SEAGRASS COMMUNITIES OF TORRES STRAIT,
NORTHERN AUSTRALIA

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Executive Summary

To describe and map the seagrass assemblages of Torres Strait, northern Australia, seagrass was sampled from 1986 to 1996 at 2,230 sites. Four spatial scales were sampled with a nested sampling technique: region (100's km^2), location (1–5 km^2), sites (400 m^2) and quadrats within-sites (0.25 m^2) at approximately six-monthly intervals. At 1,326 sites replicate 0.25 m^2 quadrats were sampled by SCUBA along a 20 m transect and the percentage cover of each seagrass species was recorded for each quadrat. Core samples (0.07 m^2) were also taken along the transect to estimate the biomass and shoot-density of seagrass.

Eleven species of seagrass were identified in Torres Strait: *Zostera capricorni* Aschers., *Cymodocea rotundata* Ehrenb. & Hempr. ex Aschers., *Cymodocea serrulata* (R.Br.) Aschers., *Halodule uninervis* (Forsk.), *Thalassia hemprichii* (Ehrenb.), *Enhalus acoroides* (L. *f.*), *Syringodium isoetifolium* (Aschers.), *Halophila ovalis* (R.Br.), *Halophila. decipiens* Ostenfeld, *Halophila spinulosa* (R.Br.) and *Thallassodendron ciliatum* (Forsk.). Species richness was high and 8 of the 11 species were widely distributed throughout the reefs, islands and seabed of the central and western regions of Torres Strait. In contrast, seagrass was found mainly on the tops of the reefs in eastern Torres Strait.

Area estimates from maps of the presence or absence of seagrass grouped by depth indicated that the largest areas of seagrass on the seafloor were in central (9,032 km^2) and western (4,259 km^2) Torres Strait with the least seagrass (457 km^2) in the eastern Torres Strait region. The ratio of seagrass to non-seagrass areas decreased westwardly across Torres Strait for comparable deep water areas (15–40 m). The ratio was lowest (1:21) in eastern Torres Strait, intermediate in central (1:2.4) and highest in western Torres Strait (1:0.94) which correlated with Sechi depth and the regional distribution of particle grain sizes across Torres Strait with finer sediments and more turbid waters generally found in the central and eastern regions of Torres Strait and coarser sediments and clearer waters in the western region.

The numerically dominant seagrass of Torres Strait was *Thalassia hemprichii* both in terms of biomass, 31.384 gDW.m^{-2} (SE = 6.4) and percentage cover of seagrass, 8.04% (SE = 1.86%). The remaining species ranked by biomass were *Syringodium isoetifolium*, 13.90 gDW.m^{-2} (SE = 4.06), 2.51% (SE = 0.44%); *Cymodocea serrulata*, 11.373 (SE = 3.0), 3.78% cover, (SE = 0.82%); *Enhalus acoroides*, 10.01 (SE = 2.0), *Halodule uninervis* (t), 9.42 gDW.m^{-2} (SE = 3.6), *H. uninervis*, 5.26 gDW.m^{-2} (SE = 1.4), *Cymodocea rotundata*, 5.01 (SE = 1.41), *Halophila ovalis*, 2.60 (SE = 0.73) and *Halophila spinulosa*, 1.39 gDW.m^{-2} (SE = 0.35) averaged over central and western Torres Strait. The percentage cover of *H. uninervis* (t), 1.42% (SE = 0.31%), *H. spinulosa*, 1.29% (SE = 0.28%), *C. rotundata*, 1.25% (SE = 0.31%), *H.ovalis* (l), 1.18% (SE = 0.24%), *H. uninervis* (b), 1.05% (SE = 0.19%), *E. acoroides*, 0.88% (SE = 0.18%) and *H. ovalis* (s), 0.53% (SE = 0.15%) were all less than 2%. The biomass and shoot-density of seagrass was greatest in the shallow bays (< 7 m) and foreshore areas of the continental islands and the reef tops of central and western Torres Strait.

For most species of seagrass most of the variation in percentage cover of seagrass was at the smaller spatial scales sampled, quadrat and sites. In contrast, differences between sampling occasions were relatively small compared to the spatial sources of variation. These general results suggest that physical factors operating at small spatial scales are important in explaining the variation in distribution and abundance of seagrass in Torres Strait.

Pattern analysis of the percentage cover of seagrass averaged by sites indicated that there were four main seagrass assemblages in Torres Strait: a deep-water ($\bar{x}$ = 12.1 m) assemblage with 48% cover of seagrass numerically dominated by *Halophila spinulosa;* an assemblage dominated by the broad-leaved morph of *Halophila ovalis* with 53% cover of seagrass in moderately deep water, 5.4 m in gravelly sand; a large site group with a mixed assemblage of seagrasses characterised by the presence of *Thalassia hemprichii* with five subgroups ranging from an assemblage dominated by the thin-leaved morph of *Halodule uninervis* in shallow nearshore areas and embayments of continental islands with high cover (71%); an assemblage dominated by *Cymodocea rotundata* also with high cover (73%); two assemblages dominated by *Thalassia hemprichii*, one with moderate (51%) and the other with low (9%) cover; and an assemblage dominated by the small-leaved morph of *Halophila ovalis*. The third main seagrass assemblage was characterised by *Cymodocea serrulata* and *Syringodium isoetifolium* and had four subgroups which were separated on the relative amounts of *Cymodocea serrulata* and *Syringodium. isoetifolium* within each subgroup.

The seagrass communities of Torres Strait were a diverse array of complex assemblages with most combinations of species recorded in the field. The communities were mostly dominated by *Thalassia hemprichii*, *Enhalus acoroides* and *Halophila ovalis*. The abundance of individual species of seagrasses were significantly correlated with water depth and species diversity was highest in intermediate (3-6 m) depths of water. Moreover, the variation of species diversity was highest in intermediate water depths. There were no significant correlations between the abundance and biomass of seagrasses and sediment grain size. These results suggest the seagrasses communities of Torres Strait were mostly composed of complex assemblages of species controlled by physical conditions of a complex environment of tides, currents, turbidity and small-scale differences in exposure due to micro topographical variations across foreshore areas. Each species showed a significant response of biomass and abundance with depth but the response curve differed among species; there were large amounts of unexplained variation in the response due to measurement error in water depth uncorrected for tidal level and other physical factors.

Introduction

Nearshore tropical marine systems throughout the world carry extensive seagrass meadows (den Hartog 1970). The biology, ecology and physiology of Caribbean seagrasses have received the most attention (Durako and Moffler 1987, Iverson and Bittaker 1986). Tropical Australia has the greatest seagrass diversity in the Indo-West Pacific region (Poiner et al. 1987) with 14 species recorded in Great Barrier Reef waters (Lanyon, 1986). However, relatively little is known of the seagrass communities in the more northern Australian waters, and most research has emphasised biogeographic distribution (den Hartog 1970) and seagrass distribution at a few localities on the Warrior reefs of Torres Strait in relation to tropical fisheries because of their importance as critical nursery habitats for commercially important species of penaeid prawns, (Turnbull and Mellors, 1990).

The first quantitative study of the distribution and abundance of seagrass in Torres Strait was by Bridges et al. (1982). Seagrasses on 14 islands and reefs were described and at three locations detailed profiles of seagrass abundance were made across the intertidal areas. However, most of the islands and reefs and the large expanses of seabed between the numerous Torres Strait islands and reefs were not sampled and consequently very little is known of the overall seagrass distribution in these waters.

The seagrass communities of Torres Strait are critical habitats for both commercial and traditional fisheries in the region, including tiger and endeavour prawns (*Penaeus esculentus*, *Metapenaeus ensis*), tropical rock lobster (*Panulirus ornatus*), pearl shell (*Pinctata maxima*) green turtle (*Chelonia midas*) and dugong (*Dugong dugon*). The purpose of this study was to map, quantify and describe the communities of seagrasses of the foreshore areas, reefs and shallow subtidal seabed of Torres Strait.

Materials and Methods

Description of the study area

The Torres Strait region is a narrow stretch of water (150 km north-south and 250 km east-west) between Cape York, tropical north Australia and Papua New Guinea (Fig. 1). The Straits proper are 20–60 km wide and 100 km long (Admiralty, 1973). The area has a complex bathymetry with many islands shoals and reefs, however, the straits can be divided into three main physiographic regions: a western, central and eastern Torres Strait (Fig. 1).

The western region extends from the western approaches to Torres Strait to a string of high relief continental islands that extends from Cape York to Papua New Guinea. Many of the islands here have fringing reefs, and platform reefs are also common in the surrounding waters. The region is shallow (< 20 m) and the northern section has extensive and well developed sand waves (Harris, 1988).

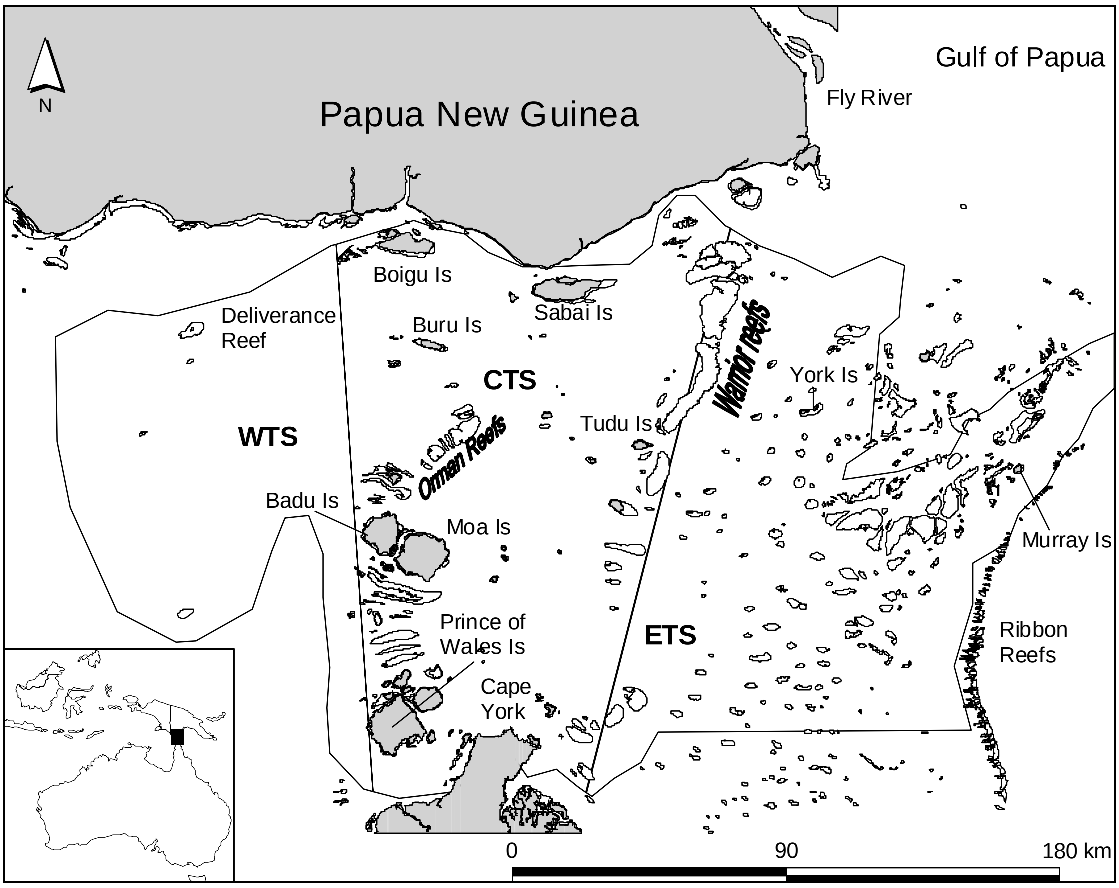


Figure 1. Map of Torres Strait showing the three regions sampled for seagrass and the main islands and reefs (WTS = Western Torres Strait, CTS = Central Torres Strait, ETS = Eastern Torres Strait).

The central region of Torres Strait is situated between the string of continental islands mentioned above and the Warrior reef complex to the west which nearly divides Torres Strait in half. The area is shallow (< 20 m) and there are small rocky islands fringed by reef in the central and southern part of this region. Coral reefs with cays lined by mangroves are found on some of the larger reefs in this region.

The eastern region of Torres Strait encompasses the numerous platform reefs and atolls east of the Warriors and is bounded to the east by the Great Barrier ribbon reefs. The depth of water increases from approximately 20 m on the western side of the Warriors to greater than 100 m approaching the ribbon reefs near Murray Island.

The physical oceanography of Torres Strait has been summarised by Wolanski (1991) and Harris et al. (1988). The winds are seasonal with strong south-east trades in the austral winter (May - October) and north-western monsoons in the austral summer (December - February). The tidal amplitude for the straits ranges from 3.4 to 4.1 m (Anon. 1995) and the strong tidal currents (> 1 $m.s^{-1}$) that flow alternately east and west through the straits keeps the water vertically well mixed (Wolanski et al., 1988). A tongue of Gulf of Papua brackish water intrudes through the Bligh Entrance down the Great North East Channel and is considered to be a permanent feature of the area (Wolanski et al., 1984). The Warrior reefs are apparently not a western boundary to this intruding lens except during transient flood events where large differences in salinity have been recorded on either side of the Warrior reefs (Wolanski et al. 1984).

Field sampling

Seagrass in Torres Strait was sampled during 15 field surveys from 1984 to 1996 (Fig. 1; Table 1). Twelve of these surveys were carried out from 1984 to 1990 specifically to study the seagrass of Torres Strait, hereafter called the seagrass study. Supplemental data on the presence or absence of seagrass or percentage cover of seagrass was collected during three other field surveys in Torres Strait as part of a lobster (Pitcher et al., 1992), by-catch of the prawn fishery in Torres Strait (Harris and Poiner, 1990) and megabenthos survey (CSIRO, 1996) and were used with the data collected during the seagrass survey to map the seagrass.

Sampling techniques

Seagrass Survey

For the seagrass study, samples were taken in a spatially nested sampling design. At each of the reefs, islands and mangrove island chosen as representative examples of the main seagrass habitat types, a variable number of locations (ranged from 1 to 3) approximately 1 km^2 in area were selected and at each location a variable number of sites (ranged from 1 to 30; $\overline{x}$ = 7.44 $sites.location^{-1}$) were sampled by dinghy. Locations were grouped into regions (100 km^2) and from 1 to 6 locations were sampled in a region on each sampling occasion ($\overline{x}$ = 1.78 $locations.region^{-1}$). From one to 15 regions were sampled on each of the 12 sampling occasion ($\overline{x}$ = 6.00 $region.cruise^{-1}$). For most locations the sampling was done approximately twice a year over 4 years from 1986 to 1990. At two locations, in addition to the six monthly sampling, sampling was undertaken every two months from June 1989 to February 1990. The sites were positioned haphazardly over the foreshore and sub-tidal areas to obtain a representative sample of the seagrass assemblages. The sites were either sampled at regular intervals along transects across a location or they were sampled haphazardly within a location. The position of the sites were fixed with an optical range finder, hand compass and triangulation, or by visually estimating the distance from a prominent landmark on shore and taking a bearing. In addition to the above sampling, quantitative samples were also taken haphazardly along the ships track between the islands and reefs to provide quantitative data on the seagrass communities in these subtidal inter reefal areas. Satellite navigation system (SatNav) was used to position the sites in the open water areas.

The above sampling program gave a temporally and spatially nested sampling design with temporal scales of approximately 6 monthly intervals at most locations, and a monthly scale over a 6 month period at two locations at Prince of Wales Island. Four spatial scales were sampled: region (100–300 km^2); location (1–5 km^2); sites (400 m^2) and within-site (0.25 m^2).

Table 1. Data from field surveys done in Torres Strait used to map the presence or absence of seagrass.

Survey	Survey dates	No. sites	Sampling technique	Data type	Location	Reference
Seagrass study	Oct. 1984	258	3 to 5, 0.25 m^2 quadrats and 3 to 5, 0.07 m^2 core samples along 20 m transects	seagrass biomass, percentage seagrass cover	Reef top, inter-reefal and foreshore areas	This study
	Oct. 1985	330				
	May 1988	94				
	Aug. 1988	125				
	Nov. 1988	168				
	Feb. 1989	197				
	Jun. 1989	60				
	Aug. 1989	60				
	Sept. 1989	60				
	Oct. 1989	113				
	Dec. 1989	60				
	Feb. 1990	60				
By-catch of prawn trawling	Mar. 1985 to 1986	274	50 mm net towed at 3.2 knots for 30 min.	seagrass presence or absence	inter-reefal areas east of Warrior reefs	Harris & Poiner, 1990
Lobster survey	Jun. 1989	539	500 m x 2 m transect	seagrass presence or absence	inter-reefal areas	Pitcher et al., 1992
East Torres Strait megabenthos survey	Aug. 1996	208	0.1 m^2 grab; 500 m video transects	seagrass presence or absence	inter-reefal areas	Skewes, et al, 1996

Two methods were used to sample seagrass quantitatively in the seagrass study. For the first method a 0.07 m^2 shovel sample was taken with SCUBA at fixed distances along a 15 m transect line laid out on the ground. At 573 sites 5 quantitative samples were taken with a shovel at 3 m intervals along the transect line; at 819 sites three samples were taken at 5 m intervals and at 63 sites two samples were taken. The number of samples taken at a site was reduced from five to two because of the results of on-going cost-benefit analysis. Samples were placed in separate nylon divers-bags and returned to the dinghy or ship where they were sieved in a 1 cm lug-basket to removed the sediment from the rhizomes. The samples were stored on ice and returned to the marine laboratory at Cleveland where they were processed for shoot-density and biomass. At the laboratory the seagrass sampled was washed in a bath of dilute orthophosphoric acid for 20 min. to remove the epiphytes and to loosen any remaining sediment. The seagrass was then rinsed with fresh water to remove the debris; separated into species and the above-ground shoots were counted and cut from the below-ground rhizomes where the stem met the rhizome. The samples were dried in an oven at 60° C until a constant weight and weighed to the nearest 0.1 gram to estimate the above ground biomass (AGB) and below ground biomass (BGB).

For the second method the percentage cover of seagrass along with the relative proportion of each of the seagrass species in 0.25 m^2 quadrats were visually estimated by SCUBA divers. The relative proportions were later converted by computer to absolute covers for each of the species recorded in the quadrats. To estimate the abundance and biomass of *Enhalus acoroides*, a large seagrass conspicuous seagrass, all shoots were counted in each of the quadrats. A sample of 5 shoots was also collected along the transect and processed back at the laboratory as above to estimate the average dry-weight of *Enhalus acoroides* shoots per site. The biomass of *Enhalus acoroides* was estimated for each quadrat by multiplying the shoot density in each quadrat by the average shoot dry-weight.

A total of 8,269 quadrats were sampled at 1,326 sites. At most sites (631) 10 quadrats were sampled, however, the number of quadrats to sample per transect was reduced from 10 to 5 over the duration of the study as part of an on-going cost-benefit analysis.

The diversity of seagrass biomass was calculated with the Shannon-Weiner information content index as:

$$H' = \sum_{i=1}^{s} p_i \log(p_i)$$

where

p_i is the proportion of the total above-ground-biomass of seagrass; summed over the s species to give the diversity, H'

Lobster survey

For the lobster survey, seagrass was scored as present or absent along 500 m x 2 m transects (Pitcher et al., 1992). The 512 sites were randomly positioned throughout central Torres Strait west of the Warrior reef complex.

Prawn trawl by-catch survey

For the prawn trawl by-catch survey, seagrass brought up by a 30 min trawl (Florida Flyer prawn trawl nets with 9.15 m headrope, 50 mm stretched mesh and 44 mm stretched-mesh cod-end) was identified and scored as present or absent at all trawl sites (Harris and Poiner, 1990). The sites were sampled on 7 different occasions over the 18 month study period to give a total of 274 prawn trawls.

Megabenthos survey

For the megabenthos survey, 208 sites were sampled in eastern Torres Strait. A 0.1m^2 grab sample and a 500 m video transect was sampled at each site and the presence or absence of seagrass was recorded (Skewes, et al, 1996).

Environmental variables

At all sites water depth was measured and at 370 sites sediment samples were taken and processed back at the laboratory with techniques given in Folk (1968) for grain size fraction analysis. For the seagrass study, Sechi depths were taken at 332 sites and sediment depth was measured at 1,387 sites by pushing a 2 m ruler into the sediment by hand as far as it would go.

Data analysis

Seagrass mapping

Quantitative data was collected during the seagrass study and qualitative presence or absence data was collected during the lobster, fish trawl and megabenthos survey; hence quantitative data from the seagrass study was converted to seagrass presence or absence data to produce a map of the presence or absence of seagrass of Torres Strait. The presence or absence data were converted to areas with unweighted tessellated polygons with a Geographic Information System (GIS) and each polygon was classified by seagrass presence or absence. The area of seagrass for the eastern, central and western Torres Strait regions were measured in the GIS by summing the areas of the polygons in a region that were classified as seagrass present.

Seagrass distribution and environmental variables

A depth contour plot was created with the GIS based on 23,563 depth recordings that were obtained by digitising nautical charts of Torres Strait (AUS 296, 292, 289, 299 and 294), by divers and also from a computer interfaced to a depth sounder and a GPS from the various CSIRO cruises in Torres Strait. The seagrass presence or absence map was superimposed on the depth contour map and cross-tabulated to give area estimates of seagrass present or absent for eight depth classes (0, 1–5; 5–10; 10–15, 15–20, 20–30, 30–40 and > 40 m) and three regions, eastern, central and western Torres Strait.

