

SEAGRASS HABITATS OF NORTHEAST AUSTRALIA: MODELS OF KEY PROCESSES AND CONTROLS

*T. J. B. Carruthers, W. C. Dennison, B. J. Longstaff, M. Waycott,
E. G. Abal, L. J. McKenzie and W. J. Lee Long*

ABSTRACT

An extensive and diverse assemblage of seagrass habitats exists along the tropical and subtropical coastline of north east Australia and the associated Great Barrier Reef. In their natural state, these habitats are characterised by very low nutrient concentrations and are primarily nitrogen limited. Summer rainfall and tropical storms/cyclones lead to large flows of sediment-laden fresh water. Macro grazers, dugongs (*Dugong dugon*) and green sea turtles (*Chelonia mydas*) are an important feature in structuring tropical Australian seagrass communities. In general, all seagrass habitats in north east Australia are influenced by high disturbance and are both spatially and temporally variable. This paper classifies the diversity into four habitat types and proposes the main limiting factor for each habitat. The major processes that categorise each habitat are described and significant threats or gaps in understanding are identified. Four broad categories of seagrass habitat are defined as 'River estuaries', 'Coastal', 'Deep water' and 'Reef', and the dominant controlling factors are terrigenous runoff, physical disturbance, low light and low nutrients, respectively. Generic concepts of seagrass ecology and habitat function have often been found inappropriate to the diverse range of seagrass habitats in north east Australian waters. The classification and models developed here explain differences in habitats by identifying ecological functions and potential response to impacts in each habitat. This understanding will help to better focus seagrass management and research in tropical habitats.

Increased awareness of human impacts on seagrass meadows has generated renewed interest in understanding the dynamic nature of seagrass communities (Short and Wyllie-Echeverria, 1996). This is particularly relevant in the tropics where some abundant species are considered very dynamic but are little studied (Duarte, 1999). Over 45,000 ha of seagrass have been lost from Australian coastal waters in recent years, this loss has been largely attributed to reductions in water quality and therefore in available light (Walker and McComb, 1992). Tropical seagrass habitats in Australia are extensive (18 405 km²), diverse and important for primary and secondary production (Hillman et al., 1989; Lee Long et al., 2000). The Queensland coastline is ca 9800 km long and extends through tropical and subtropical regions including the 2600 km of the Great Barrier Reef (Hopley, 1986). Extensive coastal lagoons, estuaries, rivers and the barrier reef with its inshore lagoon provide a high diversity of potential seagrass habitats (Fig. 1). Classifications of north east Australian seagrass communities (Poiner et al., 1987; Lee Long et al., 1998) have demonstrated a need to develop a clear framework for understanding the diversity of seagrass habitats.

Australia has the highest species diversity of seagrasses in the world, with more than half the known species of seagrass occurring in Australian waters (Kuo and McComb, 1989). This high diversity is in part due to the overlap of tropical and temperate seagrass floras and the considerable endemism present in certain bioregions (Walker and Prince, 1987). In north east Australia, the highest species diversity of seagrass occurs near the tip of Cape York, with a gradual decline in diversity moving south down the east coast (Coles

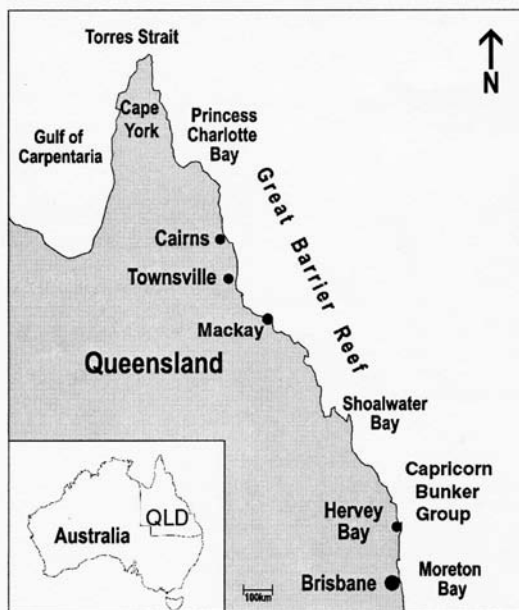


Figure 1. Map of north east Australia, detailing main locations referred to in text.

et al., 1989; Mukai, 1993). This is proposed to be the result of increasing geographic distance from the centre of diversity, between Torres Strait and Borneo, driven by dispersal in the East Australian Current which runs north to south (Mukai, 1993).

The dynamics of tropical seagrasses are modified by long term weather patterns as well as extreme flood and cyclone events, resulting in stochastic and cyclic patterns of seagrass abundance (Birch and Birch, 1984; Lanyon and Marsh, 1995). It has been well established that turbidity and other restrictions to light availability limit seagrass growth (Shepherd et al., 1989). The main turbidity source in the Great Barrier Reef lagoon is pulsed turbidity events from river discharges of summer rainfall (Hamilton, 1994). Turbidity, and therefore the potential for impact on seagrass habitat, declines in a gradient away from the coastal source, however sediment plumes do frequently reach mid-shelf coral reefs (Hamilton, 1994).

The presence of such a high diversity of seagrass habitats in north east Australia makes generalizations about seagrass communities difficult. Different habitat types have different ecological processes, different threats and therefore different management requirements. This paper defines four broad habitat types and their key features, identifying research needs and major threats with the aim of increasing our understanding of the diversity and dynamics of seagrass habitats in the Australian tropics.

NORTH EAST AUSTRALIAN HABITATS (Fig. 2, Table 1)

Queensland seagrasses occur in a variety of different habitats (Fig. 2, Table 1) and are influenced by seasonal and episodic coastal runoff (Bridges et al., 1981). Episodic terrigenous runoff events result in pulses of increased turbidity, nutrients and a zone of reduced salinity in nearshore waters.

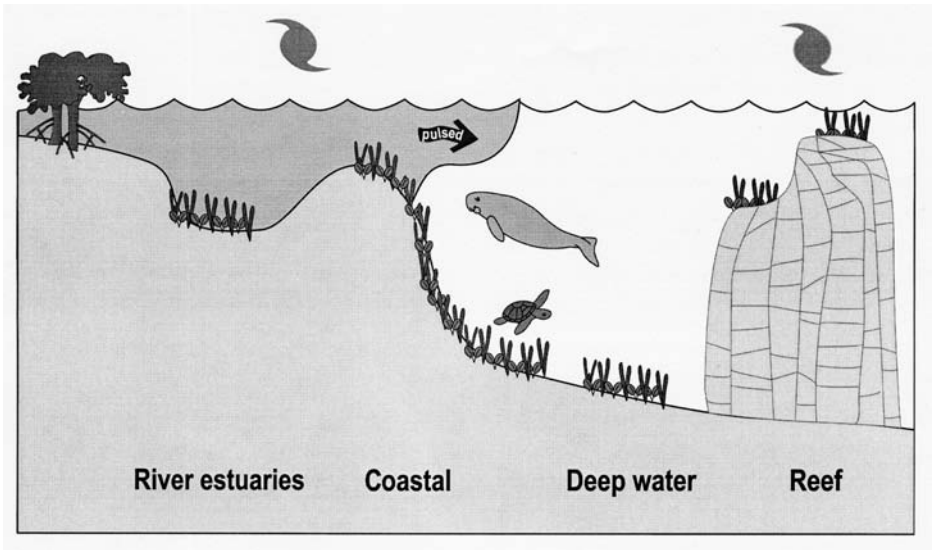


Figure 2. General conceptual model of seagrass habitats in north east Australia.

Table 1. Summary of seagrass habitats of north east Queensland.

