Vol. 392: 57–68, 2009
doi: 10.3354/meps08197

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published October 19

Spatial distribution of deepwater seagrass in the inter-reef lagoon of the Great Barrier Reef World Heritage Area

Robert Coles[1,*], Len McKenzie[1], Glenn De'ath[2], Anthony Roelofs[1], Warren Lee Long[3]

[1]Northern Fisheries Centre, Primary Industries and Fisheries, PO Box 5396, Queensland 4870, Australia
[2]Australian Institute of Marine Science, PMB 3, Townsville, Queensland 4810, Australia
[3]Wetlands International — Oceania, PO Box 4573, Kingston, ACT 2604, Australia

ABSTRACT: Seagrasses in waters deeper than 15 m in the Great Barrier Reef World Heritage Area (adjacent to the Queensland coast) were surveyed using a camera and dredge (towed for a period of 4 to 6 min); 1426 sites were surveyed, spanning from 10 to 25°S, and from inshore to the edge of the reef (out to 120 nautical miles from the coast). At each site seagrass presence, species, and biomass were recorded; together with depth, sediment, secchi, algae presence, epibenthos, and proximity to reefs. Seagrasses in the study area extend down to water depths of 61 m, and are difficult to map other than by generating distributions from point source data. Statistical modeling of the seagrass distribution suggests 40 000 km^2 of the sea bottom has a probability of some seagrass being present. There is strong spatial variation driven in part by the constraint of the Great Barrier Reef's long, thin shape, and by physical processes associated with the land and ocean. All seagrass species found were from the genus *Halophila*. Probability distributions were mapped for the 4 most common species: *Halophila ovalis, H. spinulosa*, *H. decipiens*, and *H. tricostata.* Distributions of *H. ovalis* and *H. spinulosa* show strong depth and sediment effects, whereas *H. decipiens* and *H. tricostata* are only weakly correlated with environmental variables, but show strong spatial patterns. Distributions of all species are correlated most closely with water depth, the proportion of medium-sized sediment, and visibility measured by Secchi depth. These 3 simple characteristics of the environment correctly predict the presence of seagrass 74% of the time. The results are discussed in terms of environmental dynamics, management of the Great Barrier Reef province, and the potential for using surrogates to predict the presence of seagrass habitats.

KEY WORDS: Seagrass · Trawling · Depth · Marine park · *Halophila* spp.

INTRODUCTION

The Great Barrier Reef World Heritage Area stretches 2000 km along the northeastern coast of Australia, covering 347 800 km^2 of seabed and including almost all of the coral reefs and lagoons of the Great Barrier Reef (GBR) province. Its ca. 2800 coral reefs make up ~6% of the area. The shallow inter-reef and lagoon areas are more extensive comprising ~58% of the area, with the remainder being continental shelf, slope, and deep ocean (Wachenfeld et al. 1998). The Great Barrier Reef Marine Park overlays the world heritage area and provides the legal basis for management which follows a multi-use zoning strategy. Coral reef systems of the GBR have been researched extensively, but until recently little attention has been paid to the less accessible and less charismatic soft-bottom inter-reef habitats. This is despite the fact that a major penaeid shrimp trawl fishery with a gross value of product of around AU$ 110 000 000 yr^{-1} and a scallop trawl fishery with a gross value of product of around AU$ 17 000 000 yr^{-1} operate in these inter-reef waters (Williams 2002). Recent rezoning of the marine park has focused attention on these non-reef ecosystems;

*Email: rob.coles@dpi.qld.gov.au

their connectivity to the coral reef ecosystem, the impacts of fishing, global threats from climate change, global declines of coral reef ecosystems and on the biodiversity of the system as a whole (Day et al. 2000).

In the early 1990s coastal management agencies recognised the value of seagrass meadows to coastal fisheries in the northern Australian region (Coles et al. 1993, Watson et al. 1993), and subsequent studies have reinforced the value of seagrasses as part of coastal ecosystems worldwide (Larkum et al. 2006, Kenworthy et al. 2006). Seagrasses are a functional grouping of vascular flowering plants which can grow fully submerged and rooted in soft bottom estuarine and marine environments. Seagrasses are rated the third most valuable ecosystem globally (on a per hectare basis), and the average global value for their nutrient cycling services and the raw product they provide has been estimated at US$ 19 004 ha^{-1} yr^{-1} (at 1994 prices; Costanza et al. 1997). In tropical and subtropical waters, seagrasses are also important as food for the endangered green sea turtle *Chelonia mydas* and dugong *Dugong dugon* (Lanyon et al. 1989), which are found throughout the GBR and used by traditional indigenous communities for food and ceremonies. Seagrass systems exert a buffering effect on the environment, resulting in important physical and biological support for the other communities.

Seagrasses face an array of pressures in coastal waters as human populations increase and the potential effects of global warming, such as increased storm activity, come into play. Seagrasses have been exposed to climate change in the past, but only over time scales of millions of years (Orth et al. 2006). The rapid changes in coastal waters currently being experienced (Orth et al. 2006) may exceed the capacity of seagrasses to adapt. There is a clear need to characterise initially the extent of existing meadows and their ability to adapt to change.

Comprehensive broad-scale inshore (intertidal and subtidal to 15 m depth) seagrass surveys of the Queensland coast have been completed (Coles et al. 1987, 2007; Lee Long et al. 1993), however, remarkably little work has occurred to describe benthic communities in the soft-bottom, inter-reef and lagoon parts of the Great Barrier Reef. Mapping of seagrass in intertidal zones and shallow water is relatively easy, with many techniques available (McKenzie et al. 2001); however, all rely on the ability to locate a seagrass meadow and to map edges or features that can be georeferenced. Georeferencing is simple and quick in intertidal zones and down to depths where free-divers or SCUBA divers can reasonably operate (i.e. ~15 m below mean sea level); at greater depths the logistics of diving and reduced safe dive times make meadow-edge mapping expensive, time consuming and inaccurate. Incidental collections from trawl nets, vessel anchors and taxonomic collections indicated that seagrass was present in the Great Barrier Reef lagoon at least to depths of 30 m, well below the depth feasible with conventional meadow-edge mapping techniques.

This paper describes a deepwater seagrass survey using a towed video camera at selected sites in water between depths of 15 and 90 m in the GBR, and a method of using that point data to determine the likely distribution of seagrasses. The approach to mapping seagrasses by modelling point source data is discussed, and its implications for global seagrass mapping initiatives considered. Also described is how that information has been used to establish a sophisticated zoning plan for the maintenance of biodiversity and fisheries productivity in the Great Barrier Reef Marine Park; broad-scale patterns of the seagrass meadows are examined, and their implications for fisheries and marine park management discussed.

MATERIALS AND METHODS

Sampling strategy. Because of the extent of the region covered, sampling was conducted over multiple years (1994–1999) with a different section of the GBR sampled in each year; data was collected over 5 separate cruises (of approximately 20 d each) in each of the 5 yr. Cruises were all conducted in the southern hemisphere spring/summer months October, November and December, as previous studies have shown seagrass biomass to be at a maximum during this time (Kuo et al. 1993); this is particularly important for *Halophila tricostata* which can be annual in tropical Queensland, occurring only in spring and summer.

