Marine reserves and Seascape context shape fish assemblages in seagrass ecosystems

7 authors, including:

Andrew Olds
University of the Sunshine Coast
63 PUBLICATIONS   649 CITATIONS

Shing Yip Lee
The Chinese University of Hong Kong
164 PUBLICATIONS   5,650 CITATIONS

Ben Gilby
University of the Sunshine Coast
43 PUBLICATIONS   74 CITATIONS

Tim Stevens
Griffith University, Gold Coast campus
41 PUBLICATIONS   464 CITATIONS

Some of the authors of this publication are also working on these related projects:

Project   Bird conservation View project

Project   mangrove conservation and management View project

Marine reserves and seascape context shape fish assemblages in seagrass ecosystems

**Christopher J. Henderson[1],*, Andrew D. Olds[2], Shing Y. Lee[1], Ben L. Gilby[1,2],
Paul S. Maxwell[3], Rod M. Connolly[1], Tim Stevens[1]**

[1]Australian Rivers Institute - Coasts and Estuaries, School of Environment, Griffith University, Gold Coast, Queensland 4222,
Australia
[2]School of Science and Engineering, University of the Sunshine Coast, Maroochydore DC, Queensland 4558, Australia
[3]Healthy Waterways, PO Box 13086, George Street, Brisbane, Queensland 4003, Australia

ABSTRACT: Spatial properties of landscapes modify the abundance and diversity of most animal assemblages in ways that need to be understood to plan and implement conservation initiatives, and evaluate their effectiveness. Seascape context (i.e. the spatial arrangement of ecosystems) mediates the effects of reserves on fish abundance, species richness and ecological processes in shallow coral reef and mangrove ecosystems; however, it is unclear whether this interaction exerts similar effects on reserves in other ecosystems. This study used baited remote underwater video stations (BRUVS) to test for combined effects of seascape context and reserves on fish abundance in seagrass meadows in Moreton Bay, Queensland, Australia. We demonstrate that the composition of harvested fishes in seagrass meadows was different in reserves and fished areas. Specifically, in reserves there was enhanced abundance of exploited rabbitfish *Siganus fuscescens*, a functionally important herbivore in local seagrass meadows. These reserve effects are not influenced by the area of seagrass meadows or seascape context they occur in (i.e. their spatial proximity to other ecosystems or the ocean). However, seascape context was directly correlated with the spatial distribution of harvested rabbitfish and emperors *Lethrinus* spp., which were more abundant in seagrass meadows nearer to the open ocean. Our results show that reserves and seascape context can shape spatial patterns in the abundance of harvested fishes in seagrass meadows, and that these effects may be operating on different components of fish assemblages. Further empirical data on how and where seascape features modify reserve performance are critical for effective conservation in seagrass and related ecosystems.

KEY WORDS: Seascape ecology · Seagrass · Conservation planning · Fish · Marine reserve

INTRODUCTION

Movement of organisms and matter across landscapes determines the composition of animal assemblages and alters the functioning of ecosystems (Loreau et al. 2003, Baguette et al. 2013, Hyndes et al. 2014). The spatial context of ecosystems, which is dependent on the size and shape of habitats in the landscape, and the level of spatial connectivity with other habitat, modifies spatial patterns in biodiversity and ecosystem resilience across landscapes (Massol et al. 2011, Magris et al. 2014). For this reason, functional connectivity is an important factor in conservation planning, and is commonly used to optimise the design of protected area networks on land and in the sea (Rudnick et al. 2012, Kool et al. 2013, Olds et al. 2016).

Marine reserves (e.g. no-take marine areas inside multi-purpose marine protected areas) have been widely used to promote biodiversity and enhance

productivity (Babcock et al. 2010, Edgar et al. 2014, Olds et al. 2014b, Mellin et al. 2016). These conservation responses are, however, also shaped by the spatial properties of seascapes (i.e. habitat context and connectivity). This is because animals move among habitats to forage, spawn and disperse, affecting the composition of assemblages and the spatial distribution of ecosystem functions (e.g. herbivory, predation, scavenging) (reviewed by Grober-Dunsmore et al. 2009, Sheaves 2009, Boström et al. 2011). There is widespread evidence that seascape context and connectivity can enhance effects of marine reserves on animal abundance, assemblage composition and ecosystem functioning (e.g. Huntington et al. 2010, Nagelkerken et al. 2012, Olds et al. 2012b). To date, all studies examining functional connectivity in a conservation context (i.e. within a marine reserve network) have been conducted with reef seascapes as the focal habitat in predominantly tropical habitats, and it is not clear whether similar effects of connectivity occur in other habitats (Olds et al. 2016).

In marine ecosystems, seagrass has been one of the most frequently used habitats for testing the principles of landscape ecology (Boström et al. 2011), predominantly through the study of fishes and invertebrates in seagrass meadows (Robbins & Bell 1994, Irlandi & Crawford 1997, Micheli & Peterson 1999). This is partly because seagrass meadows are of high ecological and economic significance as habitat for threatened species, and as nursery areas for the juveniles of harvested fishes and crustaceans (Heck et al. 2003, Nagelkerken et al. 2015). Like other coast habitats, seagrasses are threatened globally by coastal development, degraded water quality and sedimentation (Orth et al. 2006, Waycott et al. 2009, Gera et al. 2013). These stressors operate in concert to fragment seagrass meadows, producing heterogeneous seascapes that have been the focus for considerable research into the importance of spatial context and connectivity for seagrass-associated fishes (see reviews by Connolly & Hindell 2006, Heck et al. 2008, Boström et al. 2011). These studies have particularly focused on the size of seagrass patches, positioning within an estuary and their proximity to nearby habitats (Connolly & Hindell 2006, Olds et al. 2012a). In many cases, proximity to the ocean, coral reefs or mangroves has been correlated with higher abundances of fish, as has meadow size (Boström et al. 2006, Connolly & Hindell 2006). Despite the established importance of seascape ecology for seagrass fishes and invertebrates (Nagelkerken et al. 2015), and the conservation significance of these ecosystems (Unsworth &

Cullen 2010), the effect of spatial context of seagrass meadows on the performance of reserves is unknown (Olds et al. 2016).