To quantify the distribution of seagrass and diversity with depth, the $\log_e$-transformed above- and below ground biomass of seagrass data collected during the seagrass study was grouped into 1 m depth intervals and averaged. The averaged values were regressed against depth and depth squared. The regression model tested for both an exponential and a non-linear change of seagrass biomass with depth.

Correlation analysis was done on samples collected during the seagrass study to measure the relationship between seagrass biomass, shoot-density and percentage seagrass cover with Sechi depth, sediment grain size and sediment depth.

Nested ANOVA

A nested analysis of variance was done to estimate the variance components for sampling occasions and for the spatial scales sampled during the seagrass study: region, location, site and within-site. Maximum-likelihood estimates of the variance components were obtained with PROC VARCOMP (SAS 1988).

Pattern analysis to describe seagrass communities

Pattern analysis techniques were used to classify and ordinate the sites sampled in the seagrass study (*q*-mode analysis) based on the similarity of the percentage cover of seagrass species averaged by sites. Because of the large number of sites (1,326) they were first grouped with PROC FASTCLUS (SAS, 1988) into 50 groups based on Euclidean distance computed from the percentage cover of seagrass. The group means for the percentage cover of seagrass species were then clustered with PATN (Belbin 1991) software with the Bray-Curtis dissimilarity measure. The unweighted-group-mean-average clustering algorithm with a beta value of -0.1 was used to sort the sites based on their collective dissimilarities and a dendrogram was produced to assist with the interpretation of the groupings. ANOVA was done to test whether the environmental variables, water depth, Sechi depth, sediment depth and sediment grain size differed significantly among the groups. Sites were ordinated with multi-dimensional scaling (MDS) and the MDS scores were correlated with the environmental variables.

Species groups were obtained with *r*-mode analysis by grouping species based on similarities in the percentage cover of seagrass among sites. A two-way table was also produced to visually assist with the joint interpretation of the species and site groupings (Belbin, 1991).

Results

Seagrass mapping

A map of the presence or absence of seagrass in the foreshore and inter-reefal areas of Torres Strait created from the presence or absence of seagrass recorded at 1,477 sites sampled during the seagrass study, fish-trawl, lobster and megabenthos survey (Fig. 2a) indicated that seagrass was broadly distributed throughout central and western Torres Strait but was largely absent from the inter-reefal areas of eastern Torres Strait (Fig. 2b). Reefs were excluded from this analysis because too few reefs were sampled during the seagrass study to map the seagrass on them. The Torres Strait study area was 42,952 km^2

which was divided into eastern, 15,794 km^2, central, 17,458 km^2, and western, 9,700 km^2 regions; the total estimated area of seagrass was 13,425 km^2 which was a third (33%) of the study area (Table 2). Area estimates from the seagrass map indicated that the largest area of seagrass, 8,434 km^2, was in central Torres Strait (Table 2). There was less area of seagrass in western Torres Strait, 4,246 km^2, and relatively little, 745 km^2, in eastern Torres Strait. Differences were also evident when the estimates were adjusted for differences in study area size. The proportion of seagrass to non-seagrass areas (1: 0.93) was highest for central Torres Strait with more area mapped as seagrass than non-seagrass; decreased for western Torres Strait (1:1.2); and was low (1:35) for eastern Torres Strait. These comparisons were affected by differences in average water depths among the three regions with average water depths for Eastern Torres Strait, 40.1 m, much deeper than central, 9.0 m and western, 10.7 m, Torres Strait study area. To adjust proportions for differences in water depth a further comparison based on the ratio of seagrass to non seagrass areas in the depth range, 15 to 40 m was done. The estimated area of seagrass in the depth range of 15–40 m was 457, 970 and 1,102 km^2 for eastern, central and western Torres Strait respectively and the non-seagrass areas were 9,612, 2,352 and 1,039 km^2 respectively. The ratio of seagrass to non seagrass areas was 1:21 for eastern Torres Strait, 1:2.4 for central Torres Strait and 1:0.94 for western Torres Strait. There was a increase in the ratio of seagrass to non-seagrass areas eastwardly across the Straits for seabed areas between 15 and 40 m water depth (Table 2).

General distribution and abundance of seagrass

Eleven seagrass species were identified from the 1,326 sites sampled during the seagrass study in Torres Strait, *Zostera capricorni* Aschers., *Cymodocea rotundata* Ehrenb. & Hempr. ex Aschers., *Cymodocea serrulata* (R.Br.) Aschers., *Halodule uninervis* (Forsk.), *Thalassia hemprichii* (Ehrenb.), *Enhalus acoroides*(L. *f.*), *Syringodium isoetifolium* (Aschers.), *Halophila ovalis* (R.Br.), *Halophila decipiens* Ostenfeld, *Halophila spinulosa* (R.Br.) and *Thallassodendron ciliatum* (Forsk.). Because *H. decipiens* was difficult to distinguish from *H. ovalis* in the field they were both identified as *H. ovalis.* Two morphs of *H. ovalis* and *Halodule uninervis*, were easily distinguished in the field on the basis of leaf size and were scored separately for the percentage cover in the quadrats. *H. uninervis* occurred as a thin-leafed (leaf width up to 1 mm) and broad-leafed (width ~ 2 to 3 mm) morph. *H. ovalis* occurred as a small-leafed (leaf width ~ 5 to 8 mm) and large-leafed (leaf width ~ 15 to 20 mm) morph.

Thallassodendron ciliatum was distributed along the edge of the coral reefs west of and including the Warrior reef complex. *Zostera capricorni* was sampled only in the boat harbour at Thursday Island and was not included in subsequent data analyses because there were so few records of this seagrass.

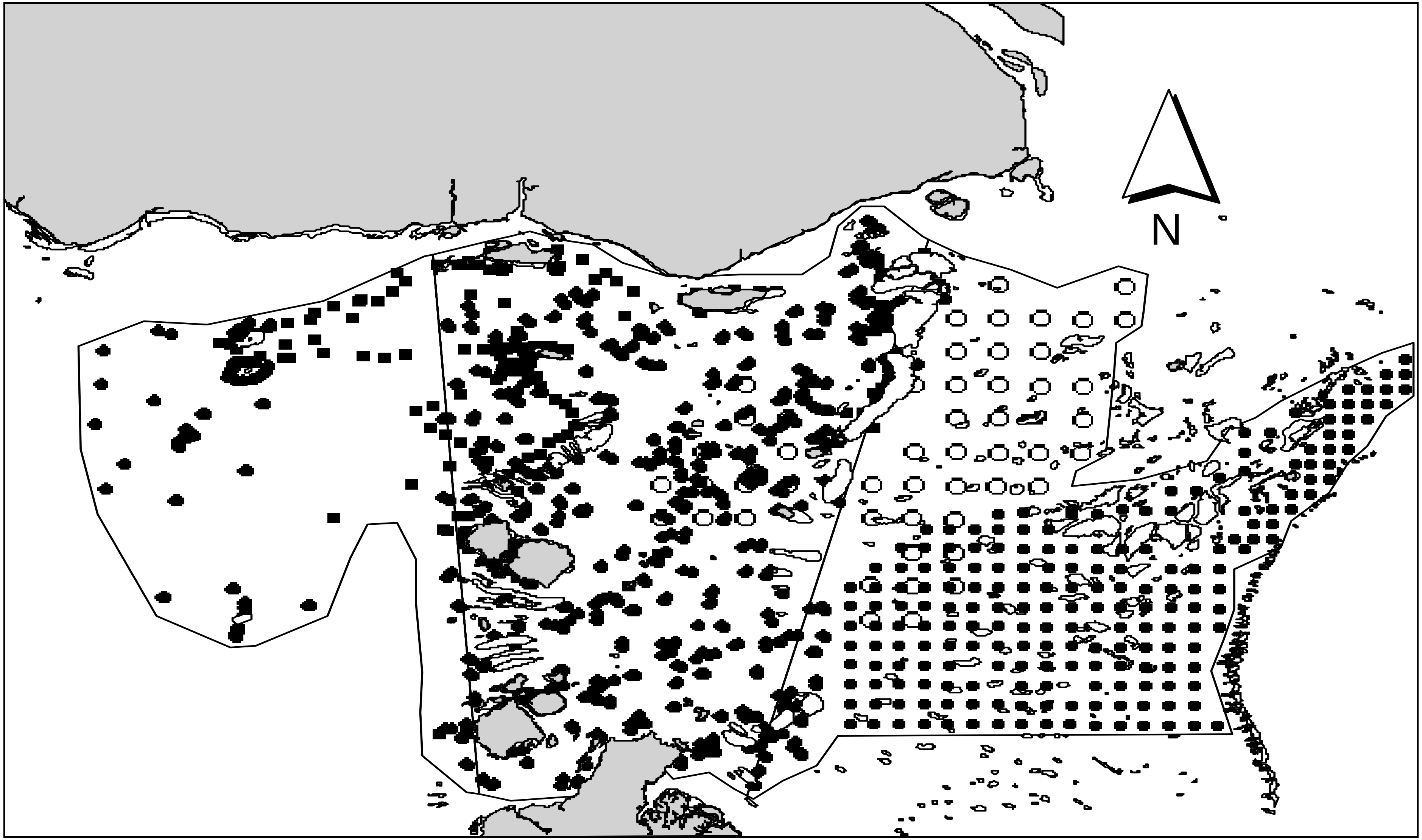
Estimates of the biomass of seagrass of Torres Strait were calculated from the location means to rank the relative numerical importance of seagrass in Torres Strait. Location means were used to reduce the bias due to different sampling intensities among locations. The numerically dominant seagrass of Torres Strait in terms of biomass was *Thalassia hemprichii* with 31.384 gDW.m^{-2} (SE = 6.4); the maximum average biomass per location of *T. hemprichii* was 416.29 gDW.m^{-2}. The next four dominant seagrasses, *Syringodium isoetifolium*, 13.90 gDW.m^{-2} (SE = 4.06), *Cymodocea serrulata*, 11.373 (SE = 3.0), *Enhalus acoroides*, 10.01 (SE = 2.0) and *Halodule uninervis* (t), 9.42 gDW.m^{-2} (SE = 3.6) were less abundant by at least a factor of two. The broad-bladed morph of *H. uninervis*, 5.26 gDW.m^{-2} (SE = 1.4) was less abundant than the thin bladed morph. *Cymodocea rotundata*, *Halophila ovalis* and *Halophila spinulosa* were least dominant in Torres Strait in terms of biomass with 5.01 (SE = 1.41), 2.60 (SE = 0.73) and 1.39 gDW.m^{-2} (SE = 0.35) respectively averaged over central and western Torres Strait. The biomass of all seagrasses were very variable shown by the high coefficients of variation which ranged from 208% for *E. acoroides* to 405% for *H. uninervis* (b).

The dominant seagrass in terms of percentage seagrass cover was also *T. hemprichii*, 8.04% (SE = 1.86%) , followed by *C. serrulata*, 3.78% (SE = 0.82%), *S. isoetifolium*, 2.51% (SE = 0.44%). The remaining seagrasses, *H. uninervis* (t), 1.42% (SE = 0.31%), *H. spinulosa*, 1.29% (SE = 0.28%), *C. rotundata*, 1.25% (SE = 0.31%), *H. ovalis* (l), 1.18% (SE = 0.24%), *H. uninervis* (b), 1.05% (SE = 0.19%), *E. acoroides*, 0.88% (SE = 0.18%), *H. ovalis* (s), 0.53% (SE = 0.15%) were all less than 2% average cover.

All species of seagrass were broadly distributed throughout the foreshore areas, reefs and subtidal areas of central and western Torres Strait (Fig. 3a-i). *Cymodocea rotundata*, *Enhalus acoroides* and *Thalassia hemprichii* were mainly found on reefs and in shallow water areas around the continental islands and reefs and were mostly absent from the deeper water inter-reefal areas (Fig. 3b, 3e & 3f). In contrast, *Halodule uninervis*, *Halophila ovalis*, *Syringodium isoetifolium* and *Cymodocea serrulata* were found throughout central and western Torres Strait (Fig. 3a, 3d, 3h & 3g). The biomass of seagrass was highest in the shallow subtidal and foreshore areas of Torres Strait and lowest in the inter-reefal areas well away from the coasts and reefs (Fig. 3).

Table 2. The estimated area (km^2) of seagrass and non seagrass areas by depth interval for the three regions, central, western and eastern Torres Strait grouped by depth.

	Central Torres Strait			Western Torres Strait			Eastern Torres Strait			
Depth	seagrass present	seagrass absent	total	seagrass present	seagrass absent	total	seagrass present	seagrass absent	total	total
0	1,397	997	2,394	33	21	54	0	0	0	2,449
1–5	1,451	1,193	2,644	982	719	1,701	0	0	0	4,344
5–10	2,718	2,152	4,869	1,150	1,245	2,394	0	76	76	7,340
10–15	2,496	1,706	4,202	993	1,974	2,967	0	486	486	7,655
15–20	927	1,940	2,867	838	845	1,683	0	978	978	5,527
20–25	39	401	440	261	135	395	0	2,212	2,212	3,047
25–30	3	8	10	4	54	58	381	3,357	3,738	3,806
30–40	1	4	6	0	6	6	76	3,814	3,890	3,902
> 40 m	0	1	1	0	0	0	0	4,883	4,883	4,884
Total	9,032	8,400	17,432	4,259	4,998	9,257	457	15,806	16,263	42,952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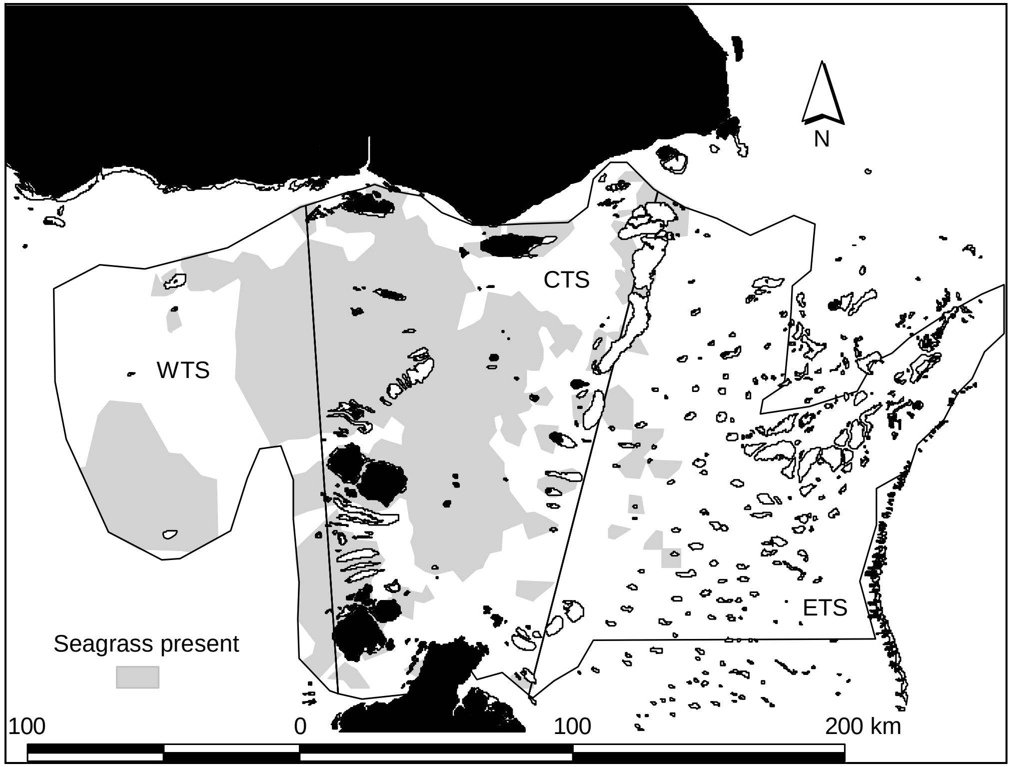
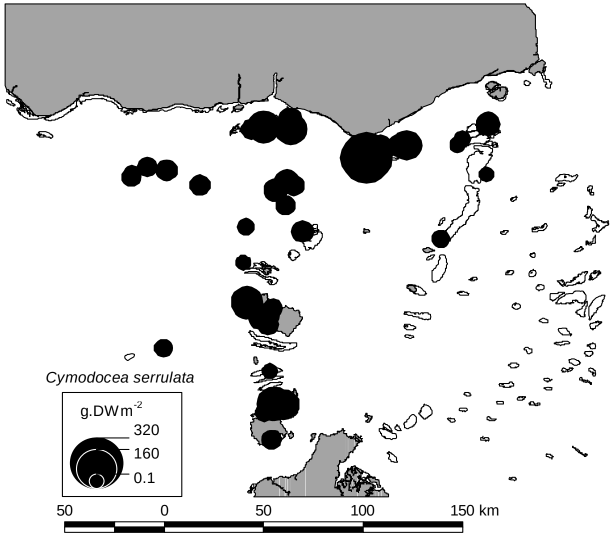
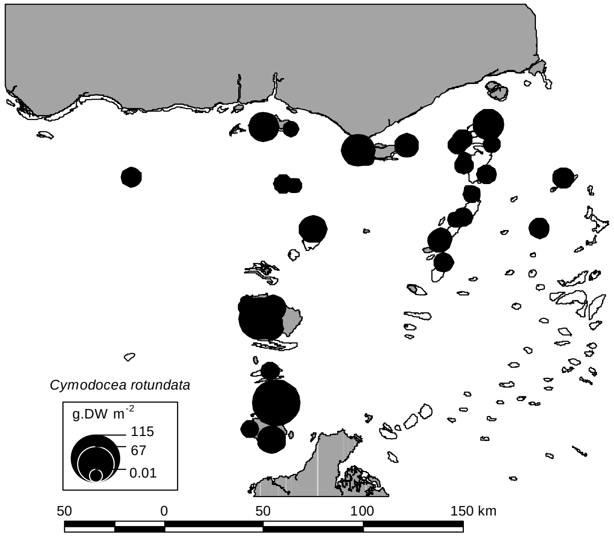


Figure 2. Map of Torres Strait showing the a). three regions sampled, east (ETS), central (CTS) and west Torres Strait (WTS). ■: seagrass study; ○: prawn trawl by-catch survey; ♦: lobster survey; ●: megabenthos survey; and b). distribution of seagrass produced form the presence or absence of seagrass at the sites sampled in Torres Strait.

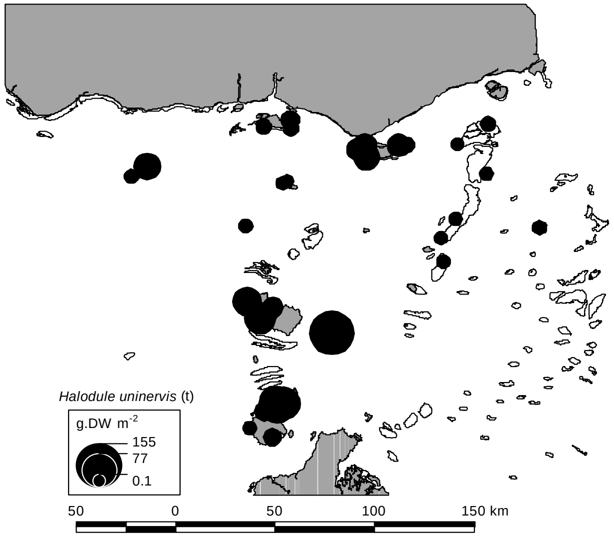
a).


Cymodocea serrulata
g.DWm^{-2}
320
160
0.1
50
0
50
100
150 km

b).


Cymodocea rotundata
g.DW m^{-2}
115
67
0.01
50
0
50
100
150 km

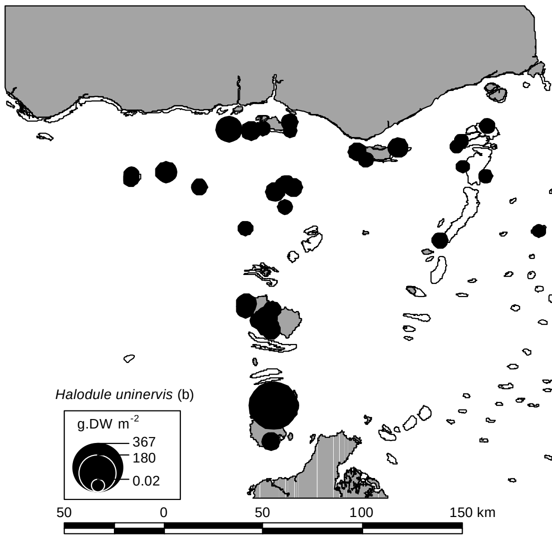
c).


Halodule uninervis (t)
g.DW m^{-2}
155
77
0.1
50
0
50
100
150 km

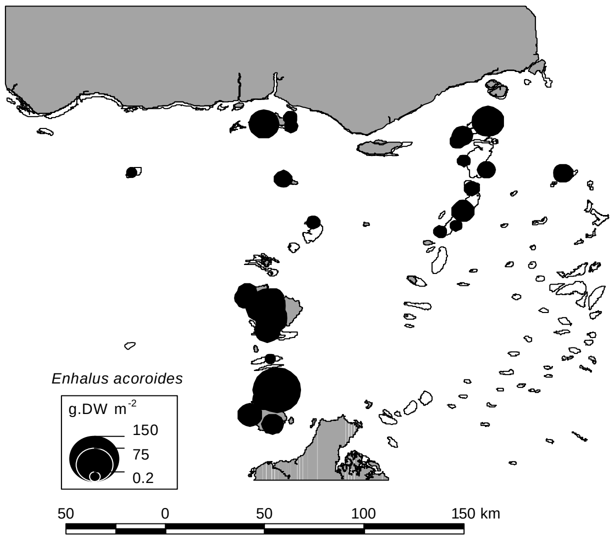
d).

e).

