* **59**: S208-S213.
- Chemello, R., and Milazzo, M. (2002) Effect of algal architecture on associated fauna: some evidence from phytal molluscs. *Marine Biology* **140**: 981-990.
- Choat, J., and Ayling, A. (1987) The relationship between habitat structure and fish faunas on New Zealand reefs. *Journal of experimental marine biology and ecology* **110**: 257-284.
- Church, J.A., Clark, P.U., Cazenave, A., Gregory, J.M., Jevrejeva, S., *et al.* (2013) Sea level change. In 'In Climate change 2013 the physical science basis: Working group I contribution to the fifth assessment report of the Intergovernmental Panel on Climate Change'. pp. 1137-1216. IPCC, Cambridge, UK.
- Chust, G., Grande, M., Galparsoro, I., Uriarte, A., and Borja, Á. (2010) Capabilities of the bathymetric Hawk Eye LiDAR for coastal habitat mapping: A case study within a Basque estuary. *Estuarine, Coastal and Shelf Science* **89**: 200-213.
- CI (2013) Conservation International. <http://www.conservation.org>. Accessed: 19/05/13.
- Cicin-Sain, B., and Belfiore, S. (2005) Linking marine protected areas to integrated coastal and ocean management: A review of theory and practice. *Ocean and Coastal Management* **48**: 847-868.
- Clarke, J. (2011) Old Salt. Royal Australian Historical Society, Port Stephens, Australia.
- Clarke, K., and Gorley, R. (2006) PRIMER v6: User Manual/Tutorial. PRIMER-E Ltd, Plymouth, UK.
- Clarke, K., and Gorley, R. (2015) PRIMER v7: User Manual/Tutorial. PRIMER-E Ltd, Plymouth, UK.
- Clarke, K.R. (1993) Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* **18**: 117-143.

- Clarke, K.R., Gorley, R.N., and Warwick, R.M. (2014) Change in marine communities : an approach to statistical analysis and interpretation 3rd Edition. PRIMER-E Ltd, Plymouth, UK.
- Claudet, J., Osenberg, C.W., Benedetti-Cecchi, L., Domenici, P., García-Charton, J.-A., *et al.* (2008) Marine reserves: size and age do matter. *Ecology Letters* **11**: 481-489.
- Coleman, M., Palmer-Brodie, A., and Kelaher, B.P. (2013) Conservation benefits of a network of marine reserves and partially protected areas. *Biological conservation* **167**: 257-264.
- Coleman, M.A., Roughan, M., Macdonald, H.S., Connell, S.D., Gillanders, B.M., *et al.* (2011) Variation in the strength of continental boundary currents determines continent-wide connectivity in kelp. *Journal of Ecology* **99**: 1026-1032.
- Colwell, R.K. (2013) EstimateS: Statistical estimation of species richness and shared species from samples. Version 9. User's Guide and application published at: <http://purl.oclc.org/estimates>.
- Colwell, R.K., and Coddington, J.A. (1994) Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society of London B Biological Sciences* **345**: 101-118.
- Connell, S., and Kingsford, M. (1998) Spatial, temporal and habitat-related variation in the abundance of large predatory fish at One Tree Reef, Australia. *Coral Reefs* **17**: 49-57.
- Connor, E.F., and McCoy, E.D. (1979) The statistics and biology of the species-area relationship. *The American Naturalist* **113**: 791-833.
- Costello, M.J., Coll, M., Danovaro, R., Halpin, P., Ojaveer, H., *et al.* (2010) A census of marine biodiversity knowledge, resources, and future challenges. *PloS one* **5**: e12110.
- Crain, C.M., Halpern, B.S., Beck, M.W., and Kappel, C.V. (2009) Understanding and managing human threats to the coastal marine environment. *Annals of the New York Academy of Sciences* **1162**: 39-62.
- Creese, R.G., Glasby, T.M., West, G., and Gallen, C. (2009) Mapping the habitats of NSW estuaries. Industry & Investment NSW, New South Wales, Australia.
- Dahan, M., and Benayahu, Y. (1997a) Clonal propagation by the azooxanthellate octocoral *Dendronephthya hemprichi*. *Coral Reefs* **16**: 5-12.
- Dahan, M., and Benayahu, Y. (1997b) Reproduction of *Dendronephthya hemprichi* (Cnidaria: Octocorallia): year-round spawning in an azooxanthellate soft coral. *Marine Biology* **129**: 573-579.
- Davis, T.R., Harasti, D., and Smith, S.D.A. (2015a) Compensating for length biases in underwater visual census of fishes using stereo video measurements. *Marine and Freshwater Research* **66**: 286-291.

- Davis, T.R., Gallen, C., Laird, R., and Harasti, D. (2015b) Mapping sub-tidal habitats in the Eastern Port of Port Stephens. NSW Department of Primary Industries, New South Wales, Australia.
- Davis, T.R., Harasti, D., Kelaher, B., and Smith, S.D.A. (2016a) Diversity surrogates for estuarine fish assemblages in a temperate estuary in New South Wales, Australia. *Regional Studies in Marine Science* **7**: 55-62.
- Davis, T.R., Harasti, D., Kelaher, B., and Smith, S.D.A. (2017a) Spatial and temporal variation in subtidal molluscan diversity amongst temperate estuarine habitats. *Marine Ecology* **38**:e12428.
- Davis, T.R., Harasti, D., Kelaher, B., and Smith, S.D.A. (2017b) Defining conservation targets for fish and molluscs in the Port Stephens estuary, Australia using species-area relationships. *Ocean & Coastal Management* **136**: 156-164.
- Davis, T.R., Harasti, D., and Smith, S.D.A. (2015c) Extension of *Dendronephthya australis* soft corals in tidal current flows. *Marine Biology* **162**: 2155-2159.
- Davis, T.R., Harasti, D., and Smith, S.D.A. (2016b) Developing a habitat classification typology for subtidal habitats in a temperate estuary in New South Wales, Australia. *Marine and Freshwater Research* **67**: 1186-1195.
- Davis, T.R., Harasti, D., Smith, S.D.A., and Kelaher, B.P. (2016c) Using modelling to predict impacts of sea level rise and increased turbidity on seagrass distributions in estuarine embayments. *Estuarine Coastal and Shelf Science* **181**: 294-301.
- Davis, T.R., and Smith, S.D.A. (2017) Proximity effects of natural and artificial reef walls on fish assemblages. *Regional Studies in Marine Science* **9**: 17-23.
- Day, J., Fernandes, L., Lewis, A., De'Ath, G., Slegers, S., *et al.* (2000) The representative areas program for protecting biodiversity in the Great Barrier Reef World Heritage Area. In 'Proceedings of the Ninth International Coral Reef Symposium', Bali, pp. 687-696.
- Desmet, P., and Cowling, R. (2004) Using the species-area relationship to set baseline targets for conservation. *Ecology and Society* **9**: 11.
- Diaz, R.J., Solan, M., and Valente, R.M. (2004) A review of approaches for classifying benthic habitats and evaluating habitat quality. *Journal of environmental management* **73**: 165-181.
- Dickens, L.C., Goatley, C.H.R., Tanner, J.K., and Bellwood, D.R. (2011) Quantifying relative diver effects in underwater visual censuses. *PLoS ONE* **6**: e18965.
- Dixon-Bridges, K., Hutchings, P., and Gladstone, W. (2013) Effectiveness of habitat classes as surrogates for biodiversity in marine reserve planning. *Aquatic Conservation: Marine and Freshwater Ecosystems* **24**: 463-477.
- Dixon, M.J.R., Loh, J., Davidson, N.C., Beltrame, C., Freeman, R., *et al.* (2016) Tracking global change in ecosystem area: The Wetland Extent Trends index. *Biological Conservation* **193**: 27-35.

- Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., *et al.* (2013) Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* **36**: 27-46.
- Downie, A.-L., von Numers, M., and Boström, C. (2013) Influence of model selection on the predicted distribution of the seagrass *Zostera marina*. *Estuarine, Coastal and Shelf Science* **121**: 8-19.
- DPWS (1998) Port Stephens tidal data collection September 1993. NSW Department of Public Works and Services, Manly Hydraulics Laboratory, New South Wales, Australia.
- DPWS (1999) Port Stephens/Myall Lakes estuary processes study. NSW Department of Public Works and Services, Manly Hydraulics Laboratory, New South Wales, Australia.
- Duarte, C.M. (2002) The future of seagrass meadows. *Environmental conservation* **29**: 192-206.
- Duarte, C.M., Marbà, N., Krause-Jensen, D., and Sánchez-Camacho, M. (2007) Testing the predictive power of seagrass depth limit models. *Estuaries and Coasts* **30**: 652-656.
- Dulvy, N.K., Sadovy, Y., and Reynolds, J.D. (2003) Extinction vulnerability in marine populations. *Fish and fisheries* **4**: 25-64.
- Edgar, G. (2012) Australian Marine Life: The Plants and Animals of Temperate Waters. New Holland Publishers Pty, Ltd, Sydney, Australia.
- Edgar, G.J., and Shaw, C. (1995) The production and trophic ecology of shallow-water fish assemblages in southern Australia I. Species richness, size-structure and production of fishes in Western Port, Victoria. *Journal of Experimental Marine Biology and Ecology* **194**: 53-81.
- Edgar, G.J., and Stuart-Smith, R.D. (2014) Systematic global assessment of reef fish communities by the Reef Life Survey program. *Scientific Data* **1**: 140007.
- Edwards, R.A., and Smith, S.D. (2005) Subtidal assemblages associated with a geotextile reef in south-east Queensland, Australia. *Marine and Freshwater Research* **56**: 133-142.
- Elgin (2014a) Merimbula Lake: Environmental monitoring in coastal lakes and lagoons of Bega Valley Shire Council region 2012-2013. Elgin Associates Pty Ltd, Bega, Australia.
- Elgin (2014b) Pambula Lake: Environmental monitoring in coastal lakes and lagoons of Bega Valley Shire Council region 2010-2013. Elgin Associates Pty Ltd, Bega, Australia.
- Emanuel, K.A. (2013) Downscaling CMIP5 climate models shows increased tropical cyclone activity over the 21st century. *Proceedings of the National Academy of Sciences* **110**: 12219-12224.

