Management and conservation of seagrass in New Zealand: an introduction

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ABSTRACT

Globally, seagrass management and conservation have received increased attention over the last decade. To date, however, there has been a paucity of available information specific to New Zealand about seagrass beds as an ecosystem component and which could be used to assist resource managers in decision making. This report has been prepared primarily for coastal resource managers, to assist in the management and conservation of seagrass. It provides a review of the current state of knowledge in New Zealand, within the context of international seagrass research. There are some key characteristics that set New Zealand seagrass habitat apart from many temperate and tropical systems. In New Zealand, the seagrass flora is represented by one genus, *Zostera*, in the family Zosteraceae. Seagrass occurs predominantly intertidally in New Zealand, although it may extend into the shallow subtidal areas of sheltered estuaries, and permanently submerged beds of seagrass have been recorded around a small number of offshore islands. While a lot is known about seagrasses in other regions, the role that these plants play and just how important they are in estuarine and coastal ecosystems in New Zealand is less well understood and to date has been the subject of limited study. The relative importance or magnitude of the multiple ecosystem functions of seagrass beds may vary considerably within and between different estuarine and coastal systems. For successful management, a specific understanding of seagrass ecology within New Zealand is required, preferably at the regional or estuary scale, rather than relying on international paradigms.

Keywords: *Zostera capricorni*, ecology, threats, monitoring, indicator species, ecosystem health

1. Introduction

Internationally, seagrass ecology has received increased attention from marine scientists in the last decade, which has in turn resulted in a number of comprehensive publications on the topic (e.g. Duarte 1999; Hemminga & Duarte 2000; Short & Coles 2001; Green & Short 2003). However, within these publications, there has been only one chapter about seagrass in New Zealand (Inglis 2003), within a treatise on global seagrasses. The current review was prepared at the conclusion of a study that assessed some aspects of the ecology of intertidal seagrass in estuaries of the North Island, New Zealand.

While a lot is known about seagrasses in other regions, the role that these plants play and just how important they are in estuarine and coastal ecosystems in New Zealand is less well understood and to date has been the subject of limited study. More research is required if we are to better understand the ecology and role of seagrass habitat in New Zealand estuarine and coastal ecosystems. In this review, we synthesise the status of knowledge of New Zealand seagrass at the time of writing and set out some guidelines for the management and monitoring of seagrass. We begin by summarising generalities about seagrass ecology globally and then focus on existing New Zealand information, utilising international examples when relevant to the New Zealand situation. We are pleased to note that with the increased appreciation of the potential significance of seagrass, a number of new initiatives have begun since this work was completed. Therefore, this document is likely to require updating within the next few years to assist in providing a sound scientific basis for the conservation and management of seagrass habitat in New Zealand.

This report has been prepared primarily for coastal resource managers, to assist in the management and conservation of seagrass, but will also be a useful resource for other interest groups and stakeholders. An increased awareness of the value of seagrass, and of the potential risks and long-term consequences of loss or degradation of seagrass habitat, will play a significant role in the successful implementation of management activities initiated to protect New Zealand's seagrass habitat. While the focus of this report is on seagrass, this is only one component of a complex ecosystem; we need to understand, manage and protect the whole ecosystem.

2. General seagrass biology

There are an estimated 50–60 named species of seagrass worldwide, represented by 12 genera in five families (Hydrocharitaceae, Cymodoceaceae, Posidoniaceae, Zosteraceae and Ruppiaceae); the greatest diversity is found in tropical regions (Larkum & Den Hartog 1989; Sullivan 1994; McCook 1998; Hemminga & Duarte 2000; Spalding et al. 2003). The species share a fundamentally similar architecture and physiology, and perform similar ecosystem functions.

Seagrasses are true flowering plants (Angiospermae), with stems, leaves, roots and flowers, which have become specialised to grow rooted and submersed in estuarine and coastal environments. While seagrasses are all monocotyledons, they are not true grasses (family Poaceae). Seagrasses are the only flowering plants that grow in the sea, and are thought to be derived from terrestrial plants that colonised the marine environment c. 100 million years ago (Den Hartog 1970; Larkum & Den Hartog 1989; but see Stevenson 1988; Sullivan 1994). Seagrasses are mainly found in intertidal (to about the mid-tide level) and shallow subtidal areas in bays, estuaries and coastal waters around many of the world's subarctic, temperate and tropical coasts (Larkum & Den Hartog 1989; Hemminga & Duarte 2000; Green & Short 2003; Spalding et al. 2003). Seagrasses reach their most northerly distribution in Norway, Russia and Alaska, and their most southerly distribution at Stewart Island, New Zealand (Spalding et al. 2003).

Typically, seagrasses are found in water depths of 2–12 m, where light intensity is greatest, but in some areas they can occur down to depths of 50–60 m (Lee Long & Coles 1997; McCook 1998; Coles et al. 2003; Spalding et al. 2003). They occur on a variety of substrata, from mud through to sand and even bedrock, generally in areas sheltered from wave action and strong currents (McCook 1998; Hemminga & Duarte 2000; Spalding et al. 2003). The most extensive seagrass beds occur in soft substrates (sand and mud), where they may form continuous expanses of vegetation extending over several square kilometres, or mosaics of discrete patches surrounded by unvegetated sediment. They often represent the dominant and most highly productive habitat type of intertidal and shallow subtidal zones (Duarte & Chiscano 1999; Hemminga & Duarte 2000; Green & Short 2003).

Seagrasses possess a number of anatomical, morphological and physiological adaptations that are unique for submerged marine plants (Stevenson 1988; Kuo & McComb 1989; Larkum et al. 1989; McConchie & Knox 1989; Tyerman 1989; McCook 1998; Hemminga & Duarte 2000; Spalding et al. 2003). These include:

- An extensive system of roots and rhizomes (horizontal underground stems), which allow the plants to withstand wave action and tidal currents, anchoring the plant in the sediment. The roots and rhizomes are specialised for extracting nutrients and minerals from the sediment pore-waters, and the rhizome also functions in the vegetative propagation of the plants and serves as a storage area for carbohydrates.

- An extensive system of veins and air channels in the leaves and stems, which enable the plants to live in oxygen-deficient sediments, facilitating the diffusion of oxygen from the leaves to the buried roots and rhizomes.

- Thin, linear, grass-like leaves (in many seagrass species) produced on vertical branches, which facilitate light penetration, adsorption of nutrients, diffusion of gases and buoyancy.

- Flowers and pollination systems that are well adapted for pollination by water (hydrophilous pollination). In most genera, the flowers are borne underwater. The pollen grains are released into the water column and are transported to other plants, where the pollen becomes attached to female flowers and fertilisation occurs to produce seeds. Asexual (vegetative) propagation may also occur via fragmentation of the rhizome, with vegetative fragments potentially providing an additional mechanism for dispersal (Cambridge et al. 1983; Ewanchuk & Williams 1996; Campbell 2003; Marbà et al. 2004).

These features enable the plants to exist in shallow coastal and estuarine areas, which have variable salinities and are subject to periods of submersion or complete submersion, wave and tidal action, and shifting sediments.

2.1 SPECIES OF SEAGRASS IN NEW ZEALAND

In New Zealand, the seagrass flora is represented by one genus, *Zostera*, in the family Zosteraceae. Until recently, it was generally considered that there were two species native to New Zealand: *Zostera capricorni* Aschers. and *Zostera novazelandica* Setchell. *Z. capricorni* was considered to be confined to the North Island, while *Z. novazelandica* was considered an endemic species reportedly found throughout coastal New Zealand (Den Hartog 1970; Moore & Edgar 1976; Johnson & Brooke 1989; Webb et al. 1990). However, there are few morphologically distinctive characteristics between the two species. Furthermore, phylogenetic analysis of morphological characters and DNA sequences of samples from a limited number of locations in New Zealand have identified a lack of molecular divergence among Australian and New Zealand *Zostera*, which were formerly segregated as four distinct species (*Z. capricorni*, *Zostera muelleri*, *Zostera mucronata* and *Z. novazelandica*), as well as a lack of reliable morphological characters to separate these four species (Les et al. 2002). Consequently, Les et al. (2002) recommended the taxonomic merger of Australian/New Zealand *Zostera* into a single species, *Z. capricorni*. Recent molecular genetic and morphological analysis has indicated that *Z. capricorni* and *Z. muelleri* should be considered synonymous (Waycott et al. 2004). However, more comprehensive surveys and phylogenetic analyses will be required to definitively confirm the existence of a single species within New Zealand.