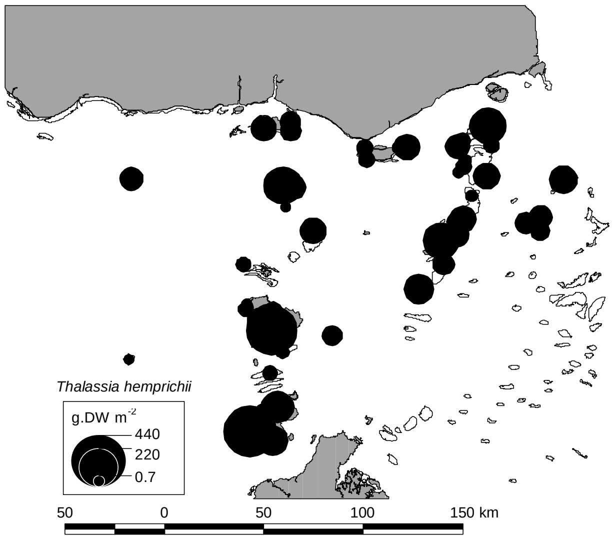
f).


Halodule uninervis (b)
g.DW m-2
367
180
0.02
50
0
50
100
150 km

g).


Enhalus acoroides
g.DW m-2
150
75
0.2
50
0
50
100
150 km

h).


Thalassia hemprichii
g.DW m-2
440
220
0.7
50
0
50
100
150 km

i).

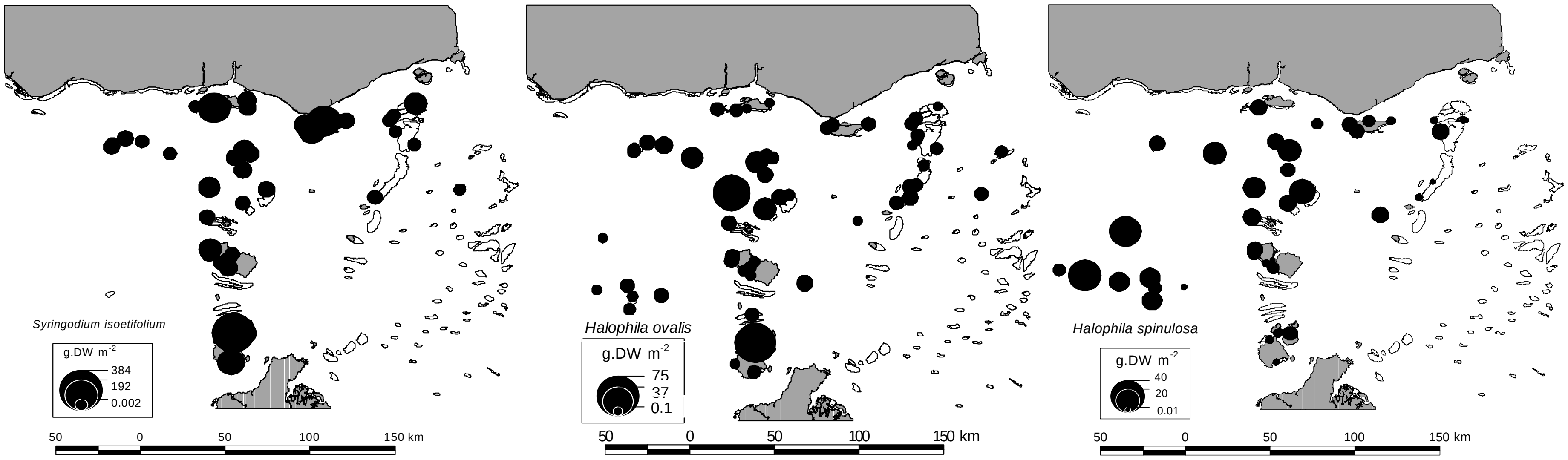


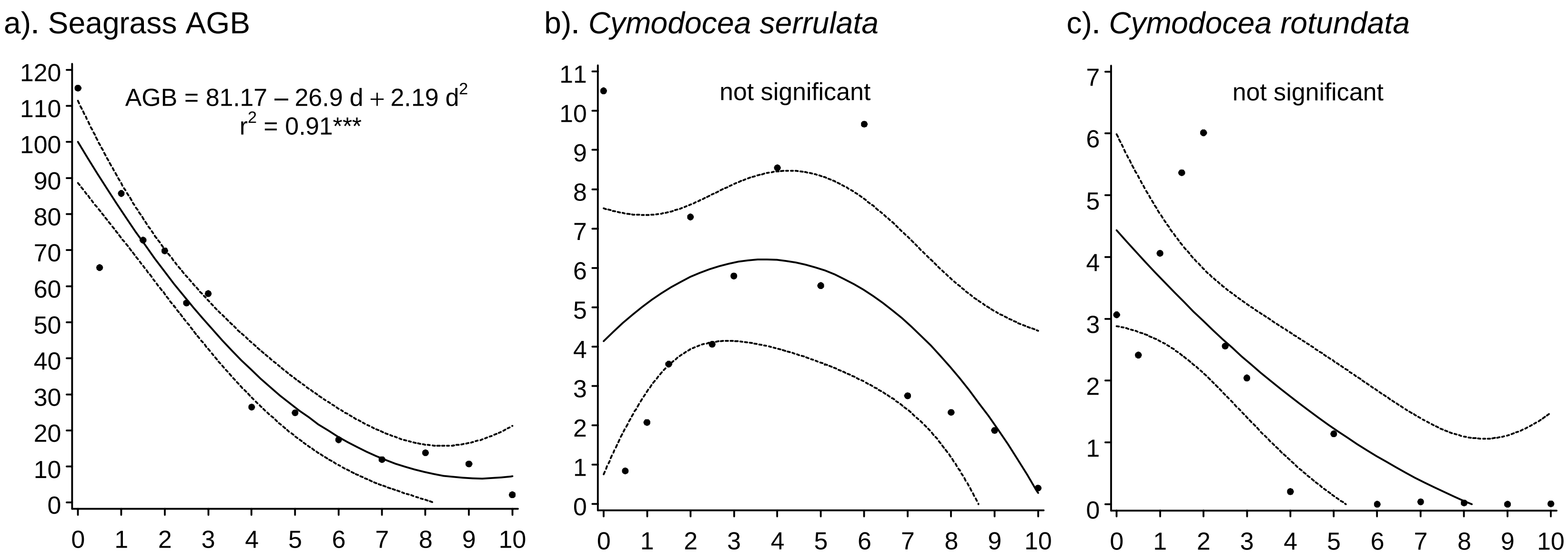
Figure 3. Bubble plot of the biomass (g.DWm^{-2}) of seagrass in Torres Strait averaged by location for the numerically dominant seagrasses a). *Cymodocea serrulata*; b). *Cymodocea rotundata*; c). *Halodule uninervis* (t); d). *Halodule uninervis* (b); e). *Enhalus acoroides*; f). *Thalassia hemprichii*; g). *Syringodium isoetifolium*; h). *Halophila ovalis*; and i). *Halophila spinulosa*.

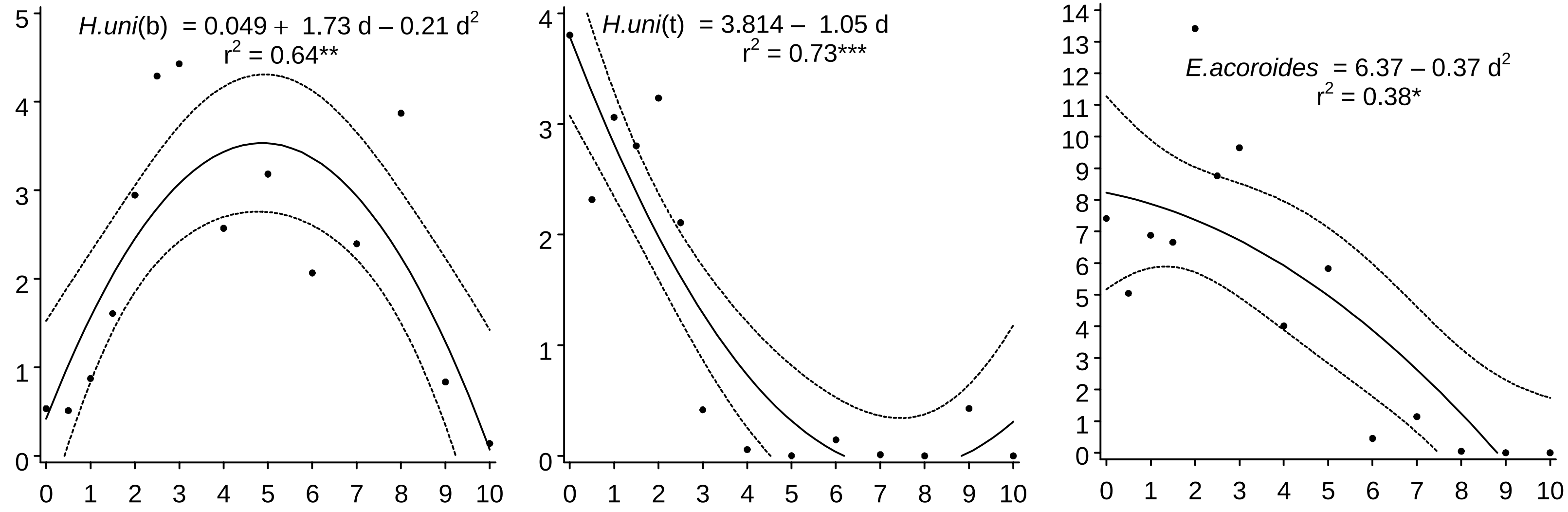
Distribution of seagrass biomass with depth

The broad scale patterns of the distribution of seagrass in Torres Strait indicated that seagrass was more abundant in shallow than deep water. The relationship between $\log_e$-transformed biomass of seagrass and water depth and depth squared was tested using a regression analysis. The squared term for depth added flexibility to the model to test for a non-linear relationship between seagrass biomass and depth. As there may have been changes in the ratio of above ground biomass (AGB) to below ground biomass (BGB) with depth, a regression analysis was first done on the ratio of above- to below-ground biomass with water depth. The results of this analysis indicated that there was no significant effect of depth on the ratio of above- to below-ground biomass except for *Thalassia hemprichii* ($P < 0.05$) where the ratio of above- to below-ground biomass decreased significantly with depth. Moreover, there was a significant correlation ($P < 0.0001$) between above- and below-ground biomass for all nine numerically dominant species which ranged from 0.80 for *Halophila ovalis* to 0.94 for *H. spinulosa*; most correlations (7 out of 9) were >= 0.90. Consequently, above-ground biomass was used as the response variable in the regression analysis of seagrass biomass with depth.

There was an exponential decrease of AGB of seagrass with depth for *Thalassia hemprichii* and pooled seagrass shown by the significant positive term for depth squared and significant negative term for depth in the regression model (Fig. 4a). Estimates of above-ground biomass of *T. hemprichii* approached zero at 10 m from an average of 81 gDW.m^{-2} on foreshore areas and reefs. In contrast there was a significant linear decrease of *Halodule uninervis* (t) with depth (Fig. 4e). The AGB for three seagrasses, *Halodule uninervis* (b), *Syringodium isoetifolium* and *Halophila ovalis* AGB was significantly lower in shallow and deep water than intermediate depths where AGB reached a maximum at 3 to 6 m water depth (Fig. 4d, h and I). The AGB of *Halophila spinulosa* increased with depth and leveled off at 8 to 10 m. There were no significant regressions of AGB with depth for *Cymodocea serrulata* and *Cymodocea rotundata* (Fig. 4b & 4c). The predicted curve was bell-shaped for *C. serrulata*, and AGB decreased with depth for C. *rotundata*, however, the variation was large and significant trends were not detected for either seagrass.

The diversity of biomass, measured with the Shannon-Wiener information content index indicated that diversity peaked at depths of 2 to 4 m and declined in shallower and deeper water (Fig. 4k). The variance of the diversity values, grouped by 1 m depth intervals was also significantly higher in intermediate water depths and was well modelled with 76% of the variation explained by depth and depth squared(Fig. 4l). Thus seagrass diversity was significantly higher and more variable in waters between 2 and 4 m.

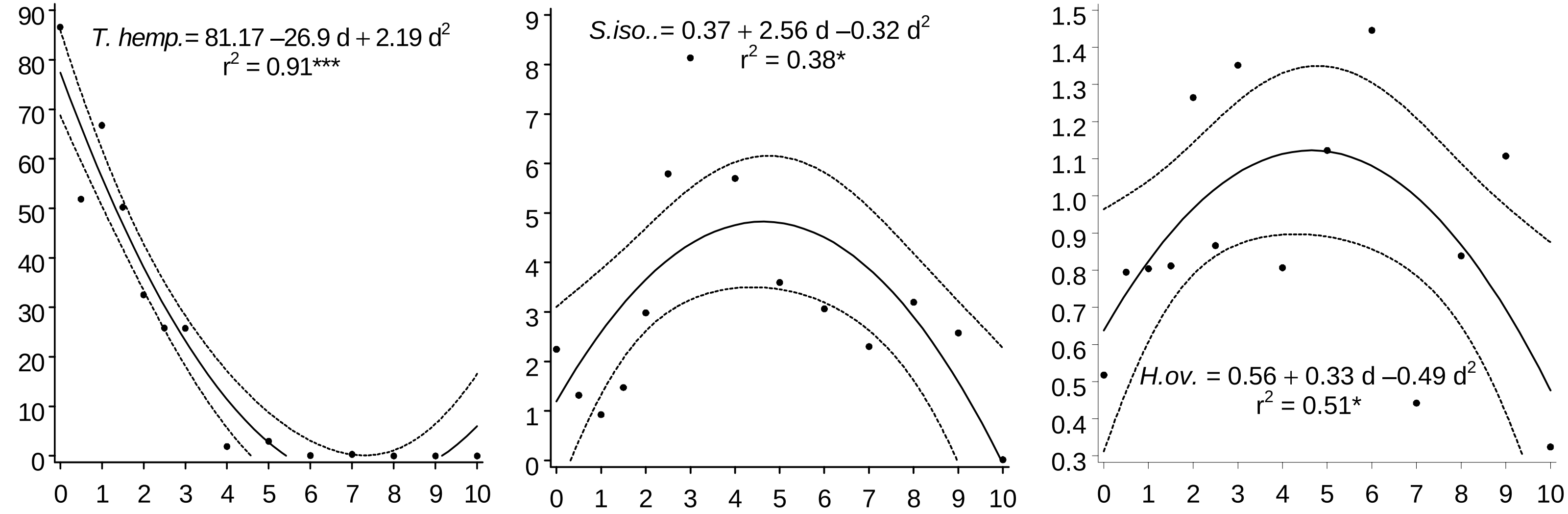

a). Seagrass AGB
AGB = 81.17 – 26.9 d + 2.19 d2
r2 = 0.91***
120
110
100
90
80
70
60
50
40
30
20
10
0
0 1 2 3 4 5 6 7 8 9 10
b). *Cymodocea serrulata*
not significant
11
10
9
8
7
6
5
4
3
2
1
0
0 1 2 3 4 5 6 7 8 9 10
c). *Cymodocea rotundata*
not significant
7
6
5
4
3
2
1
0
0 1 2 3 4 5 6 7 8 9 10



d). *Halodule uninervis* (b)

e). *Halodule uninervis* (t)

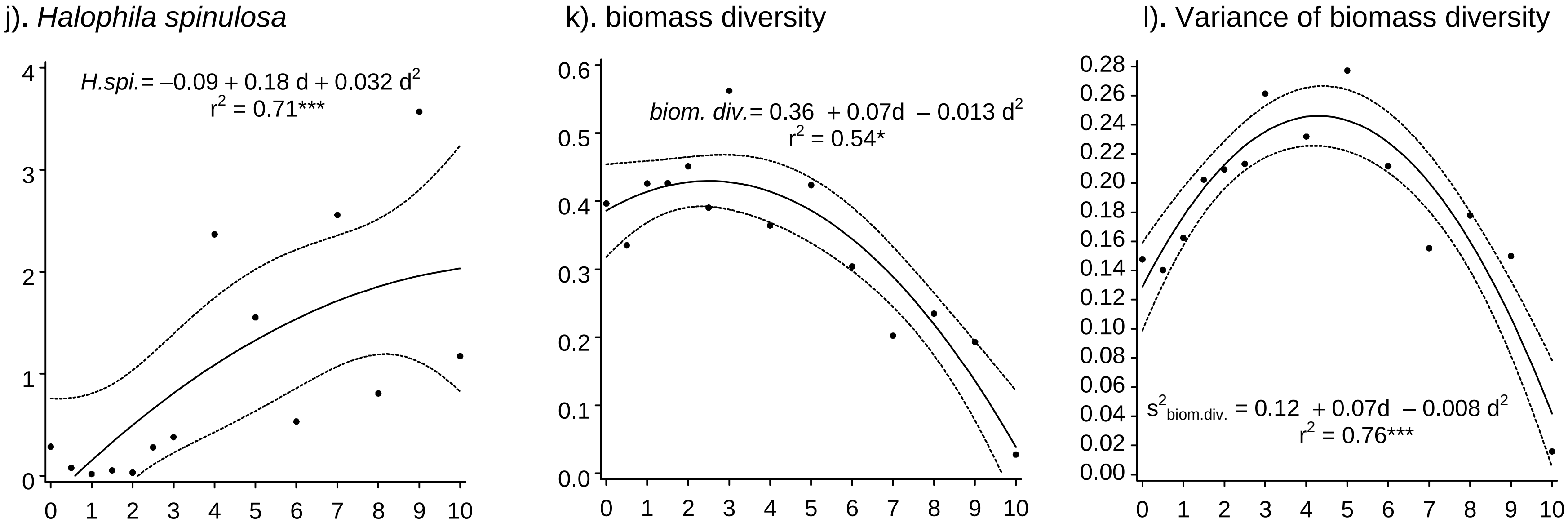
f). *Enhalus acoroides*



g). *Thalassia hemprichii*

h). *Syringodium isoetifolium*

i). *Halophila ovalis*


j). *Halophila spinulosa*

k). biomass diversity

l). Variance of biomass diversity

Figure 4. Above-ground-biomass, AGB, (gDW.m^{-2}) ± 90% confidence intervals of Torres Strait seagrasses plotted against 1 m depth intervals for a). Pooled seagrass; b). *Cymodocea serrulata*; c). *Cymodocea rotundata*; d). *Halodule uninervis* (broad-leaf); e). *Halodule uninervis* (thin-leaf); f). *Enhalus acoroides*; g). *Thalassia hemprichii*; h). *Syringodium isoetifolium*; i). *Halophila ovalis*; j). *Halophila spinulosa*; k). AGB diversity (nats) and l). variance of AGB diversity. Only significant regression equations shown.

Nested ANOVA

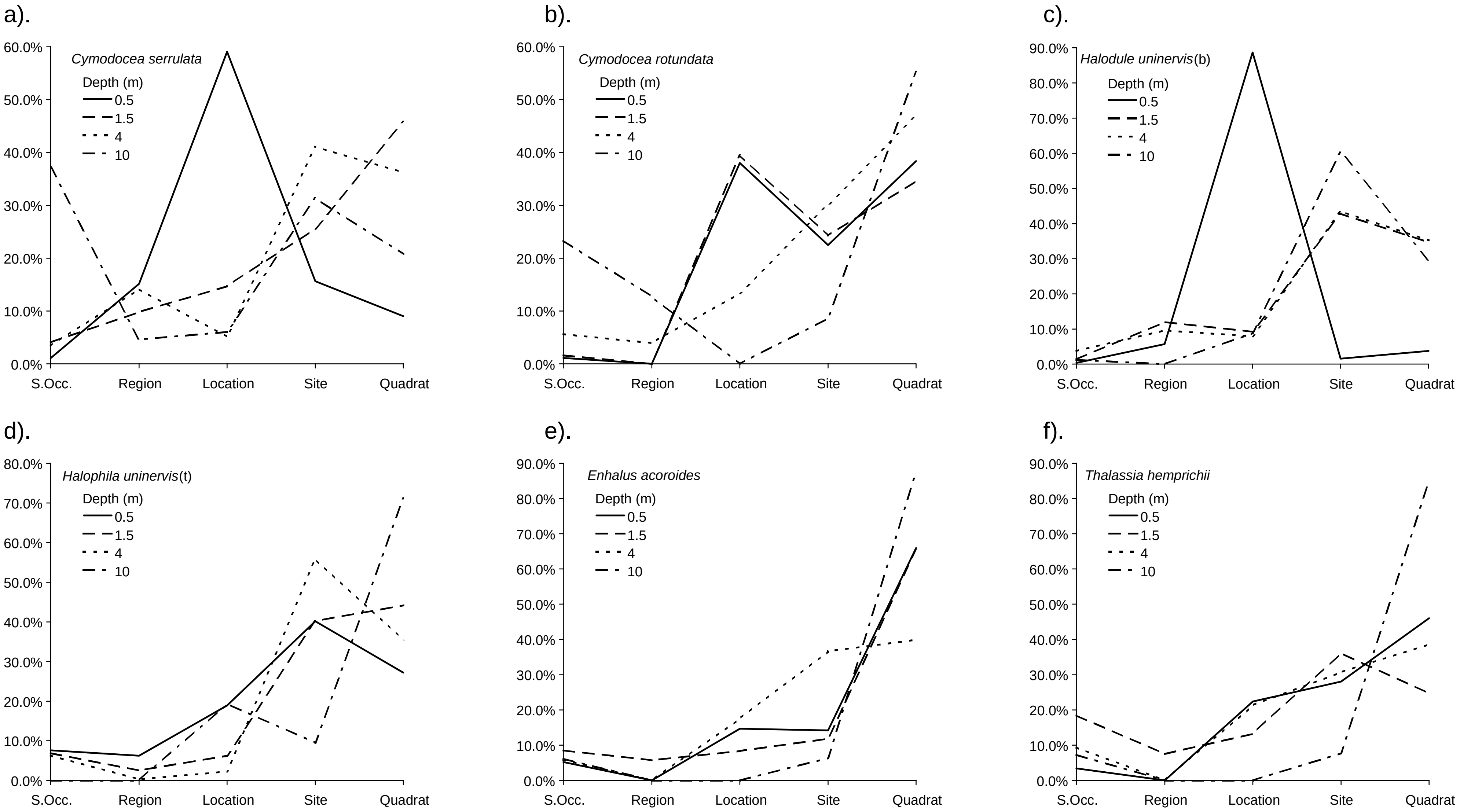
Differences among locations explained most (60%) of the variation in the percentage cover of *Cymodocea serrulata* for foreshore and shallow water (< 2 m) areas of Torres Strait. The large variation among locations was due to high cover (65%) of *Cymodocea serrulata* in the shallow subtidal areas of Boigu Island whereas this seagrass was normally absent or occurred in low abundance in this depth interval in other locations sampled in Torres Strait. For the remaining three depth intervals, differences among sites and quadrats explained most (>50%) of the variation and there were small differences among locations and regions (< 15%). Thus the patchiness of this seagrass was mostly at the site and quadrat spatial scales. In contrast, there were small differences among locations. Differences among sampling occasions explained over a third (38%) of the variation of sites sampled in deep water (> 6 m) which was due to a dense bed of *C. serrulata* which was sampled only once in western Torres Strait. This area was not sampled again and thus the high variation explained by sampling occasion in this instance was due to spatial and not temporal effects.