Habitat	Limiting factor	Seagrass species	Features/Threats
River estuaries (Fig. 4)	Terrigenous runoff	<i>Cymodocea serrulata</i> <i>Enhalus acoroides</i> <i>Halophila ovalis</i> <i>Zostera capricorni</i>	Highly productive High density, low diversity Often anoxic Highly threatened
Coastal (Fig. 5)	Physical disturbance	<i>Halophila ovalis</i> <i>Halophila spinulosa</i> <i>Halodule uninervis</i> <i>Syringodium isoetifolium</i> <i>Cymodocea serrulata</i> <i>Zostera capricorni</i>	Very diverse Highly productive Imp. for fisheries Supports Dugongs Dynamic Threatened by development
Deep water (Fig. 6)	Low light	<i>Cymodocea serrulata</i> <i>Halophila decipiens</i> <i>Halophila ovalis</i> <i>Halophila spinulosa</i> <i>Halophila tricostata</i>	15–58+ m deep Monospecific High turnover Least known habitat Threats are trawling
Reef (Fig. 7)	Low nutrients	<i>Cymodocea rotunda</i> <i>Cymodocea serrulata</i> <i>Halodule uninervis</i> <i>Halophila ovalis</i> <i>Halophila spinulosa</i> <i>Syringodium isoetifolium</i> <i>Thalassia hemprichii</i> <i>Thalassodendron ciliatum</i>	Support high biodiversity Shallow unstable sediment Variable physical environment Little studied Least threatened

Inshore seagrass communities occur in river estuaries and often display an ephemeral life history due to variation in salinity and light availability. Coastal habitats can be intertidal or subtidal and are affected by rapid increases in runoff with heavy rain or cyclone events (Preen et al., 1995). In these habitats, a large and variable seed bank facilitates recovery following disturbance (Inglis, 2000). These inshore seagrass communities occur in varying quantity all along the coastline of north east Australia. In the

shallow and turbid waters of the Gulf of Carpentaria (Fig. 1), no seagrass meadows are present along the exposed eastern coast (Poiner et al., 1989; Department of Primary Industries Queensland, unpubl. data). Extensive coastal meadows are present on the western coastline in the Gulf of Carpentaria and in the north east, which are protected from the predominantly NW winds by the continental islands of the Torres Strait. On the Queensland east coast, where the prevalent winds are south easterly, much of the northern coast is protected by the Great Barrier Reef (Fig. 1). In the central Queensland coast, the GBR offers little protection and coastal seagrass meadows are restricted to sheltered bays, behind headlands and in the lee of islands. The highest biomass coastal seagrass meadows occur in the large north-facing bays such as Moreton Bay, Hervey Bay and Shoalwater Bay.

Increasing distance from the coast decreases the immediacy of impacts from pulsed terrigenous runoff and in these regions, clear water at depth results in the capacity for deep water seagrass growth (Fig. 2, Table 1). Deepwater seagrasses are found in Torres Strait, within the Great Barrier Reef Lagoon, extending south to the Capricorn Bunker group and Hervey Bay (Pitcher et al., 1992; Lee Long et al., 1996a). Throughout the Great Barrier Reef region approximately 40,000 km² of lagoon and inter-reef area has at least some seagrass, most of low density (<5% cover) (Coles et al., 2000). Deep water seagrasses are uncommon north of Princess Charlotte Bay, a remote area of low human population and little disturbance. This may result from a lack of propagules for colonisation in this region due to the divergence of the East Australian Current at Princess Charlotte Bay (Fig. 1). Much of this coast is also silica sand as well as low in rainfall and stream run-off, consequently it is possible that limited availability of nutrients restricts seagrass growth (Coles et al., 2000). High-density seagrasses, mostly on the inner shelf, occur on the central narrow-shelf section of the east coast which experiences a moderate tidal range and is adjacent to high-rainfall rainforest catchments. Where there are large tidal ranges, just to the south of Mackay, no major deepwater seagrass areas exist, but some habitats occur further south where tide ranges moderate again (Coles et al., 2000). Clearer waters allow the development of coral reef communities and seagrasses are an integral part of these habitats along the length of the Great Barrier Reef (Lee Long et al., 2000). Reef seagrass communities may be intertidal or subtidal depending upon depth and tide range.

Intertidal seagrasses represent a significant resource and these communities, both on the coast and on the reef, are subject to a particular set of conditions that influence their survival and productivity (Fig. 2, Table 1). These seagrass meadows must be capable of coping with exposure to intense light and heat at certain times of the day. Exposure is particularly severe during the dry season (July/August) with usually clear atmospheric conditions and mid-day spring low tides (Brouns, 1987; Stapel et al., 1997). Intertidal environments are also impacted by deposition and scouring, tidal fluctuations, desiccation, fluctuating temperature and variable salinity (Bridges et al., 1981).

The following discussion of the four conceptual models details the major features and processes within each habitat type. Reference is made throughout the text to the figure legend (Fig. 3), so icons for processes can be clearly identified. Icons used are constant throughout the models, however differences in the specifics of those processes within a particular habitat are detailed in the text and indicated with superscript numbers. Full referencing is made where possible in the text to justify the processes and features summarised in the models.

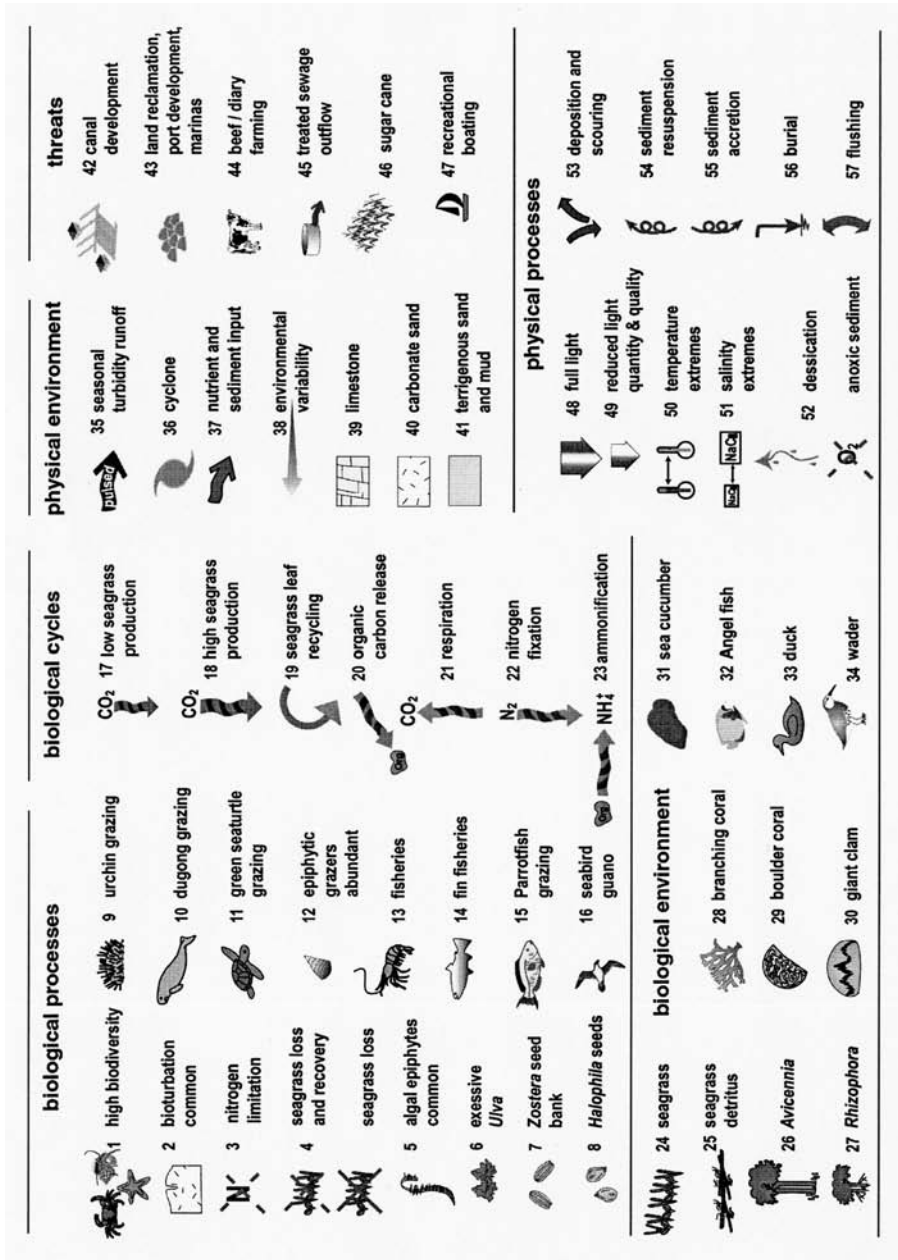


Figure 3. Legend for icons used in seagrass habitat models (NB: superscript numbers in text refer to processes represented by icons).