The sampling area included the inter-reef and lagoon waters (from the 15 m contour seaward to the outer barrier reefs, or to the inner edge of the Ribbon Reefs in the northern section). Sampling included the GBR from the tip of Cape York Peninsular (10°S) to Hervey Bay (25°S); approximately 1000 nautical miles (n miles) of coastline extending to just below the GBR in the south. (Fig. 1).

Sampling was stratified in 10 m depth zones from the 15 m contour down (15–25, 25–35, 35–45, 45–55, and 55–65 m etc.). Recorded depths were adjusted to mean sea level by reference to the nearest located tidal plane datum (Queensland Transport 1994–1999) and time of measurement. Two or three cross-shelf transects were randomly located within every 1° of latitude, with the constraint that any location less that a minimum of 10 n miles from a transect location already chosen was rejected. Sites were randomly selected within a distance increment along each transect, such that a mini-

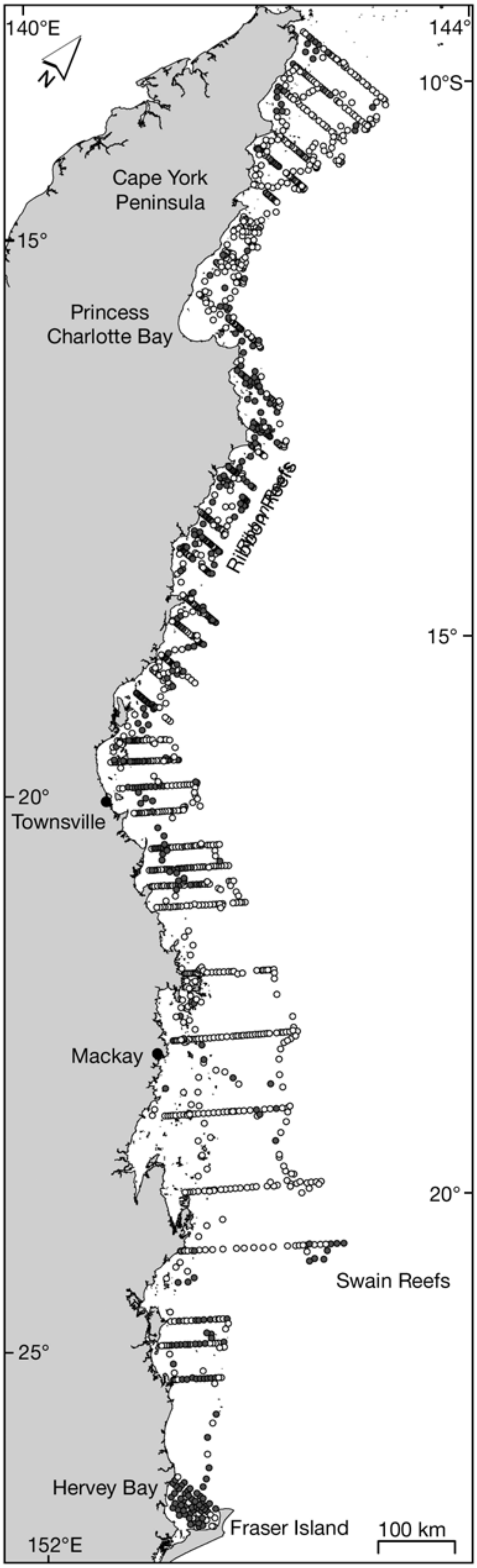

Fig. 1. Location of sampling sites on the Great Barrier Reef (GBR); filled circles: locations with seagrass

mum of 3 sites were in each of the 10 m depth zones; spot sites between transects were additionally chosen at random to check habitat continuity. Any sample location within 2 n miles of a reef or island was coded separately to examine the effect of proximity or shelter from waves. In pre-analysis of the data neither time nor location was found to have a significant effect on seagrass distribution, so the final analysis included all sample points deeper than 15 m where data was recorded.

At each site a real time video (remote colour camera, 795 × 596 PAL system, 2:1 interlace with an electronic iris slaved to an onboard monitor) was used to record an image of bottom habitat and seagrasses for 4 to 6 min of time at drift speed (minimum 100 m tow). Data on seagrass species presence and biomass, macroalgae presence, presence of other benthos (when it could be distinguished), and sediment description were all obtained from post-processed video images. In conjunction with each camera tow, a sled net sample of benthos and a grab sample of the sediment were collected, providing a qualitative benthic sample to confirm the taxonomy and sediment characterisation inferred from the video. Secchi depths were also recorded.

Data collection. Deepwater sites were checked for seagrass presence by replaying and examining the videotapes in the laboratory. Seagrass biomass estimates were based on 10 random time-frames (at a 1 s time accuracy), allocated within the 4 to 6 min of footage for each site (within-site variance was reduced by at least 50% with 10 replicates). Aboveground seagrass biomass for all species combined was determined by a visual estimate of biomass technique (Mellors 1991) adapted for use with video recordings. To standardise biomass estimates, a 0.25 m^2 quadrat (scaled to the video camera lens used in the field) was superimposed on the screen. Observer visual estimates were calibrated by regressing against a set of 50 × 50 cm quadrats videoed in front of a stationary camera (in the 15–20 m depth range), harvested by SCUBA divers, and then later dried and weighed in the laboratory. All observers achieved significant linear regressions ($r^2 = 0.98$) when above-ground biomass estimates were calibrated against the harvested quadrats for all species.

Sediment data were collected using a 6.25 cm^2 van Veen Grab and sieved into 7 fractions: shell/gravel (>2000 µm), coarse sand (<2000–1000 µm), medium sand (<1000–500 µm), sand (<500–250 µm), fine sand (<250–125 µm), very fine sand (<125–63 µm) and mud (<63 µm). An analysis of carbonate fraction was determined using a 10% HCl acid digestion and weight loss method, after first removing all organics with a 10% bleach solution (Blakemore et al. 1987).

Data on the location of trawl effort was extracted from Primary Industries and Fisheries, Queensland (PI&F) compulsory commercial daily logbook data base (CFISH) of trawl fishing log records based on a within 6 min grid (latitude and longitude) location. Great Barrier Reef Marine Park (GBRMP) zoning information was from an ArcMap (ESRI) data layer of GBRMP zoning boundaries.

Statistical analysis. Spatial distributions of the presence/absence of seagrass species were mapped using generalized additive models (GAMs) with binomial error and smoothed terms (Wood 2004) in relative distance across and along the GBR. Latitude and longitude would normally be used for the spatial component of such models; however, the physical and ecological gradients typically run across and (to a lesser degree) along the shelf. Relative distance across the GBR was defined as the distance of a site to the coast, divided by the sum of distances to the coast and to the outer edge of the GBR. Relative distance along the GBR was similarly defined as: the distance to the northern end divided by the sum of distances to the northern and southern ends of the GBR. The coordinates of the across/along system are locally orthogonal, and run at right angles and parallel to the coast, taking advantage of the fact that many processes are affected by the natural geometry of the GBR.