Differences among locations, sites and quadrats explained most (> 95%) of the variation of the percentage cover of seagrass of *Cymodocea rotundata* in shallow waters < 2 m (Fig. 5). In deeper water, however, most of the variation (> 45%) was among quadrats within sites. Thus in deeper waters, this seagrass was patchily distributed within sites and there were no strong differences among locations and regions of Torres Strait.

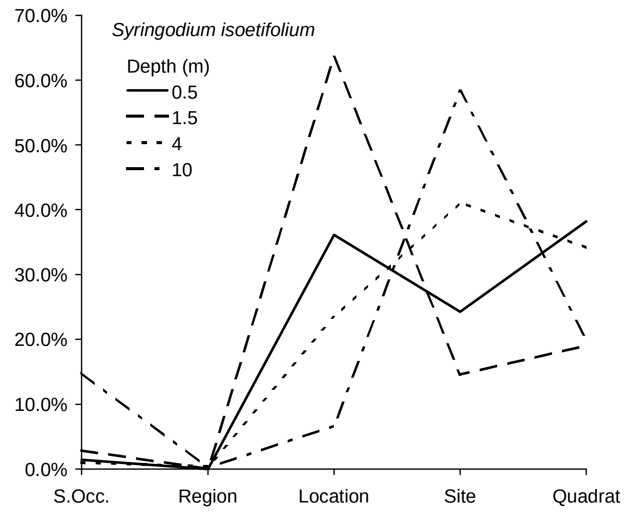
Most of the variation in the percentage cover of *Halodule uninervis* (b) was among locations in shallow water (< 1 m), however, this was due to very high cover (> 90%) at a few sites off the edge of the foreshore at Thursday Island whereas most sites at the other locations on the foreshore areas of Torres Strait had little or no cover of this broad-leaved morph. In deeper waters, most of the variation was among sites and among quadrats. Approximately the same variation was explained by these two spatial scales which indicated the same degree of patchiness at these scales. In contrast, little (< 5%) of the variation was between sampling occasions.

Differences among sites explained as much or more of the variation of *Halodule uninervis* (t) than differences among quadrats (Fig. 5d). Thus on the foreshore areas and in shallow water the distribution of *H. uninervis* (t) often occurred in patches at the spatial scale of at least sites. There were relatively few differences among locations and regions when grouped by location and region respectively.

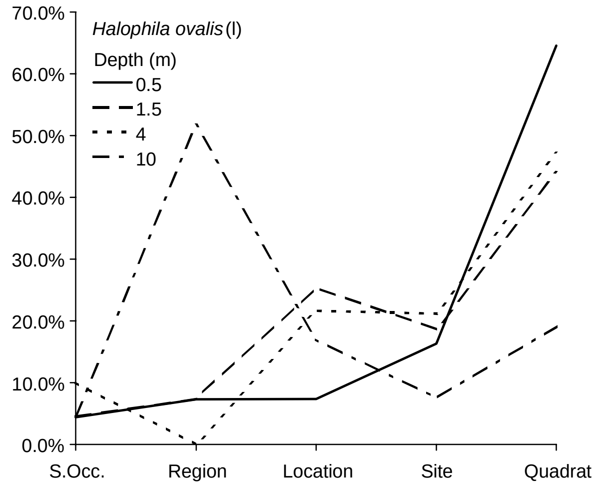
Most of the variation of percentage cover of *Enhalus acoroides* for all depth ranges was among quadrats. Very little variation was among regions and < 10% of the variation was between sampling occasions. This indicated that *E. acoroides* was very patchily distributed at the within-site spatial scale over all depth intervals and that differences among sites, locations or regions sampled in Torres Strait were far less pronounced than differences among quadrats within a site(Fig. 5e).


a).
Cymodocea serrulata
b).
Cymodocea rotundata
c).
Halodule uninervis(b)
d).
Halophila uninervis(t)
e).
Enhalus acoroides
f).
Thalassia hemprichii
Depth (m)
0.5
1.5
4
10
0.0%
10.0%
20.0%
30.0%
40.0%
50.0%
60.0%
70.0%
80.0%
90.0%
S.Occ.
Region
Location
Site
Quadrat

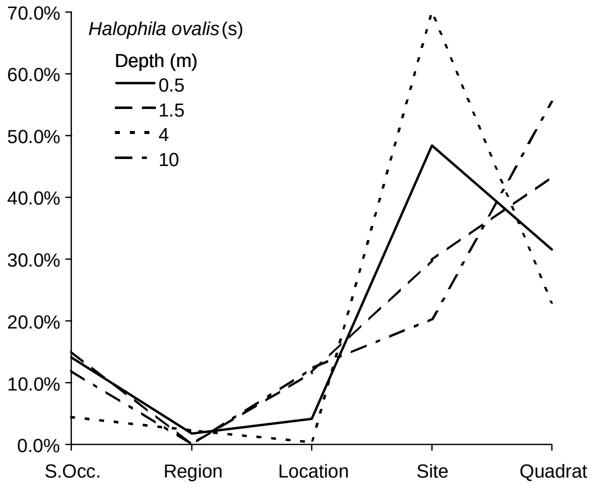
g).


70.0%
60.0%
50.0%
40.0%
30.0%
20.0%
10.0%
0.0%
Syringodium isoetifolium
Depth (m)
0.5
1.5
4
10
S.Occ.
Region
Location
Site
Quadrat

h).


70.0%
60.0%
50.0%
40.0%
30.0%
20.0%
10.0%
0.0%
Halophila ovalis (l)
Depth (m)
0.5
1.5
4
10
S.Occ.
Region
Location
Site
Quadrat

i).


70.0%
60.0%
50.0%
40.0%
30.0%
20.0%
10.0%
0.0%
Halophila ovalis (s)
Depth (m)
0.5
1.5
4
10
S.Occ.
Region
Location
Site
Quadrat

j).

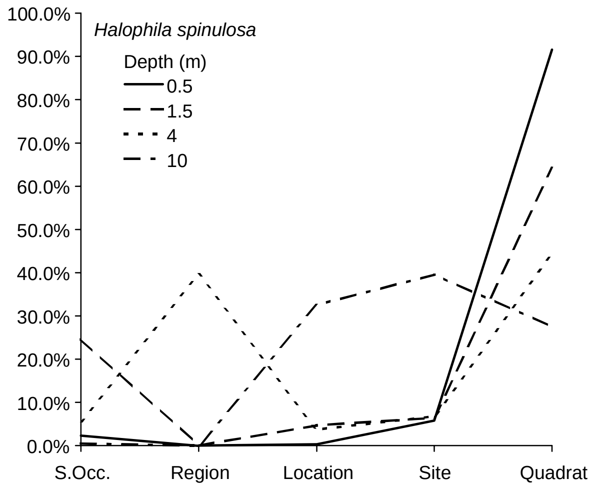

100.0%
90.0%
80.0%
70.0%
60.0%
50.0%
40.0%
30.0%
20.0%
10.0%
0.0%
Halophila spinulosa
Depth (m)
0.5
1.5
4
10
S.Occ.
Region
Location
Site
Quadrat

Figure 5. Percentage variation explained among sampling occasions, S. Occ., and four spatial levels sampled: Region, Location, Site and Quadrats within sites for a). *Cymodocea serrulata*; b). *Cymodocea rotundata*; c). *Halodule uninervis* (broad-leaf); d). *Halodule uninervis* (thin-leaf); e). *Enhalus acoroides*; f). *Thalassia hemprichii*; g). *Syringodium isoetifolium*; h). *Halophila ovalis* (large-leaf); i). *Halophila ovalis* (small-leaf); j). *Halophila spinulosa*.

The patterns of variation of percentage cover of *Thalassia hemprichii* among the spatial scales sampled indicated that there was a general decrease in variation with increase in spatial scale for all four depth ranges(Fig. 5f). There was a marked difference, however, between samples taken > 6 m and the remaining three depth intervals with 85% of the variation among quadrats for the deep water sites. Thus at the deeper end of its distribution range, *T. hemprichii* was very patchily distributed and was found in only a few quadrats. For the remaining three depth ranges the variation explained was relatively evenly partitioned among quadrats, sites and locations which indicated equivalent levels of patchiness at these spatial scales. Thus beds of *Thalassia hemprichii* were broadly distributed over many locations in Torres Strait with equivalent scales of patchiness among and within-sites. There was little regional variation and sampling occasion explained only 4 to 19% of the variation for the 4 depth intervals.

The amount of variation explained by the spatial scales sampled for *Syringodium isoetifolium* was very low for region (< 1%) and was relatively evenly partitioned among locations, sites and quadrats for most depth intervals with no obvious trends among the depth intervals. Differences between sampling occasions explained little of the variation (Fig. 5g).

Most of the variation of *Halophila ovalis* (l) (>40%) was among quadrats for three depth intervals: 0-1; 1-2 and 2-6 (Fig. 5h). When averaged over sites and locations, approximately half this variation (~20%) was each explained by these two coarser spatial scales. In contrast, most of the variation (50%) was among regions for deep water (> 6 m), however, this was due to high cover of *H. ovalis* (l) (> 50%) at sites sampled in deep water off Kerr reef in western Torres Strait whereas seagrass cover was lower in other deep water regions of Torres Strait. However the results for *H. ovalis* should be interpretedwith caution because in some cases it represents the pooled *H. ovalis* and *H. decipiens* data.

The pattern of variation in the percentage cover of *Halophila ovalis* (s) was similar to *Halodule uninervis* (t), *Enhalus acoroides*, and *Thalassia hemprichii* with most of the variation among quadrats and sites. Differences among locations and among sampling occasions explained less than 15% of the variation for all depth intervals (Fig. 5c, 5e, 5f & 5i).

There was a significant correlation between log-transformed spatial scale (100 km^2, 1 km^2, 400 m^2 and 0.25 m^2) and the percentage variation explained for the pooled seagrasses, with significantly higher amounts of variation explained at smaller spatial scales than larger ($r = 0.63$; $P < 0.0001$). Seagrass communities in Torres Strait are more variable at smaller than larger spatial scales.

Pattern analysis to describe seagrass communities

The results of the nested ANOVA indicated there was little variation between sampling occasions over the study period. Consequently, the full data set for the seagrass study was pooled for pattern analysis. A detailed study of temporal changes in seagrass is in preparation (Long and Poiner in prep.).

The percentage cover of seagrass estimated in 8,269 x 0.25 m^2 quadrats from 1,326 sites from the seagrass study were analysed with pattern analysis to describe the seagrass communities and explore relationships between seagrass assemblages and environmental factors: water depth, Sechi depth, sediment grain size and sediment depth. Biomass estimates from 4,445 x 0.07 m^2 shovel samples taken at the 1,327 sites during the seagrass study were analysed for differences among the main seagrass assemblages identified from the pattern analysis.

The 1,326 sites were grouped into 50 subgroups with PROC FASTCLUS (SAS 1986) based on the Euclidean distance between sites in terms of the percentage cover of each seagrass. The *q*-mode cluster analysis of the 50 subgroups indicated that there were 11 groups at a dissimilarity level of 0.61 (Fig. 6a).

The *r*-mode cluster analysis of seagrasses grouped on their average percentage cover in the 50 subgroups indicated that there were five clear species groups at a dissimilarity level of around 0.75 (Fig. 6b). The *q*- and *r*-mode dendrograms were combined with the two-way table showing the association between the species and site groups (Fig. 7). The number of sites for each combination of habitat type and site group were tabulated to assist with the interpretation of the species and site groups (Tables 3 & 4).

Group 1: — *Halophila ovalis* (e) dominant / *Halodule uninervis* (t) sub-dominant assemblage. A small group of 15 sites situated subtidally off reefs (4 sites) and foreshore areas of the continental islands (10 sites) (Table 3). This assemblage was strongly dominated (> 25%) by the broad-leaved morph of *Halophila ovalis* (65%) with *Halodule uninervis* (t) (11%) as a subdominant (10-25%) (Table 4). The average cover of seagrass in this assemblage was 53%, with an additional 7% cover of algae (Table 5). The average water depth was 5.4 m and was second deepest behind site group 11 (12.1 m). The sediments were predominantly muddy sands. In terms of biomass, the numerically dominant species was not *Halophila ovalis* (b) (6.2 gDW.m^{-2}); *Halodule uninervis* (t) (30.2 gDW.m^{-2}), *H. uninervis* (b) (11.4 gDW.m^{-2}), and *Enhalus acoroides* (7.5 gDW.m^{-2}) had higher biomass. However, the coefficient of variation (CV) of biomass was very high for these species and ranged from 242 to 282% whereas the CV of *H. ovalis* was low, 79% (Table 5). The average number of species was 2.27 per quadrat which was reflected by the low diversity. Two of the 15 sites were monospecifc stands of *H. ovalis* (b).

Group 2: *Halodule uninervis* (t) dominant / *Halophila ovalis* (s), *Cymodocea rotundata* subdominant assemblage — 82 sites almost exclusively from the foreshore areas around the continental islands and to a lesser extent the mangrove cays of Boigu and Saibai Island and were generally located near the landward edge of the foreshore (Table 3) shown by the shallow water depth, 1.3 m and low coefficient of variation, 69%, for this group (Table 5). This assemblage was strongly dominated numerically by the percentage cover of *Halodule uninervis* (t) (61%) (Table 4). Average seagrass cover was high, 71% and this site group was second shallowest of the 11 site groups (Table 5). Together the dominants and sub-dominant species accounted for 87% of the average seagrass cover. Biomass was moderately high, 167 gDW.m^{-2}, and the dominant seagrass in terms of biomass was also *H. uninervis* (t), 71.9 gDW.m^{-2}. However, the biomass of *Halophila ovalis* (s), 5.6 gDW.m^{-2} was much lower than for *Thalassia hemprichii*, 41 gDW.m^{-2} which was a minor component of this site group in terms of percentage cover (8%), a difference which may be explained by the supine growth form of *H. ovalis* and tissue density per mm^2 than the erect growth form of *T. hemprichii*. Sediment depth, 1.37 m, was the deepest of the 11 site groups and was because sites were mostly located in shallow muddy nearshore areas in the embayments of the continental islands and foreshore areas of mangrove cays of Torres Strait. Five of the sites were monospecific stands of *H. uninervis* (t).

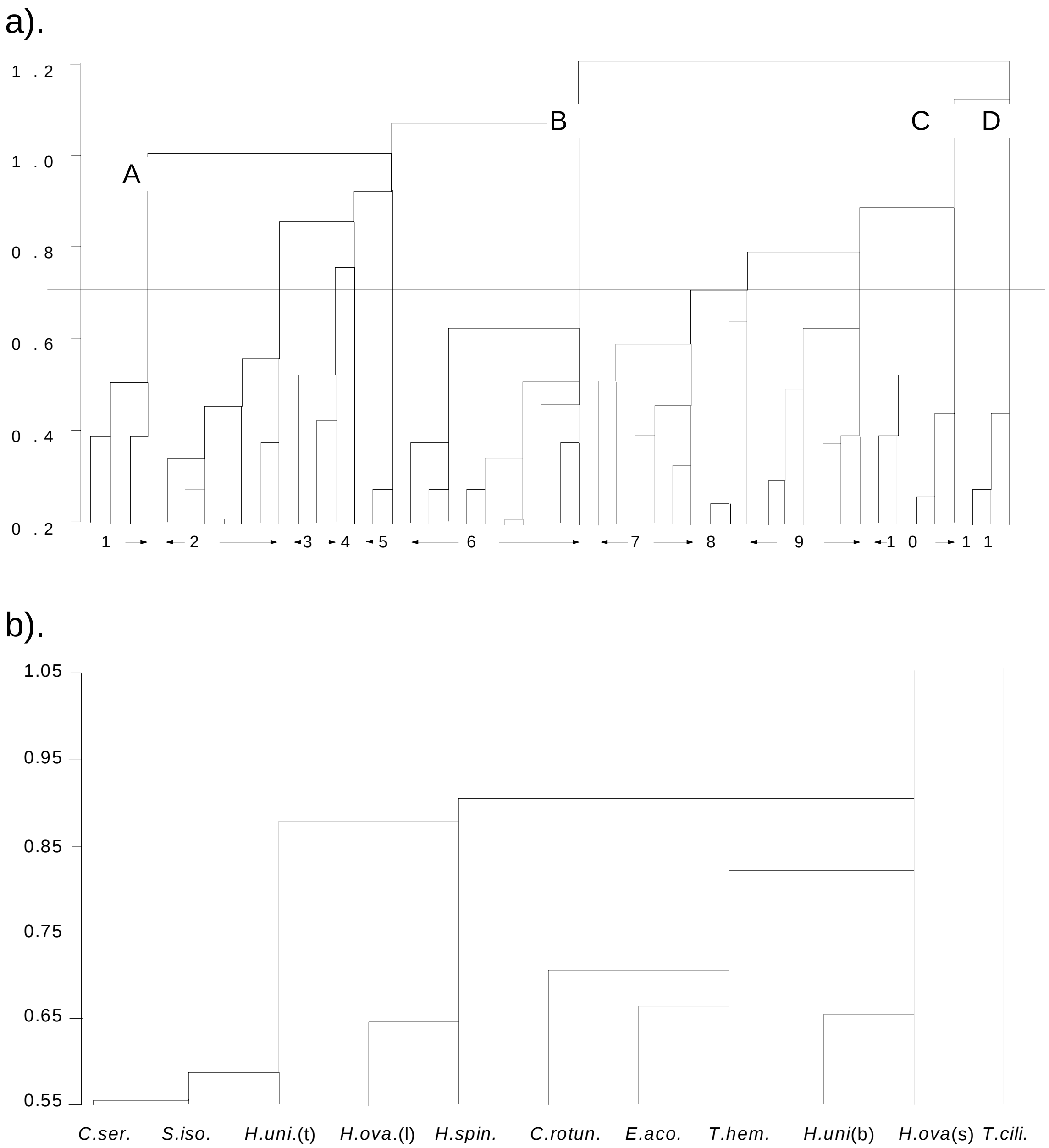


Figure 6. Dendrogram of a). four main groups, A to D and 11 subgroups of sites grouped on the basis of percentage cover of seagrass species (*q*-mode analysis) and b). species groups (r-mode analysis).

Group 3: *Halophila ovalis* (s), *Thalassia hemprichii* dominant / *Halodule uninervis* (t) sub-dominant seagrass assemblage — 57 sites similar to Group 2 and almost exclusively from the foreshore areas around the continental islands and mangrove cays. The average water depth was deeper, 1.7 m but was much more variable (CV = 123%) than Group 2 and consequently the difference was not significant ($P > 0.05$). The three dominant and subdominant species accounted for 90% of the 44% overall seagrass cover. Biomass was moderately low, 74 gDW.m^{-2} and numerically dominated by *T. hemprichii*, 45 gDW.m^{-2} like Group 2. Four of the sites were monospecific stands of *H. ovalis* (s).

Group 4: *Thalassia hemprichii / Halophila ovalis* (l) and *Halodule uninervis* (t) assemblage — 348 sites divided evenly between foreshore areas (140 sites) and reef top (137) with a substantial number (63) of sites in shallow subtidal areas and were generally deeper, 2.9 m than Group 3, although not significantly ($P > 0.05$) different due to the high CV for water depth, 134%. The overall cover of seagrass in this group was low (9%). Also present in minor abundances were *Enhalus acoroides*, *H. ovalis* (s), *H. spinulosa* and *H. uninervis* (b) (Table 5). The numerically dominant species in this site group in terms of biomass were *Thalassia hemprichii*, 18.8 gDW.m^{-2}, and *Halodule uninervis* (thin-blade), 4.2 gDW.m^{-2}. The CV was high for biomass, water, Sechi and sediment depth and was low for sediment grain size which was predominantly sandy sediments. Diversity was the lowest of the site groups, 0.355 reflected by the low number of species per quadrat, 1.97. This large site group was a sparse, mixed and variable assemblage of seagrass found throughout subtidal and foreshore areas of Torres Strait with many combination of species which occurred in low abundance and very patchy within-sites shown by the within-site high variation.