We used the heterogeneous seascape of Moreton Bay, Queensland, Australia, as a model system to test for joint effects of seascape context and marine reserves on fish assemblages in seagrass ecosystems. The effects of seascape context and marine reserves have been studied in the past in Moreton Bay; however, the focal habitat of these studies was coral reefs, with strong connectivity benefits evident for harvested fish species and key ecological functions (Olds et al. 2012a,b). This system is suitable for examining whether seascape context shapes the effectiveness of reserves for seagrass fishes because: (1) it supports extensive seagrass meadows, including meadows of a variety of sizes and spatial arrangements (Roelfsema et al. 2014); (2) seagrass meadows occur within a heterogeneous seascape comprised of several other habitats including mangroves and coral reefs that are also used by seagrass-associated fishes (Olds et al. 2012b); (3) seagrass meadows in Moreton Bay are protected in a network of marine reserves, but their effectiveness is yet to be determined (Ebrahim et al. 2014); and (4) extensive commercial and recreational fishing takes place in Moreton Bay's seagrass meadows (Department of Agriculture Fisheries and Forestry, http://qfish. fisheries.qld.gov.au/). We hypothesized that seascape context would modify the performance of reserves for harvested fish species; reserve effectiveness would be expected to increase with the size of seagrass meadows, proximity of meadows to other meadows, to other habitats (i.e. coral reefs, mangrove forests) and to the open ocean.

MATERIALS AND METHODS

Study seascape

We surveyed seagrass fish assemblages at 10 locations in Moreton Bay, a shallow subtropical embayment in Queensland, eastern Australia (Fig. 1). It is bordered to the west by the mainland, including multiple estuaries, and to the east by 3 sand islands that allow exchange with oceanic water through 3 passages (Gibbes et al. 2014). Moreton Bay supports a heterogeneous seascape comprising extensive seagrass meadows, inshore coral reefs, mangrove forests and subtidal unvegetated sediments (Stevens & Connolly 2005, Maxwell et al. 2014). This seascape is managed within the multiple-use Moreton Bay Mar-
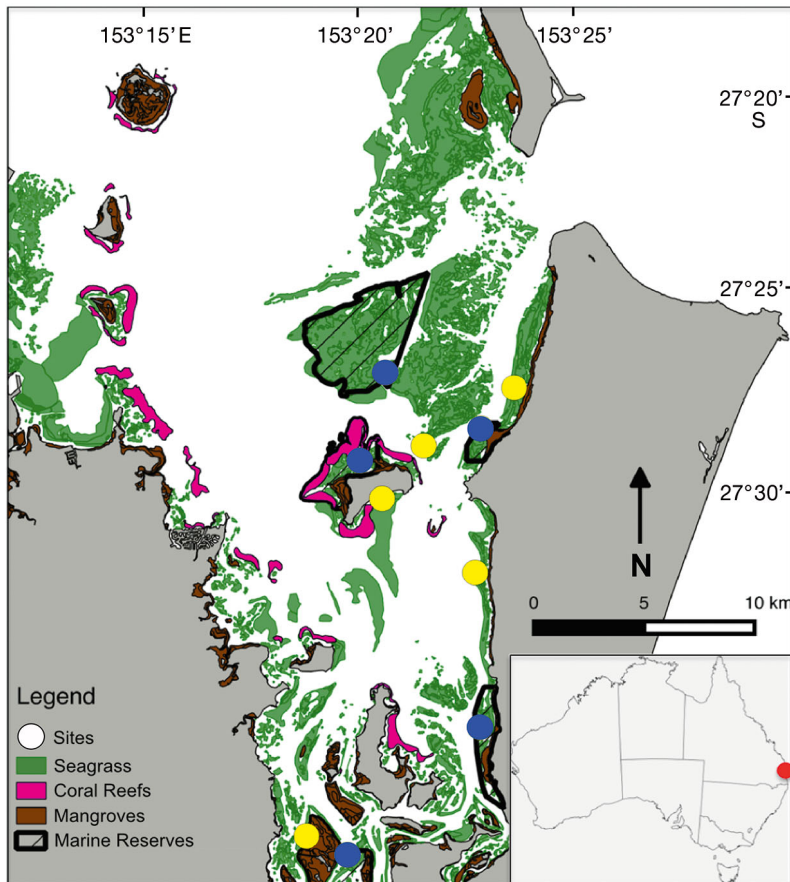
Fig. 1. Seagrass sampling sites in the Moreton Bay Marine Park, Queensland Australia, in marine reserves (blue circles) and fished areas (yellow circles)

ine Park, which contains a number of marine reserves (strict 'no-take' zones). The park was declared in 1993, and the area of reserves expanded in 2009 to 16% of the total marine park area (Queensland Government 2007). The Moreton Bay Marine Park was zoned to protect representative areas of all defined habitat types, as well as protecting areas known to be important for endangered and vulnerable species include dugong and marine turtles. The multiple-use model aims to conserve biodiversity, enhance the abundance of harvested fish species and promote ecosystem function (Queensland Government 2007).

Seascape variables were calculated in ArcGIS (ESRI) by quantifying the area of each seagrass meadow as well as the proximity of meadows to the nearest other meadow, the open ocean, subtidal coral reefs, and intertidal mangrove forests. These 5 spatial variables were, however, highly correlated, and so only one could be included in our analyses at any one time (Fig. 2). Seagrass beds closer to the ocean also experience better water clarity, increased salinity and lower concentrations of nutrients, while those

further away have lower water clarity and salinity and high nutrient concentrations (Gibbes et al. 2014). Sites were deliberately spaced along the established water quality gradient in this system. Sites in the northeast are closest to oceanic waters; sites in the southwest are closest to river discharges.

All 10 subtidal seagrass meadows were dominated by *Zostera muelleri.* Seagrass meadows in Moreton Bay also contain other seagrass species, including *Cymodocea serrulata, Syringodium isoetifolium, Halodule univervis, Halophila ovalis, Halophila spinulosa* and *Halophila decipiens.* Five meadows were conserved in marine reserves (protected since 2009, except one protected since 1997); the other 5 meadows are open to recreational and commercial fishing (but not trawling, which is excluded from all seagrass areas in the bay). Each meadow was surveyed 3 times, in the austral winter (August 2014), spring (November 2014) and summer (February 2015). The intention was to encompass the full range of seasonal temperature variability, to test for consistency in effects through time, but season was not a replicated factor and no deductions are made regarding seasonality.