Predictive models of presence/absence of species based on spatial and environmental variables were modelled using (aggregated) boosted trees (BTs) with binomial error (Friedman 2001, De'ath 2007, Fabricius & De'ath 2008). BTs were used for prediction (rather than GAMs) since substantial amounts of environmental data were not available; such data is better handled by BTs, which are also widely recognised as being very effective predictors (De'ath 2007). All analyses used the R statistical package (R Development Core Team, 2006).

RESULTS

Records were obtained from 1426 sites; of these, 1404 were used in statistical analysis for seagrasses deeper than 15 m. Seagrasses were present at 31.4% of sites (Fig. 1), and only the *Halophila* species were found: *H. capricorni* (1.2% of sites), *H. tricostata* (5.6%), *H. ovalis* (9.1%), *H. spinulosa* (11.5%), and *H. decipiens* (17.4%). Seagrass meadows were found in all depth strata, with the deepest recorded at 61 m for *H. decipiens* (Fig. 2). The frequency of occurrence of seagrasses decreased below 35 m, with *H. decipiens* the most commonly found species at all depths. Seagrass dry weight (DW) biomass ranged from less than 1 g DW m^{-2} (*H. decipiens* at a depth of 61 m) to 45 g DW m^{-2} (*H. spinulosa*-dominant meadow at a depth of 21 m). Compared with seagrass meadows in waters less than 15 m deep (Lee Long et al. 1993), the overall mean biomass for all species was low at 3.26 g DW m^{-2} (±0.36).

The across-shelf seagrass distribution (Fig. 3) showed only a weak overall signal, with a consistent tendency for all species to be found closer to the Australian coastline. This distribution was most pronounced for *Halophila tricostata,* which generally occurred adjacent to the mainland coast, preferring sheltered locations (leeward of continental islands and headlands) (Fig. 3). *H. spinulosa* occurred in more central locations of the lagoon, and *H. capricorni* was found proximal to coral reefs (Fig. 3). In comparison, *H. decipiens* was more variable in distribution, both across and along the shelf (Fig. 3).

In contrast to across-shelf distributions, there were large spatial scale discontinuities in seagrass presence with distance along the reef; this pattern was remarkably consistent across species with the exception of *Halophila tricostata*, which was more restricted in distribution than the others (Fig. 3). All seagrass species were sparse north of Princess Charlotte Bay and immediately south of Mackay where the tidal range is 4 to 6 m and tidal velocities were high. Seagrasses were most common in the central narrow shelf region, with highest densities between Princess Charlotte Bay and Townsville and in the southernmost region of the GBR south of 23° S (Fig. 3). *H. tricostata* was found mostly

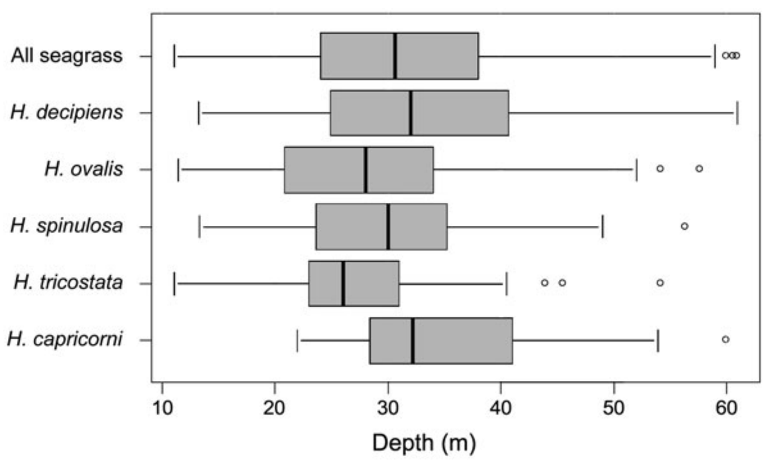

Fig. 2. *Halophila* spp. Boxplots showing the distributions of depths at which species of seagrass are found. Boxes indicate the median and upper and lower quartiles, and whiskers indicate the most extreme of the maximum (minimum) of the data or 1.25 times the inter-quartile range. Circles beyond the whiskers indicate extreme values