Group 5: *Cymodocea rotundata* assemblage — 15 sites strongly dominated by the absolute percentage cover of *C rotundata*, 55%, and to a much lesser degree *Thalassia hemprichii* and *Enhalus acoroides* which together accounted for 88% of the high overall coverage, 73% of seagrass. The pooled biomass, 273 gDW.m^{-2} of this assemblage was third highest of the 11 site groups and was dominated by *C. rotundata*, (77.81 gDW.m^{-2}) and *T. hemprichii* (16.69 gDW.m^{-2}). The majority (12) of sites in this group were located in the foreshore areas of continental islands and mangrove cays. Water depths were constant at 1.4 m (CV= 64%) and sediments were muddiest, 35% of the 11 site groups. Sediment depth, however, was shallow, 0.29 m and constant (CV=39%). Average Sechi depth, 1.3 m, was shallowest of the site groups. This seagrass was never found in monospecific stands.

Group 6: *T. hemprichii* dominant / *E. acoroides* subdominant assemblage — 527 sites found predominantly on the foreshore areas of the continental islands and on the reef tops and to a lesser degree the foreshore areas of mangrove cays (Table 4). Three species, *Thalassia hemprichii*, *E. acoroides* and *C. rotundata* together accounted for 88% of the average seagrass cover of 51% (Table 5). This was the largest site group and was characterised by high biomass of *Thalassia hemprichii* (96.21 gDW.m^{-2}) and to a lesser extent *Enhalus acoroides* (11.64 gDW.m^{-2}). The coefficient of variation was high for biomass which indicated high variability among sites. Fifty-five of the sites in this group were monospecific stands of *T. hemprichii.*

Group 7: *Cymodocea serrulata* and *Syringodium isoetifolium* dominant / *Halodule uninervis* (b) sub-dominant — 166 sites mostly located subtidally off the edge of the foreshore areas and reefs with average water depths of 3.8 m with relatively low variation (CV = 65%) of depth. Average cover was relatively low, 40%, however, species diversity, 0.77 was highest of the 11 site groups as was the number of species per quadrat, 3.5.

Table 3. Cross-tabulation of the number of sites categorised by habitat type and site groups from the cluster analysis of the percentage cover of seagrass at Torres Strait sites. FS: foreshore; OS: offshore; RF: reef top.

	Site group											
Sites	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**Total**
FS	1	71	49	88	11	280	31	4	7	24	2	568
OS	10	9	5	128	1	87	116	10	11	30	22	429
RF	4	2	3	132	3	161	19	4	0	1	1	330
Total	15	82	57	348	15	528	166	18	18	55	25	1327

Group 8: *Syringodium isoetifolium* and *Cymodocea serrulata* dominant / *Halodule uninervis* (b) sub-dominant — 18 sites similar to Group 7 in terms of species composition, however, there was a switch-over in numerical dominance from *C. serrulata* to *S. isoetifolium*. Average cover was very high, 92% and biomass was the highest of the 11 site groups, 459 gDW.m^{-2}. The number of species per quadrat, 3.9 and diversity, 0.57 were also high.

Group 9: *Halodule uninervis* (b) dominant / *E. acoroides*, *C. serrulata* and *S. isoetifolium* subdominant — 18 sites with very high seagrass cover, 90% and high biomass (Table x). This group had highest diversity and number of species per quadrat and was located in intermediate water depths, 3.2 m mostly in offshore subtidal areas and along the offshore edge of foreshore areas. None of the sites in this group were situated on reefs. Only one of the sites was a monospecific stand of *H. uninervis* (b) however, it was present at all sites and

Group 10: *Cymodocea serrulata* dominant — 55 sites with high cover of seagrass, 70% and high biomass of *C. serrulata*, 153.9 g.DWm^{-2}. Ten of the sites in this group were monospecific stands of *C. serrulata*.

Group 11: *Halophila spinulosa* assemblage — 25 sites located in deep water, 12.1 m, with minor contributions of *S. isoetifolium* and *H. ovalis* (l). Average cover was low, 50%, and biomass was the lowest of the 11 site groups, 50.44 gDW.m^{-2}. Approximately half (10) of the sites in this group were monospecific stands of *H. spinulosa*.

All species except *Enhalus acoroides* numerically dominanted at least one site group. Moreover, a single species (*T. hemprichii*) dominated eight of the 11 site groups and contributed > 60% of the total cover of seagrass at half (6) of the site groups. However, monospecific stands (sites where only one seagrass occurred) were uncommon for all species except *Halophila spinulosa* in site Group 11 where half the sites, 10, in this group were monospecific stands of *H. spinulosa*. For the full seagrass study there were 89 sites with monospecific stands of *T. hemprichii*, 22 sites with monospecific stands of *C. serrulata*, 19 sites of monospecific *H. ovalis* (s), 15 sites of *H. ovalis* (l), 7 sites of *H. uninervis* (t), 5 sites of *S. isoetifolium* and 3 sites with monospecific stands of *C. rotundata* and *H. uninervis* (b) respectively. The numerically dominant seagrass of a site group was present at all sites in the group except for site Group 4, 6 and 7. For Group 4 and 6, the numerically dominant *T. hemprichii* was present at 203 and 518 of the 348 and 528 sites respectively. For Group 7 the numerically dominant *C. serrulata* was at 148 of the 166 sites.

Table 4. Species composition of 11 site groups from classification of percentage seagrass cover at sites sampled in Torres Strait.

Site Group	Dominants (> 25%)	Sub-dominants (10–25%)	Minor (< 10 > 5%)
1	*H. ovalis* (l) (65%)	*H. uninervis* (t) (11%)	*H. uninervis* (b) (8%); *H. spinulosa* (7%)
2	H. uninervis (t) (61%)	*H. ovalis* (s) (15%); *C. rotundata* (11%)	*T. hemprichii* (8%)
3	*H. ovalis* (s) (50%); *T. hemprichii* (26%)	*H. uninervis* (t) (14%)	E. acoroides (6%)
4	*T. hemprichii* (30%)	*H. ovalis* (l) (12%); *H. uninervis* (t) (17%)	*E. acoroides* (8%); *H. ovalis* (s) (7%); *H. spinulosa* (7%); *H. uninervis* (b) (5%)
5	*C. rotundata* (76%)		*H. uninervis* (t) (8%); *T. hemprichii* (5%)
6	*T. hemprichii* (70%)	*E. acoroides* (12%)	*C. rotundata* (6%)
7	*C. serrulata* (32%); *S. isoetifolium* (30%)	*H. uninervis* (b) (13%)	*H. ovalis* (l) (6%); *H. spinulosa* (6%)
8	*S. isoetifolium* (52%); *C. serrulata* (39%)		
9	*H. uninervis* (b) (45%)	*E. acoroides* (19%); *C. serrulata* (17%); *S. isoetifolium* (16%)	
10	*C. serrulata* (78%)		*T. hemprichii* (9%); *E. acoroides* (5%)
11	*H. spinulosa* (79%)		*S. isoetifolium* (9%); *H. ovalis* (l) (5%)

Table 5. Average environmental and biological characteristics of the 11 site groups and coefficient of variation (in brackets) from the cluster analysis of percentage seagrass cover data of Torres Strait. *N*: number of sites; Depth: water depth (m); Sechi: Sechi depth (m); Sed. Depth: sediment depth (m); %Gravel: % gravel; %Sand: % sand; %Mud: % mud; Biomass: Seagrass biomass gDW.m^{-2}; *C. serrulata*: *Cymodocea serrulata* biomass gDW.m^{-2}; *C. rotundata*: *Cymodocea rotundata* biomass gDW.m^{-2}; *H. uninervis* (b): *Halodule uninervis* (broad-leaf) biomass gDW.m^{-2}; *H. uninervis* (t): *Halodule uninervis* (thin-leaf) biomass gDW.m^{-2}; *E. acoroides*: *Enhalus acoroides* biomass gDW.m^{-2}; *T. hemprichii*: *Thalassia hemprichii* biomass gDW.m^{-2}; S. isoetifolium: *Syringodium isoetifolium* biomass gDW.m^{-2}; *H. ovalis* (s): *Halophila ovalis* biomass gDW.m^{-2}; *H. spinulosa*: *Halophila spinulosa* biomass gDW.m^{-2}; *T. ciliatum*: *Thallassodendron ciliatum* biomass gDW.m^{-2}; Diversity: biomass diversity (nats); %Seagrass cover: % cover of seagrass; %Total cover: % cover of seagrass and algae; No. species: Number of seagrass species site^{-1}; —: no data.

	Site Groups										
	1	2	3	4	5	6	7	8	9	10	11
N	15	82	57	348	15	528	166	18	18	55	25
Depth	5.4	1.3	1.7	2.9	1.4	1.2	3.8	2.7	3.2	2.4	12.1
	(80)	(69)	(123)	(134)	(64)	(97)	(65)	(49)	(54)	(73)	(60)
Sed. Depth	0.39	1.37	0.33	0.22	0.29	0.46	0.26	0.20	0.46	0.27	0.10
	(84)	(548)	(83)	(315)	(39)	(695)	(96)	(103)	(81)	(70)	(67)
Sechi	4.1	1.5	1.7	3.3	1.3	1.7	3.2	3.1	4.3	2.7	4.2
	(39)	(33)	(41)	(59)	(40)	(58)	(45)	(9)	(30)	(71)	(51)
%Gravel	25.5%	5.9%	9.0%	8.0%	3.6%	8.9%	9.3%	20.7%	9.8%	10.1%	9.1%
	(-)	(82)	(93)	(77)	(78)	(75)	(118)	(30)	(84)	(62)	(62)
%Sand	61.4%	67.6%	73.2%	80.8%	60.3%	74.0%	72.4%	55.6%	63.9%	65.2%	75.0%
	(-)	(28)	(23)	(15)	(17)	(16)	(19)	(34)	(14)	(13)	(11)
%Mud	7.9%	23.1%	14.7%	8.4%	35.1%	13.5%	16.0%	19.8%	22.8%	19.4%	11.4%
	(-)	(82)	(67)	(97)	(40)	(74)	(71)	(80)	(35)	(38)	(70)
Biomass	71.133	167.021	74.083	51.909	273.226	255.250	145.669	459.675	318.213	294.781	50.441
	(134)	(78)	(121)	(123)	(57)	(103)	(104)	(47)	(54)	(66)	(115)
C. serrulata	5.886	4.042	0.644	2.167	11.243	4.334	30.826	101.407	61.682	153.890	1.247
	(236)	(541)	(755)	(532)	(214)	(428)	(112)	(95)	(116)	(88)	(274)
C. rotundata	0.179	26.526	0.190	1.675	159.948	7.706	5.215	32.721	3.911	9.520	0.014
	(361)	(233)	(557)	(390)	(71)	(292)	(403)	(203)	(400)	(345)	(399)
H. uninervis (b)	11.363	3.930	2.297	1.317	5.132	2.830	19.611	57.538	91.458	5.189	1.416
	(242)	(540)	(443)	(466)	(251)	(329)	(221)	(163)	(81)	(221)	(240)
H. uninervis (t)	30.166	71.950	5.404	4.248	32.287	1.928	2.833	0.200	9.021	1.437	0.000
	(289)	(89)	(171)	(504)	(103)	(424)	(575)	(316)	(367)	(400)	(-)
E. acoroides	7.504	11.687	9.178	8.316	21.399	29.922	23.777	30.223	107.547	39.929	1.806
	(283)	(192)	(231)	(295)	(150)	(161)	(248)	(145)	(108)	(172)	(469)

Table 5 (continued). Average environmental and biological characteristics of the 11 site groups and coefficient of variation (in brackets) from the cluster analysis of percentage seagrass cover data of Torres Strait. *N*: number of sites; Depth: water depth (m); Sechi: Sechi depth (m); Sed. Depth: sediment depth (m); %Gravel: % gravel; %Sand: % sand; %Mud: % mud; Biomass: Seagrass biomass gDW.m^{-2}; *C. serrulata*: *Cymodocea serrulata* biomass gDW.m^{-2}; *C. rotundata*: *Cymodocea rotundata* biomass gDW.m^{-2}; *H. uninervis* (b): *Halodule uninervis* (broad-leaf) biomass gDW.m^{-2}; *H. uninervis* (t): *Halodule uninervis* (thin-leaf) biomass gDW.m^{-2}; *E. acoroides*: *Enhalus acoroides* biomass gDW.m^{-2}; *T. hemprichii*: *Thalassia hemprichii* biomass gDW.m^{-2}; S. isoetifolium: *Syringodium isoetifolium* biomass gDW.m^{-2}; *H. ovalis* (s): *Halophila ovalis* biomass gDW.m^{-2}; *H. spinulosa*: *Halophila spinulosa* biomass gDW.m^{-2}; *T. ciliatum*: *Thallassodendron ciliatum* biomass gDW.m^{-2}; Diversity: biomass diversity (nats); %Seagrass cover: % cover of seagrass; %Total cover: % cover of seagrass and algae; No. species: Number of seagrass species site^{-1}; —: no data.

	Site Groups										
	1	2	3	4	5	6	7	8	9	10	11
T. hemprichii	3.403	41.052	45.201	18.814	38.906	191.448	7.642	10.043	19.408	47.514	0.187
	(361)	(217)	(182)	(182)	(196)	(134)	(308)	(229)	(161)	(153)	(456)
S. isoetifolium	0.663	0.733	0.325	1.810	0.000	4.232	28.413	203.825	19.703	19.316	6.345
	(176)	(618)	(515)	(384)	(-)	(480)	(161)	(76)	(117)	(251)	(230)
H. ovalis	6.207	5.564	9.095	2.534	0.145	1.529	4.787	1.355	1.259	0.182	1.897
	(79)	(150)	(129)	(196)	(197)	(213)	(263)	(180)	(142)	(434)	(131)
H. spinulosa	0.769	0.311	0.544	0.849	0.000	0.284	2.592	1.371	0.000	0.894	32.780
	(359)	(854)	(649)	(588)	(-)	(1185)	(320)	(118)	(-)	(491)	(105)
T. ciliatum	0.000	0.000	0.000	0.798	0.000	0.029	0.000	0.000	0.000	0.000	0.000
	(-)	(-)	(-)	(1050)	(-)	(2100)	(-)	(-)	(-)	(-)	(-)
Diversity	0.461	0.589	0.518	0.355	0.672	0.431	0.772	0.568	0.918	0.540	0.415
	(89)	(72)	(77)	(109)	(59)	(94)	(68)	(101)	(50)	(88)	(99)
%Seagrass cover	53%	71%	44%	9%	73%	51%	40%	92%	90%	70%	48%
	(36)	(26)	(49)	(82)	(29)	(49)	(50)	(8)	(13)	(36)	(45)
%Total cover	60%	76%	49%	17%	77%	56%	48%	93%	91%	75%	50%
	(38)	(24)	(48)	(95)	(26)	(46)	(49)	(8)	(12)	(31)	(44)
No. species	2.27	3.00	2.77	1.97	3.33	2.80	3.45	2.67	3.94	2.35	2.36
	(66)	(54)	(47)	(85)	(52)	(70)	(61)	(101)	(44)	(76)	(67)

The detailed analysis also indicated that there were four main groups. The first main group, Group A, was an assemblage dominated by the broad-leaved morph of *Halophila ovalis* (l) (Fig. 7). The second main group B was comprised of Groups 2 to 6 which were subgroups of a larger *Thalassia hemprichii* mixed assemblage. Although the characteristic feature of this main group was *Thalassia hemprichii*, there was a gradient in the abundance of this seagrass which progressed from an assemblage dominated by *Cymodocea rotundata* located in nearshore areas with muddy sand (Group 5) with low *T. hemprichii* (5.8% cover); an assemblage dominated by the thin-bladed morph of *Halodule uninervis* also located in nearshore areas with muddy sand and unconsolidated sediments (Group 2) with low *T. hemprichii* (5.7% cover) through mixed and sparse assemblages with *T. hemprichii* in foreshore areas and reef tops in shallow water (Group 3 and 4) and an assemblage strongly dominated by *T. hemprichii* (Group 6) with many monospecific stands of *T. hemprichii* also located in shallow waters in foreshore areas and reef tops. The vast majority of sites (77%) occurred in this main group B of mixed assemblages with highly variable diversity, biomass and cover.

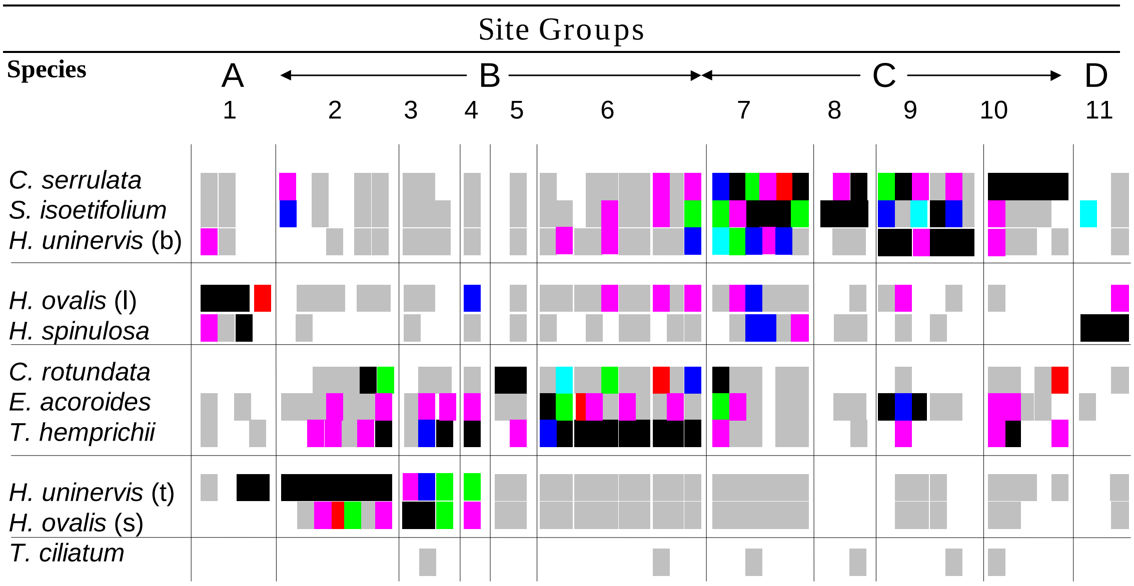


Figure 7. Two-way table of species groups by location based on seagrass species % cover. Black >50%, white 0%, grey 0 – 10%, green 10 – 20%, red 20 – 30%, lt. blue 30 – 40%, dk. Blue 40 – 50% cover. Groupings 1 – 11 based on percentage cover of seagrass species (q-mode analysis). See Figure 6.

The third main group C, was comprised of Groups 7 to 10. The diagnostic species of this group were *Cymodocea serrulata* and *Syringodium isoetifolium*. There were also gradients in the abundance of these seagrasses with a switch over from an assemblage dominated by *S. isoetifolium* (Group 8) to a mixed *S. isoetifoilum* and *C. serrulata* (Group 7) to a transition assemblage dominated by the broad-leaved morph of *Halodule uninervis*. Group 10 was a special case of the *C. serrulata* / *S. isoetifolium* assemblage with 11 of the 55 sites monospecific stands of *C. serrulata* with high cover and biomass. Sediments in this group were mostly muddy sands although sand predominated in Group 7. Species diversity was highest in this main group and ranged from 0.54 to 0.77. Highest average biomass also occurred in this main group.

The fourth main group D, (Group 11) was a distinct deep water *Halophila spinulosa* assemblage.

The MDS analysis clearly separated out the *Thalassia hemprichii* assemblage B (Group 2 to 6) from the *Cymodocea serrulata* / *Syringodium isoetifolium* assemblage C (Group 7 to 10) along MDS axes two and three (Fig. 8b). This was also shown by the significant correlations ($P < 0.001$) between the MDS scores on axes two and three with water depth (0.55 and 0.603 respectively) and MDS three with sediment depth (-0.40; $P < 0.01$). The deep water *Halophila spinulosa* (Group 11) was separated from the remaining groups along MDS axis 2 (Fig. 8b). In contrast, the *Halophila ovalis* (l) Group 1 assemblage was not separated out from the *Thalassia hemprichii* group B (Fig. 8a).

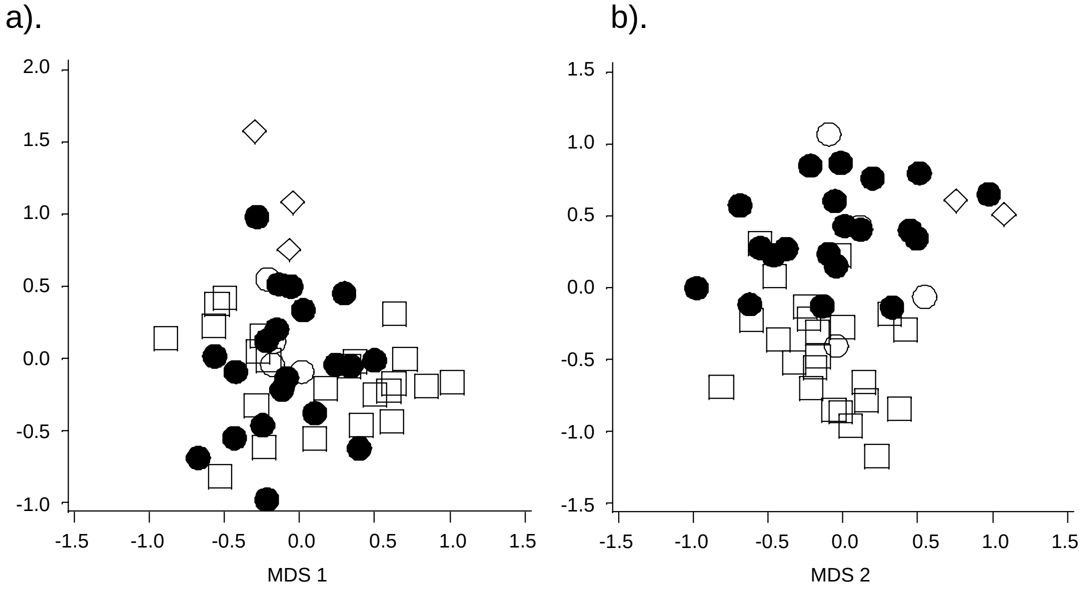


Figure 8. Plot of MDS scores a). MDS 1 and MDS 2 and b). MDS 2 and MDS 3 for the 50 groups from the classification of sites based on percentage seagrass cover. ○: *Halophila ovalis* (l) assemblage; □: *Thalassia hemprichii* assemblage; ●: *Cymodocea serrulata* / *Syringodium isoetifolium* assemblage; ◇: *Halophila spinulosa* assemblage.