Fish assemblage surveys

Fish assemblages were surveyed at 10 sites in each seagrass meadow with baited remote underwater video stations (BRUVS) (Malcolm et al. 2007, Harvey et al. 2012). BRUVS consisted of a GoPro HD video camera attached to a 5 kg weight and a bait bag (500 g of pilchards *Sardinox sagax*) fixed 0.5 m in front of the camera by a PVC pipe. The use of BRUVS to assess the fish assemblage can appear, superficially, to bias the community, but previous studies have shown that they are as effective as unbaited remote underwater video stations for sampling herbivorous fish (Harvey et al. 2007). Previous studies within this system have shown that BRUVS are able to record more herbivorous fish then underwater video systems that are baited with algae or are unbaited (Gilby et al. 2016). Each BRUVS deploy-
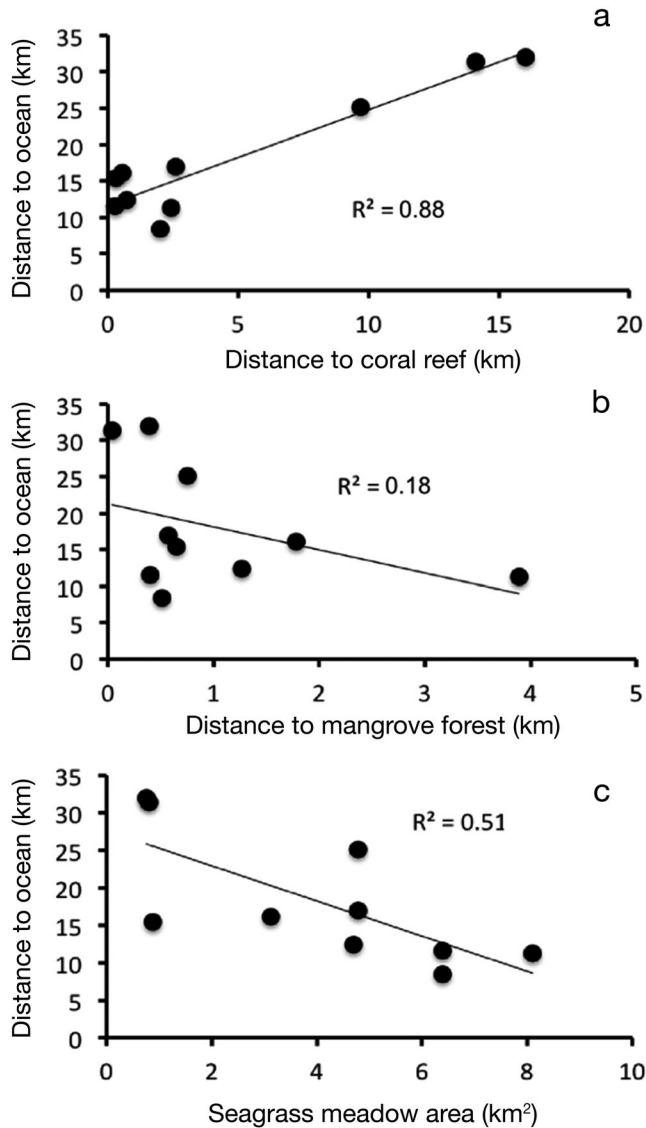
Fig. 2. Distance of seagrass meadows in Moreton Bay to the open ocean plotted against (a) distance to coral reefs, (b) distance to mangroves and (c) seagrass meadow size. Distance to the ocean was significantly (p < 0.05) correlated with all 3 seascape metrics

ment lasted for 1 h (following Harvey et al. 2007, Bernard & Götz 2012 and Santana-Garcon et al. 2014), giving a total video sampling time of 240 h for the study. All BRUVS were deployed over seagrass, positioned in water depths of 1 to 1.5 m at low tide, and spaced at least 200 m apart to avoid sampling the same individual more than once. Fish were surveyed only during daylight hours to avoid any potentially confounding influences of diel fish movement. Fish abundance, species richness, and assemblage composition was quantified from video footage using the standard Max N statistic on all fish that came into the view of the camera (Willis & Babcock 2000).

Due to extensive commercial and recreational fishing in the Moreton Bay region (Webley et al. 2015), harvested fish species, i.e. species targeted by commercial and/or recreational fisheries, are most likely to respond to ecosystem protection and were the focal point for our analyses. We used those listed as 'exploited' by Rees et al. (1999) and Johnson (1999). In Moreton Bay, a range of fish species are harvested by recreational fishers, including emperors *Lethrinus* spp. and yellowfin bream *Acanthopagrus australis*, and by a commercial net fishery, which primarily targets yellowfin bream and black rabbitfish *Siganus fuscescens* (Olds et al. 2012a).

Data analysis

A 5-factor distance-based linear model (DistLM) were used to quantify how assemblages of harvested fishes in seagrass meadows related to the composition of the surrounding seascape. Five seascape variables were included in this analysis: distance to ocean, distance to coral reef, distance to mangrove forest, distance to nearest seagrass patch and seagrass patch size (Anderson 2004). The distance of seagrass meadows to both the open-ocean and adjacent coral reefs was correlated with the composition of fish assemblages (Table 1). These 2 seascape variables were, however, highly cross-correlated (Fig. 2, p < 0.001) and so only distance-to-ocean, which explained the largest amount of variation in fish assemblage composition, was included in subsequent analyses of reserve performance on the 3 dominant harvested species. Assemblage data for harvested fish species were then examined using permutational multivariate analysis of variance (PERMANOVA) (Anderson et al. 2008). The factors were: level of protection (2 levels, fixed factor), sampling period (3 levels, fixed factor), and distance to ocean and coral reef (covariates in separate analyses). Pairwise tests were

Table 1. Results of distance-based linear models (DistLM) relating composition of harvested fish assemblages in seagrass meadows in Moreton Bay, Queensland, Australia to the proximity of different elements of the seascape. Bold text indicates significant variable (p < 0.05)

Source	p
Distance to ocean	**0.001**
Distance to coral reef	**0.005**
Distance to mangrove forest	0.655
Distance to nearest seagrass patch	0.598
Seagrass patch area	0.539

applied to significant factors following PERM-ANOVA, and canonical analysis of principal coordinates (CAP) was used to visualize significant factors (Anderson & Willis 2003). All multivariate analyses were based on modified Gower (log base 2) similarity measures, which exclude joint absences, strongly emphasize differences in species abundance, and are appropriate for dealing with multivariate heterogeneity of variance (Anderson et al. 2011). A similarity profile analysis (SIMPER) was used to determine which species were responsible for differences between reserve and fished seagrass meadows.