Whether there are one or two species of seagrass in New Zealand, its seagrass flora is extremely limited compared, for example, with Australia, which has c. 30 different species of seagrass, including the highest diversity of temperate seagrasses worldwide, and the largest single area of temperate seagrass meadow in the world (Kirkman 1997). *Z. capricorni* is one of the most common

temperate species found in Australia, occurring predominantly in sheltered bays, estuaries and in coastal lagoons (Coles et al 1989; West et al. 1989; Kirkman 1997; Coles et al. 2003; Green & Short 2003).

2.2   THE ECOSYSTEM VALUE OF SEAGRASSES

Seagrasses perform a variety of functions within estuarine and coastal ecosystems, and have both economic and ecological value. These roles are so important that seagrasses are considered to be some of the most valuable components of estuarine and coastal ecosystems in terms of the value-added benefits of the services they provide (Costanza et al. 1997). While seagrasses undoubtedly have multiple functions and attributes, their relative importance may vary considerably within and between different estuarine and coastal systems.

2.2.1   High primary productivity—including benthic and epiphytic production

Seagrasses represent important components of coastal primary productivity and support numerous detritus-based and herbivore-based food webs. Seagrasses are highly productive, with an estimated average annual production of 1012 g dry weight m^{-2} $year^{-1}$ (this estimate is conservative, as root production is under-represented), which rivals or exceeds that of terrestrially cultivated areas (Duarte & Chiscano 1999).

A large variety of micro- and macro-algae also occur in seagrass beds, attached to seagrass leaves, stones and shells, anchored in the sediment, or free living on the seafloor. These contribute significantly to the overall primary productivity of seagrass systems and represent important food sources for many animals utilising seagrass beds (Borowitzka & Lethbridge 1989; Klumpp et al. 1989; Keough & Jenkins 1995; Hemminga & Duarte 2000; Williams & Heck 2000; Kaldy et al. 2002; Hily et al. 2004; Keuskamp 2004; Connolly et al. 2005; Tomas et al. 2005). Grazers can play an important role in controlling the epiphyte loads on seagrass leaves, which enhances seagrass productivity and biomass, thereby mitigating the negative impacts of epiphytic growth that tends to occur in water columns with elevated nutrient levels (Hootsmans & Vermaat 1985; Howard & Short 1986; Neckles et al. 1993; Williams & Ruckelshaus 1993; Philippart 1995a; Jernakoff & Nielsen 1997; Heck et al. 2000; Frankovich & Zieman 2005; Hays 2005).

Direct grazing on seagrass leaves has generally been considered to be a relatively unimportant trophic pathway in temperate seagrass beds. However, recent studies have indicated that grazing on the plants, as well as predation on reproductive structures, may be significant, and that the importance of seagrasses to food webs has previously been greatly underestimated (Stevenson 1988; Klumpp et al. 1989; Fishman & Orth 1996; Rose et al. 1999; Williams & Heck 2000; Kirsch et al. 2002; Valentine et al. 2002). Cebrián & Duarte (1998) have reported that the extent of herbivory varies greatly both within and among seagrass species, ranging from negligible values to up to 50% of leaf production removed in some species.

Many seagrass systems are net exporters of organic material and thus support broader estuarine and coastal productivity (De Boer 2000; Hemminga & Duarte 2000; Valentine et al. 2002; Spalding et al. 2003; Terrados & Borum 2004). The majority of organic matter is produced by decomposition, and enters the food chain through the detrital pathway and as dissolved organic matter (Harrison 1989; Kenworthy et al. 1989; Klumpp et al. 1989; Keough & Jenkins 1995; Cebrián et al. 1997; De Boer 2000). Assimilation of plant material into food webs occurs not only within the seagrass bed itself, but also into habitats that may be considerable distances from the bed, as a result of the transport of seagrass detritus. There have been few attempts to quantify the transfer of seagrass production into coastal food webs, or to determine the importance of seagrass production relative to primary production generated by other major plant groups (phytoplankton, macroalgae, benthic microalgae, mangroves, etc.). Normally 65%–80% of organic matter produced by seagrass beds remains in the bed as detritus, while 10%–20% (in some situations up to 50%) is carried away from the beds (Keough & Jenkins 1995).

2.2.2 Habitat

Seagrasses generally occur in comparatively homogeneous, soft-sediment environments and, due to the presence of both above-ground leaves and the extensive below-ground root-rhizome system, they greatly increase both the horizontal and vertical structural complexity of the habitat above that of the surrounding seafloor.

Habitat complexity within seagrass beds has a significant influence on the diversity, abundance and spatial distribution of associated flora and fauna by:

- Increasing the variety of microhabitats around the leaves and root-rhizomes, as well as increasing the total area of available substrata (Leber 1985; Stoner & Lewis 1985; Bell & Westoby 1986; Main 1987; Bell & Pollard 1989; Howard et al. 1989; Schneider & Mann 1991; Worthington et al. 1992; Connolly 1994b; Irlandi 1997; Webster et al. 1998; Attrill et al. 2000; Bologna & Heck 2000; Williams & Heck 2000; Lee et al. 2001; Spalding et al. 2003).

- Altering predator-prey relationships as a consequence of the increased habitat complexity affording shelter from predation and inhibiting foraging (Coen et al. 1981; Heck & Thoman 1981; Peterson 1982; Orth et al. 1984; Summerson & Peterson 1984; Leber 1985; Bell & Pollard 1989; Howard et al. 1989; Pohle et al. 1991; Connolly 1994a; Irlandi 1994; Boström & Mattila 1999; Coronoa et al. 2000; Hindell et al. 2000; Williams & Heck 2000; Hovel & Lipcius 2001; Bartholomew 2002; Hindell et al. 2002; Schofield 2003; Adams et al. 2004). There is, however, considerable variation in precisely how the presence of seagrass affects the outcomes of predator-prey interactions among individual suites of predators and prey, among seagrass species, and among seasons and years (Williams & Heck 2000).

- Modifying the hydrodynamic environment by reducing the effects of currents and wave action at the sea-bed, which facilitates the settlement of planktonic larvae as well as of fine sediments and organic materials, thus altering the availability of food for benthic fauna (Peterson 1986; Eckman 1987; Howard et al. 1989; Wilson 1990; Boström & Bonsdorff 2000; Terrados

& Duarte 2000; Williams & Heck 2000; Moran et al. 2004; Peterson et al. 2004).

- Stabilising the sediment, protecting against wave disturbance and favouring sedentary species that require stable substrates for maintenance of their permanent tubes and burrows (Orth 1977b; Brenchley 1982; Posey 1987; Irlandi & Peterson 1991; Irlandi 1996).

Seagrasses are widely considered to provide critical habitat (e.g. feeding, breeding and nursery areas), as well as refuge from predation, competition, and physical and chemical stresses, for a wide variety of taxonomic and functional groups (e.g. birds, fish and invertebrates) (Heck & Thoman 1984; Fonseca et al. 1992; Hoss & Thayer 1993; Loneragan et al. 1998; Lipcius et al. 2005). This includes the juvenile stages of species that are ecologically important or are commercially or recreationally harvested in other ecosystems. However, the exclusivity of some of these widely accepted paradigms are increasingly being challenged (Hemminga & Duarte 2000; Williams & Heck 2000). While it is well established that seagrass beds provide nursery habitat for many species, juveniles that are known to occur in seagrass beds may also use alternative nursery habitats (e.g. algal reefs, oyster beds and mangroves), and different seagrass beds, even of the same species, may vary considerably in terms of their nursery value (Hemminga & Duarte 2000); for example, there is considered to be limited evidence for a significant nursery function of seagrasses in temperate Australia (Edgar & Shaw 1993, 1995a,b).