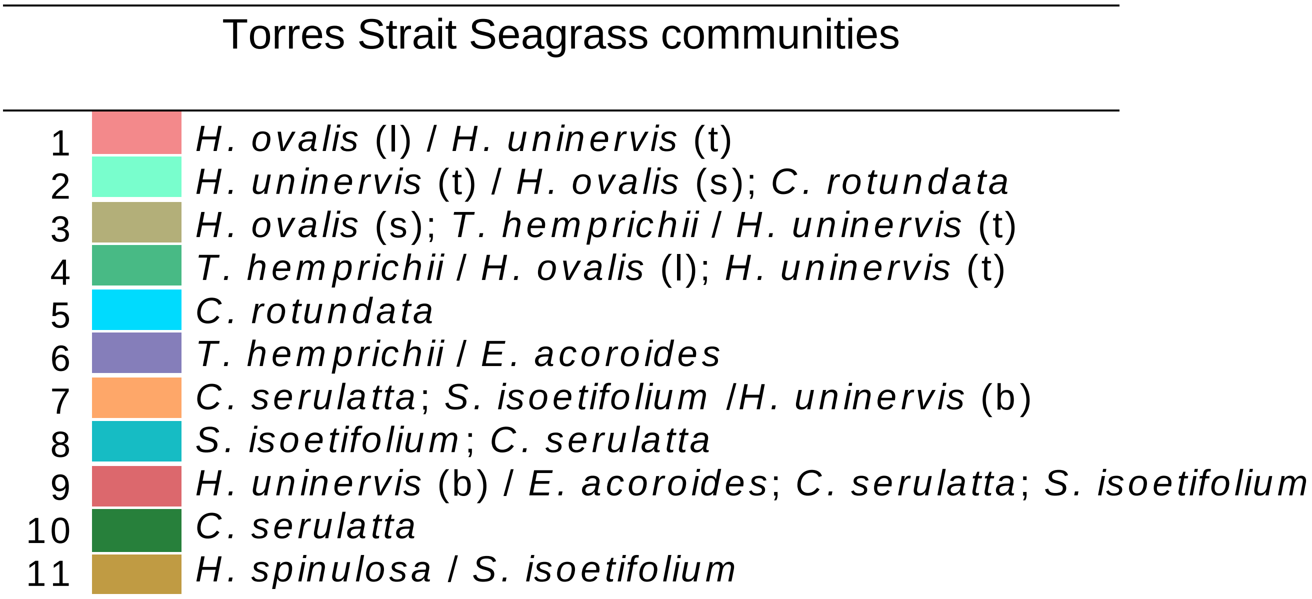
Distribution of seagrass assemblages

The eleven seagrass communities shown in Fig. 9 were found throughout Torres Strait. Plots of seagrass assemblages on the reef tops indicated that the *T. hemprichii* / *H. ovalis* (l), *H. uninervis* (t) (Group 4) and *T. hemprichii* / *E. acoroides* (Group 6) assemblages were the main assemblages of reefs (Fig. 10a-d). In contrast, the distribution of the seagrass assemblages on the foreshore areas of the sheltered embayments of the continental islands were very complex and showed little evidence of zonation (Fig. 10e-i). A typical example of this high complexity was shown at Port Lihou, Prince of Wales Island (Fig. 10i). Here the foreshore areas were mainly comprised of the *T. hemprichii* / *E. acoroides* (Group 6) assemblage and patches of the *T. hemprichii* / *H. ovalis* (l), *H. uninervis* (t) (Group 4) assemblage. There were also patches of the *H. uninervis* (t) / *H. ovalis* (s), *C.*

rotundata (Group 2) assemblage mostly in the nearshore areas; and the *H. ovalis* (s) *T. hemprichii* / *H. uninervis* (t) (Group 3) assemblage was scattered throughout the foreshore area. There were some marked differences, however, between foreshore and offshore assemblages at Port Lihou shown by the prevalence of the *C. serrulata, S. isoetifolium* / *H. uninervis* (b) (Group 7), assemblage off the foreshore area. In these subtidal areas there were only scattered patches of the *T. hemprichii* / *E. acoroides* (Group 6), assemblage which were much more prevalent on the foreshore areas. Moreover there were scattered patches of the *H. ovalis* (l) / *H. uninervis* (t) (Group 1) assemblage in the subtidal areas off the foreshore which were absent from the foreshore areas of Port Lihou.

The complex distribution patterns of seagrass assemblages at Port Lihou was also repeated at sheltered embayments sampled at the east, south and west of Badu Island (Fig. 10f-h); and foreshore and offshore areas of Thursday Island and Friday passage (Fig. 10l & m). In general there was a complex mixture of species assemblages in these embayments both on the foreshore and offshore in subtidal areas, however, the *C. serrulata* Group 10 and *H. spinulosa* Group 11 assemblage were mainly located in subtidal areas.

In the offshore areas between the reefs and islands of central and western Torres Strait the assemblages were mainly the *H. spinulosa* Group 11 assemblages, *C. serrulata*, *S. isoetifolium* / *H. uninervis* (b) Group 7 and the scattered and sparse mixed *T. hemprichii* / H. ovalis (l) ; H. uninervis (t) Group 4 assemblages (Fig. 10j& k). In some areas the *C. serrulata* Group 10 assemblage was present. The offshore areas of reefs were mostly the mixed and sparse *T. hemprichii* / *H. ovalis* (l) *H. uninervis* (t) Group 4 assemblage and *T. hemprichii* / *E. acoroides* Group 6 and the deep water *H. spinulosa* Group 11 assemblage.

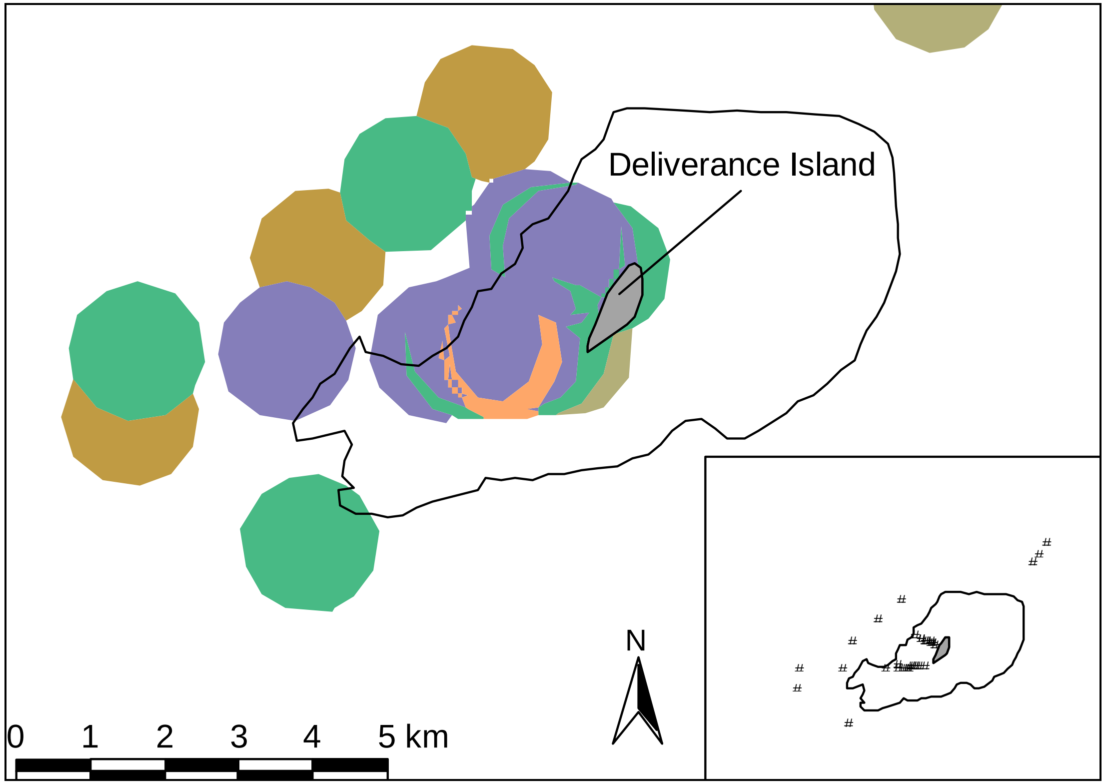


Torres Strait Seagrass communities

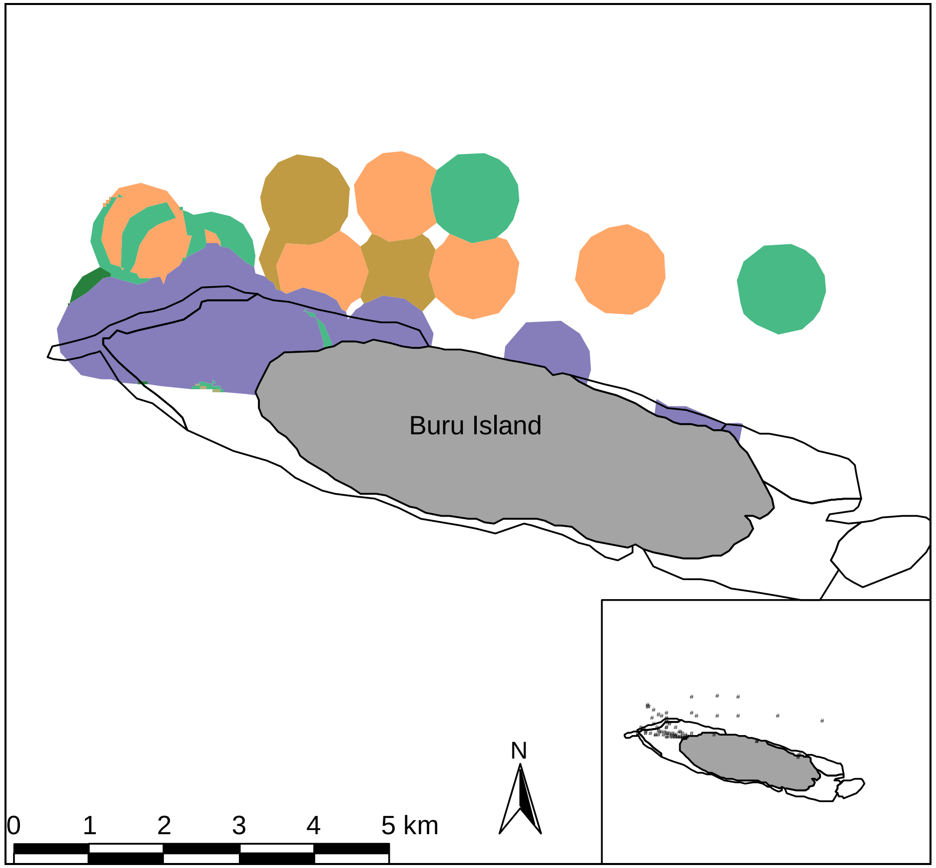
1	🟥	*H. ovalis* (l) / *H. uninervis* (t)
2	🟩	*H. uninervis* (t) / *H. ovalis* (s); *C. rotundata*
3	🟫	*H. ovalis* (s); *T. hemprichii* / *H. uninervis* (t)
4	🟩	*T. hemprichii* / *H. ovalis* (l); *H. uninervis* (t)
5	🟦	*C. rotundata*
6	🟪	*T. hemprichii* / *E. acoroides*
7	🟧	*C. serulatta*; *S. isoetifolium* /*H. uninervis* (b)
8	🟦	*S. isoetifolium*; *C. serulatta*
9	🟥	*H. uninervis* (b) / *E. acoroides*; *C. serulatta*; *S. isoetifolium*
10	🟩	*C. serulatta*
11	🟨	*H. spinulosa* / *S. isoetifolium*

Figure 9. Eleven seagrass communities identified in Torres Strait.

a).



b).



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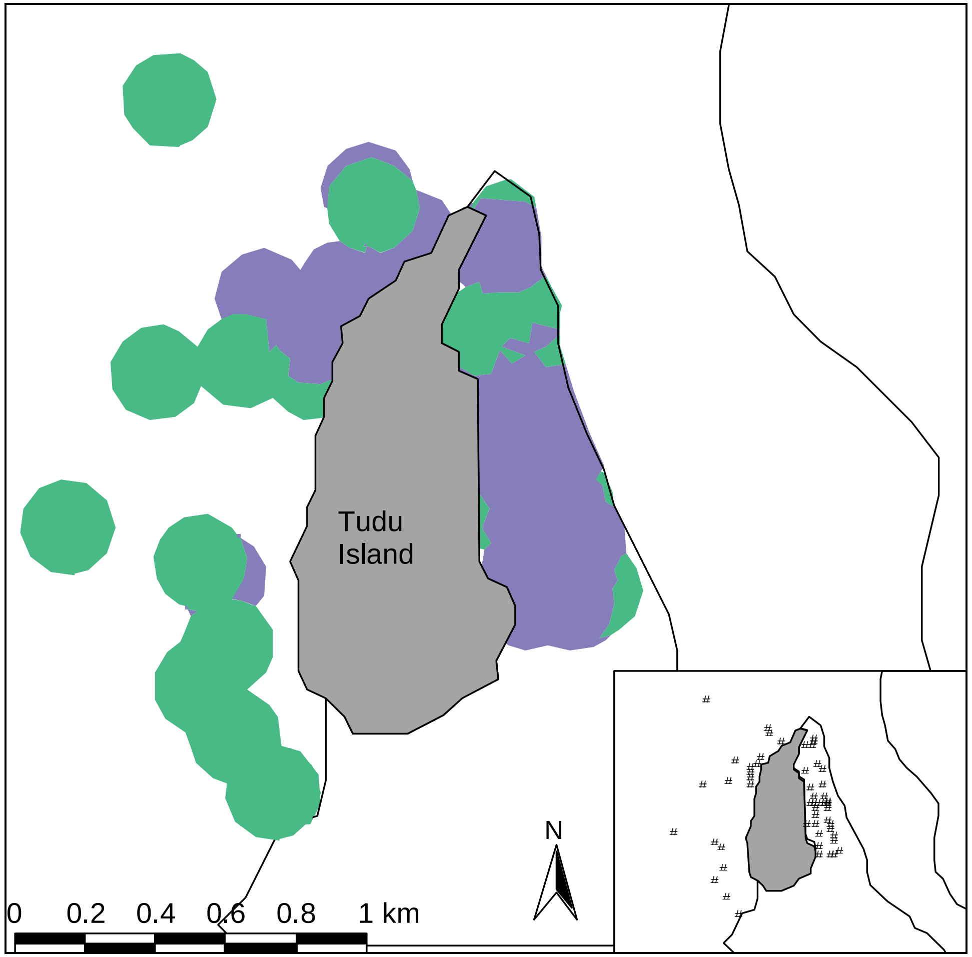

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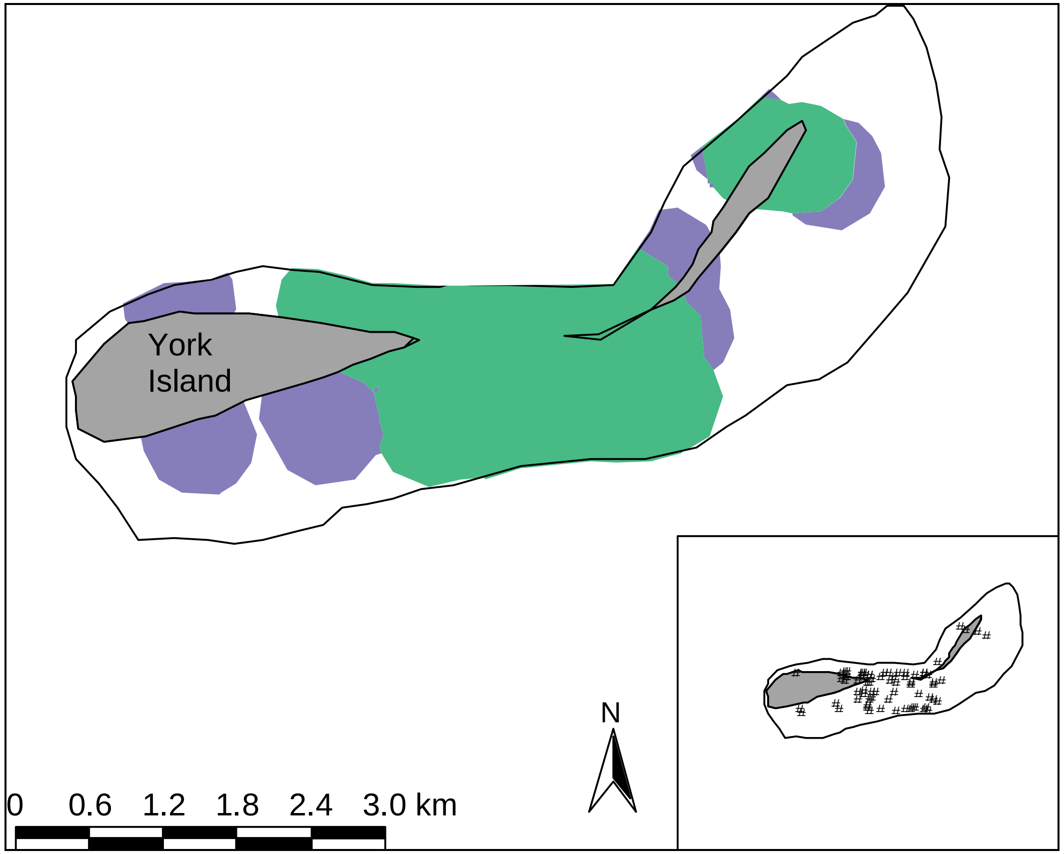

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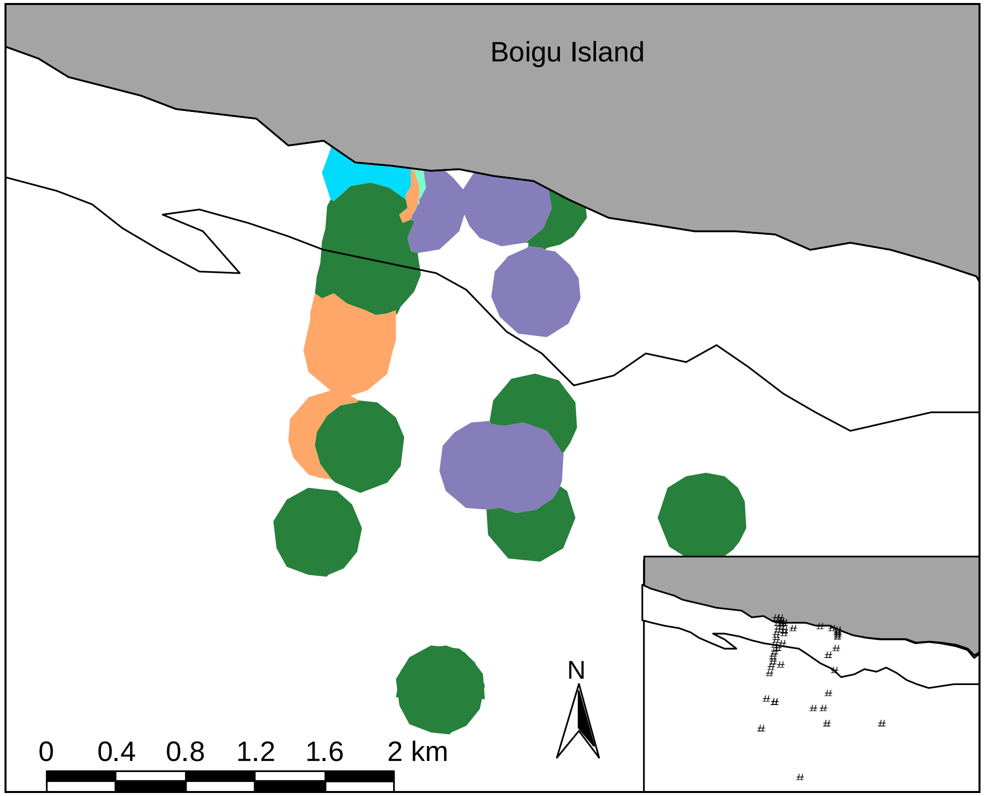