Univariate PERMANOVA was then used to examine whether seascape context modified the effect of reserves on individual fish species. Analyses were based on the design adopted for multivariate PERMANOVA tests. As well as total numbers of harvested species, 3 individual species of harvested fish were sufficiently abundant to permit analysis: black rabbitfish (commercially fished), yellowfin bream (commercially and recreationally fished) and emperors (recreationally fished). Seagrass meadows in Moreton Bay support 2 species of juvenile emperor (grassy emperor *Lethrinus laticaudis* and spangled emperor *Lethrinus nebulosus*), but these cannot be reliably identified to species level from video footage and so their abundance was pooled for analysis.

RESULTS

Overall, we recorded 61 species of fish from the seagrass meadows of Moreton Bay, including 23 species that are harvested by local commercial and recreational fisheries. The composition of assemblages of harvested fishes differed between seagrass meadows that were protected inside reserves and those that were open to fishing (Table 2, Fig. 3). CAP showed that sand whiting *Sillago ciliata*, golden trevally *Gnathanodon speciosus*, school mackerel *Scomberomorus queenslandicus*, dusky rabbitfish *Siganus fuscescens*, yellowtail kingfish *Seriola lalandi*, yellowfin bream *Acanthopagrus australis* and moses perch *Lutjanus russelli* were the species whose abundance was most strongy correlated with reserve effects (Fig. 3, Table S1 in the Supplement at www.int-res.com/articles/suppl/m566p135_supp.pdf). There was no difference in the abundance of harvested fishes in seagrass meadows that were open to fishing or in reserves, regardless of the proximity of meadows to the open ocean (Table 3, Fig. 4). While not significant, there were slightly more harvested fish in seagrass meadows that were open to

Table 2. Results of multivariate PERMANOVA of the relation between harvested fish assemblages in seagrass meadows in Moreton Bay and protection, spatial context and season. Bold text indicates significant differences (p < 0.05)

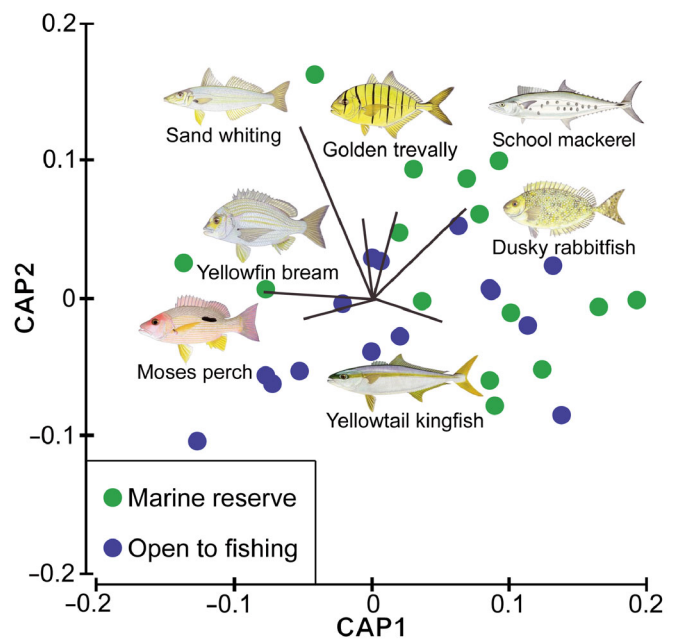| Source	Open ocean		
	df	*F*	p
Protection (P)	1	3.4378	**0.021**
Distance to seascape feature (D)	1	15.287	**0.001**
Season (S)	2	2.009	0.067
P × D	1	1.138	0.325
P × S	2	0.368	0.915
D × S	2	1.036	0.431
P × D × S	2	0.462	0.88
Residual	18		
Total	29		

Fig. 3. Constrained canonical analysis of principal coordinates (CAP) displaying spatial relationships among harvested fish assemblages in marine reserves and fished seagrass beds in Moreton Bay, and illustrating common fish species with distributions that were correlated with the canonical axes (CAP1 and CAP2). The length of vector overlays indicates an increased Spearman rank correlation value. Fish illustrations courtesy of www.efishalbum.com

fishing, but no individual fish species was significantly more abundant in fished seagrass than in protected meadows (see Table S2). Harvested fishes were more abundant in seagrass meadows that were closer to the open ocean (Table 3, Fig. 4).

Harvested fish assemblages were dominated numerically by black rabbitfish, emperors and yellowfin bream, which accounted for 17 to 32% of total

Table 3. Results of univariate PERMANOVA of the relation between the abundance of harvested fish and individual common species (black rabbitfish, emperors and yellowfin bream) in seagrass meadows in Moreton Bay and protection, spatial context and season. Bold text indicates significant differences (p < 0.05)