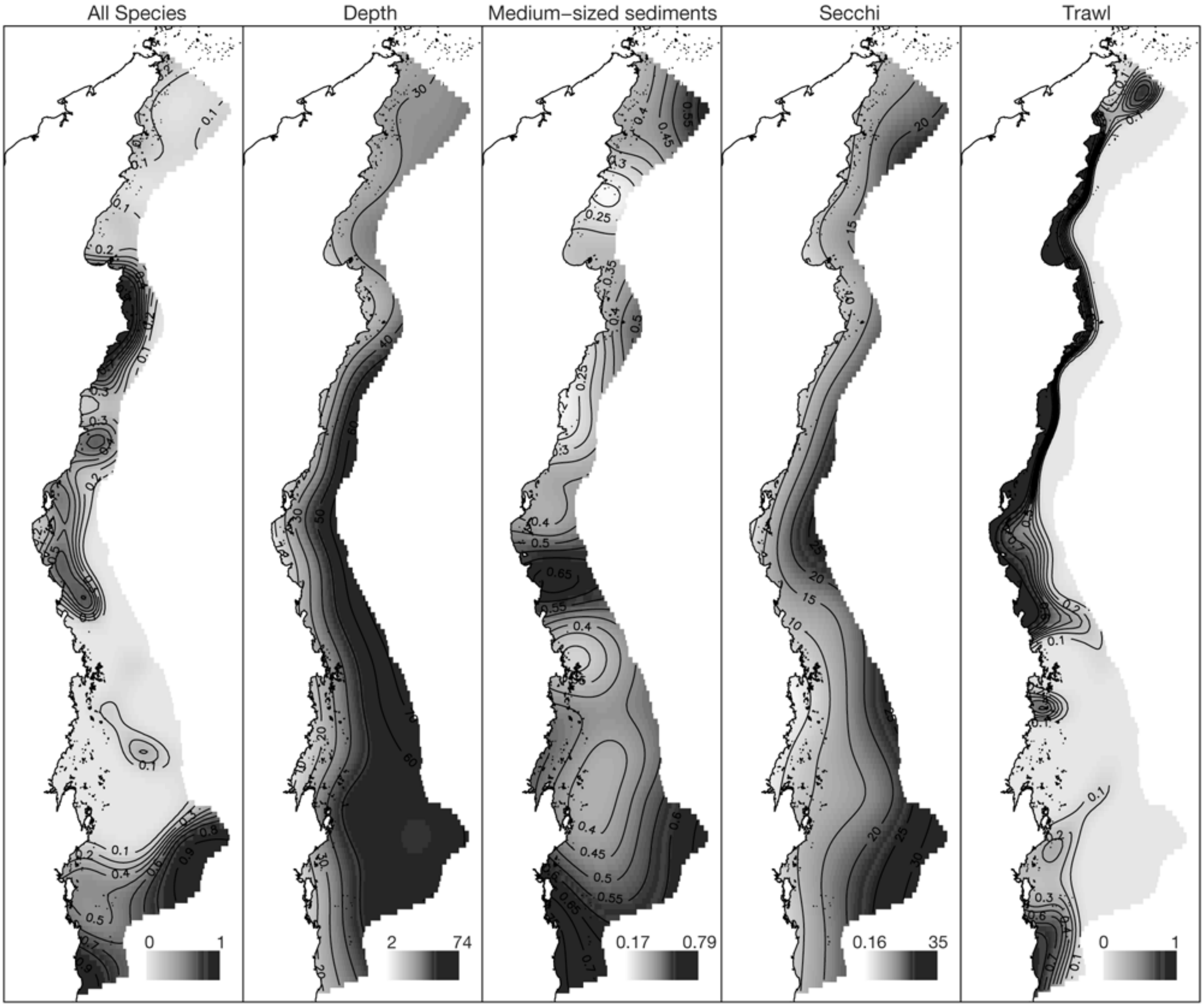

Fig. 3. *Halophila* spp. Estimated probabilities of occurrence of deep-water seagrasses in the Great Barrier Reef lagoon (contours obtained by spatial smoothing)

between Princess Charlotte Bay and Mackay. The spatial discontinuities along the north–south axis of the reef lagoon suggest that biophysical constraints may influence distribution.

A predictive analysis using boosted trees (Figs. 4 & 5; Table 1) was conducted on pooled species using 4 of the 5 species; *Halophila capricorni* was excluded due to its rarity, being only found in 17 sites. Spatial measures (relative distances across and along), physical/environmental measurements (depth, Secchi depth, grain size classification, and visibility derived from Secchi depth), and trawl effort were used as possible predictors of seagrass occurrence. A subset of these variables comprising across-shelf distribution, along-shelf distribution, depth, total medium sized sediments (sum of grain sizes from 125–500 m) and Secchi depth proved to be collectively the best predictors. As is often the case, the spatial and physical/environmental predictors were highly inter-correlated (especially across-shelf distribution, depth and Secchi depth); untangling such effects is at best difficult. For each of the seagrasses, models comprising all 5 predictors (2 purely spatial and 3 purely physical) were compared.

The analyses of the occurrence of the 5 seagrasses showed strong similarities, but there were also substantial differences. Along-shelf distribution accounted for most of the spatial variation, and Secchi depth the least. The physical/environmental effects were largely monotonic (i.e. were either consistently increasing or decreasing); depth (decreasing), sediment and Secchi depth (increasing). With the exception of models where species were pooled, both spatial and environmental predictors were found to predict seagrass occurrence with a similar error to when both spa-

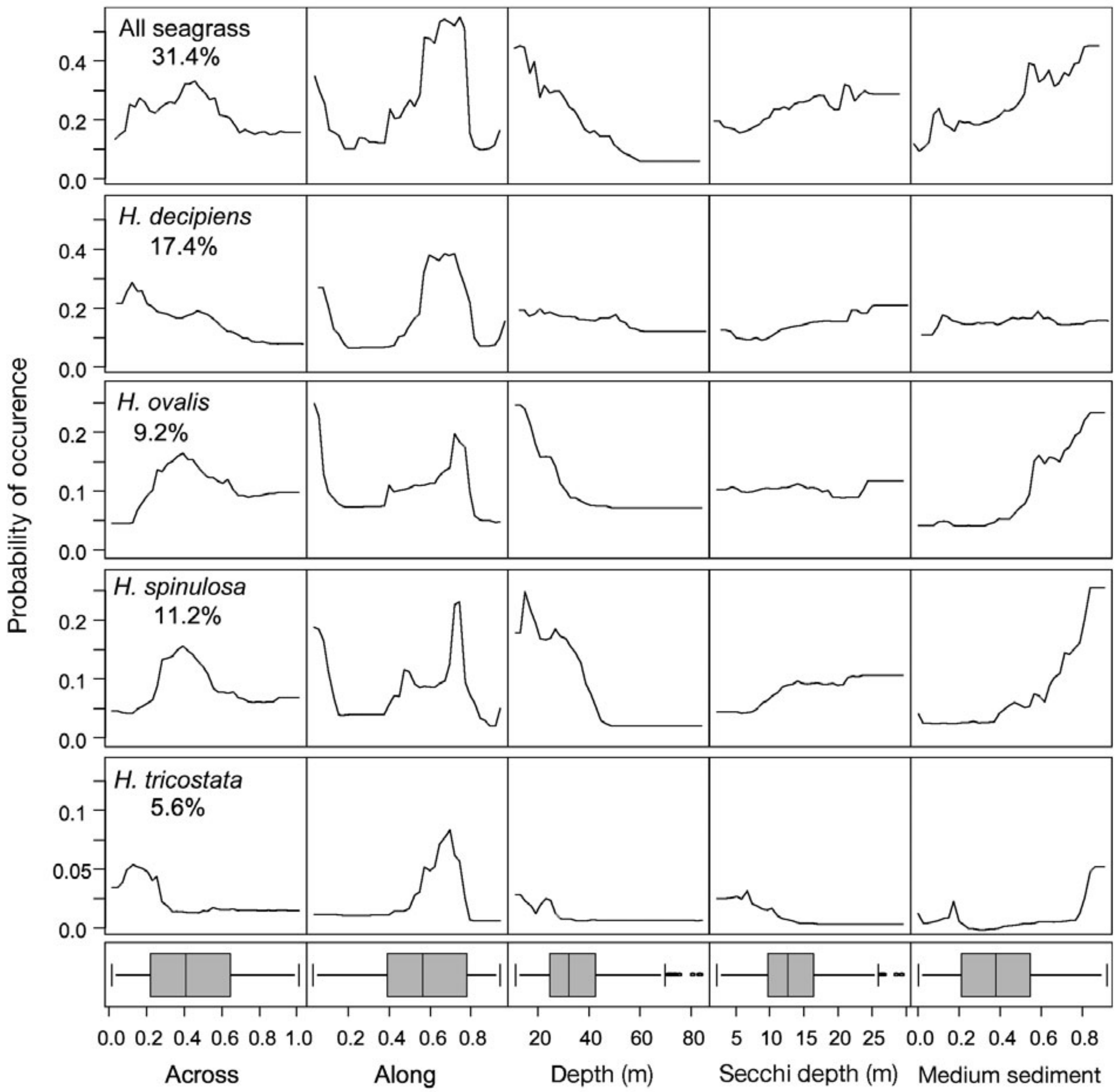

Fig. 4. *Halophila* spp. Modelled probabilities of seagrass species occurrence as a function of across distribution (0: on the coast; 1: outer reef edge), along distribution (0: southern end of GBR; 1: northern end of GBR), depth, Secchi depth and the proportion of mid-sized sediments. Each profile is adjusted for all other predictors in the model. Box plots are 5-point summaries (0, 25, 50, 75, 100 percentiles)

tial and environmental predictors were combined. All models predicted occurrence with an error rate close to half of that based on informed guessing (i.e. guessing randomly but concurring to the observed prevalence). Models comprising all 5 predictors were only marginally better than purely spatial or purely physical/environmental models (Table 1).