2.2.3 Trapping and stabilisation of bottom sediments

The well-developed canopy formed by seagrass beds slows the rate at which water flows over the seafloor by increasing resistance to water currents (Fonseca et al. 1982; Fonseca & Fisher 1986; Gambi et al. 1990; Fonseca & Cahalan 1992; Worcester 1995; Koch & Gust 1999; Heiss et al. 2000; Peterson et al. 2004). This in turn creates a low-energy microenvironment within the bed, which facilitates the deposition and retention of suspended inorganic and organic material, including sediment and planktonic larvae, and reduces turbulence and scouring (Fonseca et al. 1982; Fonseca & Fisher 1986; Fonseca 1989b; Klumpp et al. 1989; Duarte et al. 1999; Heiss et al. 2000; Gacia & Duarte 2001; Lee et al. 2001; Agawin & Duarte 2002; Spalding et al. 2003; Lepoint et al. 2004). Sediment builds up under the canopy of seagrass beds, and the extensive root-rhizome system of the plants then acts to trap and stabilise the bottom sediments, providing protection against sediment erosion (Fonseca et al. 1983; Bulthuis et al. 1984; Ward et al. 1984; Fonseca 1989b).

The trapping and stabilisation of terrestrially derived sediments from estuarine and coastal waters is an important function of seagrasses. This has an important role in contributing to reducing erosion and resuspension in coastal areas, and helping to improve water clarity in the immediate environment and adjacent habitats (Christiansen et al. 1981; Bulthuis et al. 1984; Short & Short 1984; Ward et al. 1984; Gacia & Duarte 2001).

Seagrasses also help to settle and remove contaminants (nutrients and chemical pollutants) from the water column, thereby contributing to improvements in water quality (Short & Short 1984; Ward 1987; Hoven et al. 1999).

2.2.4   Nutrient cycling

Nutrient cycling within marine sediments and between the sediments and the surrounding water is mediated by the presence of seagrasses, which provide a link between the sediment and overlying water column (Harrison 1989; Hillman et al. 1989; Moriarty & Boon 1989; Hemminga et al. 1991; De Boer 2000; Hemminga & Duarte 2000; Spalding et al. 2003). Some key processes contributing to nutrient losses from seagrass beds and their associated sediments include leaching from living and dead plant material, export of sloughed leaves and leaf fragments, nutrient transfer by foraging animals, denitrification, and diffusion from the sediment (Hemminga et al. 1991; Hemminga & Duarte 2000). Nutrients may be replenished by nitrogen fixation in the sediments, sedimentation, and nutrient uptake by the leaves. The environmental conditions for the various nutrient transformations are mediated by the photosynthesis and respiration of the seagrass plants.

Seagrass roots take up a large proportion of plant nitrogen (Short 1987; Zimmerman et al. 1987; Hemminga et al. 1991; Pedersen & Borum 1993; Pedersen et al. 1997), with rhizomes and roots representing a substantial proportion of the plant biomass in some seagrass communities (Kenworthy & Thayer 1984; Larkum et al. 1984; Pangallo & Bell 1988; Hillman et al. 1989; McKenzie 1994; Paling & McComb 2000; Turner & Schwarz in press). Given the large biomass of rhizomes and roots, and the associated pools of nitrogen within the below-ground parts of the plant and detritus, the decomposition of the below-ground organic matter makes a substantial contribution to the sediment nitrogen pool, which is available to supply plant requirements, nitrogen recycling processes or diffusion into the water column (Iizumi et al. 1982; Kenworthy et al. 1982; Kenworthy & Thayer 1984; Boon 1986; Klumpp et al. 1989).

3. Biology and ecology of *Zostera* in New Zealand

This section draws on published and unpublished studies of *Zostera* in New Zealand. In addition, references to published reports of *Z. capricorni* in Australia are included for comparison, particularly where the ecology of New Zealand *Zostera* is poorly documented.

3.1 MORPHOLOGICAL CHARACTERISTICS

The leaves of *Z. capricorni* are thin and translucent with a blunt leaf tip and smooth leaf margin. Each leaf has distinct longitudinal veins, and cross veins at right angles to the longitudinal veins. There is considerable morphological variation within natural populations of *Zostera* from different locations in New Zealand. For example, plants growing intertidally in Coromandel Peninsula estuaries have leaves up to 5.5–9.0 cm in length and 1.1–1.8 mm in width, and typically have three to five leaves per shoot (Turner & Schwarz in press). In Otago Harbour, plants generally have three to four (occasionally five) leaves per shoot, and leaves reach 10.7–11.3 cm in length (Ismail 2001). In Manukau Harbour, the plants have a mean number of three leaves per shoot, with the longest leaves reaching mean lengths of 3.9–5.5 cm (Turner et al. 1996).

The rhizome has internodes of varying length, with one to two or more groups of long, thin roots at each node. Rhizome diameters are typically 1–2 mm. The extensive root-rhizome system is usually buried several centimetres (generally < 15–20 cm) below the sediment surface. Each node along the rhizome bears a short lateral branch with erect shoots that bear the leaves and leaf sheaths. The meristems (the areas where active cell division takes place), which continuously produce new plant tissue, are located at the apices of the rhizome and its branches. The leaf base or sheath encloses the growing tip of the rhizome and protects the young leaves. Each node also bears a single translucent leaf originating from the rhizome instead of from the vertical, leaf-bearing shoot.

3.2 LIFE-HISTORY CHARACTERISTICS

Seagrasses rely on both vegetative (asexual) and sexual reproduction for the maintenance of existing beds and the colonisation of new areas (Hemminga & Duarte 2000; Marbà et al. 2004; Olesen et al. 2004). Increase in the area occupied by seagrasses, as well as the maintenance of seagrass beds, is principally through vegetative propagation, which involves the continual growth and branching of rhizomes and the production of lateral shoots, rather than by colonisation by seedlings (Tomlinson 1974; Duarte & Sand-Jensen 1990a,b; Williams 1990; Gallegos et al. 1993; Olesen & Sand-Jensen 1994a;

Vermaat et al. 1995; Marbà & Duarte 1998; Nakaoka & Aioi 1999; Hemminga & Duarte 2000; Marbà et al. 2004). Although sexual reproduction is probably not important for population maintenance in an established bed, it is likely to be important for the long-term dynamics of seagrass beds, particularly during re-establishment following large-scale declines in seagrass abundance, during which open spaces become available for establishment and growth (Rasheed 1999; Marbà et al. 2004; Olesen et al. 2004).

In New Zealand, *Zostera* is perennial and, from the limited number of studies that have been reported, appears to reproduce primarily by vegetative propagation, with reproductive structures occurring infrequently (Inglis 2003; ST & A-MS, pers. obs.). During a 3-year study of seagrass in estuaries around the central North Island, there were no observations of *Zostera* flowering (Turner & Schwarz in press). Rhizome growth and new shoot and leaf production were observed to occur throughout the year, suggesting that vegetative growth is important in the persistence of the beds at these sites.

There is little known about the reproductive ecology of seagrass in New Zealand, and in particular about the role of sexual reproduction in the establishment and maintenance of seagrass beds. Ramage (1995) has described the reproductive morphology of *Zostera* growing on intertidal platforms on the Kaikoura Peninsula. The specialised flowering shoots are comprised of several branches, each with a number of inflorescences (clusters of flowers). Each inflorescence is comprised of a spathal sheath, which encloses a spadix on which 8–12 male (anthers) and female (pistils) flowers are alternately arranged. When the male flowers are mature, dehiscence and release of the thread-like pollen grains occurs, followed by the simultaneous development of the female flowers within the spathe. Floating pollen threads are snared on stigmata that project through the spathal sheath. The simple fruit is a drupe with a single seed and one carple (Ramage 1995).

There is some information on the timing of flowering in some areas of New Zealand. Den Hartog (1970) reported observations of flowering from November to March, with fruits being found only in February and March. Ismail (2001) also recorded flowering shoots in December and March in Otago Harbour, where flowering-shoot biomass constituted < 1% of leaf standing crop.