- EOL (2014) Encyclopedia of Life. <http://www.eol.org/>. Accessed: 7/10/14.
- Erlandson, J.M. (2001) The archaeology of aquatic adaptations: paradigms for a new millennium. *Journal of Archaeological Research* **9**: 287-350.
- Fabrizius, K., Yahel, G., and Genin, A. (1998) In situ depletion of phytoplankton by an azooxanthellate soft coral. *Limnology and oceanography* **43**: 354-356.
- Fabrizius, K.E., Genin, A., and Benayahu, Y. (1995) Flow-dependent herbivory and growth in zooxanthellae-free soft corals. *Limnology and Oceanography* **40**: 1290-1301.
- Fabrizius, K.K., and Alderslade, P.P. (2001) Soft corals and sea fans: a comprehensive guide to the tropical shallow water genera of the central-west Pacific, the Indian Ocean and the Red Sea. Australian Institute of Marine Science, Queensland, Australia.
- Farré, M., Lombarte, A., Recasens, L., Maynou, F., and Tuset, V.M. (2015) Habitat influence in the morphological diversity of coastal fish assemblages. *Journal of Sea Research* **99**: 107-117.
- Favreau, J.M., Drew, C.A., Hess, G.R., Rubino, M.J., Koch, F.H., *et al.* (2006) Recommendations for assessing the effectiveness of surrogate species approaches. *Biodiversity & Conservation* **15**: 3949-3969.
- Fernandes, L., Day, J., Lewis, A., Slegers, S., Kerrigan, B., *et al.* (2005) Establishing representative notake areas in the Great Barrier Reef: Large-scale implementation of theory on Marine Protected Areas. *Conservation Biology* **19**: 1733-1744.
- Ferrari, R., McKinnon, D., He, H., Smith, R.N., Corke, P., *et al.* (2016) Quantifying multiscale habitat structural complexity: A cost-effective framework for underwater 3D modelling. *Remote Sensing* **8**: 113.
- Ferrell, D.J., and Bell, J.D. (1991) Differences among assemblages of fish associated with *Zostera capricorni* and bare sand over a large spatial scale. *Marine Ecology Progress Series* **72**: 15-24.
- Fonseca, M., Whitfield, P.E., Kelly, N.M., and Bell, S.S. (2002) Modeling seagrass landscape pattern and associated ecological attributes. *Ecological Applications* **12**: 218-237.
- Fonseca, M.S., and Bell, S.S. (1998) Influence of physical setting on seagrass landscapes near Beaufort, North Carolina, USA. *Marine Ecology-Progress Series* **171**: 109-121.
- Foster, N.L., Foggo, A., and Howell, K.L. (2013) Using species-area relationships to inform baseline conservation targets for the deep North East Atlantic. *PLoS one* **8**: e58941.
- Fretwell, S.D., and Calver, J.S. (1969) On territorial behavior and other factors influencing habitat distribution in birds. *Acta biotheoretica* **19**: 37-44.

- Friedlander, A., Brown, E., Jokiel, P., Smith, W., and Rodgers, K. (2003) Effects of habitat, wave exposure, and marine protected area status on coral reef fish assemblages in the Hawaiian archipelago. *Coral Reefs* **22**: 291-305.
- Friedlander, A.M., and Parrish, J.D. (1998) Habitat characteristics affecting fish assemblages on a Hawaiian coral reef. *Journal of Experimental Marine Biology and Ecology* **224**: 1-30.
- Fulton, C.J., and Bellwood, D.R. (2004) Wave exposure, swimming performance, and the structure of tropical and temperate reef fish assemblages. *Marine Biology* **144**: 429-437.
- GBIF (2014) Global Biodiversity Information Facility. <http://www.gbif.org/whatisgbif>. Accessed: 7/10/2014.
- Gladstone, W. (2002) The potential value of indicator groups in the selection of marine reserves. *Biological Conservation* **104**: 211-220.
- Gladstone, W. (2007) Requirements for marine protected areas to conserve the biodiversity of rocky reef fishes. *Aquatic Conservation: Marine and Freshwater Ecosystems* **17**: 71-87.
- Glasby, T., and Kingsford, M. (1994) *Atypichthys strigatus* (Pisces: Scorpididae): An opportunistic planktivore that responds to benthic disturbances and cleans other fishes. *Australian journal of ecology* **19**: 385-394.
- Grand, J., Cummings, M.P., Rebelo, T.G., Ricketts, T.H., and Neel, M.C. (2007) Biased data reduce efficiency and effectiveness of conservation reserve networks. *Ecology Letters* **10**: 364-374.
- Grantham, H.S., Pressey, R.L., Wells, J.A., and Beattie, A.J. (2010) Effectiveness of biodiversity surrogates for conservation planning: Different measures of effectiveness generate a kaleidoscope of variation. *PLOS ONE* **5**: e11430.
- Gratwicke, B., and Speight, M. (2005) The relationship between fish species richness, abundance and habitat complexity in a range of shallow tropical marine habitats. *Journal of Fish Biology* **66**: 650-667.
- Gray, C., McElligott, D., and Chick, R. (1996) Intra-and inter-estuary differences in assemblages of fishes associated with shallow seagrass and bare sand. *Marine and Freshwater Research* **47**: 723-735.
- Gray, C., and Otway, N. (1994) Spatial and temporal differences in assemblages of demersal fishes on the inner continental shelf off Sydney, south-eastern Australia. *Marine and Freshwater Research* **45**: 665-676.
- Gray, J.S. (1997) Marine biodiversity: patterns, threats and conservation needs. *Biodiversity & Conservation* **6**: 153-175.
- Gray, J.S. (2001) Marine diversity: the paradigms in patterns of species richness examined. *Scientia Marina* **65**: 41-56.

- Grech, A., and Coles, R. (2010) An ecosystem-scale predictive model of coastal seagrass distribution. *Aquatic Conservation: marine and freshwater ecosystems* **20**: 437-444.
- Green, A., Smith, S.E., Lipsett-Moore, G., Groves, C., Peterson, N., *et al.* (2009) Designing a resilient network of marine protected areas for Kimbe Bay, Papua New Guinea. *Oryx* **43**: 488-498.
- Greene, H.G., Bizzarro, J.J., O'Connell, V.M., and Brylinsky, C.K. (2007) Construction of digital potential marine benthic habitat maps using a coded classification scheme and its application. *Mapping the Seafloor for Habitat Characterization: Geological Association of Canada, Special Paper* **47**: 147-162.
- Greve, T., and Krause-Jensen, D. (2005) Predictive modelling of eelgrass (*Zostera marina*) depth limits. *Marine Biology* **146**: 849-858.
- Grober-Dunsmore, R., Frazer, T.K., Beets, J.P., Lindberg, W.J., Zwick, P., *et al.* (2008) Influence of landscape structure on reef fish assemblages. *Landscape Ecology* **23**: 37-53.
- Grumbine, R.E. (1994) What is ecosystem management? *Conservation biology* **8**: 27-38.
- Grutter, A.S. (1999) Cleaner fish really do clean. *Nature* **398**: 672-673.
- Guisan, A., and Thuiller, W. (2005) Predicting species distribution: offering more than simple habitat models. *Ecology letters* **8**: 993-1009.
- Guisan, A., and Zimmermann, N.E. (2000) Predictive habitat distribution models in ecology. *Ecological modelling* **135**: 147-186.
- Hall Jr, C.A. (1964) Shallow-water marine climates and molluscan provinces. *Ecology* **45**: 226-234.
- Halpern, B.S., Selkoe, K.A., Micheli, F., and Kappel, C.V. (2007) Evaluating and ranking the vulnerability of global marine ecosystems to anthropogenic threats. *Conservation Biology* **21**: 1301-1315.
- Halpern, B.S., Walbridge, S., Selkoe, K.A., Kappel, C.V., Micheli, F., *et al.* (2008) A global map of human impact on marine ecosystems. *Science* **319**: 948-952.
- Hamner, W., Colin, P., and Hamner, P. (2007) Export–import dynamics of zooplankton on a coral reef in Palau. *Marine Ecology Progress Series* **334**: 83-92.
- Hamner, W., Jones, M., Carleton, J., Hauri, I., and Williams, D.M. (1988) Zooplankton, planktivorous fish, and water currents on a windward reef face: Great Barrier Reef, Australia. *Bulletin of Marine Science* **42**: 459-479.
- Harasti, D. (2016) Declining seahorse populations linked to loss of essential marine habitats. *Marine Ecology Progress Series* **546**: 173-181.
- Harasti, D., Gallen, C., Malcolm, H., Tegart, P., and Hughes, B. (2014a) Where are the little ones: distribution and abundance of the threatened serranid *Epinephelus*

- daemeli* (Günther, 1876) in intertidal habitats in New South Wales, Australia. *Journal of Applied Ichthyology* **30**: 1007-1015.
- Harasti, D., Martin-Smith, K., and Gladstone, W. (2012) Population dynamics and life history of a geographically restricted seahorse, *Hippocampus whitei*. *Journal of Fish Biology* **81**: 1297-1314.
- Harasti, D., Martin-Smith, K., and Gladstone, W. (2014b) Does a no-take marine protected area benefit seahorses? *PloS one* **9**: e105462.
- Harasti, D., Martin-Smith, K., and Gladstone, W. (2014c) Ontogenetic and sex-based differences in habitat preferences and site fidelity of White's seahorse *Hippocampus whitei*. *Journal of Fish Biology* **85**: 1413-1428.
- Harborne, A.R., Mumby, P.J., Kappel, C.V., Dahlgren, C.P., Micheli, F., *et al.* (2008) Tropical coastal habitats as surrogates of fish community structure, grazing, and fisheries value. *Ecological Applications* **18**: 1689-1701.
- Harriot, V.J., Smith, S.D.A., and Harrison, P.L. (1994) Patterns of coral community structure of subtropical reefs in the Solitary Islands Marine Reserve, Eastern Australia. *Marine Ecology Progress Series* **109**: 67-76.
- Harriott, V.J., Banks, S.A., Mau, R.L., Richardson, D., and Roberts, L.G. (1999) Ecological and conservation significance of the subtidal rocky reef communities of northern New South Wales, Australia. *Marine and Freshwater Research* **50**: 299-306.
- Harrison, M.A., and Smith, S.D.A. (2012) Cross-shelf variation in the structure of molluscan assemblages on shallow, rocky reefs in subtropical, eastern Australia. *Marine Biodiversity* **42**: 203-216.
- Hastie, B.F., and Smith, S.D.A. (2006) Benthic macrofaunal communities in intermittent estuaries during a drought: comparisons with permanently open estuaries. *Journal of Experimental Marine Biology and Ecology* **330**: 356-367.
- He, F., and Legendre, P. (1996) On species-area relations. *The American Naturalist* **148**: 719-737.
- Hellström, M., and Benzie, J. (2011) Robustness of size measurement in soft corals. *Coral reefs* **30**: 787-790.
- Hervouet, J.-M. (2000) TELEMAT modelling system: an overview. *Hydrological Processes* **14**: 2209-2210.
- Hoegh-Guldberg, O., and Bruno, J.F. (2010) The impact of climate change on the world's marine ecosystems. *Science* **328**: 1523-1528.
- Holmes, R.W. (1970) The Secchi disk in turbid coastal waters. *Limnology and Oceanography* **15**: 688-694.
- Holt, R.D., Lawton, J.H., Polis, G.A., and Martinez, N.D. (1999) Trophic rank and the species-area relationship. *Ecology* **80**: 1495-1504.