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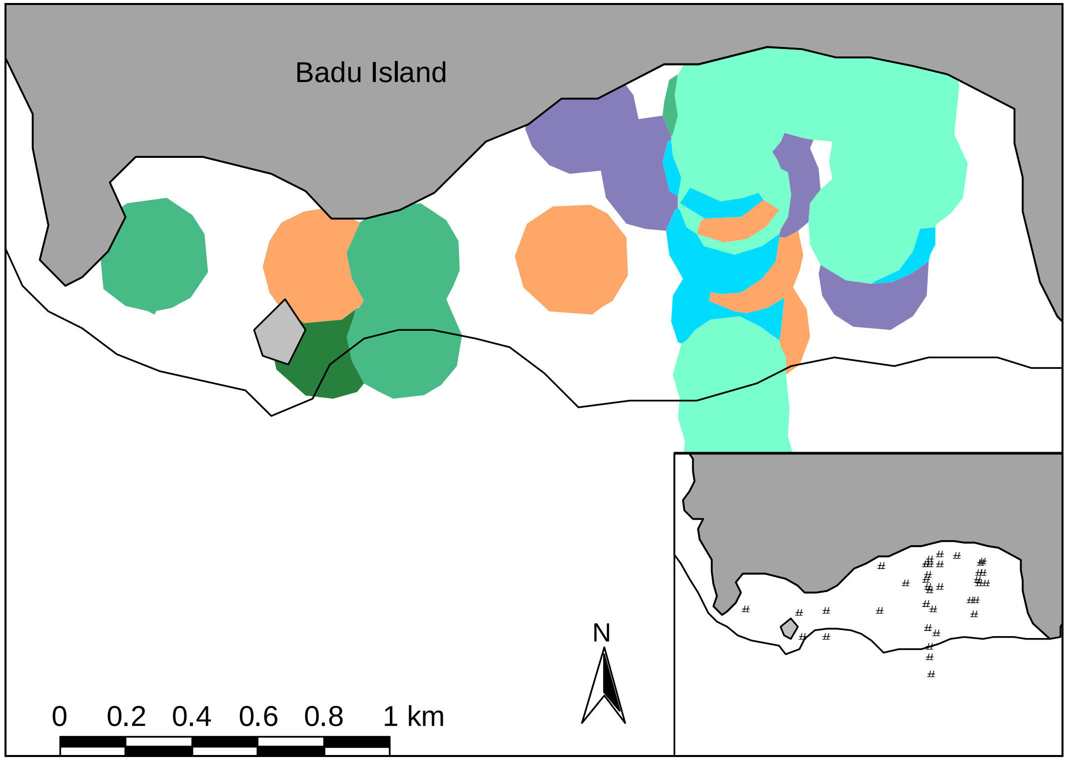

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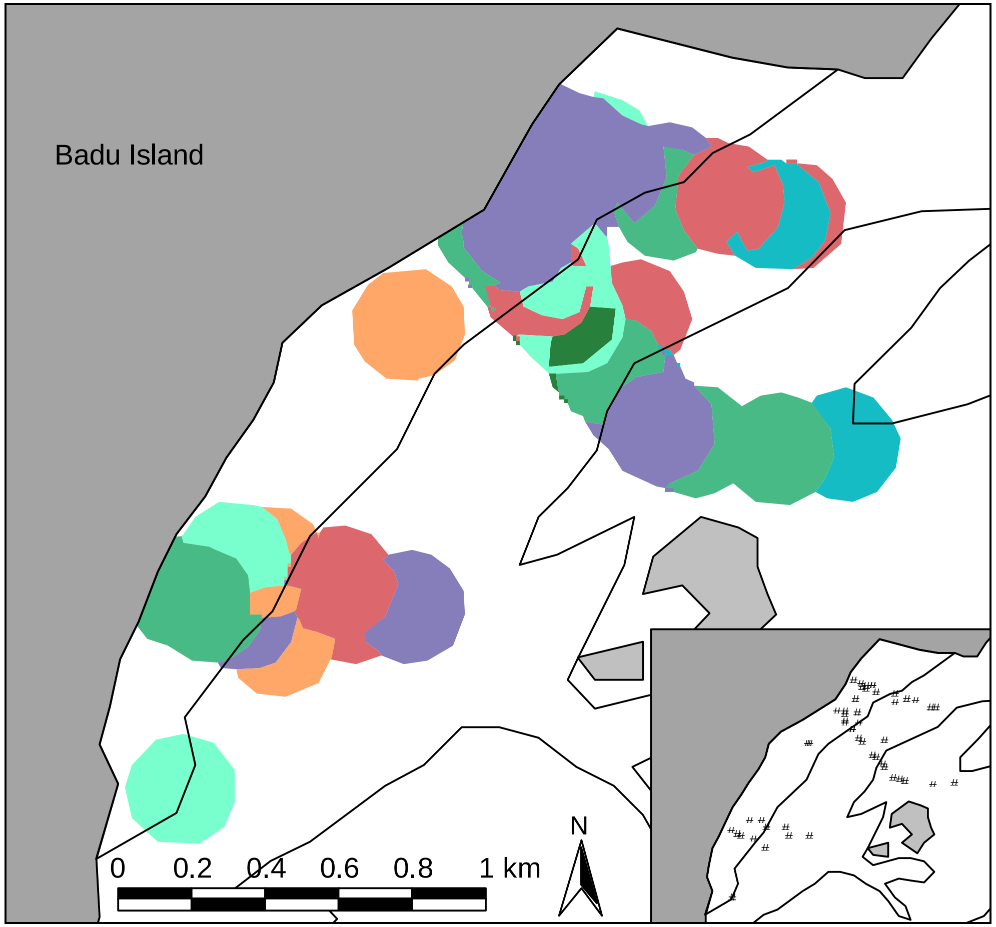

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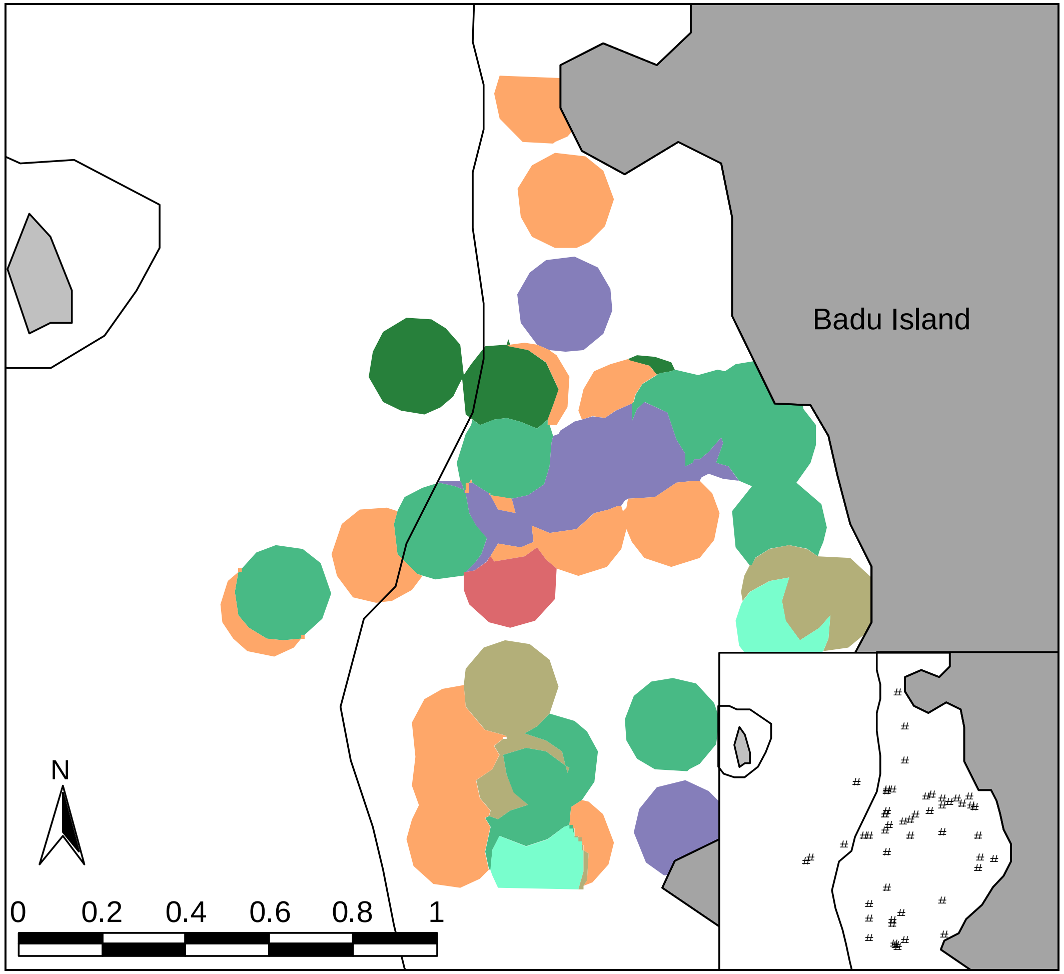

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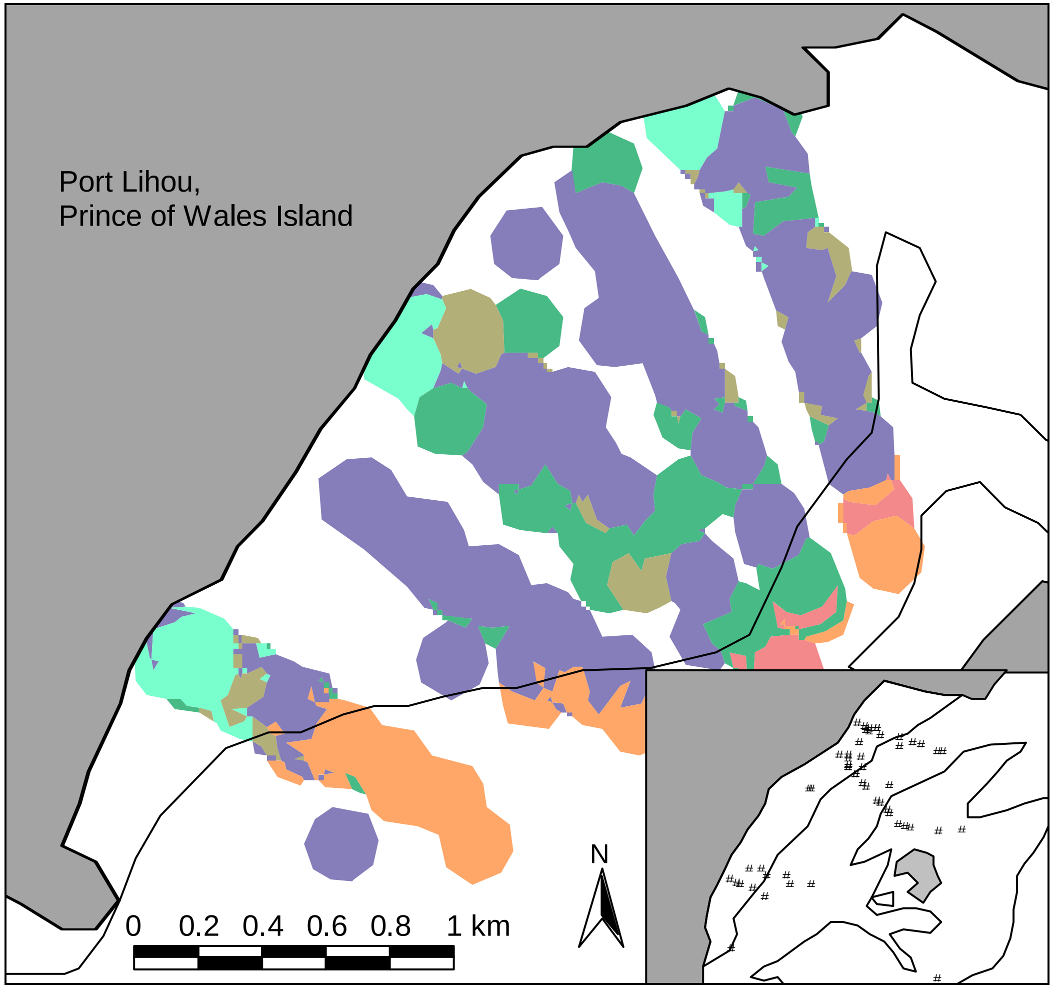
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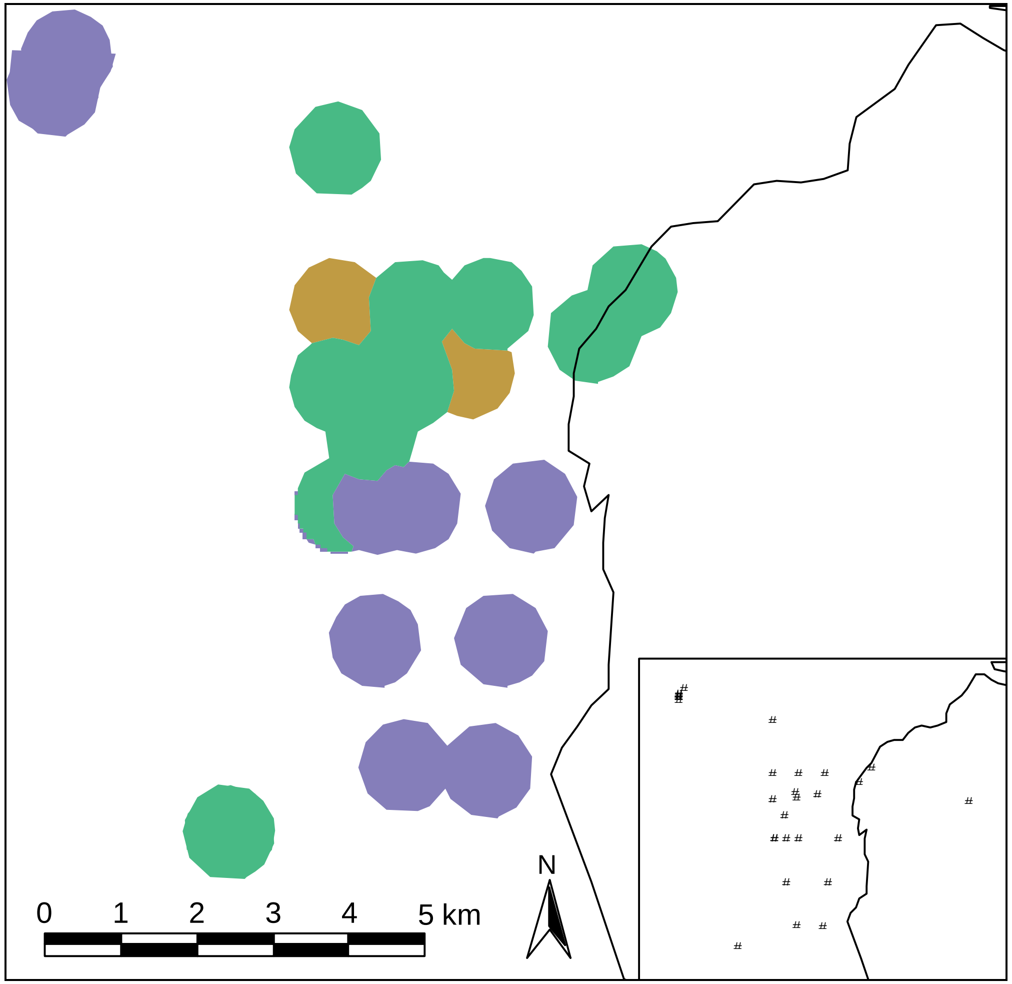
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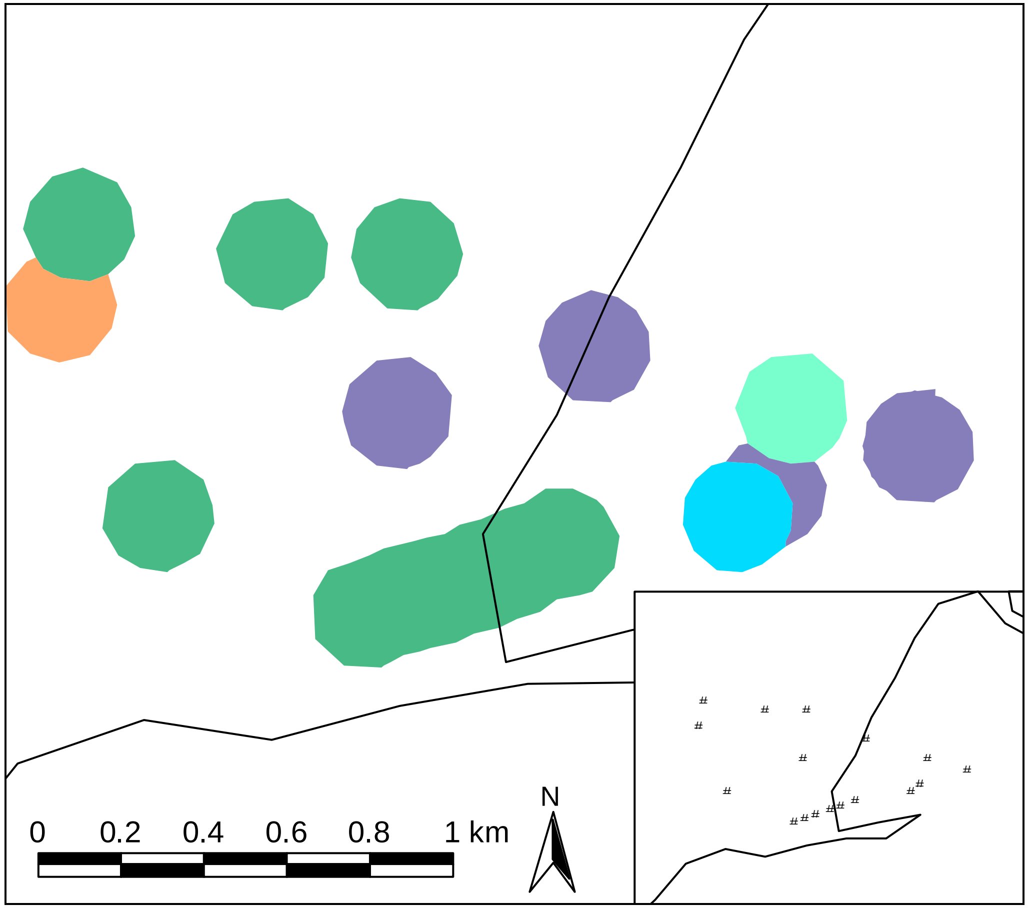

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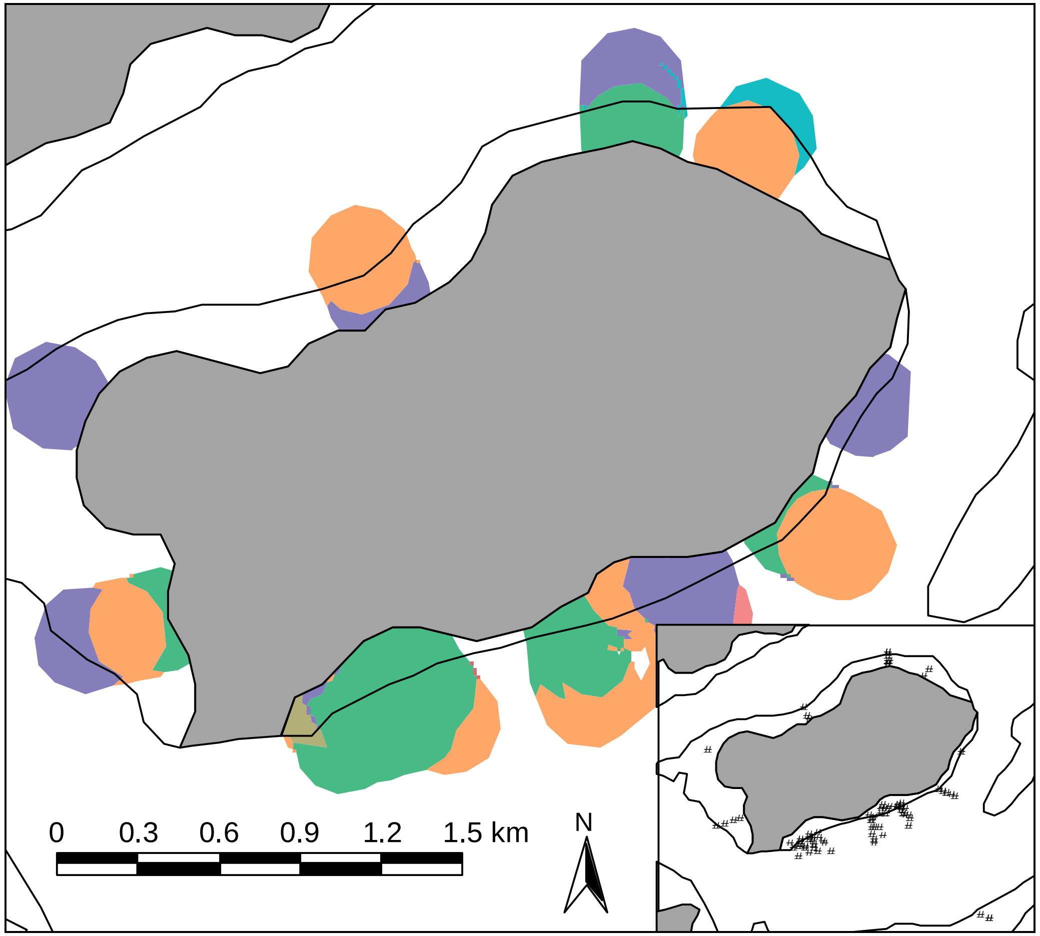