A comprehensive study published by Ramage & Schiel (1998, 1999) has described flowering patterns and characteristics for *Zostera* growing on intertidal platforms on the Kaikoura Peninsula. Here *Zostera* was reported to reproduce during summer, with seedlings found in tide-pools or water-filled crevices during late autumn. The flowering season lasts for up to 8 months of the year, from October to June, with peak flower production in January to March—a reproductive pattern typical of *Zostera* species at higher latitudes (Ramage & Schiel 1998). Flowering lasted longest in the low intertidal zone, while plants high on the shore that were not associated with tide-pools were reproductive for only 3 months. At the flowering peak, reproductive shoots corresponded to > 15% of leaf standing crop. Reproductive output was related to plant biomass, and varied significantly with site, association with tide-pools and shore-level. Plants low on the shore and those associated with tide-pools or crevices produced more flowering shoots (up to 55 flowering shoots/0.1 m²) and more inflorescences per shoot (up to nine inflorescences per flowering

shoot) than those high on the shore or not associated with tide-pools (Ramage & Schiel 1998). Temperature, light intensity and salinity were all found to contribute to the regulation of formation of reproductive shoots and the onset of flowering under laboratory conditions (Ramage & Schiel 1998).

At the Kaikoura Peninsula sites, mature embryos and seeds were seen from late December to March, with seeds apparently over-wintering and germinating the following spring (September) (Ramage & Schiel 1998). Seedlings were found mostly associated with turfing coralline algae, which accumulates sediment and thereby provides a suitable substratum for seed germination. Seedlings represented 40% of new patches that were formed at the sites in spring, but mortality due to removal by wave action was high, with no seedlings surviving for more than a few months. Ramage & Schiel (1999) concluded that the successful recruitment of seedlings was either episodic or occurred at very low levels at these sites.

In sub-tropical Queensland, the flowering season of *Z. capricorni* lasts for up to 8 months of the year, from September to March/April, with peak flower production from September to November (Young & Kirkman 1975; Conacher et al. 1994b; Rasheed 1999). Conacher et al. (1994b) found that both the timing and production of flowers and seeds differed between sites and different morphological types of *Z. capricorni* in Moreton Bay, Queensland. The density of flowering shoots varied between an average of 4 to 340 flowering shoots/m², with an average of three inflorescences per shoot. Further south in New South Wales, *Z. capricorni* has been recorded flowering over 6 months of the year, from September to April (Larkum et al. 1984), and throughout the year (Harris et al. 1979). Inglis & Lincoln Smith (1998) sampled nine *Z. capricorni* beds in three estuaries in New South Wales, and found that although reproductive shoots were widespread, the timing and intensity of flowering varied widely among estuaries and exhibited considerable patchiness within individual beds. The percentage of flowering shoots of *Z. capricorni* varied between < 5% to 37% in eastern Australia (Conacher et al. 1994b). Reproduction is probably controlled by several environmental factors, rather than by any one variable. Inglis & Lincoln Smith (1998) found that the initiation of flower production was apparently triggered by regional changes in environmental conditions, such as water temperature or photoperiod, whereas the abundance of flowers varied significantly among estuaries and was influenced by both within-estuary processes and by local conditions within each bed.

Information from *Z. capricorni* beds in subtropical Queensland suggests that it takes 1.5–2 months for female flowers to be fertilised and to develop into mature seeds (Conacher et al. 1994b). Most seeds are found in the spring and summer, which coincides with the period of seed production, and few seeds are found over the winter (Conacher et al. 1994b). The seeds of *Z. capricorni* do not appear to have any specialised adaptations for dispersal, and are thus likely to settle rapidly, dispersing only a few metres from where they are released even under strong winds and currents (Rasheed 1999). Only a small proportion of the total number of seeds produced was found in the sediment, suggesting that there was no evidence for the formation of large seed banks. *Z. capricorni* seeds are thought to have a relatively short dormancy period (in the order of 4 months). Given the lack of observations of seedlings, germination rates are

thought to be low, with many seeds presumably exported, eaten or destroyed (Conacher et al. 1994b). The highest recorded seed density was 542 ± 194 seeds/m^2, although in another study Conacher et al. (1994a) recorded seed densities of 2904 ± 149 seeds/m^2 during the flowering season; this increase was attributed to the comparatively high flowering frequency and shoot density. Most of the annual seed production by species of *Zostera* germinates within a few months of release, with only a small proportion persisting for longer periods. Burial and anoxia have been shown to stimulate germination under field conditions (Inglis 2000). Depending on the relative success of vegetative versus sexual reproduction, the fate of seeds has important implications for the natural maintenance and recolonisation of seagrass beds.

3.3   SEAGRASS BED AND PATCH DYNAMICS

There have been a few studies in New Zealand on the dynamics of seagrass colonisation, expansion, recession and mortality processes at the patch or bed scale. Turner et al. (1996) documented the spatial and temporal dynamics of intertidal patches of *Zostera* over a 2-year period at two sites in Manukau Harbour and one site in Whangapoua Harbour (Coromandel Peninsula). Patch size increased at all three sites over the first year, but at one of the Manukau Harbour sites there was a marked decline in patch size over the second year of the study, which was also reflected in decreases in patch biomass and percentage cover. Over the summer (October 1994–April 1995), the period of greatest change in patch size, patches expanded horizontally on average by > 3 m along the main patch axis at the two Manukau sites, and by > 1 m at the Whangapoua Harbour site. Over the winter (April–October), the increase in patch size was generally < 1 m. At one of the Manukau Harbour sites, mean patch size increased by at least 200% along the main axis, from 5.6 m to 12.3 m over the 2-year study. It is not understood what caused this reduction in patch size at one of the Manukau Harbour sites, and why similar changes were not observed at the second site. The significant differences in the rate and pattern of patch expansion or contraction among the sites, as well as observed differences in rhizome growth patterns and shoot demographics, were considered to be a response to local environmental conditions (Turner et al. 1996). These differences reflected differential resource allocation under different conditions, in particular exposure to wind-generated wave activity or tidal flows. This work highlighted the importance of studying seagrass systems concurrently at several different spatial scales (e.g. rhizome demography, patch expansion and contraction, and landscape patterns) if the dynamics of these systems are to be understood.

Ramage & Schiel (1999) documented the patch dynamics of *Zostera* over a 1-year period on two intertidal platforms on the Kaikoura Peninsula. Patches were formed by the germination of seeds or by fragmentation of large established patches during winter and spring. Despite fluctuations in patch size, recruitment and mortality throughout the year, there was little variation in the total cover of seagrass patches after 1 year. During winter, there was a general deterioration of patches and a reduction in patch size, which was

attributed to increased wave action and erosion of sediment around the patch margins. Variability between the sites was attributed to differences in the intensity of wave action. Patch loss was also greatest during the winter and spring, as newly germinated seedlings and small patches experienced severe erosion and were removed by storms. Loss of patches was generally confined to patches less than 0.4 m² (c. 800 shoots), of which 60% were lost during the study; large patches (> 1 m²) were much more resilient to disturbance and appeared to be relatively long-lived. While there was an overall decrease in the number of patches over the year, the natural expansion of established patches maintained a relatively constant coverage. Patches expanded over the spring-summer, when there was also an increase in shoot density and biomass. The proportional expansion and contraction of patches was independent of initial patch size.

In a study to map changes (0.25-m² resolution) in the percentage cover and position of the edge of the seagrass bed in permanent quadrats at four sites in Whangamata, Wharekawa and Whangapoua Harbours on the east coast of the Coromandel Peninsula, it was found that at all sites there was an overall increase in the area occupied by the beds within the quadrats over 2 years (ST, unpubl. data). There was considerable spatial (between replicates at a site, and among sites) and temporal (summer/winter and inter-annual) variability. Bed margins extended by 1–3 m, with extension over any 6-month period varying between 0.5 m and 1.5 m.

Ismail (2001) documented changes in the spatial extent and cover of *Zostera* in an intertidal area of Otago Harbour over a 1-year period. Total seagrass cover declined from autumn to spring; there was then little change in total cover over the following spring to autumn period. Over the same period, there was an increase in the area occupied by sparse seagrass (< 30% ground cover).