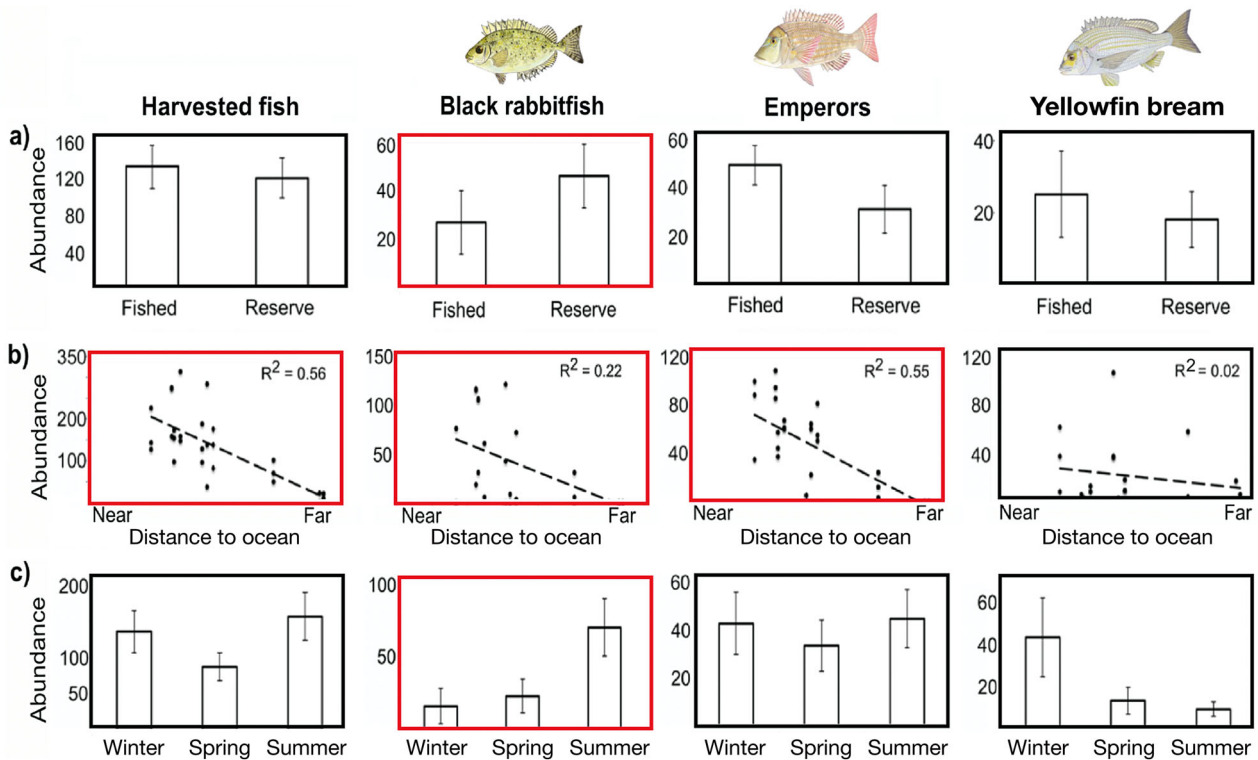|		Harvested fish		Black rabbitfish		Emperors		Yellowfin bream	
Source	df	F	p	F	p	F	p	F	p
Protection (P)	1	3.8	0.06	**6.1**	**0.027**	2.3	0.156	0.1	0.823
Distance to ocean (D)	1	**98.8**	**0.001**	**14.9**	**0.003**	**38.3**	**0.001**	1.4	0.247
Season (S)	2	2.7	0.104	**5.3**	**0.021**	0.2	0.784	1.8	0.193
P × D	1	3.5	0.068	1.8	0.196	0.2	0.69	0.3	0.568
P × S	2	1.1	0.32	0.1	0.935	0.5	0.616	0.3	0.756
D × S	2	**5.4**	**0.018**	1.0	0.354	0.3	0.708	0.1	0.925
P× D × S	2	2.7	0.1	0.4	0.694	0.0	0.986	0.1	0.934

Fig. 4. Abundance of harvested fish and common fish species (black rabbitfish *Siganus fuscescens*, yellowfin bream *Acanthopagrus australis*, and emperors *Lethrinus* spp.) in seagrass in Moreton Bay, Australia, plotted against protection, distance to ocean and season. 'Distance to ocean' is analysed as a continuous variable and is fitted with a linear trend line, with R^2 indicated. Values for the categorical variables 'protection' and 'season' are means ± SD (error bars). Red outlines identify significant factors identified by pairwise PERMANOVA. Fish illustrations courtesy of www.efishalbum.com

fish abundance across all meadows. SIMPER analysis showed that fish assemblages in fished meadows were characterized by large numbers of emperors (60%) and yellowfin bream (13%), and reserve meadows were dominated by black rabbitfish (37%) and emperors (23%). This SIMPER analysis showed that emperor species accounted for 60% of the similarity between different fished seagrass meadows. Black rabbitfish were more abundant in meadows

inside reserves than those open to fishing, regardless of the proximity of meadows to the open ocean, or the season in which surveys were conducted (Table 3, Fig. 4). Rabbitfish were also most abundant in meadows nearer to the open ocean, regardless of protection status or season (Table 3, Fig. 4). Emperors were most abundant in meadows that were closer to the open ocean, regardless of protection status or season (Table 3, Fig. 4). By contrast, the abundance of yel-

lowfin bream was not related to the conservation status or location of meadows, or the season in which surveys were conducted (Table 3, Fig. 4).

DISCUSSION

Joint effects of seascape context and marine reserves for fish assemblages and ecosystem functioning have been reported from the western Pacific Ocean, Caribbean Sea and Florida Keys, but to date these have only been examined in studies with coral reefs as the focal seascapes (Berkström et al. 2012, Pittman & Olds 2015, Olds et al. 2016). Our results show that the composition of harvested fish assemblages were different in reserves and fished areas. Specifically, in reserves there was enhanced abundance of exploited black rabbitfish in seagrass meadows. The seascape context of seagrass meadows was also important to the spatial distribution of harvested fishes: both rabbitfish and emperors were more abundant in meadows that were closer to the open ocean. This is where our results show that reserves and seascape context can exert separate effects on seagrass fish communities. Reserve effectiveness was, however, not influenced by the spatial proximity of meadows to other meadows, other habitats, or to the open ocean. Unlike other studies that have highlighted the importance of seagrass meadow size and proximity to other meadows, in our study these factors were not as influential as other spatial factors, likely due to the larger spatial scale of the study (Connolly & Hindell 2006). This finding runs counter to the results of numerous other studies that have reported positive effects of seascape context on reserve performance in Moreton Bay (Olds et al. 2012a), and elsewhere (Huntington et al. 2010, Nagelkerken et al. 2012, Olds et al. 2014a, Martin et al. 2015). This result is surprising because: (1) the seagrass meadows we studied occur in a heterogeneous seascape that includes numerous other habitats (e.g. coral reefs and mangrove forests) (Stevens & Connolly 2005, Gibbes et al. 2014); (2) seagrass-associated fishes move among these habitats to feed, spawn and disperse (Grober-Dunsmore et al. 2009, Sheaves 2009); and (3) fish are harvested in Moreton Bay in a tunnel net fishery that captures individuals as they move tidally between adjacent seagrass, mangrove and coral habitats (Tibbetts & Townsend 2010, Olds et al. 2012b).