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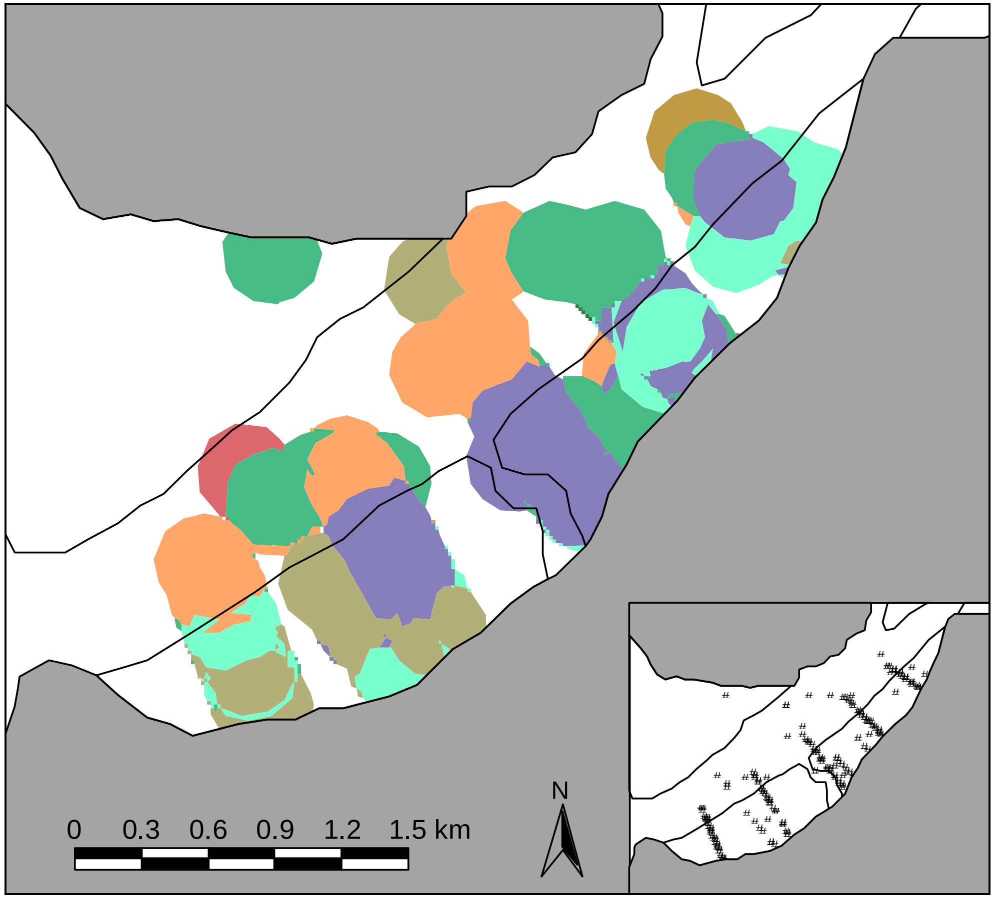

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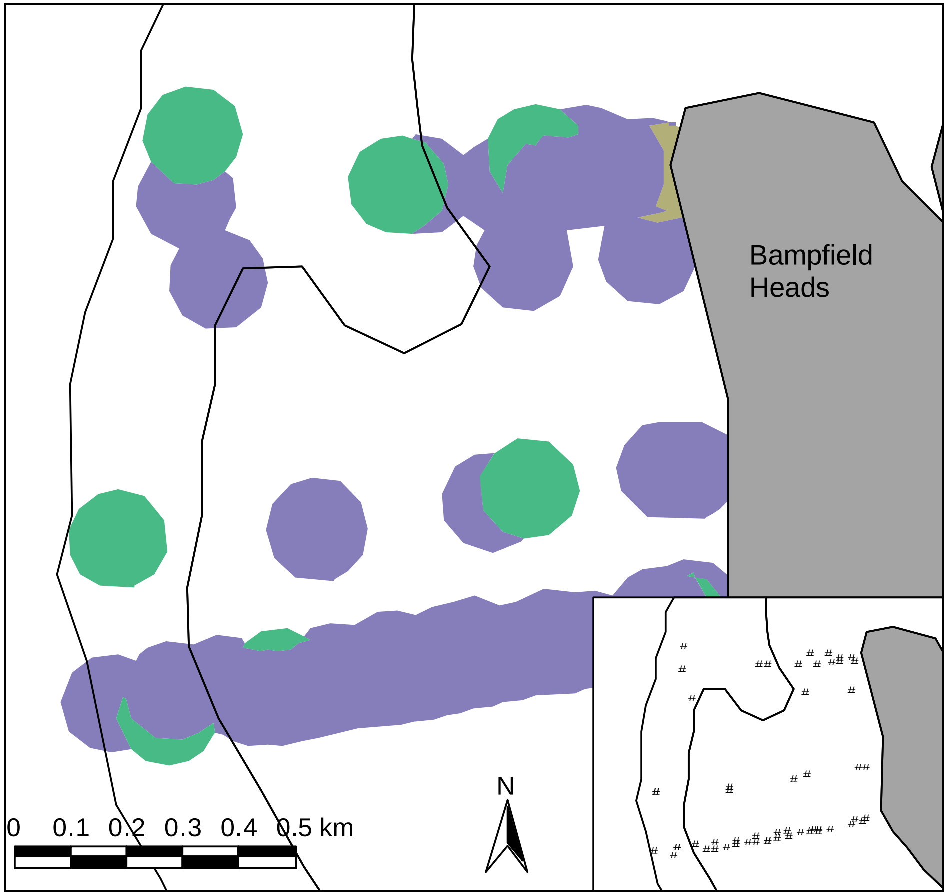

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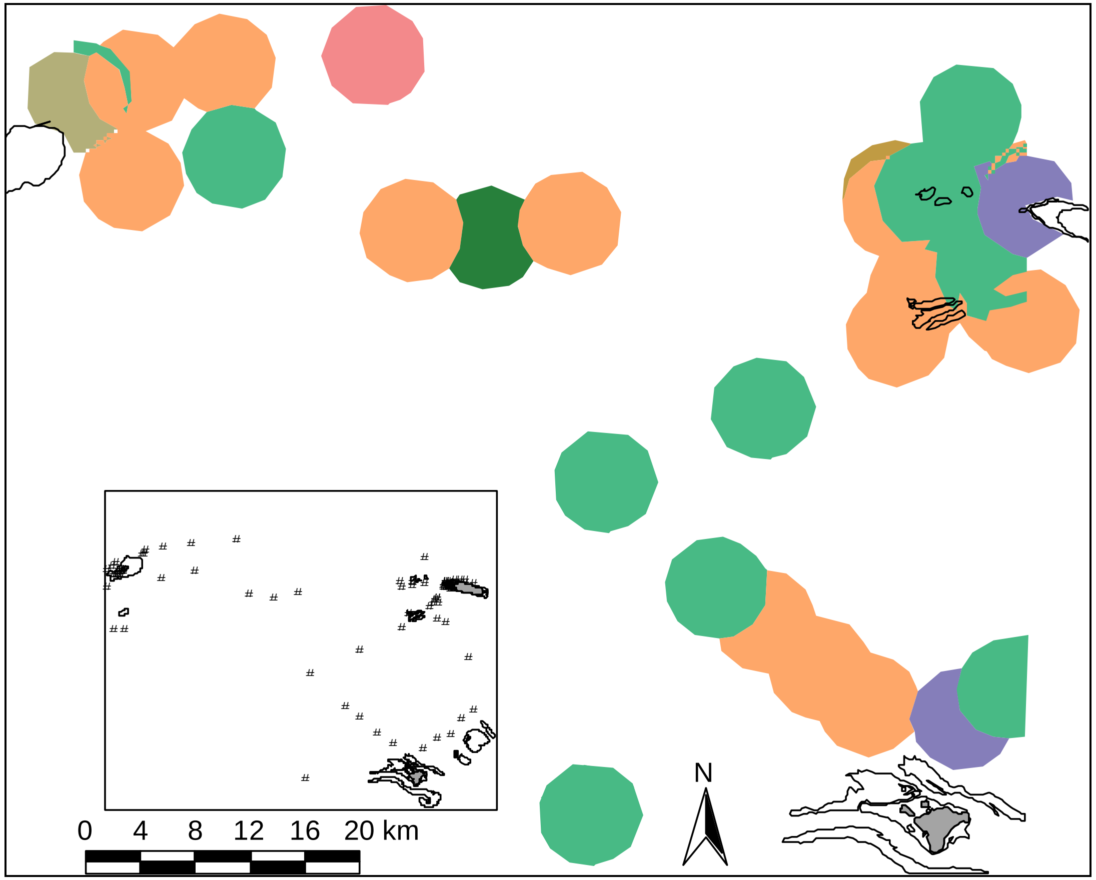

Figure 10. Seagrass communities of Torres Strait for a). Deliverance reef; b). Buru reef; c). Tudu reef; d). Yorke reef; e). south Boigu Island foreshore and shallow subtidal; f). South Badu Island foreshore and shallow subtidal; g). East Badu Island foreshore and shallow subtidal; h). west Badu foreshore and shallow subtidal; i). Port Lihou foreshore and shallow subtidal; offshore Wapa reef; k). Offshore south Warrior reef; l). Thursday Island foreshore and shallow subtidal; m). Friday Passage foreshore and shallow subtidal; n). Bampfield Head foreshore and shallow subtidal; o). Inter-reefal communities between Buru Island reef and Deliverance Island reef.

Discussion

Seagrass mapping

Large areas of the seabed of central and western and to a lesser extent eastern Torres Strait had seagrass (~13,000 km^2) in a 42,000 km^2 study area. This estimate contrasts markedly with an estimated 900 km^2 area of seagrass supporting habitat in the Gulf of Carpentaria next to Torres Strait, which is lower by factor of 10 despite the much larger area of the Gulf < 20 m (~100,000 km^2) and length of coastline (1,800 km) (Poiner et al., 1987). Estimates for Torres Strait are higher by a factor of 5 for the nearshore (< 15 m) seagrass beds (2,464 km^2) for the 1,200 km stretch of coastline from Cape York to Townsville (19° 15'S; 146° 45' E) in a study area of ~6,000 km^2 (Lee Long et al., 1993). The estimates for Torres Strait compares well with the area of deep-water (15–58 m) seagrass, ~14,000 km^2, between Cape York and Cairns (16° 50'S; 145° 45' E) in a study area of 36,000 km^2 based on maps in Lee Long et al. (1996). However, the deep water seagrass assemblages reported by Lee Long et al. (1996) for the northern Great Barrier Reef (GBR) lagoon were not present along the inside margin of the ribbon reefs in eastern Torres Strait. There is a decrease in deep water seagrass along the inside margin of the ribbon reefs from the northern GBR seagrass north of Princess Charlotte Bay (14° S; 144° E) (Lee Long et al. 1996) into the far northern GBR (Poiner et al., 1997) and eastern Torres Strait (this study). Without further environmental data it is not possible to determine probable causes for this pattern. The percentage cover of seagrass on the reefs of Torres Strait was inversely correlated with distance from the Mai and Fly Rivers in Papua New Guinea; a factor associated with the influence of river runoff (Long et al. submitted). Lee Long et al. (1996) suggested that factors associated with river runoff may be implicated in the low abundance of deep-water seagrass in the northern GBR.

Distribution and abundance of seagrass

Seagrass was broadly distributed throughout Torres Strait with all 12 species except *Thallassodendron ciliatum* found on reefs, foreshore and shallow subtidal areas off the reefs and continental island embayments and coastline. *T. ciliatum* was mainly found in high energy environments on a coral rubble matrix with little overlying soft sediment. *Halophila ovalis* and *H. spinulosa* had the broadest distribution with depth and the deep-water *Halophila* spp. assemblages in Torres Strait appear to be a general feature of the seagrass assemblages of inter-reefal areas of northern Australia (Great Barrier Reef: Lee Long et al., 1996). They were not present in the Gulf of Carpentaria where exposed reefs are uncommon (Poiner et al., 1987).

The dominant seagrass in Torres Strait was *Thalassia hemprichii* which is also the dominant seagrass in mixed meadows throughout the tropical West Pacific (Brouns 1985). The seagrass, *Zostera capricorni* was only sampled in the boat harbour at Thursday Island on one occasion. den Hartog (1970) also reported this seagrass from Thursday Island harbour. Coles et al. (1987) sampled *Z. capricorni* south of 15° S which they considered to be the northern limit of the seagrass on the east coast of Queensland. Transplantation by ground tackle from small ships may explain the presence of *Z. capricorni* in the boat harbour at Thursday Island, but the seagrass is probably transient and does not permanently establish itself there. Coles et al. (1987) considered that the far northern distribution of *Z. capricorni* was from transplanted material carried from site to site on the ground tackle of small craft and these results supports this hypothesis.

Monospecific beds of seagrass were uncommon in Torres Strait with less than 15% of the 1,327 sites composed of single species of seagrass. Monospecific beds of *C. serrulata, C. rotundata, H. uninervis* and *S. isoetifolium* were reported for Papua New Guinea, however, they were rare and normally these seagrasses were found in mixed assemblages (Brouns, 1987). Monospecific beds of seagrass have been reported from the northern Great Barrier reef (Coles et al., 1987), however, they were uncommon and mixed assemblages were the norm. Mixed assemblages of *Halophila* spp. occur in the deep-water regions of the northern Great Barrier lagoon (Lee Long et al., 1996). In contrast, seagrass beds along the open coastline in the Gulf of Carpentaria were predominantly monospecific beds of *H. ovalis* and *H. uninervis* intertidally and *C. serrulata* and *S. isoetifolium* subtidally (Poiner et al., 1987). Monospecific beds of *S. isoetifolium* have been reported for Fiji but only over small areas (Aioi and Pollard, 1993).

The above-ground biomass of most species (7) of seagrass was significantly correlated with water depth and for many there was a significant bell-shaped relationship with depth with biomass increasing to a maximum around 4 to 6 m water depth before decreasing again. Biomass was pooled for selected depth intervals as we could not adjust depths for tidal height up to ~ 4 m (Anon., 1995). The low amount of variation explained by the regressions of biomass with depth may be explained by the complex physical environment of Torres Strait. There is a complex spatial and temporal distribution of suspended sediments in Torres Strait which affects the light regime at a variety of spatial and temporal scales which ranges from a semi-permanent turbidity maximum zone in central Torres Strait (Harris et al., 1988) to high suspended sediments occurring at peak tidal currents which returns to relatively clear water at the change of the tide in areas with coarse, poorly sorted sediments in regions of western Torres Strait (Wolanski et al., 1984; Harris et al., 1988). The light regime is a primary environmental factor influencing photosynthesis, growth and depth distribution of seagrass (Dennison, 1986). Complex micro topography on foreshore areas and reefs resulting in water ponding, levels of exposure correlated with complex tides and high temperatures up to 40° C in shallow pools during the day would further contribute to the poor relationship between seagrass biomass and water depth in intertidal areas. The diversity of seagrass was highest in intermediate water depths (4–6 m) and significantly lower in shallower and deeper water. The low diversity in the shallowest waters was due to an assemblage dominated by the thin-bladed morph of *Halodule uninervis* and the small leafed morph of *Halophila ovalis.* Diversity is depressed and the variation in diversity is low as few seagrass can tolerate the extreme conditions of exposure, however, biomass and cover can be high largely due to abundant *Halodule uninervis*. Where *Thalassia hemprichii* occur the shoots are often sun-burnt, broken off and stunted. Off the foreshore areas and reefs were a complex array of seagrass assemblages. Diversity and the variation of diversity is highest in these areas. Biomass is highest, but is also variable. Complex and varying environmental conditions of tidal heights, water turbidity and water currents in combination with heterogeneous substrates of rubble, sand and coral and muddy substrates off the reefs and foreshore areas can explain the high diversity and complexity of the assemblages in intermediate water. Climax species such as *C. serrulata* and *S.*

isoetifolium are unable to dominate over the full range of environmental conditions and substrates in Torres Strait and overlap with pioneering *Halophila* species, stress tolerant *Halodule uninervis, Thalassia hemprichii* and *Enhalus acoroides* (Birch and Birch, 1984). At the other deep-water extreme, diversity is again depressed and a *Halophila spinulosa* assemblage dominates.

Spatial and temporal sources of variation

Almost half of the variation in the biomass of seagrass was among quadrats within a site and the remaining variation was relatively evenly partitioned among the larger spatial scales sampled for most of the seagrasses. In contrast little of the variation was between sampling occasions. There was a significant correlation between spatial scale and variation with significantly more variation in percentage cover of seagrass at smaller than larger spatial scales. These results indicate that processes operating at small spatial scales in the order of metres were important in structuring the seagrass assemblages on the reefs, foreshore and subtidal areas of Torres Strait. Complex micro-topological relief over the wide range of coral reef, rubble and sand habitats with complex tides and currents interacting with strong prevailing winds resulting in complex, small-scale spatial and temporal variations in environmental stress can explain the patterns of variation in seagrass at the small spatial scales sampled. The extent and duration of water ponded on the reefs and foreshore areas would vary greatly between tides and shallow ponded water can reach temperatures as high as 38°C. Small-scale heterogenous matrix of rubble, sand, mud and structural megabenthos on the reefs would increase the spatial complexity of environmental conditions experienced by seagrass and affect distribution and abundance at this scale. At larger, regional, spatial scale, the strong currents and tides act to break down environmental gradients across Torres Strait which can explain the relatively low variation in seagrass cover among locations and regions.

The maps of the distribution of seagrass in the deeper water areas indicates that there are regional differences among the eastern, central and western Torres Strait with high seagrass in western Torres Strait and very little seagrass in the inter-reefal areas of eastern Torres Strait. Prawn trawling may explain the absence of seagrass east of the Warrior reefs in the main trawling grounds. Alternately, this an area of greater depths, fewer sediments and higher turbidity (Wolanski et al., 1984); consequently low light availability may explain the absence of seagrass in this region. In contrast, the deep water areas of western Torres Strait with coarse sediments and clear water supported dense beds of *Halophila spinulosa* as deep as 20 m.

Seagrass assemblages

There were 11 seagrass assemblages in Torres Strait which were grouped into four main communities: a mixed assemblage most often characterised by the presence of *Thalassia hemprichii* and with sparse cover (< 10%) of seagrass found throughout the reefs and foreshore and shallow subtidal areas of Torres Strait; an assemblage characterised by *C. serrulata* and *S. isoetifolium* located mainly in subtidal waters; a deep-water assemblage dominated by and was often a monospecific stand of *Halophila spinulosa*; and an assemblage found in intermediate water depths characterised by *Halophila ovalis* (b) and *Halodule uninervis* (t). Within the main *Thalassia hemprichii* shallow water group there were examples of monospecific stands of *Halophila ovalis* (s) and *Halodule uninervis* (t) located mainly in areas with high environmental stress close to the shore, however, these two species mostly occurred together. There were also examples of assemblages dominated by *Cymodocea rotundata* and many examples where all possible combinations of seagrasses were sampled together as scattered, mixed assemblages with low abundance.

The species groups classified in this study were similar to the species groups in the Gulf of Carpentaria (Poiner et al., 1987). There was an equivalent *C. rotundata*, *E. acoroides* and *T. hemprichii* species association in both the Gulf of Carpentaria and Torres Strait. Both the Gulf and Torres Strait also had a distinct *C. serrulata, S. isoetifolium, H. uninervis* (b) and *H. spinulosa* association and whereas *H. uninervis* (t) and *H. ovalis* (s) formed an association in Torres Strait, these two seagrasses were often monospecific communities in the Gulf. There were marked differences between the seagrass assemblages in Torres Strait and the Gulf. There was an open coastline assemblage with well defined zonation patterns related to water depth which was absent from Torres Strait. The differences in the seagrass assemblages between Torres Strait and the Gulf of Carpentaria can be explained by differences in tidal regimes and bathymetry. Torres Strait has an extremely complex spatial pattern of tides and associated currents. The phase of the dominant M_2 constituent of the tide varies by 120° through the Straits between Booby (10° 36' S; 141° 56'E) and Twin Island, Torres Strait (10° 28' S; 142° 26'E) yet these two islands are separated by just 30 nm (Bode and Mason, 1994). The resultant large pressure gradients generate strong tidal currents. There are also large differences in the diurnal and semidiurnal constituents between the Coral Sea and Gulf of Carpentaria which results in a rapid change in amplitude and phase between Cape York and Papua New Guinea (Bode and Mason, 1994). In the summer months of December and January the low tides occur at night and high tides during the day. This may reduce the extremes in temperature and desiccation that seagrasses would be exposed to if there were low tides in the middle of the day during summer. The tidal range is ~4.0 m at many locations in Torres Strait (Anon., 1995). The result of this complexity is to integrate and blur the depth boundaries of the seagrass assemblages.

Most assemblages were numerically dominated by a single seagrass and all species except *E. acoroides* was strongly dominant for at least one site group. Individual species showed a significant correlation with depth, with peak abundance at different depths and a non-linear distribution for most. This pattern at the species level was responsible for significant differences in depth among the four main site groups. The *H. spinulosa* site group located in deep waters was significantly deeper than the *H. ovalis* (b) site group. The *C. serrulata* and *S. isoetifolium* group was located in deeper water than the *Thalassia hemprichii* mixed group. However, within the *T. hemprichii* main assemblage there were also significant differences. The two shallowest sub-groups dominated by *C. rotundata* and *H. uninervis* (t) respectively showed little variation in water depth. However, the two sub-groups with mixed assemblages and the sub-group dominated by *T. hemprichii* showed great variation in water depth. This complex pattern of seagrass assemblages with depth can also be explained by the large variations in environmental conditions experienced in Torres Strait. The patterns of diversity with depth and more importantly the patterns in the variation in diversity with depth indicated that diversity and variation in diversity peaked at intermediate depths. Lower diversity was at the two extremes of exposure. Thus the complex array of environmental factors can account for the complex array of seagrass assemblages in Torres Strait and lack of zonation with depth which is a feature characteristic of open coastline areas in the Gulf of Carpentaria (Poiner et al., 1987). Thus the seagrass assemblages of Torres Strait appear to be regulated and controlled by a complex interaction between physical factors of the environment and the individual niche requirements of each species.

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