- Hughes, T.P., Bellwood, D.R., and Connolly, S.R. (2002) Biodiversity hotspots, centres of endemism, and the conservation of coral reefs. *Ecology Letters* **5**: 775-784.
- Infantes, E., Terrados, J., Orfila, A., Cañellas, B., and Álvarez-Ellacuría, A. (2009) Wave energy and the upper depth limit distribution of *Posidonia oceanica*. *Botanica Marina* **52**: 419-427.
- Irving, A., and Connell, S. (2002) Sedimentation and light penetration interact to maintain heterogeneity of subtidal habitats: algal versus invertebrate dominated assemblages. *Marine Ecology Progress Series* **245**: 83-91.
- Jaccard, P. (1912) The distribution of the flora in the alpine zone. *New phytologist* **11**: 37-50.
- Jackson, J.B. (2001) What was natural in the coastal oceans? *Proceedings of the National Academy of Sciences* **98**: 5411-5418.
- Jackson, J.B., Kirby, M.X., Berger, W.H., Bjorndal, K.A., Botsford, L.W., *et al.* (2001) Historical overfishing and the recent collapse of coastal ecosystems. *Science* **293**: 629-637.
- Jennerjahn, T.C., and Mitchell, S.B. (2013) Pressures, stresses, shocks and trends in estuarine ecosystems—An introduction and synthesis. *Estuarine, Coastal and Shelf Science* **130**: 1-8.
- Jiang, A., Ranasinghe, R., Cowell, P., and Savioli, J. (2011) Tidal asymmetry of a shallow, well-mixed estuary and the implications on net sediment transport: A numerical modelling study. *Australian Journal of Civil Engineering* **9**: 1-18.
- Jiang, A.W., Ranasinghe, R., and Cowell, P. (2013) Contemporary hydrodynamics and morphological change of a microtidal estuary: a numerical modelling study. *Ocean Dynamics* **63**: 21-41.
- Jones, A., Watson-Russell, C., and Murray, A. (1986) Spatial patterns in the macrobenthic communities of the Hawkesbury estuary, New South Wales. *Marine and Freshwater Research* **37**: 521-543.
- Jones, G.P., and Srinivasan, M. (2007) Conservation of Marine Biodiversity. *Oceanography* **20**: 100-111.
- Jordan, A., Davies, P., Ingleton, T., Mesley, E., Neilson, J., *et al.* (2010a) Developments in mapping of seabed habitats for Marine Protected Area planning and monitoring. In 'OCEANS 2010 IEEE', Sydney, pp. 1-10.
- Jordan, A., Davies, P., Ingleton, T., Mesley, E., Neilson, J., *et al.* (2010b) Seabed habitat mapping of the continental shelf waters of NSW. NSW Department of Environment, Climate Change and Water, New South Wales, Australia.
- Jordan, A., Lawler, M., Halley, V., and Barrett, N. (2005) Seabed habitat mapping in the Kent Group of islands and its role in marine protected area planning. *Aquatic Conservation: Marine and Freshwater Ecosystems* **15**: 51-70.

- Kaschner, K., Watson, R., Trites, A., and Pauly, D. (2006) Mapping world-wide distributions of marine mammal species using a relative environmental suitability (RES) model. *Marine Ecology Progress Series* **316**: 2-3.
- Kelaker, B.P., Castilla, J.C., and Prado, L. (2007a) Is there redundancy in bioengineering for molluscan assemblages on the rocky shores of central Chile. *Revista Chilena de Historia Natural* **80**: 173-186.
- Kelaker, B.P., Castilla, J.C., Prado, L., York, P., Schwindt, E., *et al.* (2007b) Spatial variation in molluscan assemblages from coralline turfs of Argentinean Patagonia. *Journal of Molluscan Studies* **73**: 139-146.
- Kelaker, B.P., Castilla, J.C., and Seed, R. (2004) Intercontinental test of generality for spatial patterns among diverse molluscan assemblages in coralline algal turf. *Marine Ecology Progress Series* **271**: 221-231.
- Kelaker, B.P., Coleman, M.A., Broad, A., Rees, M.J., Jordan, A., *et al.* (2014) Changes in fish assemblages following the establishment of a network of no-take marine reserves and partially-protected areas. *PLoS ONE* **9(1)**: e85825.
- Kelly, N.M., Fonseca, M., and Whitfield, P. (2001) Predictive mapping for management and conservation of seagrass beds in North Carolina. *Aquatic Conservation: Marine and Freshwater Ecosystems* **11**: 437-451.
- Kendrick, G.A., Aylward, M.J., Hegge, B.J., Cambridge, M.L., Hillman, K., *et al.* (2002) Changes in seagrass coverage in Cockburn Sound, Western Australia between 1967 and 1999. *Aquatic Botany* **73**: 75-87.
- Kennish, M.J. (2002) Environmental threats and environmental future of estuaries. *Environmental Conservation* **29**: 78-107.
- Kidwell, S.M. (2001) Preservation of species abundance in marine death assemblages. *Science* **294**: 1091-1094.
- Kingsford, M., and Battershill, C. (1998) Studying temperate marine environments: a handbook for ecologists. Canterbury University Press, University of Canterbury, UK.
- Knott, T., Lunney, D., Coburn, D., and Callaghan, J. (1998) An ecological history of koala habitat in Port Stephens Shire and the Lower Hunter on the central coast of New South Wales, 1801-1998. *Pacific Conservation Biology* **4**: 354-368.
- Kohler, K.E., and Gill, S.M. (2006) Coral Point Count with Excel extensions (CPCe): A Visual Basic program for the determination of coral and substrate coverage using random point count methodology. *Computers and Geosciences* **32**: 1259-1269.
- Laliberté, E., Legendre, P., and Shipley, B. (2014) Measuring functional diversity (FD) from multiple traits, and other tools for functional ecology. R package, version 1.0-12.
- Last, P.R., Lyne, V.D., Williams, A., Davies, C.R., Butler, A.J., *et al.* (2010) A hierarchical framework for classifying seabed biodiversity with application to

- planning and managing Australia's marine biological resources. *Biological Conservation* **143**: 1675-1686.
- Lathrop, R.G., Styles, R.M., Seitzinger, S.P., and Bognar, J.A. (2001) Use of GIS mapping and modeling approaches to examine the spatial distribution of seagrasses in Barnegat Bay, New Jersey. *Estuaries* **24**: 904-916.
- Lefebvre, A., Thompson, C., Collins, K., and Amos, C. (2009) Use of a high-resolution profiling sonar and a towed video camera to map a *Zostera marina* bed, Solent, UK. *Estuarine, Coastal and Shelf Science* **82**: 323-334.
- Leslie, H.M. (2005) A synthesis of marine conservation planning approaches. *Conservation Biology* **19**: 1701-1713.
- Lilley, S.A., and Schiel, D.R. (2006) Community effects following the deletion of a habitat-forming alga from rocky marine shores. *Oecologia* **148**: 672-681.
- Lincoln-Smith, M. (1989) Improving multispecies rocky reef fish censuses by counting different groups of species using different procedures. *Environmental Biology of Fishes* **26**: 29-37.
- Lindegarth, M., and Hoskin, M. (2001) Patterns of distribution of macro-fauna in different types of estuarine, soft sediment habitats adjacent to urban and non-urban areas. *Estuarine, Coastal and Shelf Science* **52**: 237-247.
- Lindsay, M.J., Patterson, H.M., and Swearer, S.E. (2008) Habitat as a surrogate measure of reef fish diversity in the zoning of the Lord Howe Island Marine Park, Australia. *Marine Ecology Progress Series* **353**: 265-273.
- Long, E.R., MacDonald, D.D., Smith, S.L., and Calder, F.D. (1995) Incidence of adverse biological effects within ranges of chemical concentrations in marine and estuarine sediments. *Environmental management* **19**: 81-97.
- Lotze, H.K., Lenihan, H.S., Bourque, B.J., Bradbury, R.H., Cooke, R.G., *et al.* (2006) Depletion, degradation, and recovery potential of estuaries and coastal seas. *Science* **312**: 1806-1809.
- Lowry, M., Glasby, T., Boys, C., Folpp, H., Suthers, I., *et al.* (2014) Response of fish communities to the deployment of estuarine artificial reefs for fisheries enhancement. *Fisheries Management and Ecology* **21**: 42-56.
- Magierowski, R.H., and Johnson, C.R. (2006) Robustness of surrogates of biodiversity in marine benthic communities. *Ecological Applications* **16**: 2264-2275.
- Malcolm, H., Foulsham, E., Pressey, R., Jordan, A., Davies, P., *et al.* (2012) Selecting zones in a marine park: early systematic planning improves cost-efficiency; combining habitat and biotic data improves effectiveness. *Ocean & coastal management* **59**: 1-12.
- Malcolm, H., and Smith, S.A. (2010) Objective selection of surrogate families to describe reef fish assemblages in a subtropical marine park. *Biodiversity and Conservation* **19**: 3611-3618.