The composition of fish assemblages differed between seagrass meadows that were open to fishing and those that were protected inside marine reserves. However, given that marine reserves in Moreton Bay are designed with the primary aim of representing all habitats (Queensland Government 2007), the strength of the marine reserve effect on fish assemblages seen here may be diminished. Seagrass meadows that are open to fishing support a high abundance of juveniles of fish species, which are harvested as adults by recreational fishers (e.g. bream, emperors, flathead and snapper) (Pillans et al. 2007, Webley et al. 2015); however, with the BRUVS method using a single camera, no size measurements could be made for this study. The addition of stereo-BRUVS to assess size of fish in future studies would provide more information regarding the influences that spatial context and marine reserves have on fish of different sizes, allowing a larger range of the benefits of conservation initiatives to be addressed. Fishing pressure is higher in the southeast Queensland region than anywhere else in the state; however, juvenile fish are protected by size limits and when juveniles are inadvertently captured they are promptly released to avoid potential financial penalties from the fisheries management authority (Webley et al. 2015). While size estimates were not used in this study, a large number of juvenile emperors were recorded. They most likely feed on small invertebrate prey, which would be more abundant in large seagrass beds near the ocean (Boström et al. 2006). The fishing pressure that is experienced in these fished seagrass beds may result in a reduction in competitive pressure, allowing for an increase in the abundance of juvenile fish species. Seagrass meadows that were protected inside marine reserves supported more black rabbitfish, a species that is harvested heavily in a net fishery that targets aggregations of both adults and sub-adults across Moreton Bay (Tibbetts & Townsend 2010, Olds et al. 2012b, Gilby et al. 2016). Commercial fisheries within southeast Queensland heavily target black rabbitfish within a net fishery (Olds et al. 2012a), with 162 t removed from Moreton Bay alone in the last 5 yr (Department of Agriculture Fisheries and Forestry, http://qfish.fisheries.qld.gov.au/). Black rabbitfish are functionally important herbivores, and numerically dominate assemblages of herbivorous fish in seagrass meadows across the study area (Ebrahim et al. 2014, Maxwell et al. 2014). Black rabbitfish have been shown to benefit from reserves in Moreton Bay; their biomass inside protected areas is approximately double that outside, and provides an increased functional role, resulting in a reduction in macroalgal cover (Olds et al. 2012c). The conservation of this important herbivore within marine reserves might,

therefore, promote herbivory and ecosystem functioning in protected seagrass meadows across Moreton Bay (Prado et al. 2008, Davis et al. 2014, Vergés et al. 2014); however, this hypothesis is yet to be tested with empirical data.

The proximity of seagrass meadows to the open ocean was positively correlated with the abundance of total harvested fish, black rabbitfish and emperors (*Lethrinus laticaudis* and *L. nebulosus*). This finding is consistent with the long-standing hypothesis that the position of meadows in estuaries and embayments is pivotal in structuring the spatial distribution of juvenile fishes in seagrass patches (sensu Bell et al. 1988). Moreover, it is widely known that the spatial proximity of seagrass meadows to the open sea is of fundamental significance to the abundance of fish in seagrass (see reviews by Connolly et al. 1999, Nagelkerken et al. 2015). However, due to the heterogeneous nature of seagrass meadows, empirical data on the effects of spatial context on reserve effects are required for effective conservation. Many fish species are more abundant in meadows nearer to the mouths of estuaries, and this is believed to correspond to these areas receiving a greater supply of larvae from offshore locations (Jenkins et al. 1998, Jelbart et al. 2007, Ford et al. 2010). The larger numbers of juveniles in seagrass meadows that are closer to the ocean might also be linked to effects of salinity and turbidity. Both black rabbitfish and emperors undertake ontogenetic habitat shifts in their lives; their larvae recruit into seagrass and juveniles use seagrass meadows as nurseries, before moving offshore as adults to deeper reefs where spawning takes place (Sumpton et al. 2008, Kimirei et al. 2011, Olds et al. 2012c, Gilby et al. 2016). The results of this study, and the findings of previous work on the importance of seascape context to fishes in seagrass meadows (Connolly & Hindell 2006), suggest that the spatial effects of recruitment from offshore locations may be of greater importance to seagrass fishes in Moreton Bay than spatial links with other meadows or other habitats.

We demonstrate that the composition of fish assemblages in seagrass meadows was different in marine reserves compared with fished areas and that reserves enhanced the abundance of black rabbitfish, a functionally important herbivore that is heavily fished in this region. The proximity of seagrass meadows to the open ocean also affected the spatial distribution of 2 harvested fish species; however, the effectiveness of reserves was not modified by the seascape context of individual meadows. Our results show, for the first time, that marine reserves and sea-scape context exert separate effects on seagrass fishes, possibly because reserves and seascape content affect fish at different stages of their lives. Marine reserves prohibit fishing and promote the abundance of sub-adults and adults of harvested fish species in seagrass; this 'reserve effect' is seen most clearly to operate on the commercially fished black rabbitfish. By contrast, the position of seagrass meadows in estuaries is of primary importance in structuring larval recruitment dynamics and, consequently, modifies the spatial distribution of juvenile fishes in seagrass patches. We suggest that empirical data on how and where seascape features modify reserve performance are critical for effective conservation in seagrass ecosystems.

LITERATURE CITED

Anderson MJ (2004) DISTLM v. 5: a FORTRAN computer program to calculate a distance-based multivariate analysis for a linear model. Department of Statistics, University of Auckland

Anderson MJ, Willis TJ (2003) Canonical analysis of principal coordinates: a useful method of constrained ordination for ecology. Ecology 84:511–525

Anderson MJ, Gorley RN, Clarke KR (2008) PERMANOVA+ for PRIMER: guide to software and statistical methods. PRIMER-E, Plymoth

Anderson MJ, Crist TO, Chase JM, Vellend M and others (2011) Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist. Ecol Lett 14: 19–28

Babcock RC, Shears NT, Alcala AC, Barrett NS and others (2010) Decadal trends in marine reserves reveal differential rates of change in direct and indirect effects. Proc Natl Acad Sci USA 107:18256–18261

Baguette M, Blanchet S, Legrand D, Stevens VM, Turlure C (2013) Individual dispersal, landscape connectivity and ecological networks. Biol Rev Camb Philos Soc 88: 310–326