3.4 GROWTH AND PRODUCTION

There have been a limited number of studies documenting the demography and productivity of *Zostera* in New Zealand. In general, however, it appears that a seasonal pattern is evident across a wide latitudinal range, with a winter minimum in above-ground biomass recorded at sites from the Coromandel Peninsula to Otago Harbour (Ramage & Schiel 1999; Ismail 2001; Turner & Schwarz in press). The reported average above- and below-ground biomass and production of *Zostera* at different locations throughout its range are summarised in Table 1.

In estuaries on the Coromandel Peninsula, both biomass and shoot density were found to vary between summer (January) and winter (July), with above- and below-ground biomass and shoot density generally lowest in winter and highest in summer (Turner & Schwarz in press). Below-ground biomass was more variable than above-ground biomass, and comprised the greatest proportion of total biomass; there was an indication of a shift towards a greater accumulation of resources in the form of below-ground biomass at those sites where the plants were more productive (i.e. more total biomass production). The relatively high below-ground biomass may be a reflection of a comparatively

TABLE 1. SHOOT DENSITY, ABOVE- AND BELOW-GROUND BIOMASS (g DRY WEIGHT (DW)/m^2), RELATIVE LEAF GROWTH RATE (g DRY WEIGHT (DW) g^{-1} DAY^{-1}) AND ABOVE-GROUND PRODUCTION (g DRY WEIGHT (DW) m^{-2} DAY^{-1}) OF *Zostera* AT INTERTIDAL LOCATIONS AROUND NEW ZEALAND AND AUSTRALIA.

Values are means (± SEM) or ranges, as reported in the literature. Different computations were used to calculate proportional leaf growth rates and above-ground production.

SPECIES	LOCATION	SHOOT DENSITY (NO./m^2)	BIOMASS ABOVE GROUND (g DW/m^2)	BELOW GROUND (g DW/m^2)	RELATIVE LEAF GROWTH RATE (g DW g^{-1} DAY^{-1})	ABOVE-GROUND PRODUCTION (g DW m^{-2} DAY^{-1})
Zostera capricorni	Port Hacking (New South Wales, Australia)[1]	–	Mean: 55 Range: 22 (July)–74 (Mar)	Approx. range: 160 (Mar)–200 (Jan) 150 (Nov)–290 (Jan)	Feb/Mar: 0.035 June/Sept: < 0.01	Feb/Mar: 2.5 June/Sept: 0.3
Zostera capricorni	Botany Bay (New South Wales, Australia)[2]	Jan: 2176 ± 82 July: 1797 ± 93 19 sites Jan: 68 ± 144–4106 ± 320	Jan: 290 ± 10 July: 64 ± 4	Jan: 707 ± 50 July: 610 ± 54	Jan: 0.031 July/Aug: 0.021	Jan: 8.9 July/Aug: 1.4
Zostera capricorni	Moreton Bay (Queensland, Australia)[3]	1135 ± 90–5037 ± 198	38 ± 2.3–68 ± 4.5	–	–	–
Zostera capricorni	Cairns Harbour (Queensland, Australia)[4]	–	Mean: 96 ± 2 Range: 7 (Feb)–243 (Nov)	Mean: 177 ± 4 Range: 15 (Feb)–658 (Nov)	–	–
Zostera novazelandica	Manukau Harbour (North Island, New Zealand)[5]	336 ± 152–557 ± 148	Range total biomass: April: 7 ± 2–160 ± 13 Oct: 3 ± 0.5–192 ± 24		–	–
Zostera novazelandica	Whangapoua Harbour (North Island, New Zealand)[5]	–	Range total biomass: April: 156 ± 17–320 ± 23 Oct: 148 ± 20–213 ± 23		–	–
Zostera novazelandica	Otago Harbour (New Zealand)[6]	4800–8700	Mar: 93–97 Oct: 40–50	180–235	Dec/Mar: 0.021–0.028 June/July: < 0.01	Dec/Mar: 1.8–2.0 June/July: 0.2–0.7
Zostera capricorni	Whangamata Harbour (Coromandel, New Zealand)[7]	Jan: 3365 ± 166–4270 ± 417 July: 2759 ± 349–2889 ± 279	Jan: 49 ± 15.5–51 ± 7.6 July: 48 ± 4.1–54 ± 4.8	Jan: 165 ± 32.1–168 ± 23.1 July: 120 ± 11.9–133 ± 14.0	Jan: 0.031–0.041 July: 0.022–0.028	Jan: 1.6–2.0 July: 1.1–1.5

Table 1—continued

SPECIES	LOCATION	SHOOT DENSITY (NO./m²)	BIOMASS ABOVE GROUND (g DW/m²)	BELOW GROUND (g DW/m²)	RELATIVE LEAF GROWTH RATE (g DW g⁻¹ DAY⁻¹)	ABOVE-GROUND PRODUCTION (g DW m⁻² DAY⁻¹)
Zostera capricorni	Wharekawa Harbour (Coromandel, New Zealand)[7]	Jan: 3202 ± 347– 3564 ± 223	Jan: 65 ± 10.8– 69 ± 6.4	Jan: 256 ± 30.2– 260 ± 51.5	Jan: 0.033–0.037	Jan: 2.3–2.4
		July: 2040 ± 222– 2318 ± 248	July: 49 ± 8.2– 164 ± 27.7	July: 223 ± 49.7– 310 ± 65.2	July: 0.016–0.027	July: 0.8–4.4
Zostera capricorni	Whangapoua Harbour (Coromandel, New Zealand)[7]	Jan: 3136 ± 540– 3931 ± 617	Jan: 85 ± 10.1– 101 ± 19.7	Jan: 638 ± 96.6– 665 ± 110.0	Jan: 0.029–0.033	Jan: 2.4–3.3
		July: 2048 ± 213– 3069 ± 429	July: 47 ± 3.6– 123 ± 8.7	July: 479 ± 82.5– 587 ± 123.1	July: 0.027–0.028	July: 1.3–3.5
Zostera capricorni	Ten central North Island harbours[8]	Jan: 437 ± 108– 5365 ± 1505	Jan: 19 ± 2.4– 150 ± 21.4	Jan: 78 ± 5.0– 481 ± 116.3	–	–

[1] Kirkman et al. (1982): data from two sites in Port Hacking studied over 14 months.

[2] Larkum et al. (1984): January and July data from one site studied over 1 year; other data from 19 sites in Botany Bay over December–January period.

[3] Conacher et al. (1994b): data from one site in Moreton Bay studied over 18 months.

[4] McKenzie (1994): data from one site in Cairns Harbour studied over 2 years.

[5] Turner et al. (1996): data from two sites in Manukau Harbour and one site in Whangapoua Harbour studied over 2 years.

[6] Ismail (2001): data from one site in Otago Harbour studied over 2 years.

[7] Turner & Schwarz (in press): data from four sites in three Coromandel estuaries studied over 2 years.

[8] A-MS & ST (unpubl. data): data from 10 harbours studied in January 2002.

low turnover of below-ground material, resulting in a greater capacity for the long-term accumulation of material, as well as a lower loss of below-ground material through disturbance and grazing. There were also seasonal differences in shoot characteristics and plant morphology, which contributed to variations in biomass and shoot density. At some sites, the lengths of the primary rhizome internodes, the frequency of rhizome branching and the lengths of leaves at the edge of the bed were longer in winter than summer, indicating that winter may be an important period for growth of *Z. capricorni*, despite the lower ambient temperatures.

In Otago Harbour, there was a clear seasonal trend in above-ground biomass that was consistent between years, with maximum biomass recorded in autumn (March) and minimum biomass recorded during winter and spring (July–October) (Ismail 2001). Below-ground biomass, which contributed most to the total biomass, did not vary markedly over the course of the study. Shoot density and the number of leaves per shoot did not vary seasonally. However, there was marked seasonal variation in leaf length: the longest leaves were recorded in March, corresponding to the period of high leaf growth rates, and the shortest in October–December, associated with the formation of new shoots and the shedding of dead leaves from the previous winter. Ismail (2001) attributed the observed variation in above-ground biomass to changes in leaf dimensions.