- Malcolm, H.A., Jordan, A., and Smith, S.D.A. (2011) Testing a depth-based Habitat Classification System against reef fish assemblage patterns in a subtropical marine park. *Aquatic Conservation: Marine and Freshwater Ecosystems* **21**: 173-185.
- Malcolm, H.A., Smith, S.D.A., and Jordan, A. (2010) Using patterns of reef fish assemblages to refine a Habitat Classification System for marine parks in NSW, Australia. *Aquatic Conservation: Marine and Freshwater Ecosystems* **20**: 83-92.
- Mapstone, B.D., and Ayling, A. (1998) An investigation of optimum methods and unit sizes for the visual estimation of abundances of some coral reef organisms. Great Barrier Reef Marine Park Authority, Townsville, Australia.
- Margules, C.R., and Pressey, R.L. (2000) Systematic conservation planning. *Nature* **405**: 243-253.
- Martins, R., Sampaio, L., Quintino, V., and Rodrigues, A. (2014) Diversity, distribution and ecology of benthic molluscan communities on the Portuguese continental shelf. *Journal of Sea Research* **93**: 75-89.
- McClanahan, T.R., Graham, N.A.J., Maina, J., Chabanet, P., Bruggemann, J.H., *et al.* (2007) Influence of instantaneous variation on estimates of coral reef fish populations and communities. *Marine Ecology Progress Series* **340**: 221-234.
- McCormick, M.I. (1994) Comparison of field methods for measuring surface topography and their associations with a tropical reef fish assemblage. *Marine Ecology Progress Series* **112**: 87-96.
- McDonald, G.R., and Nybakken, J.W. (1997) List of the Worldwide Food Habits of Nudibranchs. *Veliger* **40**: 157-159.
- Mendes, C.L.T., Tavares, M., and Soares-Gomes, A. (2007) Taxonomic sufficiency for soft-bottom sublittoral mollusks assemblages in a tropical estuary, Guanabara Bay, Southeast Brazil. *Marine Pollution Bulletin* **54**: 377-384.
- Metcalf, K., Delavenne, J., Garcia, C., Foveau, A., Dauvin, J.C., *et al.* (2013) Impacts of data quality on the setting of conservation planning targets using the species–area relationship. *Diversity and Distributions* **19**: 1-13.
- Micallef, A., Le Bas, T.P., Huvenne, V.A., Blondel, P., Hühnerbach, V., *et al.* (2012) A multi-method approach for benthic habitat mapping of shallow coastal areas with high-resolution multibeam data. *Continental Shelf Research* **39**: 14-26.
- Middleton, M., Bell, J., Burchmore, J., Pollard, D., and Pease, B. (1984) Structural differences in the fish communities of *Zostera capricorni* and *Posidonia australis* seagrass meadows in Botany Bay, New South Wales. *Aquatic botany* **18**: 89-109.
- Morton, J.K., and Gladstone, W. (2014) Changes in rocky reef fish assemblages throughout an estuary with a restricted inlet. *Hydrobiologia* **724**: 235-253.
- Mount, R., Bricher, P., and Newton, J. (2007) National/Intertidal/Subtidal Benthic (NISB) Habitat Classification Scheme version 1.0 October 2007. School of Geography and Environmental Studies, University of Tasmania, Australia.

- Mumby, P.J., and Edwards, A.J. (2002) Mapping marine environments with IKONOS imagery: enhanced spatial resolution can deliver greater thematic accuracy. *Remote sensing of environment* **82**: 248-257.
- Mumby, P.J., and Harborne, A.R. (1999) Development of a systematic classification scheme of marine habitats to facilitate regional management and mapping of Caribbean coral reefs. *Biological Conservation* **88**: 155-163.
- Mumby, P.J., and Steneck, R.S. (2011) The resilience of coral reefs and its implications for reef management. In 'Coral Reefs: An Ecosystem in Transition'. pp. 509-519. Springer.
- Nearmap (2014) Nearmap. <http://www.nearmap.com.au/>. Accessed: 8/10/2014.
- Neigel, J.E. (2003) Species-area relationships and marine conservation. *Ecological Applications* **13**: 138-145.
- Nell, J.A. (2001) The history of oyster farming in Australia. *Marine Fisheries Review* **63**: 14-25.
- Nelson, R.C. (1994) Depth limited design wave heights in very flat regions. *Coastal Engineering* **23**: 43-59.
- Nhancale, B.A., and Smith, R.J. (2011) The influence of planning unit characteristics on the efficiency and spatial pattern of systematic conservation planning assessments. *Biodiversity and Conservation* **20**: 1821-1835.
- Nielsen, S.L., Sand-Jensen, K., Borum, J., and Geertz-Hansen, O. (2002) Depth colonization of eelgrass (*Zostera marina*) and macroalgae as determined by water transparency in Danish coastal waters. *Estuaries* **25**: 1025-1032.
- Nimbs, M.J., Larkin, M., Davis, T.R., Harasti, D., Willan, R.C., *et al.* (2016) Southern range extensions for twelve heterobranch sea slugs (Gastropoda: Heterobranchia) on the eastern coast of Australia. *Marine Biodiversity Records* **9**: 27.
- Nixon, S.W. (1995) Coastal marine eutrophication: a definition, social causes, and future concerns. *Ophelia* **41**: 199-219.
- NSW-DPI (2008) Primefact 825: Commercial fishing in New South Wales. NSW Department of Primary Industries, New South Wales, Australia.
- NSW-DPI (2013a) Government response to the Report of the Independent Scientific Audit of Marine Parks in NSW. NSW Department of Primary Industries, New South Wales, Australia.
- NSW-DPI (2013b) NSW recreational saltwater fishing guide 2013. NSW Department of Primary Industries, New South Wales, Australia.
- NSW-DPI (2014) Discharge from Karuah River at Booral (ML/d). <http://realtimedata.water.nsw.gov.au>. Accessed: 25/6/14.

- NSW-MPA (2007) Port Stephens-Great Lakes Marine Park Zoning Plan User Guide. pp. 8. NSW Marine Parks Authority, New South Wales, Australia.
- NSW-MPA (2010a) Port Stephens-Great Lakes Marine Park Operational Plan - November 2010. NSW Marine Parks Authority, New South Wales, Australia.
- NSW-MPA (2010b) Seabed mapping in the Solitary Islands and Jervis Bay Marine Parks. NSW Marine Parks Authority, New South Wales, Australia.
- Olabarria, C. (2006) Faunal change and bathymetric diversity gradient in deep-sea prosobranchs from Northeastern Atlantic. *Biodiversity and Conservation* **15**: 3685-3702.
- OzCoasts (2015) OzCoasts Australian online coastal information. <http://www.ozcoasts.gov.au/>. Accessed: 5/12/2015.
- Pais, M.P., Henriques, S., Costa, M.J., and Cabral, H.N. (2013) Improving the “chain and tape” method: A combined topography index for marine fish ecology studies. *Ecological Indicators* **25**: 250-255.
- Patterson, M. (1980) Hydromechanical adaptations in *Alcyonium sidereum* (Octocorallia). In 'Biofluid Mechanics · 2'. (Ed. D Schneck) pp. 183-201. Springer, USA.
- Pauly, D., and Christensen, V. (1995) Primary production required to sustain global fisheries. *Nature* **374**: 255-257.
- Pickering, H., and Whitmarsh, D. (1997) Artificial reefs and fisheries exploitation: a review of the ‘attraction versus production’ debate, the influence of design and its significance for policy. *Fisheries research* **31**: 39-59.
- Pitcher, T.J., and Parrish, J.K. (1993) Functions of shoaling behaviour in teleosts. In 'Behaviour of teleost fishes'. (Ed. TJ Pitcher) pp. 363-427. Chapman & Hall, London.
- Poulos, D. (2011) Unique soft coral habitat in a temperate estuary: significance to biodiversity and marine park management. University of Technology, Sydney, Sydney, Australia.
- Poulos, D., Gallen, C., Davis, T., Booth, D., and Harasti, D. (2015) Distribution and spatial modelling of a soft coral habitat in the Port Stephens-Great Lakes Marine Park: implications for management. *Marine and Freshwater Research* **67**: 256-265.
- Poulos, D.E., Harasti, D., Gallen, C., and Booth, D.J. (2013) Biodiversity value of a geographically restricted soft coral species within a temperate estuary. *Aquatic Conservation: Marine and Freshwater Ecosystems* **23**: 838-849.
- Powles, H., Bradford, M.J., Bradford, R., Doubleday, W., Innes, S., *et al.* (2000) Assessing and protecting endangered marine species. *ICES Journal of Marine Science: Journal du Conseil* **57**: 669-676.