Overall seagrass distribution varied strongly with depth (Fig. 4); all species of seagrass were more common in shallower water, with a steady decline in occurrence down to depths of 60 m. The relationship was strongest for *Halophila ovalis* and *H. spinulosa* (*H. spinulosa* was slightly less common in the shallowest depth range). With the exception of *H. tricostata*, all species were more common in areas where the Secchi depth was greatest, although Secchi effects were weaker than other predictors. Seagrasses commonly occurred where large quantities of medium-sized sediments were present. (Fig. 4). This relationship was strongest for *H. ovalis* and *H. spinulosa.*

These results suggest that the presence of seagrasses can be predicted based on a subset of physical/environmental characteristics. For example, for pooled species in the BT regression, the effect of depth was

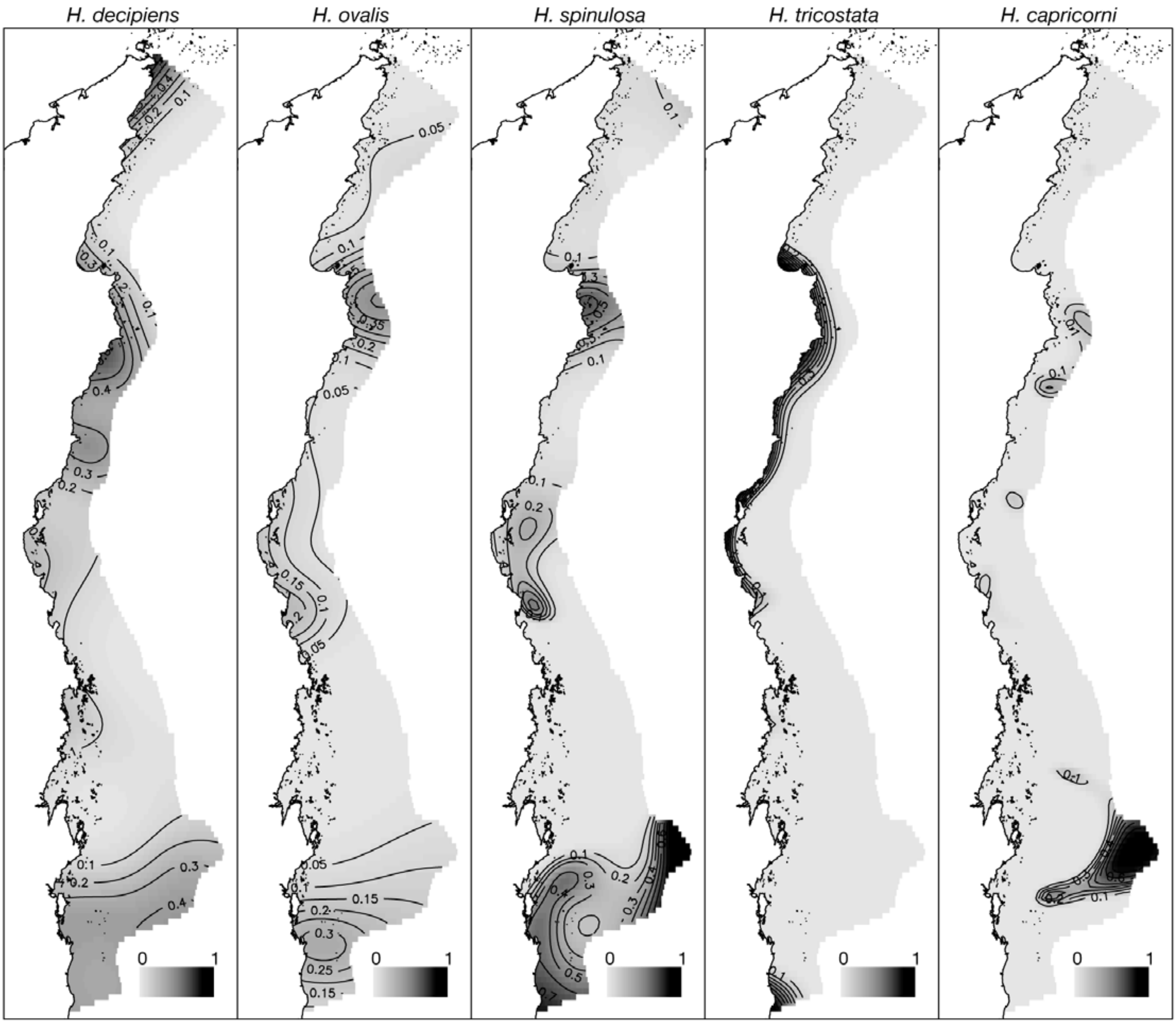

Fig. 5. *Halophila* spp. Spatially smoothed distributions of the presence of seagrass and the 3 environmental variables (depth, medium-sized sediments and Secchi depth) used for prediction of seagrass presence, and presence of trawl effort

Table 1. *Halophila* spp. Results of predictive analysis of occurrence of pooled species of seagrass and 4 individual species based on boosted trees. The prevalence varied from 5.6 to 31.4%. Of the 5 predictors used in the model, 2 were spatial (S: Across and Along distribution) and 3 were environmental (E: Depth, Medium-sized sediment [M-Sed] and Secchi depth). The importance of predictors assigns the percentage of variation predicted to each predictor

Species	Prevalence (%)	Importance of predictors (%)					Prediction error (%)			
		Across	Along	Depth	M-Sed	Secchi	S+E	E	S	Informed guess
Pooled	31.4	15.8	48.0	14.5	16.0	5.6	24.8	26.1	25.4	43.1
H. decipiens	17.4	19.0	49.9	11.2	11.3	8.5	17.1	17.4	17.7	28.8
H. ovalis	9.1	27.0	29.9	18.9	20.0	4.2	9.0	9.2	9.3	16.6
H. spinulosa	11.5	25.1	36.3	15.6	18.7	4.2	11.1	11.8	11.3	20.4
H. tricostata	5.6	17.5	65.6	5.0	8.4	3.6	5.6	5.6	5.6	10.6

strongest, increasing the odds of presence of seagrass increasing by a factor of 9 (equivalent to a shift from p = 0.1 to p = 0.5) in shallow depths (15 m) compared with the deep (60 m). For medium sediments, the odds of seagrass being present increased by a factor of 6 (equivalent to a shift from p = 0.17 to p = 0.5) for 80% compared with 5% medium-sized sediments, and for Secchi depth there was a weaker relationship — the odds of presence of an increase in the probability of presence of seagrass for a shift in Secchi distance from 5 to 25 m depth was 3.5 (equivalent to a shift from p = 0.15 to p = 0.35).

Using the model that only included spatial and depth variables and making the assumption that the reef lagoon is divided into units of 500 m^2 (an individual video tow area), the mean probability of seagrass being present was 0.38, and 23% of those 500 m^2 units would have a probability of >0.5 for the presence of seagrass. This would be equivalent to ~40 000 km^2 of lagoon and inter-reef area within the GBR province having at least a chance of some seagrass being present.