Bell JD, Steffe AS, Westoby M (1988) Location of seagrass beds in estuaries: effects on associated fish and decapods. J Exp Mar Biol Ecol 122:127–146

Berkström C, Gullström M, Lindborg R, Mwandya AW, Yahya SA, Kautsky N, Nyström M (2012) Exploring 'knowns' and 'unknowns' in tropical seascape connectivity with insights from East African coral reefs. Estuar Coast Shelf Sci 107:1–21

Bernard A, Götz A (2012) Bait increases the precision in count data from remote underwater video for most subtidal reef fish in the warm-temperate Agulhas bioregion. Mar Ecol Prog Ser 471:235–252

Boström C, Jackson EL, Simenstad CA (2006) Seagrass landscapes and their effects on associated fauna: a review. Estuar Coast Shelf Sci 68:383–403

Boström C, Pittman SJ, Simenstad C, Kneib RT (2011) Seascape ecology of coastal biogenic habitats: advances, gaps, and challenges. Mar Ecol Prog Ser 427:191–217

Connolly RM, Hindell JS (2006) Review of nekton patterns and ecological processes in seagrass landscapes. Estuar Coast Shelf Sci 68:433–444

Connolly R, Jenkins G, Loneragan N (1999) Seagrass dynamics and fisheries sustainability. In: Bulter AJ, Jernakoff P (eds) Seagrass in Australia: strategic review and development of an R&D plan. CSIRO Publishing, Collingwood, p 25–64

Davis JP, Pitt KA, Fry B, Olds AD, Connolly RM (2014) Seascape-scale trophic links for fish on inshore coral reefs. Coral Reefs 33:897–907

Ebrahim A, Olds AD, Maxwell PS, Pitt KA, Burfeind DD, Connolly RM (2014) Herbivory in a subtropical seagrass ecosystem: separating the functional role of different grazers. Mar Ecol Prog Ser 511:83–91

Edgar GJ, Stuart-Smith RD, Willis TJ, Kininmonth S and others (2014) Global conservation outcomes depend on marine protected areas with five key features. Nature 506:216–220

Ford JR, Williams RJ, Fowler AM, Cox DR, Suthers IM (2010) Identifying critical estuarine seagrass habitat for settlement of coastally spawned fish. Mar Ecol Prog Ser 408:181–193

Gera A, Romero J, Alcoverro T (2013) Combined effects of fragmentation and herbivory on *Posidonia oceanica* seagrass ecosystems. J Ecol 101:1053–1061

Gibbes B, Grinham A, Neil D, Olds A and others (2014) Moreton Bay and its estuaries: a sub-tropical system under pressure from rapid population growth. In: Wolanski E (ed) Estuaries of Australia in 2050 and beyond. Springer, Dordrecht, p 203–222

Gilby BL, Tibbetts IR, Stevens T (2016) Low functional redundancy and high variability in *Sargassum* browsing fish populations in a subtropical reef system. Mar Freshw Res, 68:331–341

Grober-Dunsmore R, Pittman SJ, Caldow C, Kendall MS, Frazer TK (2009) A landscape ecology approach for the study of ecological connectivity across tropical marine seascapes. In: Nagelkerken I (ed) Ecological connectivity among tropical coastal ecosystems. Springer, Dordrecht, p 493–530

Harvey ES, Cappo M, Butler JJ, Hall N, Kendrick GA (2007) Bait attraction affects the performance of remote underwater video stations in assessment of demersal fish community structure. Mar Ecol Prog Ser 350:245–254

Harvey E, Dorman S, Fitzpatrick C, Newman S, McLean D (2012) Response of diurnal and nocturnal coral reef fish to protection from fishing: an assessment using baited remote underwater video. Coral Reefs 31:939–950

Heck KL, Hays G, Orth RJ (2003) Critical evaluation of the nursery role hypothesis for seagrass meadows. Mar Ecol Prog Ser 253:123–136

Heck KL Jr, Carruthers TJ, Duarte CM, Hughes AR, Kendrick G, Orth RJ, Williams SW (2008) Trophic transfers from seagrass meadows subsidize diverse marine and terrestrial consumers. Ecosystems 11: 1198–1210

Huntington BE, Karnauskas M, Babcock EA, Lirman D (2010) Untangling natural seascape variation from marine reserve effects using a landscape approach. PLOS ONE 5:e12327

Hyndes GA, Nagelkerken I, McLeod RJ, Connolly RM, Lavery PS, Vanderklift MA (2014) Mechanisms and ecological role of carbon transfer within coastal seascapes. Biol Rev Camb Philos Soc 89:232–254

Irlandi EA, Crawford MK (1997) Habitat linkages: the effect of intertidal saltmarshes and adjacent subtidal habitats on abundance, movement, and growth of an estuarine fish. Oecologia 110:222–230

Jelbart JE, Ross PM, Connolly RM (2007) Patterns of small fish distributions in seagrass beds in a temperate Australian estuary. J Mar Biol Assoc UK 87:1297–1307

Jenkins G, Keough M, Hamer P (1998) The contributions of habitat structure and larval supply to broad-scale recruitment variability in a temperate zone, seagrass-associated fish. J Exp Mar Biol Ecol 226:259–278

Johnson JW (1999) Annotated checklist of the fishes of Moreton Bay, Queensland, Australia. Mem Queensl Mus 43:709–762

Kimirei IA, Nagelkerken I, Griffioen B, Wagner C, Mgaya YD (2011) Ontogenetic habitat use by mangrove/seagrass-associated coral reef fishes shows flexibility in time and space. Estuar Coast Shelf Sci 92:47–58

Kool JT, Moilanen A, Treml EA (2013) Population connectivity: recent advances and new perspectives. Landsc Ecol 28:165–185

Loreau M, Mouquet N, Holt RD (2003) Meta-ecosystems: a theoretical framework for a spatial ecosystem ecology. Ecol Lett 6:673–679

Magris RA, Pressey RL, Weeks R, Ban NC (2014) Integrating connectivity and climate change into marine conservation planning. Biol Conserv 170:207–221

Malcolm HA, Gladstone W, Lindfield S, Wraith J, Lynch TP (2007) Spatial and temporal variation in reef fish assemblages of marine parks in New South Wales, Australia — baited video observations. Mar Ecol Prog Ser 350:277–290