- Preen, A., Long, W.L., and Coles, R. (1995) Flood and cyclone related loss, and partial recovery, of more than 1000 km² of seagrass in Hervey Bay, Queensland, Australia. *Aquatic Botany* **52**: 3-17.
- Preskitt, L.B., Vroom, P.S., and Smith, C.M. (2004) A rapid ecological assessment (REA) quantitative survey method for benthic algae using photoquadrats with scuba. *Pacific Science* **58**: 201-209.
- Pressey, R., and Logan, V. (1998) Size of selection units for future reserves and its influence on actual vs targeted representation of features: a case study in western New South Wales. *Biological Conservation* **85**: 305-319.
- Pressey, R.L. (1994) Ad Hoc reservations: Forward or backward steps in developing representative reserve systems? *Conservation Biology* **8**: 662-668.
- Pressey, R.L., Cabeza, M., Watts, M.E., Cowling, R.M., and Wilson, K.A. (2007) Conservation planning in a changing world. *Trends in ecology & evolution* **22**: 583-592.
- Pressey, R.L., Cowling, R.M., and Rouget, M. (2003) Formulating conservation targets for biodiversity pattern and process in the Cape Floristic Region, South Africa. *Biological Conservation* **112**: 99-127.
- Purvis, A., Gittleman, J.L., Cowlishaw, G., and Mace, G.M. (2000) Predicting extinction risk in declining species. *Proceedings of the Royal Society of London B: Biological Sciences* **267**: 1947-1952.
- R Core Team (2014) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Ready, J., Kaschner, K., South, A.B., Eastwood, P.D., Rees, T., *et al.* (2010) Predicting the distributions of marine organisms at the global scale. *Ecological Modelling* **221**: 467-478.
- Redford, K.H., Coppolillo, P., Sanderson, E.W., Da Fonseca, G.A., Dinerstein, E., *et al.* (2003) Mapping the conservation landscape. *Conservation biology* **17**: 116-131.
- Rees, M.J., Jordan, A., Price, O.F., Coleman, M.A., and Davis, A.R. (2014) Abiotic surrogates for temperate rocky reef biodiversity: implications for marine protected areas. *Diversity and distributions* **20**: 284-296.
- Rilov, G., and Benayahu, Y. (2000) Fish assemblage on natural versus vertical artificial reefs: the rehabilitation perspective. *Marine Biology* **136**: 931-942.
- Roberts, D., Davis, A., and Cummins, S. (2006) Experimental manipulation of shade, silt, nutrients and salinity on the temperate reef sponge *Cymbastela concentrica*. *Marine Ecology Progress Series* **307**: 143-154.
- Rohweder, J., Rogala, J., Johnson, B., Anderson, D., Clark, S., *et al.* (2012) Application of wind fetch and wave models for habitat rehabilitation and enhancement projects—2012 update. US Army Corps of Engineers, St. Paul, Minnesota, USA.

- Rondinini, C. (2011) Meeting the MPA network design principles of representativity and adequacy: Developing species-area curves for habitats. Joint Nature Conservation Committee, Peterborough, UK.
- Rooper, C.N. (2008) Underwater video sleds: Versatile and cost effective tools for habitat mapping. In 'Marine habitat mapping technology for Alaska'. pp. 100-107. University of Alaska, Fairbanks, USA.
- Ross, S.T. (1986) Resource partitioning in fish assemblages: a review of field studies. *Copeia* **1986**: 352-388.
- Roy, P.S., and Matthei, L. (1996) Late Cainozoic clay deposits in the Port Stephens area, New South Wales. *Australian Journal of Earth Sciences* **43**: 395-400.
- Roy, P.S., Williams, R.J., Jones, A.R., Yassini, I., Gibbs, P.J., *et al.* (2001) Structure and Function of South-east Australian Estuaries. *Estuarine, Coastal and Shelf Science* **53**: 351-384.
- Rule, M.J., and Smith, S.D.A. (2007) Depth-associated patterns in the development of benthic assemblages on artificial substrata deployed on shallow, subtropical reefs. *Journal of Experimental Marine Biology and Ecology* **345**: 38-51.
- Sala, E., Aburto-Oropeza, O., Paredes, G., Parra, I., Barrera, J.C., *et al.* (2002) A general model for designing networks of marine reserves. *Science* **298**: 1991-1993.
- Salomon, A.K., Shears, N.T., Langlois, T.J., and Babcock, R.C. (2008) Cascading effects of fishing can alter carbon flow through a temperate coastal ecosystem. *Ecological Applications* **18**: 1874-1887.
- Sanvicente-Añorve, L., Hermoso-Salazar, M., Ortigosa, J., Solís-Weiss, V., and Lemus-Santana, E. (2012) Opisthobranch assemblages from a coral reef system: the role of habitat type and food availability. *Bulletin of Marine Science* **88**: 1061-1074.
- Schroeder, R.E. (1987) Effects of patch reef size and isolation on coral reef fish recruitment. *Bulletin of Marine Science* **41**: 441-451.
- Schultz, A.L., Malcolm, H.A., Bucher, D.J., and Smith, S.D.A. (2012) Effects of reef proximity on the structure of fish assemblages of unconsolidated substrata. *PloS one* **7**: e49437.
- Schultz, S.T., Goddard, J.H., Gosliner, T.M., Mason, D.E., Pence, W.E., *et al.* (2011) Climate-index response profiling indicates larval transport is driving population fluctuations in nudibranch gastropods from the northeast Pacific Ocean. *Limnology and oceanography* **56**: 749-763.
- Sebens, K. (1984) Water flow and coral colony size: interhabitat comparisons of the octocoral *Alcyonium siderium*. *Proceedings of the National Academy of Sciences* **81**: 5473-5477.
- Sepkoski Jr, J.J. (1988) Alpha, Beta, or Gamma: where does all the diversity go? *Paleobiology* **14**: 221-234.

- Sheaves, M. (2016) Simple processes drive unpredictable differences in estuarine fish assemblages: baselines for understanding site-specific ecological and anthropogenic impacts. *Estuarine, Coastal and Shelf Science* **170**: 61-69.
- Shimeta, J., and Jumars, P.A. (1991) Physical mechanisms and rates of particle capture by suspension feeders. *Oceanography and Marine Biology : An Annual Review* **29**: 1-257.
- Shmida, A., and Wilson, M.V. (1985) Biological determinants of species diversity. *Journal of Biogeography* **12**: 1-20.
- Shokri, M.R., and Gladstone, W. (2013) Limitations of habitats as biodiversity surrogates for conservation planning in estuaries. *Environmental Monitoring and Assessment* **185**: 3477-3492.
- Short, F.T., and Neckles, H.A. (1999) The effects of global climate change on seagrasses. *Aquatic Botany* **63**: 169-196.
- Skilleter, G., and Warren, S. (2000) Effects of habitat modification in mangroves on the structure of mollusc and crab assemblages. *Journal of Experimental Marine Biology and Ecology* **244**: 107-129.
- Smith, A.B. (2010) Caution with curves: caveats for using the species–area relationship in conservation. *Biological Conservation* **143**: 555-564.
- Smith, A.K., and Pollard, D.A. (1996) The best available information—some case studies from NSW, Australia, of conservation-related management responses which impact on recreational fishers. *Marine Policy* **20**: 261-267.
- Smith, S.D.A. (2005) Rapid assessment of invertebrate biodiversity on rocky shores: where there's a whelk there's a way. *Biodiversity and Conservation* **14**: 3565-3576.
- Smith, S.D.A. (2008) Interpreting molluscan death assemblages on rocky shores: are they representative of the regional fauna? *Journal of Experimental Marine Biology and Ecology* **366**: 151-159.
- Smith, S.D.A. (2011) Densities of the endolithic bivalve *Lithophaga lessepsiana* (Vaillant, 1865) in *Pocillopora damicornis*, Solitary Islands Marine Park, northern NSW, Australia. *Molluscan Research* **31**: 42-46.
- Smith, S.D.A., and Edgar, R.J. (2014) Documenting the density of subtidal marine debris across multiple marine and coastal habitats. *PloS one* **9**: e94593.
- Smith, S.D.A., Jordan, A., Creese, R.G., and Gladstone, W. (2010) The marine environment of the Hunter-Central Rivers region of New South Wales. A review of current knowledge. National Marine Science Centre, Southern Cross University, Coffs Harbour, Australia.
- Smith, S.D.A., Rule, M.J., Harrison, M., and Dalton, S.J. (2008) Monitoring the sea change: preliminary assessment of the conservation value of nearshore reefs, and existing impacts, in a high-growth, coastal region of subtropical eastern Australia. *Marine Pollution Bulletin* **56**: 525-34.

- Stevens, T., and Connolly, R.M. (2004) Testing the utility of abiotic surrogates for marine habitat mapping at scales relevant to management. *Biological Conservation* **119**: 351-362.
- Stevens, T., and Connolly, R.M. (2005) Local-scale mapping of benthic habitats to assess representation in a marine protected area. *Marine and Freshwater Research* **56**: 111-123.
- Stewart, M., and Fairfull, S. (2007) Primefact 629: Seagrasses. NSW Department of Primary Industries, New South Wales, Australia.
- Stewart, R., Noyce, T., and Possingham, H. (2003) Opportunity cost of ad hoc marine reserve design decisions: an example from South Australia. *Marine Ecology Progress Series* **253**: 25-38.
- Stewart, R.R., and Possingham, H.P. (2005) Efficiency, costs and trade-offs in marine reserve system design. *Environmental Modeling & Assessment* **10**: 203-213.
- Stolt, M., Bradley, M., Turenne, J., Payne, M., Scherer, E., *et al.* (2011) Mapping shallow coastal ecosystems: a case study of a Rhode Island lagoon. *Journal of Coastal Research* **27**: 1-15.
- Stuart-Smith, R.D., Bates, A.E., Lefcheck, J.S., Duffy, J.E., Baker, S.C., *et al.* (2013) Integrating abundance and functional traits reveals new global hotspots of fish diversity. *Nature* **501**: 539-542.
- Stuart-Smith, R.D., Edgar, G.J., Stuart-Smith, J.F., Barrett, N.S., Fowles, A.E., *et al.* (2015) Loss of native rocky reef biodiversity in Australian metropolitan embayments. *Marine pollution bulletin* **95**: 324-332.
- Sumich, J.L., and Morrissey, J.F. (2004) Introduction to the biology of marine life. Jones & Bartlett Learning, London, UK.
- Svancara, L.K., Scott, M., Groves, C.R., Noss, R.F., and Pressey, R.L. (2005) Policy-driven versus evidence-based conservation: a review of political targets and biological needs. *BioScience* **55**: 989-995.
- Tear, T.H., Kareiva, P., Angermeier, P.L., Comer, P., Czech, B., *et al.* (2005) How much is enough? The recurrent problem of setting measurable objectives in conservation. *BioScience* **55**: 835-849.
- Terlizzi, A., Scuderi, D., Fraschetti, S., and Anderson, M. (2005) Quantifying effects of pollution on biodiversity: a case study of highly diverse molluscan assemblages in the Mediterranean. *Marine Biology* **148**: 293-305.
- Tittensor, D.P., Micheli, F., Nyström, M., and Worm, B. (2007) Human impacts on the species–area relationship in reef fish assemblages. *Ecology Letters* **10**: 760-772.
- Tittensor, D.P., Mora, C., Jetz, W., Lotze, H.K., Ricard, D., *et al.* (2010) Global patterns and predictors of marine biodiversity across taxa. *Nature* **466**: 1098-1101.