The temporal growth pattern of *Zostera* patches on intertidal platforms on the Kaikoura Peninsula exhibited similar unimodal seasonal trends, with vegetative, reproductive and below-ground biomass being greatest in summer and declining to low levels in winter (Ramage & Schiel 1999). Shoot densities and the number of leaves per shoot exhibited seasonal patterns, with the lowest densities and the smallest number of leaves per shoot recorded in winter and the highest densities and greatest numbers of leaves recorded in summer. There was no evidence of seasonal trends in leaf length.

Seasonal patterns in biomass and shoot density of seagrasses are generally consistent with the high growth rates that have been reported for temperate intertidal seagrasses during spring-summer (Kirkman et al. 1982; Larkum et al. 1984; Hillman et al. 1989; Conacher et al. 1994b; McKenzie 1994; Campbell & Miller 2002). These patterns have generally been attributed to annual cycles in photosynthetically available radiation, as well as factors such as temperature and available nutrients, or some combination of these factors. This is supported by the observed winter biomass minima recorded for New Zealand populations (Ramage & Schiel 1999; Ismail 2001; Turner & Schwarz in press). In a study of *Zostera* in Whangapoua Harbour, Schwarz (2004) predicted that total production of plants at mean sea-level would be reduced during the winter to < 20% of that in summer because of reduced solar radiation and shorter day length. Nevertheless, for the North Island at least, winter probably remains an important time for photosynthetic gains for intertidal plants, as high irradiance stress is reduced (Turner & Schwarz in press).

Seagrasses grow by the reiteration of rhizome internodes, shoots and roots (Tomlinson 1974; Duarte 1991a; Duarte et al. 1994; Marbà & Duarte 1998; Hemminga & Duarte 2000). The time interval between the initiation of two successive rhizome internodes or leaves is termed the plastochrone interval (Ford 1982; Brouns 1985). In estuaries on the Coromandel Peninsula, *Zostera*

has been found to produce one new rhizome internode every 5.4–13.0 days and one new leaf every 8.1–11.2 days in the summer (January–February) (ST, unpubl. data). These figures are similar to the values reported for *Z. capricorni* growing in other locations; for example, Larkum et al. (1984) reported that in Botany Bay, New South Wales, a new leaf was produced on each shoot on average every 13 days.

During the summer (January) period of highest productivity, leaf-blade elongation averaged 2.0–4.4 mm/day, and rhizome extension rates averaged 0.3–5.2 mm/day in Coromandel Peninsula estuaries (ST, unpubl. data). Turner et al. (1996) reported average leaf-blade elongation rates of 1.9–2.6 mm/day in October at sites in the Manukau Harbour, and rhizome extension rates of 2.1–2.7 mm/day between October and April at the same sites. Larkum et al. (1984) recorded *Z. capricorni* leaf growth rates as high as 16.2 mm/day in January at a site in Botany Bay, New South Wales.

3.5 LIMITS TO SEAGRASS BIOMASS AND PRODUCTION

There are a number of environmental factors that are critical determinants of whether seagrasses will grow and persist at a site. These include light and nutrients, which limit the photosynthetic activity of the plants, and physical-chemical parameters that regulate the physiological activity of seagrasses, including temperature, salinity, waves, currents and substrate characteristics. Broadly speaking, seagrasses occur between an upper limit imposed by exposure to desiccation at low tide, wave action and associated turbidity, and reduced salinity from freshwater inflows, and a lower limit imposed by light penetration to an intensity sufficient for net photosynthesis (Hemminga & Duarte 2000). Understanding the physiological and environmental factors required for *Zostera* growth is the first step to understanding the potential effects of environmental change, and therefore the ability of the plant to occupy space and survive, at any particular site.

3.5.1 Light

The annual photosynthetically available radiation that can be utilised by seagrasses is one of the primary environmental factors influencing photosynthesis, growth and productivity, as well as the depth distribution of seagrasses (Dennison & Alberte 1982, 1985; Dennison 1987; Hillman et al. 1989; Duarte 1991b; Dennison et al. 1993; Olesen & Sand-Jensen 1993). Plants will colonise suitable substrates to the depth at which the light intensity allows photosynthesis to exceed respiration on an annual basis; thus any significant reduction in light transmission through the water column will bring about a reduction in the depth to which the plants are able to survive. The consequences of physiological stress associated with light limitation include diminished growth and productivity, increased shoot mortality, and limited depth distribution (Bulthuis 1983; Zimmerman et al. 1991; Gordon et al. 1994; Czerny & Dunton 1995; Philippart 1995b; Kenworthy & Fonseca 1996; Longstaff et al. 1999; Peralta et al. 2002; Biber et al. 2005). Changes in light

regime are thought to have caused large-scale loss of seagrasses in the natural environment, and it is evident from international studies that maintaining adequate light regimes is a minimal requirement for the preservation of seagrass beds (Kenworthy & Haunert 1991; Duarte 1999; Batiuk et al. 2000). Therefore, it is important to understand the responses of seagrasses to different light conditions and the light conditions that will permit the maintenance and growth of seagrasses at a given site.

Seagrasses require high levels of light (generally 15%–25% incident radiation, which is more than some marine macroalgae and phytoplankton, which typically require < 5%) because of their complex below-ground structures, which include considerable amounts of non-photosynthetic tissues (Bulthuis 1983; Duarte 1991b; Kenworthy & Haunert 1991; Dennison et al. 1993; Hemminga & Duarte 2000; Spalding et al. 2003; Walker 2003). Light transmission in coastal waters is much lower than in clear ocean water, due to generally higher loads of particulates and dissolved organic substances. The resulting reduction in penetration of light through the water column can limit photosynthesis. Globally, there is a general relationship between the depth to which seagrasses can grow and water clarity, and the majority of seagrasses are confined to depths of less than 20 m, which is roughly equivalent to 11% of surface irradiance (Duarte 1991b). The same species may, however, have different light requirements in different habitats (Dennison et al. 1993), although the reasons for this are not well understood. Seagrasses that grow predominantly in the intertidal zone, such as those in New Zealand, must deal with fluctuating irradiance while submerged, as well as while exposed to the air during periods of low tide.

Photosynthetic rates of seagrass leaves are usually determined experimentally as the response to increasing light levels from complete darkness (Beer et al. 2001). A number of parameters, such as the maximum rate of light saturated photosynthesis and the intensity at which the onset of saturation occurs, can then be calculated and used to describe the degree of acclimation to the light environment of the target species at a given location. Photosynthetic rates of intertidal *Zostera* have been recorded as becoming light saturated at an irradiance intensity of c. 200 μmol photons m^{-2} s^{-1}, both in New Zealand (Schwarz 2004) and elsewhere (Vermaat & Verhagen 1996; Vermaat et al. 1997), which is consistent with acclimation to a high light environment (Schwarz 2004). Such characteristics enable the plants to deal with occasionally extremely high irradiance when exposed to the air during low tide.

A wide range of morphological and physiological responses to changes in light intensity, at all levels of plant structure and function, have been reported for *Z. capricorni* from Moreton Bay, Queensland, in seawater aquaria experiments (Abal et al. 1994; Grice et al. 1996). For example, plants grown under high light conditions were found to have smaller shoots, higher biomass, higher productivity, lower leaf nitrogen content, and less chlorophyll-*a* and -*b*, than plants grown under low light conditions (Abal et al. 1994).

3.5.2 Nutrients

Light has generally been considered to be the primary resource that limits the growth of most seagrasses, with nutrient (nitrogen and phosphorus) availability regarded as a secondary factor (Short 1987; Hillman et al. 1989; Hemminga & Duarte 2000; Touchette & Burkholder 2000; but see also Alcoverro et al. 2001). However, there has been relatively limited research towards understanding the nutritional ecology of seagrasses or their physiological responses.