RIVER ESTUARIES: TERRIGENOUS RUNOFF (Figs. 3,4)

DESCRIPTION.—River estuary habitats can be subtidal or intertidal, containing many seagrass species, and are often highly productive. These seagrass meadows, influenced by fresh water, often have high shoot densities but low species diversity (Lee Long et al., 1993). *Zostera capricorni* is common in this habitat south of Cairns, often growing in large monospecific meadows (Coles et al., 1993). Rivers estuaries are characterized by fine sediments and are prone to high sedimentation and anoxic conditions, often damaging to seagrass. River estuary habitats have higher loadings of micro and macro-algal epiphytes than other Queensland seagrass habitats⁵.

PRIMARY CONTROL.—The dominant feature of river estuary habitats is terrigenous runoff from summer (December/January) rains. Increased river flow results in higher sediment loads which combine with reduced atmospheric light to create potential light limitation for seagrass⁴⁹ (McKenzie, 1994). Due to differences in catchment size and annual rainfall, some estuarine systems periodically close while others have year round flow. Associated salinity fluctuations and scouring make river and inlet habitats a seasonally extreme environment for seagrass growth³⁸.

PROCESSES.—Catchments to river estuary habitats support a large range of agricultural land use, predominantly sugar cane, beef cattle and dairy farming, as well as extensive forestry. These land use practices result in increased nutrient and sediment inputs through fertiliser⁴⁶, manure⁴⁴ and increased erosion³⁷. Discharge from sewage treatment plants and urban runoff are also potential nutrient sources^{45,42}; excessive growth of *Ulva* sp. can provide a strong indication of high nutrient loadings⁶. Ocean flushing and tidal exchange moderate both nutrient and sediment input to these habitats⁵⁷. Rates of water exchange are often impacted by canal and port developments⁴², which also displace mangrove habitat^{26,27} and increases rates of sediment deposition and scouring⁵³ (Neil, 1998).

Intertidal seagrasses show variable resilience to light reduction resulting from pulsed turbidity events during flood conditions³⁵ (Longstaff and Dennison, 1999; Longstaff et al., 1999). *Halophila ovalis* died after 38 days at <5% ambient light, however *Halodule pinifolia* showed high resilience and was estimated to have survived up to 100 days of severe light deprivation (Longstaff and Dennison, 1999). Reductions in water quality (light penetration) resulting from anthropogenic influences resulted in measurable reductions in the maximum depth distribution of *Z. capricorni* in regions influenced by rivers in Moreton Bay (Abal and Dennison, 1996).

Differences in life history strategy of different seagrass species, results in varying species assemblages in different river estuary systems. *Enhalus acoroides* is persistent and relatively slow growing¹⁷ and can survive periodic burial with shifting sediment⁵³ (Bridges et al., 1981). However, *E. acoroides* is susceptible to disturbance and it is predicted that removal of a 1m² area from a meadow would take more than 10 years for full recovery (Rollon et al., 1998). In contrast, *Cymodocea serrulata*, *Z. capricorni*, *Halodule uninervis* and *H. ovalis* are more ephemeral (Birch and Birch, 1984). *Halodule uninervis* and *Halophila ovalis* are considered pioneer species growing rapidly¹⁸ and surviving well in unstable or depositional environments (Bridges et al., 1981; Birch and Birch, 1984). *Cymodocea serrulata* grows in deeper sediments, and has been linked to increased sediment accretion⁵⁵ (Birch and Birch, 1984). *Z. capricorni* meadows recolonise through vegetative growth and can therefore survive small scale (<1 m²) disturbance (Rasheed, 1999).

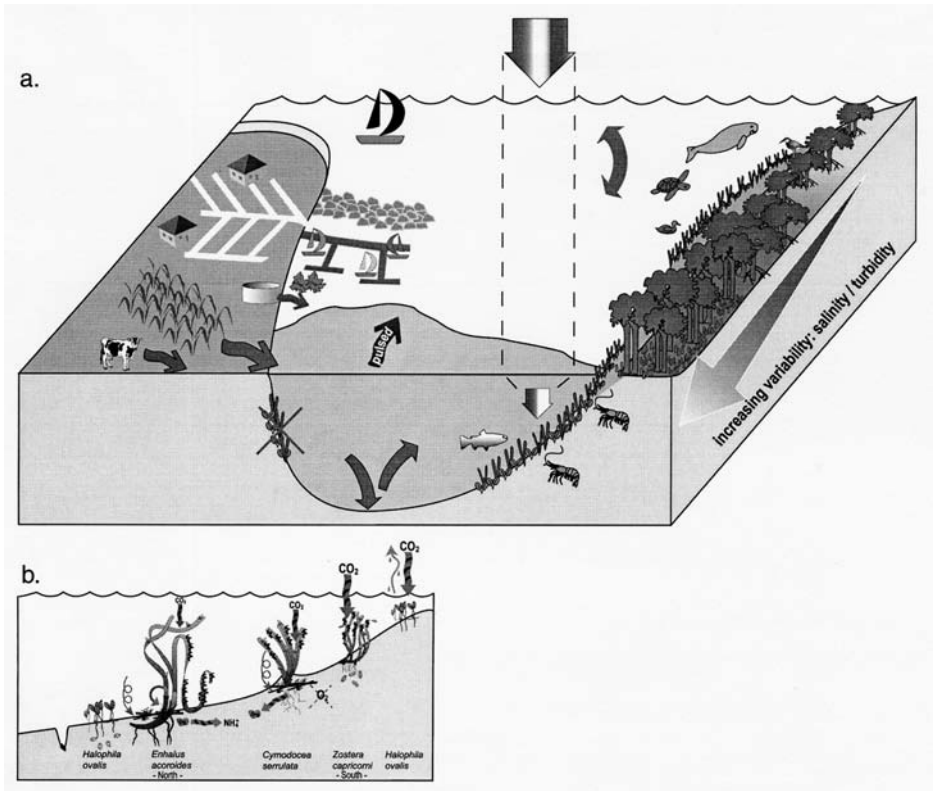


Figure 4. Model of River estuary habitat – major control terrigenous runoff: a.) general habitat processes; b.) seagrass meadow processes.

However, understanding of seagrass recovery from large scale (e.g., >1 km²) disturbance is very limited.

As a result of catchment runoff and high nutrient loading, macro-algal epiphytes are abundant on seagrass leaves in river estuary habitats. *E. acoroides* often has heavy epiphyte loads and measured high leaf turnover rates in this species are considered to be a mechanism to avoid epiphyte shading (Johnstone, 1979; Brouns and Heijs, 1986). The relatively high nutrient levels in these habitats support epiphytes, and excess growth will reduce seagrass production rates and may result in seagrass decline (Shepherd et al., 1989). *E. acoroides* occurs in river estuary habitats off northern Queensland, in the Gulf of Carpentaria (Poiner et al., 1987) and Torres Strait (Bridges et al., 1981).

Fine grain sediments and high organic loading causes anoxia in river estuary sediments, representing a specific physiological stress to the seagrasses in this habitat. *H. ovalis* shows a gradient in oxygen release from intact roots, with maximum oxygenation at the growing root tip (Connell et al., 1999). Oxygen release from roots is commonly seen in wetland macrophytes and is considered as an adaptation for survival in anaerobic sediments, such as those in river estuary habitats (Connell et al., 1999). *Z. capricorni* is well adapted to these conditions as seed germination is higher under anaerobic conditions, allowing meadow maintenance in this dynamic habitat (Brenchley and Probert, 1998). *Z. capricorni* flowers for up to eight months a year, however seed coats are soft

and seeds germinate rapidly, without forming a residual seed bank (Conacher et al., 1994; Inglis and Smith, 1998).