- Tjørve, E. (2003) Shapes and functions of species–area curves: a review of possible models. *Journal of Biogeography* **30**: 827-835.
- Tran, M. (2013) Mapping and predicting benthic habitats in estuaries using towed underwater video. University of Technology, Sydney, Sydney, Australia.
- Troncoso, J.S., Moreira, J., and Ugorri, V. (2005) Soft-bottom mollusc assemblages in the Ría de Ares-Betanzos (Galicia, NW Spain). *Iberus* **23**: 25-38.
- Umwelt (2000) Port Stephens and Myall Lakes estuary management plan. Umwelt (Australia) Pty Ltd, Toronto, NSW, Australia.
- Umwelt (2009) Living on the Edge - A Foreshore Management Plan for Port Stephens. Umwelt (Australia) Pty Ltd, Toronto, NSW, Australia.
- Underwood, A.J., Kingsford, M.J., and Andrew, N.L. (1991) Patterns in shallow subtidal marine assemblages along the coast of New South Wales. *Australian Journal of Ecology* **16**: 231-249.
- Unsworth, R.K.F., van Keulen, M., and Coles, R.G. (2014) Seagrass meadows in a globally changing environment. *Marine Pollution Bulletin* **83**: 383-386.
- USACE (1984) Shore Protection Manual. US Army Corps of Engineers, Washington, DC, USA.
- Valesini, F., Tweedley, J., Clarke, K., and Potter, I. (2014) The importance of regional, system-wide and local spatial scales in structuring temperate estuarine fish communities. *Estuaries and coasts* **37**: 525-547.
- Van der Heide, T., Peeters, E., Hermus, D., Van Katwijk, M., Roelofs, J., *et al.* (2009) Predicting habitat suitability in temperate seagrass ecosystems. *Limnology and Oceanography* **54**: 2018-2024.
- Vegter, A., Barletta, M., Beck, C., Borrero, J., Burton, H., *et al.* (2014) Global research priorities to mitigate plastic pollution impacts on marine wildlife. *Endangered Species Research* **25**: 225-247.
- Verseveldt, J., and Alderslade, P. (1982) Descriptions of types and other *Alcyonacean* material (Coelenterata: Octocorallia) in the Australian Museum, Sydney. *Records of the Australian Museum* **34**: 619-647.
- Vila-Concejo, A., Austin, T., Harris, D., Hughes, M., Short, A., *et al.* (2011) Estuarine beach evolution in relation to a flood-tide delta. *Journal of Coastal Research* **64**: 190-194.
- Villéger, S., Mason, N.W., and Mouillot, D. (2008) New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology* **89**: 2290-2301.
- Walker, B.K., Jordan, L.K., and Spieler, R.E. (2009) Relationship of reef fish assemblages and topographic complexity on southeastern Florida coral reef habitats. *Journal of Coastal Research* **53**: 39-48.

- Ward, T., Vanderklift, M., Nicholls, A., and Kenchington, R. (1999) Selecting marine reserves using habitats and species assemblages as surrogates for biological diversity. *Ecological applications* **9**: 691-698.
- Ward, T.J. (2014) The condition of Australia's marine environment is good but in decline—An integrated evidence-based national assessment by expert elicitation. *Ocean & Coastal Management* **100**: 86-100.
- Warwick, R., and Turk, S. (2002) Predicting climate change effects on marine biodiversity: comparison of recent and fossil molluscan death assemblages. *Journal of the Marine Biological Association of the UK* **82**: 847-850.
- Watson, R., Kitchingman, A., Gelchu, A., and Pauly, D. (2004) Mapping global fisheries: sharpening our focus. *Fish and fisheries* **5**: 168-177.
- Waycott, M., Collier, C., McMahon, K., Ralph, P., McKenzie, L., *et al.* (2007) Vulnerability of seagrasses in the Great Barrier Reef to climate change. Great Barrier Reef Marine Park Authority and Australian Greenhouse Office, Queensland, Australia.
- Wells, F. (1998) Marine molluscs of Milne Bay Province, Papua New Guinea. A rapid biodiversity assessment of the coral reefs of Milne Bay Province, Papua New Guinea. *RAP Working Papers* **11**: 35-38.
- Wernberg, T., Coleman, M., Fairhead, A., Miller, S., and Thomsen, M. (2003) Morphology of *Ecklonia radiata* (Phaeophyta: Laminariales) along its geographic distribution in south-western Australia and Australasia. *Marine Biology* **143**: 47-55.
- West, G., Williams, R., Authority, N.M., and Wales, N.S. (2008) A preliminary assessment of the historical, current and future cover of seagrass in the estuary of the Parramatta River. NSW Department of Primary Industries, New South Wales, Australia.
- West, R., and Gordon, G. (1994) Commercial and recreational harvest of fish from two Australian coastal rivers. *Marine and Freshwater Research* **45**: 1259-1279.
- Whittaker, R.H. (1960) Vegetation of the Siskiyou mountains, Oregon and California. *Ecological monographs* **30**: 279-338.
- Whittaker, R.H. (1972) Evolution and measurement of species diversity. *Taxon* **21**: 213-251.
- Widdig, A., and Schlichter, D. (2001) Phytoplankton: a significant trophic source for soft corals? *Helgoland marine research* **55**: 198-211.
- Williams, G.A. (1993) Seasonal variation in algal species richness and abundance in the presence of molluscan herbivores on a tropical rocky shore. *Journal of Experimental Marine Biology and Ecology* **167**: 261-275.

- Williams, S.L., and Grosholz, E.D. (2008) The invasive species challenge in estuarine and coastal environments: marrying management and science. *Estuaries and Coasts* **31**: 3-20.
- Williamson, M., Gaston, K.J., and Lonsdale, W. (2001) The species–area relationship does not have an asymptote! *Journal of Biogeography* **28**: 827-830.
- Willis, T.J., Millar, R.B., and Babcock, R.C. (2000) Detection of spatial variability in relative density of fishes: comparison of visual census, angling, and baited underwater video. *Marine Ecology Progress Series* **198**: 249-260.
- Wiszniewski, J., Allen, S.J., and Möller, L.M. (2009) Social cohesion in a hierarchically structured embayment population of Indo-Pacific bottlenose dolphins. *Animal Behaviour* **77**: 1449-1457.
- WoRMS Editorial Board (2017). World Register of Marine Species. Available from <http://www.marinespecies.org>. Accessed: 20/11/15.
- Zharikov, Y., Skilleter, G.A., Loneragan, N.R., Taranto, T., and Cameron, B.E. (2005) Mapping and characterising subtropical estuarine landscapes using aerial photography and GIS for potential application in wildlife conservation and management. *Biological Conservation* **125**: 87-100.

Appendix A - Extension of *Dendronephthya australis* soft corals in tidal current flows.

Appendix A contains a manuscript that was prepared in parallel with Chapter 2, where the effects of tidal current flows on the behavioural responses of the soft coral *Dendronephthya australis* were examined. Habitat mapping from Chapter 2 was used to identify locations of *D. australis* colonies and the hydrodynamic model from Chapter 2 was used to provide tidal current data as an explanatory variable for observed species responses. This manuscript was published in Marine Biology (Davis *et al.* 2015c):

Davis T.R., Harasti D., Smith S.D.A. (2015c) Extension of *Dendronephthya australis* soft corals in tidal current flows. *Marine Biology* **162**: 2155-2159.

Extension of *Dendronephthya australis* soft corals in tidal current flows

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Abstract

Soft corals from the *Dendronephthya* genus (Family Nephtheidae) can change size over short periods by pumping water into their internal hydro-skeletons. However, the drivers behind these size changes are not well understood. In a tidal-dominated estuary in eastern Australia, it was hypothesised that short-term changes in the size of *Dendronephthya australis* colonies occur in response to changes in tidal currents. This was tested by monitoring colonies over a period of several days using time-lapse photography. Colony extensions of up to 360% were observed, and size changes exhibited a repeated pattern, with two maxima and two minima occurring in each tidal cycle, matching patterns in semi-diurnal tidal flows. A significant positive correlation between colony size and current velocity was identified, with size changes lagging currents. The results of the study provide valuable new information on the behaviour of *D. australis* and improve understanding of the environmental requirements for this species.

Introduction

Soft corals (Alcyonacea) occur throughout the world's oceans, and the Nephtheidae family, including the *Dendronephthya* genus, are widely distributed occurring in current-prone areas from Africa eastwards into the Pacific (Fabricius and Alderslade 2001). *Dendronephthya* spp. occur in both tropical and temperate waters, and are characterised by a branching growth form, with stems and polyps supported and protected by calcareous sclerites (Edgar 2012; Fabricius and Alderslade 2001). *Dendronephthya* spp. are known to expand and contract over short periods (Fabricius *et al.* 1995; Hellström and Benzie 2011), with size changes generated through variation in water pumping in the internal canal systems forming their hydro-skeletons (Dahan and Benayahu 1997a; Fabricius and Alderslade 2001). The drivers behind these short-term size changes are not well understood, but they are thought to occur in response to physical and environmental factors including current strength, availability of food, and predation (Dahan and Benayahu 1997b; Fabricius and Alderslade 2001).

Dendronephthya australis Kükenthal, 1905 is a geographically restricted species that has only been found in large abundance within the Port Stephens estuary, New South Wales (NSW), Australia (Poulos *et al.* 2015; Verseveldt and Alderslade 1982). Substantial changes in colony size have been observed over periods of less than an hour (pers. obs.), but drivers behind these changes have not previously been investigated. Understanding the environmental requirements for *D. australis* is particularly important as the species is thought to be under threat (Harasti *et al.* 2014c; Poulos *et al.* 2015; Poulos *et al.* 2013; Smith and Edgar 2014).