Seagrasses can use nitrogen and phosphorus from both sediment pore-water and the water column, the former generally being considered the primary source (Short 1987; Hillman et al. 1989; Lopez et al. 1998; Hemminga & Duarte 2000). In general, seagrasses are considered to be nitrogen-limited when growing in sandy or organic sediments, and phosphorus-limited in carbonate sediments (Short 1987; Hemminga & Duarte 2000; Touchette & Burkholder 2000). Nutrient limitation of seagrass production has been demonstrated experimentally for populations located at various sites around the world, with evidence that seagrass morphology, physiology, growth, photosynthetic performance, distribution and abundance, and seasonal cycles may be linked to available nutrient resources (Harlin & Thorne-Miller 1981; Short 1987; Fourqurean et al. 1995; Lee & Dunton 1999; Touchette & Burkholder 2000).

Many seagrasses respond favourably to low or moderate nitrogen or phosphorus enrichment (Harlin & Thorne-Miller 1981; Williams 1990; Reusch et al. 1994; Agawin et al. 1996; Reusch & Williams 1998; Peterson & Heck 1999, 2001; Udy et al. 1999). Following nitrogen enrichment at a site in Otago Harbour, Ismail (2001) reported an increase in canopy height, below-ground biomass and chlorophyll-*a* and -*b* content, but not in shoot density, above-ground biomass, leaf growth rates or tissue carbon and nitrogen content in *Zostera*, indicating that the plants may have been nutrient limited during the summer. Udy & Dennison (1997a,b) reported changes in morphological and physiological characteristics (e.g. increased growth and biomass, increased total amino acid content of leaves, and increased tissue nutrient contents) of *Z. capricorni* in response to elevated nitrogen and phosphorus levels in Moreton Bay, Queensland.

The nutritional content of seagrass tissue has been used to infer nutrient limitation for seagrass growth. Duarte (1990) has suggested that the growth of seagrasses is likely to be limited by nitrogen when leaf-tissue nitrogen content is below 1.8% dry weight or the atomic carbon:nitrogen ratio is above 20; or by phosphorus when leaf-tissue phosphorus content is below 0.2% or the atomic carbon:phosphorus ratio is greater than 474. While there are limited data available for New Zealand, comparison of the leaf nitrogen and phosphorus contents of seagrass collected from Coromandel Peninsula estuaries with median values for seagrass beds, suggests that these plants may have been slightly deficient in both nitrogen and phosphorus at some sites and during some periods of the year, especially during the summer (Turner & Schwarz in press). A similar tendency is inferred for Otago Harbour, where Ismail (2001) presented results to show that in summer, pore-water ammonium concentrations were below the threshold values that were suggested as limiting for growth of *Zostera marina* by Dennison et al. (1987).

Excessive nitrogen loading in the water column can inhibit seagrass growth and survival. This may be an indirect effect resulting from stimulation of phytoplankton and epiphytic algal growth and associated light reduction, or a direct physiological effect resulting from high internal nitrogen concentrations causing a metabolic imbalance (Burkholder at al. 1992; Van Katwijk et al. 1997; Hemminga & Duarte 2000; Touchette & Burkholder 2000; Invers et al. 2004).

Compared with rates reported internationally, moderate rates of nitrogen fixation (measured as acetylene reduction) have been reported in New Zealand estuarine sediments in which *Zostera* plants were growing (mean $\pm$ 95% confidence interval: 15.2 ± 2.8 µmol C_2H_4 m^{-2} h^{-1}), with rates of nitrogen fixation being closely correlated with the dry weight of the roots (Hicks & Silvester 1990). Hicks & Silvester (1990) suggested that nitrogen fixation may contribute significantly to the nutrition of seagrass in these estuaries, with inputs of 8.3 kg nitrogen ha^{-1} year^{-1} predicted for areas with *Zostera* compared with 1.6 kg nitrogen ha^{-1} year^{-1} in adjacent open areas. However, the assimilation of fixed nitrogen was not proven in this study, and the ecological significance of nitrogen fixation in the context of associated de-nitrification in New Zealand seagrass systems remains to be quantified.

3.5.3   Sediment

Seagrasses depend directly on sediment for nutrients and anchorage; thus seagrass distribution and abundance is strongly related to sediment characteristics. In their literature review, Batiuk et al. (2000) found that seagrasses have a limited range in their ability to tolerate selected sedimentological variables, including sediment grain-size (0.4%–30% fines: < 64 µm), sediment organic matter content (0.4%–12%) and pore-water sulphide concentrations (< 1 mM). Seagrasses themselves also have a marked effect on the chemical and microbiological characteristics and dynamics in their sediment environment through their production of detritus and the flux of oxygen from their roots and rhizomes (Moriarty & Boon 1989; Hemminga & Duarte 2000).

The relative proportion of above-ground (comprising shoots and leaves) to below-ground (comprising roots and rhizomes) biomass differs from place to place. For example, where *Zostera* grows in sandy sediment in Whangapoua Harbour, Coromandel Peninsula, there were persistent root and rhizome layers to a depth of 7 cm below the surface, and there was a higher relative proportion of below-ground to above-ground biomass (Schwarz et al. 2004). In contrast, a seagrass bed in much muddier sediments in Whaingaroa (Raglan) Harbour had live rhizomes and roots to a depth of only 3 cm, and there was a lower relative proportion of below-ground to above-ground biomass, despite the above-ground biomass being similar at the two sites. There may be several possible explanations for the differences in root development, but the most likely is related to the characteristics of the sediment: because estuarine sediments are periodically covered with water, they contain low levels of oxygen; these oxygen-poor sediments can be a harsh habitat as, with ample organic matter, sediment bacteria produce reduced compounds, such as sulphide, which are toxic to plants (Moriarty & Boon 1989; Carlson et al. 1994; Mills & Fonseca 2003). Nevertheless, healthy seagrasses can counter this stress by transporting

oxygen from their leaves to their roots, and using this for respiration and nutrient uptake (Sand-Jensen et al. 1982). Some of the oxygen is also lost from the roots to the surrounding sediment, which helps to maintain an oxidised zone around the plant roots and reduces the likelihood of harmful toxins accumulating (Carlson et al. 1994; Pederson et al. 1998; Terrados et al. 1999; Hemminga & Duarte 2000; Azzoni et al. 2001; Enríquez et al. 2001).

In New South Wales and Queensland, *Z. capricorni* has generally been found to grow better in coarse than fine sediments, with areas where *Z. capricorni* is sparse being characterised by the presence of relatively fine sediments (Young & Kirkman 1975; Larkum et al. 1984; Conacher et al. 1994b). However, coarser sediments are generally lower in nutrients and organic matter, so that there is a need for better developed nutrient absorptive systems at sites where sediments become sandier (McKenzie 1994). McKenzie (1994) suggested that the increase in sand at a site in Cairns Harbour might have contributed to observed decreases in the distribution and biomass of *Z. capricorni*, because the availability of nutrients affects growth, distribution, morphology and seasonal population cycles. *Zostera capricorni* has also been found to grow best in reducing substrates, so oxidised areas (e.g. sediment re-worked by wave-action) may not be an optimal environment for colonisation by seedlings or for vegetative growth (Larkum et al. 1984).

3.5.4 Tidal regime and aerial exposure

At the upper intertidal limit of seagrass distribution, environmental factors other than the photosynthetically available radiation, including exposure to desiccating winds or direct sunlight, restrict seagrass growth and productivity. In New Zealand, *Zostera* is predominantly intertidal, and during periods of the tidal cycle when the plants are exposed to air they can experience extended periods of high light intensities and higher temperatures than found in the surrounding water. Although exposure at low tide can be an important time for photosynthetic gains for intertidal seagrasses (Vermaat et al. 1997; Schwarz 2004), long exposure times and the absence of a protective layer of water may result in desiccation and photoinhibition due to high irradiance, which in turn can lead to a decline in growth and productivity (Harrison 1982; Bulthuis & Woelkering 1983b; Bulthuis 1987; Adams & Bate 1994; Erftemeijer & Herman 1994; McKenzie 1994; Björk et al. 1997, 1999; Hemminga & Duarte 2000; Enríquez et al. 2002; Boese et al. 2003; Tanaka & Nakaoka 2004).