These habitats are important for the commercially caught shrimp species, *Penaeus semisulcatus* and *P. esculentus*, which use seagrass meadows as a nursery habitat^{13,14} (Haywood et al., 1995). Many cases document loss of fisheries associated with seagrass declines (Bell and Pollard, 1989). However, in some cases, reduction in seagrass cover has resulted in maintained commercial value, but with a change from herbivorous fish (*Metapenaeus bennettiae*) to shrimp species (*P. plebejus*) (Halliday, 1995).

THREATS/ISSUES.—River estuaries are the most threatened seagrass communities in north east Australia. They are particularly threatened by anthropogenic nutrient inputs from agriculture, sewage and urban runoff as well as disturbance due to marina and port developments and dredging (Coles et al., 1989; Lee Long et al., 1996b). As provincial centres develop along the Queensland coast, river estuaries are the most severely affected and need careful management to maintain these seagrass habitats and the fisheries they support (Coles et al., 1993).

COASTAL: PHYSICAL DISTURBANCE (Figs. 3,5)

DESCRIPTION.—Coastal habitats are both subtidal and intertidal and support the most diverse seagrass assemblage of all habitat types (14+ species) (Lee Long et al., 2000). These seagrass meadows are also highly productive¹⁸, support a high biodiversity¹ and provide important nursery grounds for commercial fisheries^{14,15} (Loneragan et al., 1994).

PRIMARY CONTROL.—Physical disturbance due to storm and cyclone related waves and swell, associated sediment movement and macro-grazers primarily control seagrass growing in coastal habitats. Episodic events such as cyclones or periods of storms can have severe impacts at local scales, making this a dynamic and variable habitat.

PROCESSES.—Sediment movement due to prevalent wave exposure creates an unstable environment where it is difficult for seagrass seedlings to establish or persist. Physical removal of seagrass by periodic cyclones has resulted in removal of habitat, which may take many years to regrow (Preen et al., 1995). Succession or recolonization after extreme loss has been suggested to be directional, modified by small scale perturbations resulting in patchiness in seagrass distributions (Birch and Birch, 1984). The end result of this successional process, however, varies with geographic location. Along the temperate (southern) Australian coastline, the dominant *Posidonia* spp. are the typical 'climax' species, however in northern Australian waters, multi species complexes are considered to be the climax community (Young and Kirkman, 1975).

Grazing by macroherbivores (dugong, green sea turtle), has a significant impact on the structure of seagrass communities in northern Australia^{10,11} (Preen, 1995; Aragonés and Marsh, 2000). Coastal surveys indicate highest densities of dugongs on inshore seagrass beds and areas <5 m deep (Marsh and Saalfeld, 1989; 1990). Grazing by dugongs has been found to prevent expansion of *Z. capricorni* in favor of rapidly growing, opportunistic species of *Halophila*, a process analogous to cultivation grazing (Preen, 1995). The green sea turtle (*Chelonia mydas*) is also abundant in coastal habitats and grazes a wide range of seagrass species (Lanyon et al., 1989). Dugongs graze on whole plants, digging up roots and rhizomes whereas turtles graze on leaf material only. Intensity of grazing also varies: dugongs will sometimes feed in large herds, while turtles are usually solitary

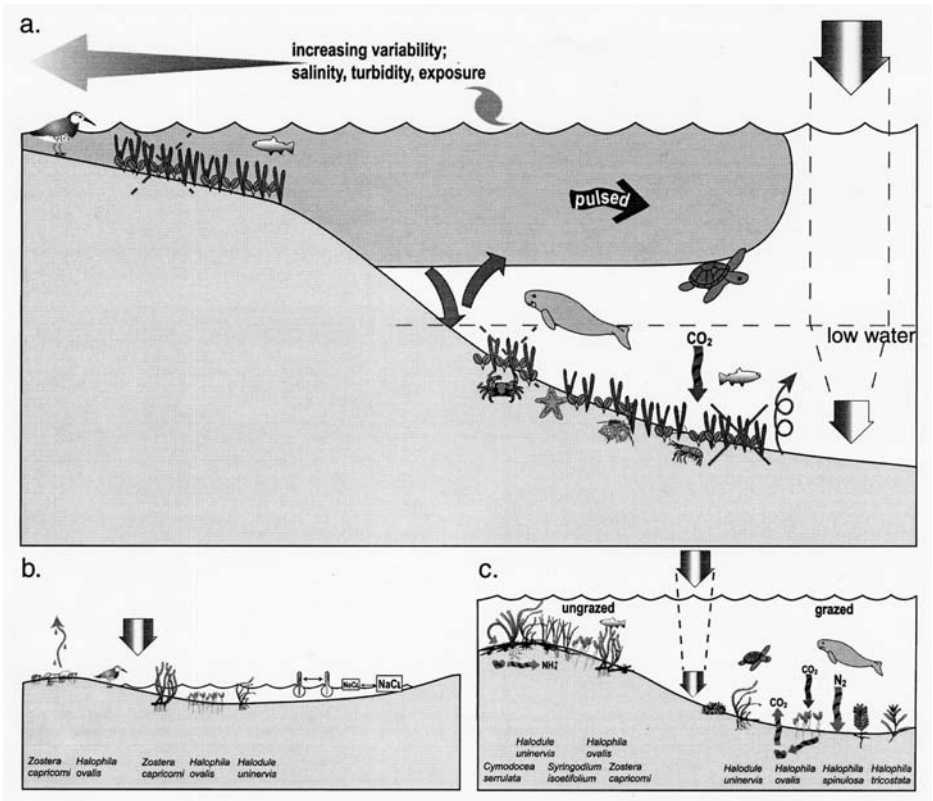


Figure 5. Model of Coastal habitat – major control physical disturbance: a.) general habitat processes; b.) intertidal seagrass processes; c.) subtidal seagrass processes, separating areas grazed and ungrazed by macro-grazers.

grazers. While macro-grazers have a large influence on coastal seagrass meadows, they depend heavily on the maintenance of meadows. It has been estimated that one dugong requires from 0.4 to 3.5 ha of seagrass per year (Heinsohn et al., 1977). Large declines of seagrass resulting from two large flood events in Hervey Bay were correlated with large scale dugong relocation and mortality (Preen and Marsh, 1995)⁴.

Seagrass meadows in coastal environments have a wide range of nutrient cycling processes, differences occur both between species and with grazing. Ungrazed meadows tend towards tight detrital nutrient cycling¹⁹ whereas grazed meadows continually rely on replenishment of external nutrient sources. Bacterial nitrogen fixation rates amongst seagrass roots and rhizomes are comparable to rates determined for terrestrial crops and legumes²² (Moriarty and O'Donohue, 1993). Rich bacterial floras are reported from the rhizospheres of the tropical seagrasses²², *Thalassia hemprichii*, *Cymodocea serrulata*, *C. rotunda*, *E. acoroides*, *H. uninervis* and *Syringodium isoetifolium* (Kuo, 1993). These microbial communities are supported by dissolved organic carbon released from the seagrass roots and rhizomes, up to 18% of the carbon fixed by *Z. capricorni* has been measured leaking into sediments surrounding the rhizosphere²⁰ (Hansen et al., 2000). These rates are calculated to provide from a third to a half of the nitrogen required to support summer growth of *Z. capricorni* (O'Donohue et al., 1991). Dugong grazing trails disturb the surface sediments of the seagrass meadow, enhancing rates of nitrogen fixation in these meadows (Perry and Dennison, 1999).

Nutrient limitation in coastal environments has been found to differ in different seagrass species. In Moreton Bay, *Halodule uninervis* and *Heterozostera tasmanica* showed exclusive N limitation, *Z. capricorni* displayed balanced N and P limitation and *Cymodocea serrulata* indicated neither N or P limitation (Udy and Dennison, 1997). These results may also be influenced by light intensity, as under high light culture conditions *Z. capricorni* does display indications of N limitation (Abal et al., 1994).

THREATS/ISSUES.—Coastal habitats are the most understood seagrass habitat in tropical Australia. However, they are threatened by extensive coastal development resulting from increasing population pressure and heavy industry as well as the impacts of runoff from impacted catchments, particularly to large embayments such as Moreton Bay and Hervey Bay.