It is hypothesised that, as passive suspension-feeders, *D. australis* colonies rely on current flows to supply food, and that changes to colony size therefore occur in response to changes in tidal current velocity. To test this hypothesis, we measured the heights of soft coral colonies *in situ* over a period of several days, and explored their relationship with tidal current velocities over the same period. This study builds on previous work examining factors influencing distributions of *D. australis* (Poulos *et al.* 2015), by clarifying the important relationship between tidal currents and *D. australis* behaviour.

Materials and methods

The study was conducted between January and March 2015 at four sites on the southern shoreline of the Port Stephens estuary (Figure 1), where the majority of *D. australis* habitat occurs (Poulos *et al.* 2015). The Port Stephens estuary is classified as a tide-dominated drowned river valley, and is subject to strong semi-diurnal tidal flows (peak tidal currents $>1 \text{ m s}^{-1}$) (DPWS 1998).

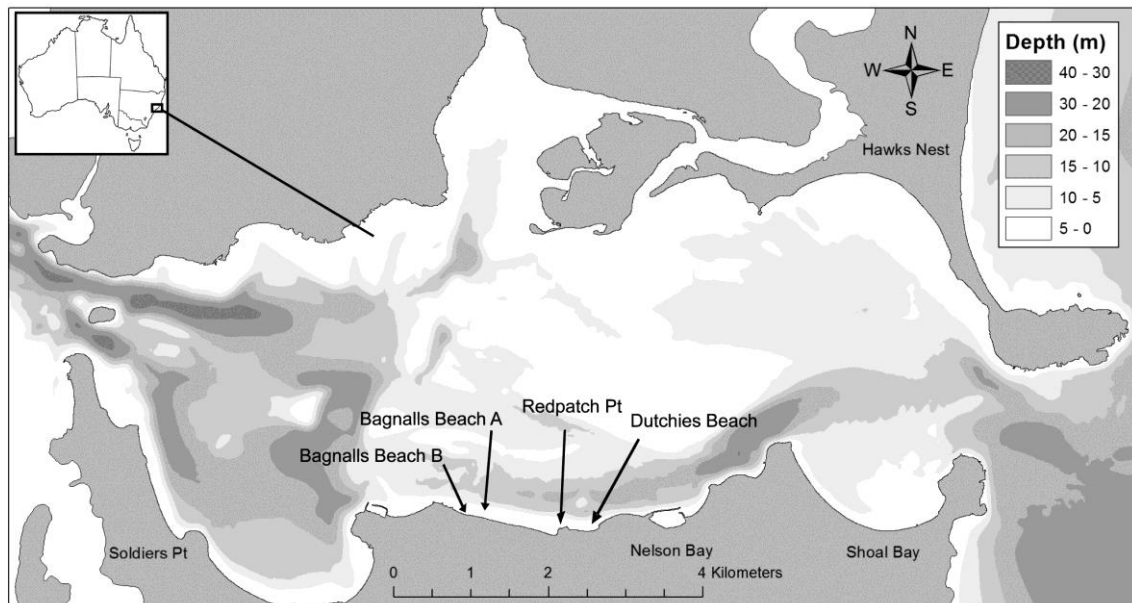


Figure 1. Study sites in the Port Stephens estuary (Bagnalls Beach A/B -32.717, 152.120; Redpatch Pt -32.719, 152.131; Dutchies Beach -32.719, 152.135)

Soft corals were monitored using GoPro Hero2 cameras fitted with Cam-Do (<http://www.cam-do.com/>) time-lapse controllers. Three colonies were photographed at 15-minute intervals at each site, over a 4.5 day period, during daylight hours. Each photograph was analysed to determine colony height and polyp extension. Measurements of soft coral heights were made using the Coral Point Count with Excel extensions (CPCe) software package (Kohler and Gill 2006). Calibration of measurements was conducted using a scale-bar positioned in the field of view at the same distance from the camera as the soft corals.

Depth averaged tidal current velocities were calculated at each site using the existing tidal model of the estuary (Poulos *et al.* 2015), validated using tidal data and measured velocities from sites spanning the study region (DPWS 1998). The model was created in the TELEMAC-2D hydrodynamic analysis package (Hervouet 2000), and data from the tidal gauge at Shoal Bay, for the periods of interest, were used as input at the model boundary.

To allow comparisons to be made for the height changes of soft coral colonies of differing sizes (i.e. fully retracted volumes (Hellström and Benzie 2011)), analyses were conducted using a dimensionless variable (extension) calculated from the ratio of: colony height increase, to colony minimum height (i.e. $\text{extension} = (\text{height} - \text{minimum height}) / \text{minimum height}$). Cross-correlation analyses were conducted in R (R Core Team 2014) to test for significant relationships between *D. australis* colony extensions and current velocities, and to determine lags between colony responses and current changes.

Results and discussion

Cameras were in situ for 4.5 days at each site, generating 2139 data points for colony height from 12 soft coral colonies. Colony extensions of up to 360% were observed (Figure 2) with maximum heights of monitored colonies ranging from 32-67 cm. Maximum current velocities of 0.70 m s^{-1} were calculated at the “Bagnalls Beach A” site on 6 March 2015 when tidal heights varied between 0.52 m to 1.78 m. *Dendronephthya australis* colonies showed a consistent cycle of behaviour, with extensions, averaged across colonies, sites, and days, exhibiting two maxima and two minima in each tidal cycle, while semi-diurnal tidal currents exhibited a similar pattern (Figure 3). During low-flow conditions (slack water) colonies were generally fully retracted with polyps closed. As currents increased, polyps opened and colonies extended, with maximum extension occurring 1-3 h after maximum flow. Then, as slack water approached, colonies retracted and polyps closed, with height minima occurring 15 and 30 min after current minima (Figure 3). Height increases (extensions) were observed to occur at up to 6 mm min^{-1} and height reductions (retractions) at up to 10 mm min^{-1} . Cross-correlation analyses identified correlations between extension and current velocity at all study sites (Table 1), indicating that *D. australis* actively controls expansion and contraction of its hydro-skeleton.

Table 1. Maximum cross-correlation index between *Dendronephthya australis* extension and current velocity with associated time lag and significance level

Site	Cross-correlation index	Time lag (min)	Significance level
Bagnalls Beach B	$R^2 = 0.333$	15	$P < 0.001$
Bagnalls Beach A	$R^2 = 0.293$	30	$P < 0.001$
Redpatch Point	$R^2 = 0.067$	60	$P < 0.001$
Dutchies Beach	$R^2 = 0.181$	30	$P < 0.001$

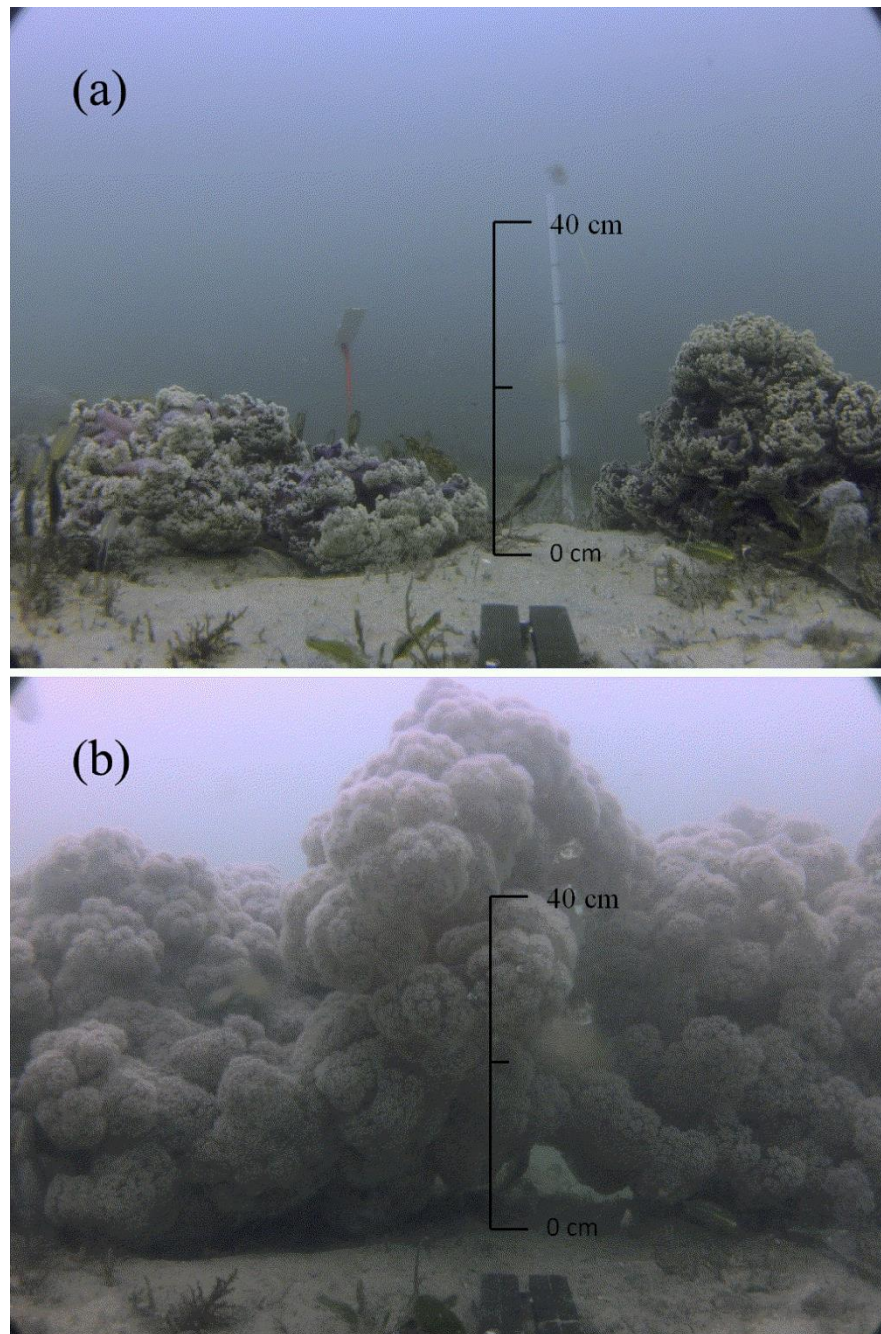


Figure 2. Series of two photos showing height changes in *Dendronephthya australis* colonies at Redpatch Point on 26 January 2015. (a) Heights 15-28 cm at 1445 hrs (high tide, current = 0.0 m s^{-1}); (b) Heights 49-67 cm at 1945 hrs (run out tide, current = 0.23 m s^{-1})