When overlaid on the distribution of trawl fishing effort (which is recorded in grids of 6 min of latitude and longitude) there is considerable overlap; 42% of the grids with catch recorded in 1999 have a >50% chance of seagrass occurrence, and only 29% of grids have a <50% chance of seagrass occurrence are trawled (Fig. 5).

Within the GBR, ~33% of the seagrass area predicted to be present in this study is now included in highly protected no-take zones, and between 50 and 60% is in an area not allowed for trawl fishing (or is in an area where trawling does not take place due to some physical or operational constraint). For areas of the GBR with a greater than 50% chance of seagrass occurrence, modelled trawl data (from electronic monitoring of the Queensland East Coast Trawl Fishery; Coles et al. 2008) shows that only 36.3% is now trawled, and only 14% is trawled more than once in any one year under present management arrangements.

DISCUSSION

Approach to mapping

Making spatial sense of seagrass distributions over an area as large, and in water as deep, as in the GBR province is an enormous challenge. Ideally, the meadow types should be aerially photographed and mapped, with species composition characterised and edge-mapped by GPS (as would be the approach for intertidal seagrass). As this is not possible, we have only the option to infer distributions from point source data, and by investigating mathematical correlations to make some sense of them; in effect, a modeling method is used as a surrogate for remote sensing.

The sheer size of the task is compounded by the potential for temporal variability both within and between years, and by inferences necessarily drawn from a relatively sparse data density and in the absence of any defined seagrass meadow edges. Time and logistics made it impossible to complete the surveys within a season for any one year, or to repeat widely dispersed samples across years. There was no *a priori* reason (unusual weather, etc.) to expect annual GBR-wide differences in deep-water seagrasses over the time of the study; the much more intensively sampled coastal seagrasses in the GBR remain relatively constant through time (Coles et al. 2007). Previous studies in the reef lagoon have shown little change other than slight increases over a 12 yr period; almost certainly the result of improved sampling technique (Coles et al. 2002, 2007). A comparison between this study and a more recent biodiversity study of the GBR lagoon (Pitcher et al. 2007) shows that the strong spatial patterns accounted for 79% of the spatial and temporal variation over a 10 yr period, with only 21% due to variation over time (De'ath et al. 2007).

Seagrass species

Finding only one genus of seagrass (*Halophila*) was a surprising result, although all of the seagrass species that were found are common in the GBR. There are 15 seagrass species in Queensland waters, representing 9 genera; some genera (such as *Enhalus* and *Ruppia*) are restricted to shallow inshore waters and would not be expected in deep-water collections. *Thalassodendron* is usually found associated with reefs. Other (mostly inshore) genera were expected in the distributions, albeit in small numbers. *Halophila* spp. have clearly adapted to survive in the low light conditions of deeper waters in the region, and completely dominate this environment.

Halophila tricostata is a species considered to be endemic to northern Australia (Greenway 1979, Kuo et al. 1993). It has a clumped distribution in this survey and is mostly found close to the coast on medium-sized terrigenous sediments in the central wet tropic area (between Princess Charlotte Bay and Townsville), with some meadows as far south as Mackay. It was among the least known of the *Halophila* species (Kuo et al. 1993), but is now shown to be common in the GBR lagoon, highlighting the extent and importance of the reef lagoon seagrass community as an ecological component of the biodiversity of coastal waters.

Halophila capricorni is found only in the southern Indo-Pacific (Larkum 1995); it is uncommon, and its absence from shallow water collections means it is rarely seen. All other species are broadly distributed throughout the Indo-Pacific region (Fortes 1989, Short & Coles 2001).

Compared with intertidal above-ground biomass measurements from seagrass meadows in Queensland, 3 g DW m^{-2} is low. *Halophila spinulosa* and *H. tricostata* at times formed large and dense meadows. The majority of samples were of isolated plants or of specimens that were very small-leaved species in the *Halophila* genus. Low light levels in deep water influence not only the species suite, but also biomass. *H. spinulosa* had the largest biomass found, at a depth of 21 m. Both *H. spinulosa* and *H. tricostata* are di-meristematic non-leaf-replacing species with an erect stem. They are able to produce additional new leaves on a shoot during the life of the plant (Short & Duarte 2001), allowing them to increase the surface area of a leaf cluster; this maximises photosynthesis in response to low light conditions, and has the effect of contributing to a greater above-ground biomass.

Spatial representation

Prior to this study there was little to suggest large meadows of seagrass existed within the GBR lagoon in water deeper than 15 m; coastal meadows in Queensland had only been surveyed down to 15–20 m, and these were intermittent and of low biomass at the outer edge, even at these depths. There are few other reports of seagrass meadows as extensive as those found at these depths in the GBR from around the world. Den Hartog (1970) reported *Halophila decipiens* to 85 m with records deeper than 50 m in the GBR, Seychelles and Cargados Carajos (Mauritius), but made no attempt to assess the extent of the meadows. Fourqurean et al. (2001), Hammerstrom et al. (2006) and Fonseca et al. (2008) have described aspects of a 20 000 km^2 seagrass meadow on the west Florida shelf, USA. This meadow extends down to the 35 m isobath, although the outer edge is poorly delineated and could presumably extend deeper. The Florida meadows have only one species (*H. decipiens*) in common with our study, and this has a much greater coverage and density, so making comparisons difficult. However the fact that large meadows of seagrass are found in deep water in such (e.g. see Kenworthy et al. 1989) widely separated parts of the world, Florida and northeast Australia, suggests that other deep water meadows are likely to exist, particularly in the tropics.

The natural geometry of the GBR and its lagoon (a long strip, shallow at the reef edge and coast and deep in the middle) forces the geometry of habitat types such as seagrass meadow to run in long NW to SE strips. Because of this geometry, it was assumed in the sampling design that there would be distinct bands of meadow across the narrow E–W axis, with species zonation reflecting the mirrored depth zones in the outer and inner reef lagoon; these were assumed to be more or less consistent throughout the N–S axis. However, the E–W banding was more a concentration of seagrasses within a 15–25 m depth band of the western edge of the lagoon; this area is associated with the presence of terrigenous sediments and mid-range particle sizes. The shallow eastern lagoon, with coarse coralline and *Halimeda* sands and probably low nutrient availability (Udy et al. 1999), supports patchy seagrass meadows of very low biomass.

There are however very strong spatial discontinuities in seagrass meadows along the N–S axis, and these spatial effects alone explain much of the overall variation in seagrass distribution. Seagrasses were uncommon north of Princess Charlotte Bay, a remote area of low human population and little disturbance. The East Australian Current diverges at Princess Charlotte Bay with deep oceanic water flowing shorewards and splitting north and south (Church 1987), and it is possible there is recruitment limitation. Much of the coast north of the Princess Charlotte Bay coast is also silica sand and low in stream run-off, possibly limiting the availability of nutrients for seagrass growth.