Martin TS, Olds AD, Pitt KA, Johnston AB, Butler IR, Maxwell PS, Connolly RM (2015) Effective protection of fish on inshore coral reefs depends on the scale of mangrove-reef connectivity. Mar Ecol Prog Ser 527:157–165

Massol F, Gravel D, Mouquet N, Cadotte MW, Fukami T, Leibold MA (2011) Linking community and ecosystem dynamics through spatial ecology. Ecol Lett 14:313–323

Maxwell PS, Pitt KA, Burfeind DD, Olds AD, Babcock RC, Connolly RM (2014) Phenotypic plasticity promotes persistence following severe events: physiological and morphological responses of seagrass to flooding. J Ecol 102: 54–64

Mellin C, Aaron MacNeil M, Cheal AJ, Emslie MJ, Julian Caley M (2016) Marine protected areas increase resilience among coral reef communities. Ecol Lett 19:629–637

Micheli F, Peterson CH (1999) Estuarine vegetated habitats as corridors for predator movements. Conserv Biol 13: 869–881

Nagelkerken I, Grol MG, Mumby PJ (2012) Effects of marine reserves versus nursery habitat availability on structure of reef fish communities. PLOS ONE 7:e36906

Nagelkerken I, Sheaves M, Baker R, Connolly RM (2015) The seascape nursery: a novel spatial approach to identify and manage nurseries for coastal marine fauna. Fish Fish 16:362–371

Olds AD, Connolly RM, Pitt KA, Maxwell PS (2012a) Habitat connectivity improves reserve performance. Conserv Lett 5:56–63

Olds AD, Connolly RM, Pitt KA, Maxwell PS (2012b) Primacy of seascape connectivity effects in structuring coral reef fish assemblages. Mar Ecol Prog Ser 462:191–203

Olds AD, Pitt KA, Maxwell PS, Connolly RM (2012c) Synergistic effects of reserves and connectivity on ecological resilience. J Appl Ecol 49:1195–1203

Olds AD, Connolly RM, Pitt KA, Maxwell PS, Aswani S, Albert S (2014a) Incorporating surrogate species and seascape connectivity to improve marine conservation outcomes. Conserv Biol 28:982–991

Olds AD, Pitt KA, Maxwell PS, Babcock RC, Rissik D, Connolly RM (2014b) Marine reserves help coastal ecosystems cope with extreme weather. Glob Change Biol 20: 3050–3058

Olds AD, Connolly RM, Pitt KA, Pittman SJ and others (2016) Quantifying the conservation value of seascape connectivity: a global synthesis. Glob Ecol Biogeogr 25:3–15

Orth RJ, Carruthers TJ, Dennison WC, Duarte CM and others (2006) A global crisis for seagrass ecosystems. Bioscience 56:987–996

Pillans S, Ortiz JC, Pillans RD, Possingham HP (2007) The impact of marine reserves on nekton diversity and community composition in subtropical eastern Australia. Biol Conserv 136:455–469

Pittman SJ, Olds AD (2015) Seascape ecology of fishes on coral reefs. In: Mora C (ed) Ecology of fishes on coral reefs. Cambridge University Press, Cambridge, p 274–282

Prado P, Farina S, Tomas F, Romero J, Alcoverro T (2008) Marine protection and meadow size alter fish herbivory in seagrass ecosystems. Mar Ecol Prog Ser 371:11–21

Queensland Government (2007) Moreton Bay Marine Park — scientific guiding principles. Queensland Government, Department of National Parks, Sport and Racing, Brisbane. www.npsr.qld.gov.au/parks/moreton-bay/zoning/moreton_bay_marine_park__scientific_guiding_principles.html

Rees A, Yearsley G, Gowlett-Holmes K, Pogonoski J (1999) Codes for Australian aquatic biota (on-line version). CSIRO Marine and Atmospheric Research, Canberra www.marine.csiro.au/caab/

Robbins BD, Bell SS (1994) Seagrass landscapes: a terrestrial approach to the marine subtidal environment. Trends Ecol Evol 9:301–304

Roelfsema CM, Lyons M, Kovacs EM, Maxwell P, Saunders MI, Samper-Villarreal J, Phinn SR (2014) Multi-temporal mapping of seagrass cover, species and biomass: a semi-automated object based image analysis approach. Remote Sens Environ 150:172–187

Rudnick DA, Ryan SJ, Beier P, Cushman SA and others (2012) The role of landscape connectivity in planning and implementing conservation and restoration priorities. Issues Ecol 16:1–23

Santana-Garcon J, Newman SJ, Harvey ES (2014) Development and validation of a mid-water baited stereo-video technique for investigating pelagic fish assemblages. J Exp Mar Biol Ecol 452:82–90

Sheaves M (2009) Consequences of ecological connectivity: the coastal ecosystem mosaic. Mar Ecol Prog Ser 391: 107–115

Stevens T, Connolly RM (2005) Local-scale mapping of benthic habitats to assess representation in a marine protected area. Mar Freshw Res 56:111–123

Sumpton W, Mayer D, Brown I, Sawynok B, McLennan M, Butcher A, Kirkwood J (2008) Investigation of movement and factors influencing post-release survival of line-caught coral reef fish using recreational tag-recapture data. Fish Res 92:189–195

Tibbetts IR, Townsend KA (2010) The abundance, biomass and size of macrograzers on reefs in Moreton Bay, Queensland. Mem Queensl Mus 54:373–384

Unsworth RK, Cullen LC (2010) Recognising the necessity for Indo-Pacific seagrass conservation. Conserv Lett 3:63–73

Vergés A, Tomas F, Cebrian E, Ballesteros E and others (2014) Tropical rabbitfish and the deforestation of a warming temperate sea. J Ecol 102:1518–1527

Waycott M, Duarte CM, Carruthers TJ, Orth RJ and others (2009) Accelerating loss of seagrasses across the globe threatens coastal ecosystems. Proc Natl Acad Sci USA 106:12377–12381

Webley J, McInnes K, Teixeira D, Lawson A, Quinn R (2015) Statewide recreational fishing survey 2013–14. Queensland Government, Department of Agriculture and Fisheries, Brisbane

Willis TJ, Babcock RC (2000) A baited underwater video system for the determination of relative density of carnivorous reef fish. Mar Freshw Res 51:755–763