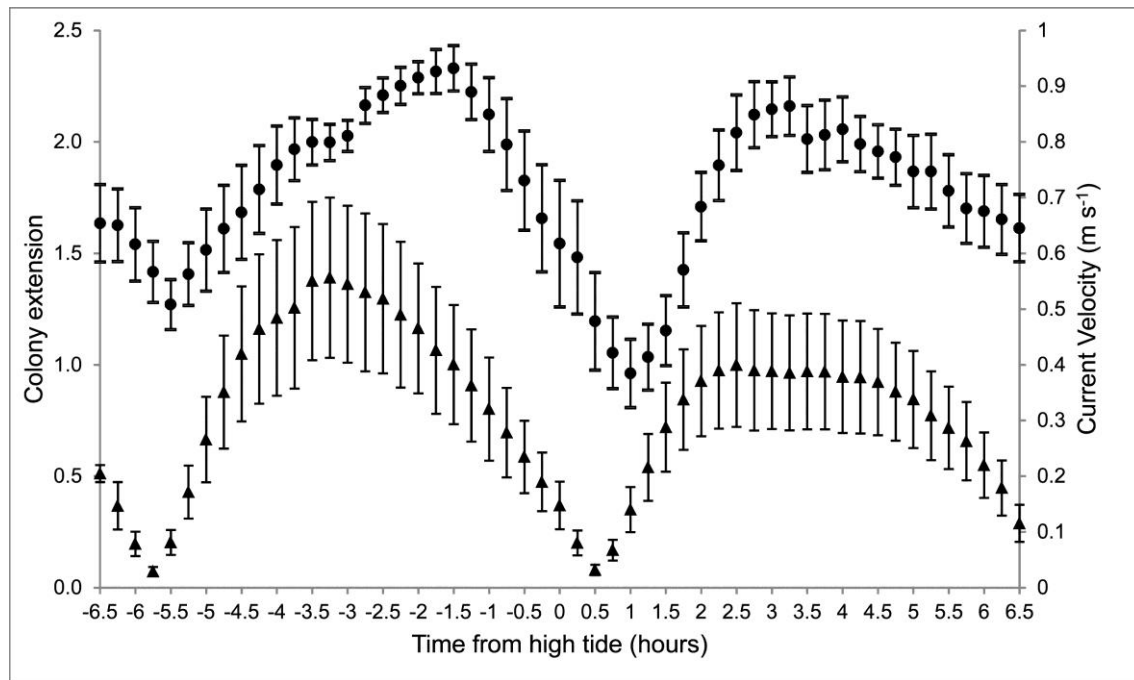


Figure 3. *Dendronephthya australis* extension averaged across sites and days plotted against time from high tide (solid circles, left scale bar - $\pm$ SE). Current velocity averaged across sites and days (solid triangles, right scale bar - $\pm$ SE)

Dendronephthya soft corals are azooxanthellate, passive suspension feeders (Fabricius and Alderslade 2001), and phytoplankton, zooplankton, detritus, and dissolved organic matter are all thought to contribute to the food requirements for azooxanthellate soft coral species (Fabricius *et al.* 1998; Fabricius *et al.* 1995; Widdig and Schlichter 2001). Efficiency of passive suspension feeding is highly dependent on both current speed, and particle concentrations, with encounter rates between feeding structures and food particles increasing as current velocities and particle concentrations increase (Sebens 1984; Shimeta and Jumars 1991). Therefore for suspension feeders, the ability to increase in size in response to increased current flows, as exhibited by *D. australis* in this study, positively impacts on particle capture by: spreading polyps over a larger area; reducing overlaps between polyps; and locally reducing currents increasing food retention rates (Shimeta and Jumars 1991).

Considerable variability was observed in *D. australis* colony response to velocity changes across sites and days (Figure 4) indicating that factors other than velocity affect colony height. One potential source of variability was the concentration of particles in the water column which visibly differed between tides, being generally higher on outgoing tides than incoming tides. Differences in colony response between incoming and outgoing tides were visible (Figure 4), indicating that *D. australis* colony extensions were potentially influenced by both current speed, and variation in the density of food particles in the water column. Retraction has also been observed in soft coral species in response to excessive currents (Fabricius and Alderslade 2001; Patterson 1980), and retraction was observed in *D. australis* colonies at the Bagnalls Beach sites when flows $>0.5 \text{ m s}^{-1}$

occurred (Figure 4 a,b), indicating that *D. australis* may actively reduce height at high flows to avoid damage or uprooting. Another source of variability observed in the study was interaction between adjacent colonies, with neighbouring colonies sometimes moving in synchrony in response to currents, while at other times, one colony appeared to dominate, extending over and shading adjacent colonies, potentially restricting food flows to them. Colony behaviour may also have been influenced by additional factors; including diel variation, and fish predation, although these effects could not be examined using the time-lapse techniques used.

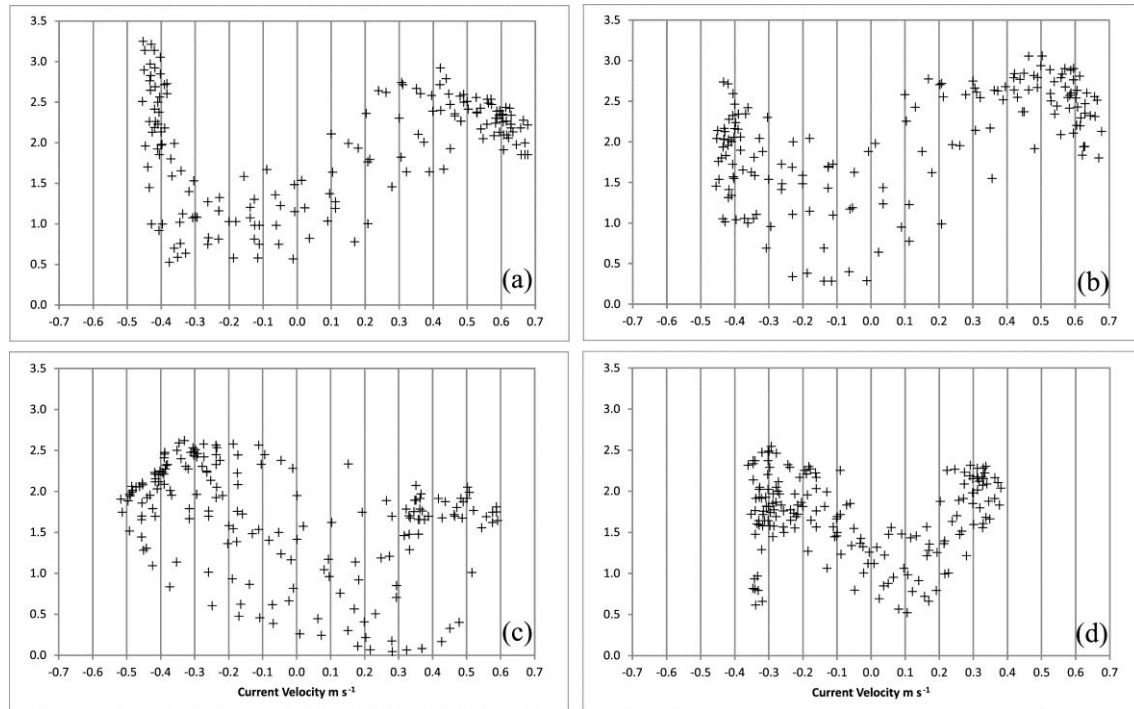


Figure 4. *Dendronephthya australis* extensions at study sites plotted against lagged current velocities. (a) Bagnalls Beach B, lag 15 minutes. (b) Bagnalls Beach A, lag 30 minutes. (c) Redpatch Point, lag 60 minutes. (d) Dutchies Beach, lag 30 minutes. Positive current velocity indicates incoming tidal flows.

This study improves the understanding of the environmental requirements for this geographically restricted soft coral species and this has important implications for conservation management. For example, these data will help to identify other estuarine areas where current velocities may successfully support colonies, allowing informed decisions about sites that could be used for rehabilitation of the species. Further work is required to determine how other factors contribute to changes in *D. australis* behaviour including the effects of particle concentrations in the water column, fish predation, diel variation, and whether intra-specific competition for food occurs between adjacent colonies.

Appendix B - Proximity effects of natural and artificial reef walls on fish assemblages.

Appendix B contains a manuscript that was prepared after fieldwork for Chapter 4 highlighted localised variations in fish assemblages in the vicinity of vertical walls. This manuscript examines variations in fish assemblages at both natural and artificial walls and was published in *Regional Studies in Marine Science* (Davis and Smith 2017):

Davis T.R., Smith S.D.A. (2017) Proximity effects of natural and artificial reef walls on fish assemblages. *Regional Studies in Marine Science* **9**: 17–23.

Proximity effects of natural and artificial reef walls on fish assemblages

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Abstract

Habitat complexity is recognised as a key driver of fish diversity and abundance. However, the effects of small (10s m) reef structures in otherwise uniform reef areas have received little attention. Here, we assessed proximity effects of small natural and artificial vertical walls on patterns of fish assemblages, at a scale relevant to fish survey transects. We tested whether wall size affected assemblages, and whether assemblages differed between wall types. Fish assemblages were found to change in the immediate vicinity of both natural and artificial walls, with significantly higher species richness and abundance occurring at reef walls than in surrounding, flatter reef areas. The size of the effect generated by walls was found to be proportional to the size of the wall, with species richness and abundance generally increasing with wall height and length. Differences between natural and artificial walls were detected, but these were confounded by differences in size between wall types. The study builds on previous work by showing that, within reefs, local areas of higher species richness and abundance can occur in the vicinity of small but important reef features such as vertical walls. This effect introduces considerable variability into data for reef fish surveys and has implications for the design of such studies. In addition, walls appear to act as localised biodiversity “hotspots” and consideration should be given to inclusion of areas containing such features within marine reserves.

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