Seagrasses formed extensive meadows in a band from Princess Charlotte Bay to just south of Townsville. All species were found in this region which abuts the coastal wet tropics with a moderate tidal range, high annual rainfall and numerous coastal rivers, as well as estuaries (many of which have extensive mangrove forests and large intertidal and shallow subtidal seagrass meadows). There are suitable areas of seafloor at a depth where seagrass can grow, a large supply of potential reproductive material (seeds and vegetative fragments), and ample nutrient input to sustain seagrass growth (Schaffelke et al. 2005). This is a highly productive coastal region mirrored in the adjacent shallow reef lagoon by the extensive seagrass meadows. South of Townsville the extent of seagrass presence declines until reaching an area of large tidal ranges (up to 6 m) just to the south of Mackay, where no major deepwater seagrass meadows exist. This is a region of high current stress, low Secchi readings and coarse mobile sediments; habitat unsuitable for seagrass growth.

The predictive spatial analysis demonstrates surprisingly good accuracy (74 %) based on depth, sediment and visibility measured by Secchi depth (Table 1). The 2 areas where analysis does not accurately predict seagrass presence is in the very north and in the offshore region to the south in the Swain Reef area. Both regions are remote from available reproductive material, and in regions very low in nutrients or removed from the coast. Physically, seagrass could grow in these regions, but that is likely to be prevented by biological constraints specific to those areas. While a 'map' of seagrass derived from physical surrogates may provide a reasonable guide to the likelihood of seagrass presence, local effects will always be difficult to include in a model that describes such a large area; a certain level of uncontrolled error would always have to be allowed for in such a predictive model. Nevertheless, the predictive 'map' generated by the model is a good first approximation of seagrass distribution. This suggests that simple spatial and environmental surrogates can be used to explore the possibility of seagrass in tropical deep-water environments on the coastal shelf, and to 'map' potential areas of seagrass meadows at other locations with similar species.

The ecological role of inter-reef seagrasses and associated algal meadows at these depths is not well understood (Carruthers et al. 2002); it is likely they provide ecosystem services similar to those provided by the coastal and intertidal seagrasses that have been extensively studied worldwide. It is possible productivity is low compared to seagrass meadows in shallow waters (Primary Industries & Fisheries unpubl. data), but this effect would be offset by the very large areas found.

Management implications

The seagrass and benthic community database from this sampling program was one of the major databases that supported development of a multi-use zoning plan in the GBR, the Representative Areas Plan (Kenworthy et al. 2006). This was designed to maintain reef biodiversity, and to determine the location of activities in the Great Barrier Reef Marine Park.

When all spatial closures are included, bottom trawling is now restricted to just 34 % of the park (Coles et al. 2008). There is also an informal agreement by the commercial fishing industry that trawl operators will avoid areas of known seagrass meadows, and repeated trawling in grids with seagrass is not common (with only 14 % of grids trawled more than once in a fishing season). However, trawling is common in the 6 minute (latitude, longitude) fishing grids where seagrass was recorded, and less common where there was no seagrass. This is probably a scale dependent result, as the fishing grids are very large and seagrass may occur within a grid without being affected by trawlers operating on smaller scale fishing grounds. It may also be simple spatial coincidence, with both trawling and seagrass tending to occur on bottom areas with shallow to medium depths and open soft sediments.

Conversely, it is possible that the low intensity bottom trawling (that occurs in most of the survey area) transports viable seagrass vegetative fragments to new sites, or may stimulate growth *in situ* through disturbance of the seed bank. *Halophila ovalis* and *H. decipiens* produce their seeds at or below the surface of marine sediments, where they are unavailable for immediate dispersal (Inglis 2000). Seeds of *Halophila* are persistent, and under laboratory conditions can remain viable for up to 2 yr (Inglis 2000). Laboratory germination trials have shown that seeds of at least 4 species of *Halophila* germinate when they are exposed to light (Inglis 2000), and that light exposure and day length are important in successful flowering and seed production (McMillan 1976). Seagrass seed banks for species such as *H. decipiens* can be comparable in size to the largest seed banks reported for tropical forests and grasslands, and may have an important ecological role in maintaining these seagrass ecosystems (Hammerstrom et al. 2006).

It has been established worldwide that bottom-fishing activities involving the use of mobile gear have a physical impact upon the seabed and the biota that live there (Kaiser et al. 2002). However, our study indicates that at the scale of the whole of GBR, trawling the bottom for penaeid shrimp and scallop over the last 40 yr has not reduced the probability of finding seagrass to levels less than that found in the non-trawled areas.

Changes in GBR deepwater seagrasses are not detectable by surface observation, and large areas could be lost before secondary ecological signals were noticed. Changes in light penetration and the possible effects of climate change (such as increased run-off and turbidity) will be integrated by the plants over long time scales in this region, and changes in distribution patterns, particularly the location of the deep edge, would be a valuable indicator for any long-term climate change.

Acknowledgements. The authors are very grateful to G. Chisholm, P. Leeson and C. Cant for support in the vessel-based sampling program. We thank the many people who assisted us in the field and laboratory, including: P. Daniel, C. Roder, M. Rasheed, K. Vidler, M. Short, A. Grice, B. Deeley, C. Shootingstar, J. Slater, L. Makey, R. Bennett, R. Thomas, S. Hollywood and V. Hall. We also thank T. Done, G. Inglis, H. Marsh, B. Mapstone, C. Crossland, J. Phillips, J. Mellors and D. Reid for comments on sampling design. This project was funded by the CRC Reef Research Centre, the Great Barrier Reef Marine Park Authority and the Queensland Primary Industries & Fisheries.

LITERATURE CITED

Blakemore, LC, Serale PL, Daly BR (1987) Methods of chemical analysis of soils. NZ Soil Bur, Sci Rep 80

Carruthers TJB, Dennison WC, Longstaff BJ, Waycott M, Abal EG, McKenzie LJ, Lee Long WJ (2002) Seagrass habitats of northeast Australia: models of key processes and controls. Bull Mar Sci 71:1153–1169

Church JA (1987) East Australian Current adjacent to the Great Barrier Reef. Aust J Mar Freshw Res 38:671–683

Coles RG, Lee Long WJ, Squire BA, Squire LC, Bibby JM (1987) Distribution of seagrasses and associated juvenile commercial penaeid prawns in north-eastern Queensland waters. Aust J Mar Freshw Res 38:103–119

Coles RG, Lee Long WJ, Watson RA, Derbyshire KJ (1993) Distribution of seagrasses, and their fish and penaeid prawn communities, in Cairns Harbour, a tropical estuary, northern Queensland, Australia. Aust J Mar Freshw Res 44:193–210

Coles RG, Lee Long WJ, McKenzie LJ (eds) (2002) Seagrass and marine resources in the Dugong protection areas of Upstart Bay, Newry Region, Sand Bay, Llewellyn Bay, Ince Bay and the Clairview Region: April/May 1999 and October 1999. Res Publ No 72. Great Barrier Reef Marine Park Authority, Townsville

Coles RG, McKenzie LJ, Rasheed MA, Mellors JE and others (2007) Status and trends of seagrass in the Great Barrier Reef World Heritage Area: report (PR07–3258) to the Marine and Tropical Sciences Research Facility. Reef and Rainforest Research Centre, Cairns