DEEP WATER: LOW LIGHT (Figs. 3,6)

DESCRIPTION.—Deep water seagrasses occur at depths of 15 to 58m. Within these regions, they are restricted to the mid and outer shelf of the Great Barrier Reef where high water clarity allows sufficient light penetration for survival (Lee Long et al., 1993). Deep water seagrass areas are extensive and dominated by species of *Halophila* (Lee Long et al., 1993, 1996a). Large monospecific meadows of seagrass occur in this habitat (e.g., *Halophila decipiens*), this contrasts coastal and reef habitats where the seagrass meadows are generally diverse and mixed (Coles et al., 1987).

PRIMARY CONTROL.—Low light availability resulting from absorption and refraction through the water column is of primary importance to deep water seagrass meadows. Not only is the total amount of light greatly reduced at depth, but also the spectral composition varies⁴⁹, only blue wavelengths reaching depths greater than 30 m. Distribution of seagrass meadows in deep water habitats is particularly affected by light reduction from pulse turbidity events³⁵ (Preen et al., 1995; Longstaff and Dennison, 1999).

PROCESSES.—*Halophila* spp. display morphological, physiological and life history adaptations to survive low light conditions. *H. decipiens* has an open canopy structure with relatively little below ground biomass and high leaf turnover and rhizome elongation rates (Josselyn et al., 1986; Kenworthy et al., 1989). The production of fruits and seeds at the base of the petiole is also beneficial for surviving in fluctuating light environments (Kenworthy, 2000). *Halophila* species are often annual, have rapid growth rates and are considered opportunistic species (Birch and Birch, 1984). An important characteristic of this strategy is high seed production: rates of 70 000 seeds m⁻² yr⁻¹ have been estimated from field observations of *H. tricostata*⁸ (Kuo et al., 1993), and *H. decipiens* also has high reported seed sets of 176 880 seeds m⁻² (Kuo and Kirkman, 1995). The distribution of deep water seagrasses, while mainly influenced by water clarity, is also modified by propagule dispersal, nutrient supply, and current stress.

The ecological role of deep water seagrasses is little understood. Some deepwater meadows of *H. ovalis* and *H. spinulosa* are important dugong feeding habitat, as feeding trails have been recorded to 33 m (Lee Long et al., 1996a), and adults have been observed in water up to 37 m deep¹⁰ (Marsh and Saalfeld, 1989; Anderson, 1994). The impact of dugong grazing in this habitat is unknown. The abundance of commercial fish and crustacean species per unit area is less in deep water habitats than in coastal inter-tidal and

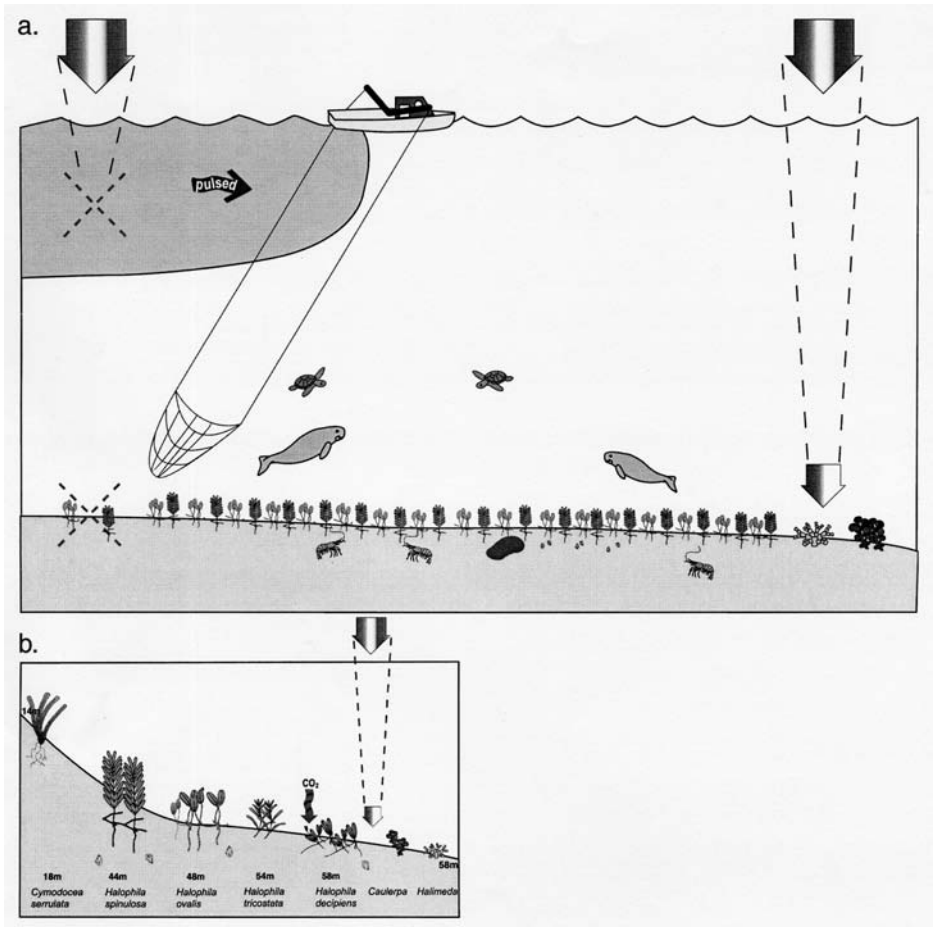


Figure 6. Model of Deep water habitat – major control low light: a.) general habitat processes; b.) detail of seagrass species and maximum depth limits.

shallow sub-tidal meadows, however the large area of this habitat suggests it is still important (Derbyshire et al., 1995).

THREATS/ISSUES.—Deep water systems are the least understood seagrass community. This habitat is impacted by coastal runoff and to some extent by prawn trawling (Coles et al., 1987; 1989), the scale of these impacts is largely unknown.

REEF: LOW NUTRIENTS (Figs. 3,7)

DESCRIPTION.—Seagrass reef communities support a high biodiversity¹ and can be highly productive. Shallow unstable sediment⁵³, fluctuating temperature⁵⁰ and variable salinity⁵¹ in intertidal regions characterise these habitats.

PRIMARY CONTROL.—Low nutrient availability characterises reef habitats (Stapel et al., 1997).

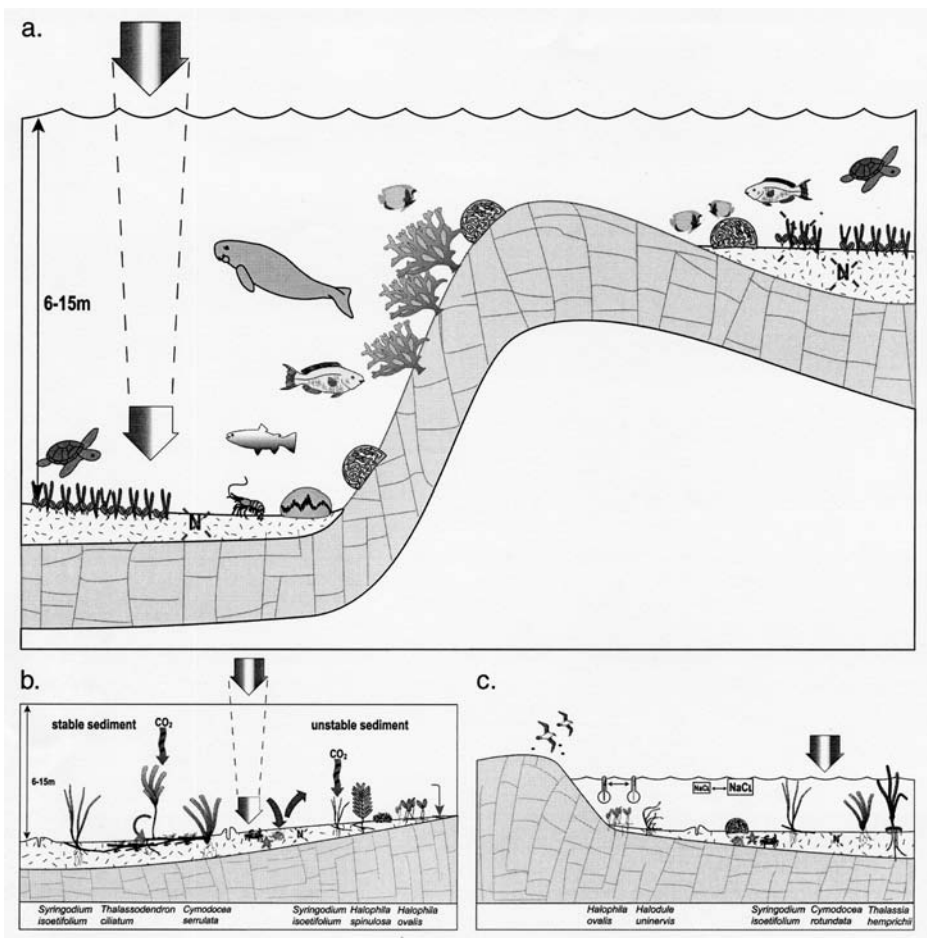


Figure 7. Model of Reef habitat – major control low nutrients: a.) general habitat model; b.) subtidal seagrass processes, separating areas of stable and unstable sediment; c.) intertidal seagrass processes.

PROCESSES.—Nutrient concentrations are generally low³ in reef habitats, however intermittent sources of nutrients are added by seasonal runoff reaching the reef (Gabric and Bell, 1993). In some localized areas, particularly coral cays, seabirds can add high amounts of phosphorus to reef environments¹⁶. In north east Australia, reef carbonate sediments are N limited³ (Udy et al., 1999), however carbonate sediments vary in the primary limiting nutrient at different geographic locations around the world (Short et al., 1990; Fourqurean et al., 1992; Erftemeijer and Middelburg, 1993). Tight nutrient recycling strategies of *T. hemprichii*¹⁹, by location of N in rhizomes when leaves are shed due to desiccation stress, aids in survival in the nutrient poor reef habitat (Stapel et al., 1997).

Reef seagrass communities have unique faunal interactions¹⁵. The Indo-Pacific has less fish and urchin grazing than the Caribbean, although low rates of grazing do still occur on many broad bladed species, such as *Enhalus* (Ogden and Ogden, 1982). Urchins have been reported to have periodic and large influences upon seagrass meadows⁹ (Rose et al., 1999). In the Torres Strait, reduction in seagrass abundance correlated with an increase in

abundance of the urchin *Prionocidaris* sp. (Long and Skews, 1996). Bioturbation by shrimps and polychaete worms is so prevalent in some reef environments as to prevent seagrass growth² (Ogden and Ogden, 1982). A region of bare sand often separates coral heads from seagrass beds, previous research suggests this is maintained by parrotfish and surgeonfish associated with the coral¹⁵ (Randall, 1965).

THREATS/ISSUES.—Seagrass reef habitats are the least threatened seagrass community. However they are little studied and therefore assessing change in this habitat is extremely difficult.

CONCLUSIONS

The seagrass systems of north east Australia can be divided into river estuaries, coastal, deep water and reef habitats. All habitats are influenced to some degree by pulses of sediment laden, nutrient rich river flows, resulting from high volume summer rainfall. Cyclones and severe storms or wind waves as well as macrograzers (dugongs and turtles) influence all habitats to varying degrees. The result is a series of dynamic, spatially and temporally variable seagrass meadows.

Defined habitats contain a large range of life history strategies (Walker et al., 1999), which provides some insight into the dynamic but variable physical nature of north east Australia seagrass habitats. *E. acoroides* is a slow turnover, persistent species with low resistance to perturbation (Walker et al., 1999), suggesting that there are some areas in river estuary habitats that are quite stable over time. *Cymodocea* and *Zostera* are seen as intermediate genera that can survive a moderate level of disturbance, while *Halophila* and *Halodule* are described as ephemeral species with rapid turnover and high seed set, well adapted to high disturbance and high rates of grazing (Walker et al., 1999). Therefore the species present in the different habitats reflect the observed physical and biological impacts summarized in the models, suggesting that reef, deep water and coastal environments are particularly variable and dynamic, while river estuary habitats have stable areas but are extremely harsh.

All identified habitats have high ecological and/or economic value, whether supporting commercial fisheries (all) or high biodiversity (coastal and reef). River estuary and coastal habitats are considered to be the most threatened, due to extensive coastal development, however the limited knowledge of reef and deep water seagrass habitats suggests that impacts to these habitats are extremely difficult to determine. The conceptual models presented in this paper help to identify gaps in our knowledge and allow for improved strategies to manage a series of diverse seagrass habitats.

ACKNOWLEDGMENTS

This paper resulted from a workshop held in Cairns in July 2000, funded by CRC for the Great Barrier Reef World Heritage Area and with the support of: The Marine Plant Ecology Group of the Queensland Fisheries Service, Department of Primary Industries, Qld; The School of Tropical Environment Studies and Geography, James Cook University; The Marine Botany Group of The University of Queensland and The Great Barrier Reef Marine Park Authority. The authors thank all participants: S. Campbell, A. Calladine, R. Coles, T. Done, D. Haynes, J. Kunzelman, D. Kwan, I. Lawler, J. Mellors, P. Ralph, M. Rasheed, A. Roelofs, C. Roder and D. Wachenfeld. J. Kenworthy, M. Van Keulen and two anonymous reviewers provided valuable comments on the manuscript. Thanks to D. Kleine for production of graphics.

LITERATURE CITED

- Abal, E. G. and W. C. Dennison. 1996. Seagrass depth range and water quality in Southern Moreton Bay, Queensland, Australia. Mar. Freshw. Res. 47: 763–771.
- _____, Loneragan, N., Bowen, P., Perry, C. J., Udy, J. W. and Dennison, W. C. 1994. Physiological and morphological responses of the seagrass *Zostera capricorni* Aschers. to light intensity. J. Exp. Mar. Biol. Ecol. 178: 113–129.
- Anderson, P. K. 1994. Dugong distribution, the seagrass *Halophila spinulosa*, and thermal environment in winter in deeper waters of eastern Shark Bay, Western Australia. Wildlif. Res. 21: 381–388.
- Aragones, L. and H. Marsh. 2000. Impact of dugong grazing and turtle cropping on tropical seagrass communities. Pac. Cons. Biol. 5: 277–288.
- Bell, J. D. and D. A. Pollard. 1989. Ecology of fish assemblages and fisheries associated with seagrasses. Pages 565–609 in A. W. D. Larkum, A. J. McComb and S. A. Shepherd, eds. Biology of seagrasses: a treatise on the biology of seagrasses with special reference to the Australian region. Elsevier, Amsterdam.
- Birch, W. R. and M. Birch. 1984. Succession and pattern of tropical intertidal seagrasses in Cockle Bay, Queensland, Australia: a decade of observations. Aquat. Bot. 19: 343–367.
- Brenchley, J. L. and R. J. Probert. 1998. Seed germination responses to some environmental factors in the seagrass *Zostera capricorni* from eastern Australia. Aquat. Bot. 62: 177–188.
- Bridges, K. W., R. C. Phillips and P. C. Young. 1981. Patterns of some seagrass distribution in the Torres Strait, Queensland. Aust. J. Mar. Freshw. Res. 33: 273–283.
- Brouns, J. W. M. 1987. Aspects of production and biomass of four seagrass species (Cymodoceidae) from Papua New Guinea. Aquat. Bot. 27: 333–362.
- _____, and F. M. L. Heijs. 1986. Production and biomass of the seagrass *Enhalus acoroides* (L.f.) Royle and its epiphytes. Aquat. Bot. 25: 21–45.
- Coles, R. G., Lee Long, W. J., McKenzie, L. J., Roelofs, A. J. and De'ath, G. 2000. Stratification of seagrasses in the Great Barrier Reef World Heritage Area, Northeastern Australia, and the implications for management. Biol. Mar. Medit. 7: 345–348.
- Coles, R. G., Lee Long, W. J., Squire, B. A., Squire, L. C. and Bibby, J. M. 1987. Distribution of seagrasses and associated juvenile commercial penaeid prawns in northeastern Queensland waters (Australia). Aust. J. Mar. Freshw. Res. 38: 103–120.
- Coles, R. G., Lee Long, W. J., Watson, R. A. and Derbyshire, K. J. 1993. Distribution of seagrasses, and their fish and penaeid prawn communities, in Cairns Harbour, a tropical estuary, northern Queensland, Australia. Aust. J. Mar. Freshw. Res. 44: 193–210.
- Coles, R. G., I. R. Poiner and H. Kirkman. 1989. Regional studies - seagrasses of north-eastern Australia. Pages 261–278 in A. W. D. Larkum, A. J. McComb and S. A. Shepherd, eds. Biology of seagrasses: a treatise on the biology of seagrasses with special reference to the Australian region. Elsevier, Amsterdam.
- Conacher, C. A., I. R. Poiner and M. J. O'Donohue. 1994. Morphology, flowering and seed production of *Zostera capricorni* Aschers, in subtropical Australia. Aquat. Bot. 49: 33–46.
- Connell, E. L., T. D. Colmer and D. I. Walker. 1999. Radial oxygen loss from intact roots of *Halophila ovalis* as a function of distance behind the root tip and shoot illumination. Aquat. Bot. 63: 219–228.
- Derbyshire, K. J., S. R. Willoughby, A. L. McColl and D. M. Hocroft. 1995. Small prawn and recruitment study - final report to the Fisheries Research and Development Corporation and the Queensland Fisheries Management Authority. Cairns: Queensland Department of Primary Industries.
- Duarte, C. M. 1999. Seagrass ecology at the turn of the millennium: Challenges for the new century. Aquat. Bot. 65: 7–20.