Coles RG, Grech A, Dew K, Zeller B, McKenzie L (2008) A preliminary report on the adequacy of protection provided to species and benthic habitats in the east coast otter trawl fishery by the current system of closures (PR08–3576). Department of Primary Industries and Fisheries, Brisbane

Costanza R, d'Arge R, de Groot R, Farber S and others (1997) The value of the world's ecosystem services and natural capital. Nature 387:253–260

Day JC, Fernandes L, Lewis A, De'ath G and others (2000) The representative area program for protecting biodiversity in the Great Barrier Reef World Heritage Area. Proc 9th Int Coral Reef Symp 2:687–696

De'ath G (2007) Boosted trees for ecological modeling and prediction. Ecology 88:243–251

De'ath G, Coles RG, McKenzie L, Pitcher R (2007) Spatial distributions and temporal change in distributions of deep water seagrasses in the Great Barrier Reef region. Report to the Marine and Tropical Sciences Research Facility. Reef and Rainforest Research Centre, Cairns

Den Hartog C (1970) The seagrasses of the world. North-Holland, Amsterdam

Fabricius KE, De'ath G (2008) Photosynthetic symbionts and energy supply determine octocoral biodiversity in coral reefs. Ecology 89:3163–3173

Fonseca MS, Kenworthy JW, Griffith E, Hall MO, Finkbeiner M, Bell SS (2008) Factors influencing landscape pattern of the seagrass *Halophila decipiens* in an oceanic setting. Estuar Coast Shelf Sci 76:163–174

Fortes MD (1989) Seagrasses: a resource unknown in the ASEAN region. ICLARM Education Series Vol 5. International Centre for Living Aquatic Resources Management, Manila

Fourqurean JW, Willsie A, Rose CD, Rutten LM (2001) Spatial and temporal pattern in seagrass community composition and productivity in South Florida. Mar Biol 138:341–354

Friedman JH (2001) Greedy function approximation: a gradient boosting machine. Ann Stat 29:1189–1232

Greenway M (1979) *Halophila tricostata* (Hydrocharitaceae), a new species of seagrass from the Great Barrier Reef region. Aquat Bot 7:67–70

Hammerstrom KK, Kenworthy JW, Fonseca MS, Whitfield PE (2006) Seed bank, biomass and productivity of *Halophila decipiens*, a deep water seagrass on the west Florida continental shelf. Aquat Bot 84:110–120

Inglis GJ (2000) Variation in the recruitment behaviour of seagrass seeds: implications for population dynamics and resource management. Pac Conserv Biol 5:251–259

Kaiser MJ, Collie JS, Hall SJ, Jennings S, Poiner IR (2002) Modification of marine habitats by trawling activities: prognosis and solutions. Fish Fish 3:114–136

Kenworthy WJ, Currin CA, Fonseca MS, Smith G (1989) Production, decomposition, and heterotrophic utilization of the seagrass *Halophila decipiens* in a submarine canyon. Mar Ecol Prog Ser 51:277–290

Kenworthy WJ, Wyllie-Echeverria S, Coles RG, Pergent G, Pergent C (2006) Seagrass conservation biology: an interdisciplinary science for protection of the seagrass biome. In: Larkum (eds) Seagrass biology, ecology and conservation. Springer, Dordrecht, p 595–623

Kuo J, Lee Long W, Coles RG (1993) Fruits and seeds of *Halophila tricostata* Greenway (Hydrocharitacea) with special notes on its occurrence and biology. Aust J Mar Freshw Res 44:43–57

Lanyon JM, Limpus CJ, Marsh H (1989) Dugongs and turtles: grazers in the seagrass system. In: Larkum AWD, McComb AJ, Shepherd SA (eds) Biology of seagrasses: a treatise on the biology of seagrasses with special reference to the Australian region. Elsevier, Amsterdam, p 610–634

Larkum AWD (1995) *Halophila capricorni* (Hydrocharitaceae): a new species of seagrass from the coral sea. Aquat Bot 51:319–328

Larkum AWD, Orth RJ, Duarte CM (2006) Seagrasses: biology, ecology and conservation. Springer, Dordrecht

Lee Long WJ, Mellors JE, Coles RG (1993) Seagrasses between Cape York and Hervey Bay, Queensland, Australia. Aust J Mar Freshw Res 44:19–31

McKenzie LJ, Finkbeiner MA, Kirkman H (2001) Methods for mapping seagrass distribution. In: Short FT, Coles RG (eds) Global seagrass research methods, Chap 5. Elsevier, Amsterdam, p 101–122

McMillan C (1976) Experimental studies on flowering and reproduction in seagrasses. Aquat Bot 2:87–92

Mellors JE (1991) An evaluation of a rapid visual technique for estimating seagrass biomass. Aquat Bot 42:67–73

Orth RJ, Carruthers TJB, Dennison WC, Duarte CM (2006) Global crises for seagrass ecosystems. Bioscience 56: 987–997

Pitcher CR, Doherty P, Arnold P, Hooper J and others (2007) Seabed biodiversity on the continental shelf of the Great Barrier Reef World Heritage Area. AIMS/CSIRO/QM/DPI CRC Reef Research Task final report, CSIRO Marine and Atmospheric Research, Cleveland, QLD

Queensland Transport (1994–1999) The official tide tables and boating guide. Queensland Transport, Brisbane

R Development Core Team (2006) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Schaffelke B, Mellors J, Duke N (2005) Water quality in the Great Barrier Reef region: responses of mangrove, seagrass and macroalgal communities. Mar Pollut Bull 51: 279–296

Short FT, Coles RG (eds) (2001) Global seagrass research methods. Elsevier, Amsterdam

Short FT, Duarte CM (2001) Methods of the measurement of seagrass growth and production. In Short FT, Coles RG (eds) Global seagrass research methods. Elsevier, Amsterdam, p 154–182

Udy JW, Dennison WC, Lee Long WJ, McKenzie LJ (1999) Responses of seagrass to nutrients in the Great Barrier Reef, Australia. Mar Ecol Prog Ser 185:257–271

Wachenfeld DR, Oliver JK, Morrissey JI (eds) (1998) State of the Great Barrier Reef World Heritage Area 1998. Great Barrier Reef Marine Park Authority, Townsville

Watson RA, Coles RG, Lee Long WJ (1993) Simulation estimates of annual yield and landed value for commercial penaeid prawns from a tropical seagrass habitat, northern Queensland, Australia. Aust J Mar Freshw Res 44: 211–220

Williams LE (2002) Queensland's fisheries resources. Current condition and trends 1988–2000. Information Series QI02012, Queensland Department of Primary Industries, Brisbane

Wood SN (2004) Stable and efficient multiple smoothing parameter estimation for generalized additive models. J Am Stat Assoc 99:673–686

Editorial responsibility: Kenneth Heck Jr., Dauphin Island, Alabama, USA

Submitted: December 22, 2006; Accepted: July 6, 2009
Proofs received from author(s): October 7, 2009