- Erfemeijer, P. L. A. and J. J. Middelburg. 1993. Sediment-nutrient interactions in tropical seagrass beds: a comparison between a terrigenous and a carbonate sedimentary environment in South Sulawesi (Indonesia). Mar. Ecol. Prog. Ser. 102: 187–198.
- Fourqurean, J. W., J. C. Zieman and G. V. N. Powell. 1992. Relationship between porewater nutrients and seagrass in a subtropical carbonate environment. Mar. Biol. 114: 57–65.
- Gabric, A. J. and P. R. F. Bell. 1993. Review of the effects of non-point nutrient loading on coastal ecosystems. Aust. J. Mar. Freshw. Res. 44: 261–283
- Halliday, I. A. 1995. Influence of natural fluctuations in seagrass cover on commercial prawn nursery grounds in a subtropical estuary. Mar. Freshw. Res. 46: 1121–1126.
- Hamilton, L. J. 1994. Turbidity in the northern Great Barrier Reef Lagoon in the wet season, March 1989. Aus. J. Mar. Freshw. Res. 45: 585–615.
- Hansen, J. W., J. W. Udy, C. J. Perry, W. C. Dennison and B. A. Lomstein. 2000. Effect of the seagrass *Zostera capricorni* on sediment microbial processes. Mar. Ecol. Prog. Ser. 199: 83–96.
- Haywood, M. D. E., D. J. Vance and N. R. Loneragan. 1995. Seagrass and algal beds as nursery habitats for tiger prawns (*Penaeus semisulcatus* and *P. esculentus*) in a tropical Australian estuary. Mar. Biol. 122: 213–223.
- Heinsohn, G. E., J. H. M. Wake and A. V. Spain. 1977. The dugong (*Dugong dugon*) in the seagrass system. Aquaculture 12: 235–248.
- Hillman, K., D. I. Walker, A. W. D. Larkum and A. J. McComb. 1989. Productivity and nutrient limitation. Pages 635–685 in A. W. D. Larkum, A. J. McComb and S. A. Shepherd, eds. *Biology of seagrasses: a treatise on the biology of seagrasses with special reference to the Australian region.* Elsevier, Amsterdam.
- Hopley, D. 1986. The Queensland coastline: attributes and issues. Pages 73–94 in J. H. Holmes, ed. *Queensland: A geographical interpretation.* Booralong Publications, Brisbane.
- Inglis, G. J. 2000. Variation in the recruitment behaviour of seagrass seeds: implications for population dynamics and resource management. Pac. Cons. Biol. 5: 251–259.
- _____ and M. P. L. Smith. 1998. Synchronous flowering of estuarine seagrass meadows. Aquat. Bot. 60: 37–48.
- Johnstone, I. M. 1979. Papua New Guinea seagrasses and aspects of the biology and growth of *Enhalus acoroides* (L.f.) Royle. Aquat. Bot. 7: 197–208.
- Josselyn, M., M. Fonseca, T. Niesen and R. Larson. 1986. Biomass, production and decomposition of a deep water seagrass, *Halophila decipiens* Ostenf. Aquat. Bot. 25: 47–61.
- Kenworthy, W. J. 2000. The role of sexual reproduction in maintaining populations of *Halophila decipiens*: implications for the biodiversity and conservation of tropical seagrass ecosystems. Pac. Cons. Biol. 5: 260–268.
- _____, Currin, C. A., Fonseca, M. S. and Smith, G. 1989. Production, decomposition and heterotrophic utilization of the seagrass *Halophila decipiens* in a submarine canyon. Mar. Ecol. Prog. Ser. 51: 277–290.
- Kuo, J. 1993. Root anatomy and rhizosphere ultrastructure in tropical seagrasses. Aust. J. Mar. Freshw. Res. 44: 75–84.
- _____ and Kirkman, H. 1995. *Halophila decipiens* Ostenfeld in estuaries of southwestern Australia. Aquat. Bot. 51: 335–340.
- _____, W. Lee Long and R. G. Coles. 1993. Occurrence and fruit and seed biology of *Halophila tricostata* Greenway (Hydrocharitaceae). Aust. J. Mar. Freshw. Res. 44: 43–57.
- _____ and A. J. McComb. 1989. Seagrass taxonomy, structure and development. Page 6–69 in A. W. D. Larkum, A. J. McComb and S. A. Shepherd, eds. *Biology of seagrasses: a treatise on the biology of seagrasses with special reference to the Australian region.* Elsevier, Amsterdam.
- Lanyon, J. M., C. J. Limpus and H. Marsh. 1989. Dugong and turtles: grazers in the seagrass system. Pages 610–634 in A. W. D. Larkum, A. J. McComb and S. A. Shepherd, eds. *Biology of seagrasses: a treatise on the biology of seagrasses with special reference to the Australian region.* Elsevier, Amsterdam.

- _____ and H. Marsh. 1995. Temporal changes in the abundance of some tropical intertidal seagrasses in North Queensland. Aquat. Bot. 49: 217–237.
- Lee Long, W. J., R. G. Coles and K. J. McKenzie. 1996a. Deepwater seagrasses in Northeastern Australia - How deep, how meaningful. Pages 41–50 in J. Kuo, R. C. Phillips, D. I. Walker and H. Kirkman, eds. *Seagrass Biology: Proc. International workshop, Rottneest Island, Western Australia*. The University of Western Australia, Nedlands.
- _____, _____ and L. J. McKenzie. 2000. Issues for seagrass conservation management in Queensland. *Pac. Cons. Biol.* 5: 321–328.
- _____, L. J. McKenzie, M. A. Rasheed and R. C. Coles. 1996b. Monitoring seagrasses in tropical ports and harbours. In *Seagrass biology: proceedings of an international workshop*. Faculty of Science, University of Western Australia, Perth. 385 p.
- _____, _____, A. J. Roelofs, L. J. Makey, R. G. Coles and C. A. Roder. 1998. Baseline survey of Hinchinbrook region seagrasses - October (spring) 1996. Great Barrier Reef Marine Park Authority, Townsville. 26 p.
- _____, J. E. Mellors and R. G. Coles. 1993. Seagrasses between Cape York and Hervey Bay, Queensland, Australia. Aust. J. Mar. Freshw. Res. 44: 19–31.
- Loneragan, N. R., R. A. Kenyon, M. D. E. Haywood and D. J. Staples. 1994. Population dynamics of juvenile tiger prawns (*Penaeus esculentus* and *P. semisulcatus*) in seagrass habitats of the western gulf of Carpentaria, Australia. Mar. Biol. 119: 133–143.
- Long, B. G. and T. D. Skews. 1996. On the trail of seagrass dieback in Torres Strait. *Professional Fisherman*. Feb. 15–18.
- Longstaff, B. J. and W. C. Dennison. 1999. Seagrass survival during pulsed turbidity events: The effects of light deprivation on the seagrasses *Halodule pinifolia* and *Halophila ovalis*. *Aquat. Bot.* 1999: 65: 105–121.
- _____, N. R. J. Loneragan, M. J. O'Donohue and W. C. Dennison. 1999. Effects of light deprivation on the survival and recovery of the seagrass *Halophila ovalis* (R.Br.) Hook. *J. Exp. Mar. Biol. Ecol.* 234: 1–27.
- Marsh, H. and W. K. Saalfeld. 1989. Distribution and abundance of dugongs in the northern Great Barrier Reef Marine Park (Australia). *Aust. Wildl. Res.* 16: 429–440.
- _____ and _____. 1990. The distribution and abundance of dugongs in the Great Barrier Reef Marine Park south of Cape Bedford (Queensland, Australia). *Aust. Wildl. Res.* 17: 511–524.
- McKenzie, L. J. 1994. Seasonal changes in biomass and shoot characteristics of a *Zostera capricorni* Aschers. dominant meadow in Cairns Harbour, northern Queensland. Aust. J. Mar. Freshw. Res. 45: 1337–1352.
- Moriarty, D. J. W. and M. J. O'Donohue. 1993. Nitrogen fixation in seagrass communities during summer in the Gulf of Carpentaria, Australia. Australian J. Mar. Freshw. Res. 44: 117–125.
- Mukai, H. 1993. Biogeography of the tropical seagrasses in the western Pacific. *Australian J. Mar. Freshw. Res.* 44: 1–17.
- Neil, D. T. 1998. Moreton Bay and its catchment: seascape and landscape, development and degradation. Pages 3–54 in I. R. Tibbets, N. J. Hall and W. C. Dennison, eds. *Moreton Bay and catchment*. School of Marine Science, University of Queensland, Brisbane.
- O'Donohue, M. J., D. J. Moriarty and I. C. Mac Rae. 1991. Nitrogen fixation in sediments and the rhizosphere of the seagrass *Zostera capricorni*. Microb. Ecol. 22: 53–64.
- Ogden, J. C. and N. B. Ogden. 1982. A preliminary study of two representative seagrass communities in Palau, Western Caroline Islands (Micronesia). *Aquat. Bot.* 12: 229–244.
- Perry, C. J. and W. C. Dennison. 1999. Microbial nutrient cycling in seagrass sediments. *AGSO J. Aust. Geol. Geophys.* 17: 227–231.
- Pitcher, C. R., T. D. Skewes, D. M. Dennis and J. H. Prescott. 1992. Distribution of seagrasses, substratum types and epibenthic macrobiota in Torres Strait, with notes on Pearl Oyster abundance. *Aust. J. Mar. Freshw. Res.* 43: 409–419.

- Poiner, I. R., D. J. Staples and R. Kenyon. 1987. Seagrass communities of the Gulf of Carpentaria, Australia. *Aust. J. Mar. Freshw. Res.* 38: 121–132.
- _____, D. I. Walker and R. G. Coles. 1989. Regional studies - seagrasses of tropical Australia. Pages 279–303 in A. W. D. Larkum, A. J. McComb and S. A. Shepherd, eds. *Biology of seagrasses: a treatise on the biology of seagrasses with special reference to the Australian region*. Elsevier, Amsterdam.
- Preen, A. R. 1995. Impacts of dugong foraging on seagrass habitats: Observational and experimental evidence for cultivation grazing. *Mar. Ecol. Prog. Ser.* 124: 201–213.
- _____, W. J. L. Long and R. G. Coles. 1995. Flood and cyclone related loss, and partial recovery, of more than 1000 km² of seagrass in Hervey Bay, Queensland, Australia. *Aquat. Bot.* 52: 3–17.
- _____, and Marsh, H. 1995. Response of dugongs to large-scale loss of seagrass from Hervey Bay, Queensland, Australia. *Wildlif. Res.* 22: 507–519.
- Randall, J. E. 1965. Grazing effects on seagrass by herbivorous reef fishes in the West Indies. *Ecol.* 46: 255–260.
- Rasheed, M. A. 1999. Recovery of experimentally created gaps within a tropical *Zostera capricorni* (Aschers.) seagrass meadow, Queensland Australia. *J. Exp. Mar. Biol. Ecol.* 235: 183–200.
- Rollon, R. N., E. D. D. Van Steveninck, W. Van Vierssen and M. D. Fortes. 1998. Contrasting recolonization strategies in multi-species seagrass meadows. *Mar. Poll. Bull.* 37: 450–459.
- Rose, C. D., W. C. Sharp, W. J. Kenworthy, W. G. Hunt, W. G. Lyons, E. J. Prager, J. F. Valentine, M. O. Hall, P. E. Whitfield and J. W. Fourqurean. 1999. Overgrazing of large seagrass bed by the sea urchin *Lytechinus variegatus* in Outer Florida Bay. *Mar. Ecol. Prog. Ser.* 190: 211–222.
- Shepherd, S. A., A. J. McComb, D. A. Bulthuis, V. Neveraskas, D. A. Steffensen and R. West. 1989. Decline of Seagrasses. Pages 346–387 in A. W. D. Larkum, A. J. McComb and S. A. Shepherd, eds. *Biology of seagrasses: a treatise on the biology of seagrasses with special reference to the Australian region*. Elsevier, Amsterdam.
- Short, F. T., W. C. Dennison and D. G. Capone. 1990. Phosphorus- limited growth of the tropical seagrass *Syringodium filiforme* in carbonate sediments. *Mar. Ecol. Prog. Ser.* 62: 169–174.
- _____, and S. Wyllie-Echeverria. 1996. Natural and human-induced disturbance of seagrasses. *Environ. Conserv.* 23: 17–27.
- Stapel, J., R. Manuntun and M. A. Hemminga. 1997. Biomass loss and nutrient redistribution in an Indonesian *Thalassia hemprichii* seagrass bed following seasonal low tide exposure during daylight. *Mar. Ecol. Prog. Ser.* 148: 251–262.
- Udy J. and W. C. Dennison. 1997. Growth and physiological responses of three seagrass species to elevated sediment nutrients in Moreton Bay, Australia. *J. Exp. Mar. Biol. Ecol.* 217: 253–277.
- _____, _____, W. J. L. Long and L. J. McKenzie. 1999. Responses of seagrass to nutrients in the Great Barrier Reef, Australia. *Mar. Ecol. Prog. Ser.* 185: 257–271.
- Walker, D. I., W. C. Dennison and G. Edgar. 1999. Status of Australian seagrass research and knowledge. Pages 1–18 in A. Butler and P. Jernakoff, eds. *Seagrass in Australia*. CSIRO Australia, Collingwood.
- _____, and A. J. McComb. 1992. Seagrass degradation in Australian coastal waters. *Mar. Poll. Bull.* 25: 191–195.
- _____, and R. T. Prince. 1987. Distribution and biogeography of seagrass species on the northwest coast of Australia. *Aquat. Bot.* 29: 19–32.
- Young, P. C. and H. Kirkman. 1975. The seagrass communities of Moreton Bay, Queensland. *Aquat. Bot.* 1: 191–202.

ADDRESSES: (T.J.B.C., W.C.D., E.G.A.) *Marine Botany, Botany Department, University of Queensland, Brisbane, QLD 4072, Australia.* (M.W.) *School of Tropical Environment Studies and Geography, James Cook University, Townsville, QLD 4811, Australia.* (L.J.K., W.J.L.L.) *Northern Fisheries Centre, Department of Primary Industries Queensland, P.O. Box 5396, Cairns QLD 4870, Australia.* CURRENT ADDRESS: (T.J.B.C., W.C.D.) *University of Maryland Center for Environmental Science, 2020 Horn Point Rd., P.O. Box 775, Cambridge, Maryland 21613* CORRESPONDING AUTHOR: (T.J.B.C.) *E-mail: <tcarruth@ca.umces.esu>*.