In three estuaries on the eastern Coromandel Peninsula, seagrass at sites with moderate periods of emersion had greater biomass production than at sites with extended periods of emersion (Turner & Schwarz in press). The differences in observed biomass between sites could reflect site-specific differences in elevation above mean low water, exposure times when low spring tides coincide with daylight hours (especially during the summer), and tidal-flat topography (which affects the way water drains from the beds at each of the sites) (Turner & Schwarz in press). On intertidal platforms on the Kaikoura Peninsula, *Zostera* patches on the low shore and associated with tide-pools had larger leaf area indices and greater total biomass than patches further up the shore or not associated with tide-pools (Ramage & Schiel 1999).

3.5.5 Water movement

Based on an extensive review of the literature, Batiuk et al. (2001) reported that seagrasses appear to have a limited range in their ability to tolerate water movement and wave activity.

Various seagrass-bed attributes (e.g. bed fragmentation, continuity of cover, patch size and shape, and complexity of patch perimeter), as well as attributes of the plants themselves (e.g. biomass, shoot density, plant architecture, and colonisation rates), have been found to be strongly related to the physical setting of an area (Kirkman & Kuo 1990; Marbà et al. 1994; Robbins & Bell 1994; Marbà & Duarte 1995; Fonseca 1996; Turner et al. 1996; Fonseca & Bell 1998; Van Katwijk & Wijergangs 2004). The spatial configuration of seagrass beds, which may vary from continuous cover over hundreds of metres to discrete patches that are metres to tens of metres across the largest dimension, is strongly related to the level of wind-generated wave action and currents (Fonseca et al. 1983; Fonseca & Kenworthy 1987; Fonseca 1996; Turner et al. 1996; Fonseca & Bell 1998; Koch & Gust 1999; Frederiksen et al. 2004b). Seagrass beds may be affected directly through impacts on bed development (e.g. transportation of seeds and vegetative propagules, uprooting of seedlings, and damage to mature plants), or indirectly through the erosion, transport and deposition of sediment, nutrients or organic matter. Increased mechanical disturbance associated with wave exposure and current speed may lead to a reduction in the vegetative spread of the plants and the inhibition of seedling colonisation, resulting in patchy seagrass beds.

Wind-generated wave dynamics and tidal currents are also important factors influencing the physical, chemical and biological attributes of seagrass beds (Pihl 1986; Fonseca & Kenworthy 1987; Murphey & Fonseca 1995; Fonseca 1996; Turner et al. 1999; Hovel et al. 2002; Moran et al. 2004).

3.6 THE SEAGRASS COMMUNITY

Seagrasses are important in sustaining a wide range of plant and animal species. The emergent leaves and subsurface root-rhizome system of seagrasses provides greater physical heterogeneity and structural complexity than found in the surrounding sediment (Howard et al. 1989; Hemminga & Duarte 2000). Through habitat modification and the associated changes in local biological, chemical and/or physical conditions, seagrasses may strongly influence the structure and functioning of associated plant and animal communities. A sound understanding of the functioning of seagrass communities is important if seagrass habitats are to be managed successfully.

There is a large diversity and abundance of organisms associated with seagrass habitats compared with unvegetated habitats. Seagrass communities typically include epiphytes (microscopic organisms, single-celled plants, filamentous algae, algal sporelings and encrusting algae), microfauna and sessile epifauna that colonise the seagrass; algal films, macroalgae and sessile and mobile epifauna on the sediment surface; infauna living in the sediment among the

rhizomes; phytoplankton and zooplankton in the water column associated with seagrass beds; and epibenthic fauna, which are larger mobile animals (e.g. fish and crabs) associated loosely with the seagrass bed. The precise components of the community will depend on the sediment type, salinity, tidal position and location, as well as the seagrass species itself.

There is still relatively little understanding of the importance of seagrass habitat for associated plant, invertebrate and fish communities in estuarine and shallow coastal-water areas around New Zealand, although a small number of quantitative investigations have been undertaken.

3.6.1 Benthic communities

It has been widely documented in international studies that seagrass habitat supports greater macrofauna species diversity, abundance and biomass than adjacent unvegetated, soft-sediment habitat, and that there are correlations between increased faunal abundance and diversity and some measures of seagrass structural complexity (e.g. shoot density and leaf length) (Virnstein et al. 1983; Summerson & Peterson 1984; Posey 1988; Ansari et al. 1991; Edgar et al. 1994; Heck et al. 1995; Boström & Bonsdorff 1997; Connolly 1997; Mattila et al. 1999; Lee et al. 2001; Somerfield et al. 2002). A comparison of macrofauna abundances in seagrass habitat with those in unvegetated habitats from around the world demonstrates the habitat value of seagrass beds to estuarine fauna: animal densities in seagrass beds are 2–25 times greater than in adjacent unvegetated areas (Dunton 1998). However, the faunal assemblages associated with seagrass beds are generally not specific to seagrass habitat, but largely comprise species that are also found in other habitats. Furthermore, other vegetated systems in the direct environment of seagrass beds may harbour equally abundant and diverse or even richer assemblages. Therefore, although seagrass beds provide valuable benthic substratum, they offer no exceptionally favourable habitat compared with other habitats (Howard et al. 1989; Hemminga & Duarte 2000; Spalding et al. 2003).

In New Zealand, studies of the animal communities associated with seagrass beds and the adjacent unvegetated sediment have included meiofauna (e.g. Hicks 1986, 1989; Bell & Hicks 1991) and macrofauna (e.g. Alderson 1997; Woods & Schiel 1997; Turner et al. 1999; Berkenbusch et al. 2000; Van Houte-Howes et al. 2004; and see review by Inglis 2003). From these studies, it has been suggested that there is a greater abundance and diversity of macrofauna, as well as different functional or taxonomic groups, within *Zostera* beds than in the surrounding unvegetated sediments in New Zealand estuaries (see Inglis 2003). However, this generality has been challenged by a recent study of macrofauna communities within seagrass beds and the adjacent unvegetated sediment in Coromandel Peninsula estuaries (Van Houte-Howes et al. 2004). The results from this study indicate that the presence of seagrass does have an effect on macrofauna communities but that this effect is complex. Rather than being a reflection of the presence or absence of seagrass per se, macrofaunal community characteristics were found to vary with distance from the seagrass-unvegetated sediment boundary, both within the seagrass bed itself and the adjacent unvegetated sediment. These results emphasise the importance of

understanding the linkages between habitats in heterogeneous estuarine landscapes and their effects on the abundance, diversity and biomass of macrofauna communities, as the effect of the seagrass itself may extend beyond the margins of any one patch or bed.

Other New Zealand studies have resulted in similar conclusions. For example, a study of the influence of seagrass on the recruitment of meiofaunal copepods in a seagrass bed in Pauatahanui Inlet (near Wellington) found that variation in landscape features and events that cause variation over the spatial scale of a seagrass bed may produce localised differences in copepod densities (Bell & Hicks 1991). This demonstrates that in order to understand the importance of landscape patterns on seagrass fauna it is important to understand vegetation patch dynamics as well as faunal responses. The results of a study of the macrofauna communities associated with seagrass patches in Manukau Harbour and Whangapoua Harbour (Coromandel Peninsula) demonstrated that the spatial patterning of seagrass habitat at the landscape scale (e.g. fractal dimension and patch isolation) can affect community composition, independent of the patch-scale characteristics (e.g. patch size, seagrass biomass and percentage cover) of the seagrass beds (Turner et al. 1999).

It is increasingly recognised that there is considerable variability in the faunal assemblages associated with seagrass beds (Howard et al. 1989; Hemminga & Duarte 2000). This may be a reflection of the varying physical-chemical environment between seagrass beds (with respect to hydrodynamic conditions, depth, etc.), the variable landscape setting of seagrass beds within the broader coastal system, and that many species only spend part of their life-cycle associated with seagrass beds, resulting in alternating periods of presence and absence of a species.

3.6.2 Fish assemblages

One of the most widely cited functions of seagrasses is their role in providing both habitat (e.g. seagrass leaves provide protection from predators) and sources of food (e.g. organic matter produced by decaying seagrass and epiphytic organisms) for fish, crabs and shrimps, including many species that are ecologically or commercially important in other ecosystems (Heck & Thoman 1984; Bell et al. 1988; Bell & Pollard 1989; Heck et al. 1989; Ferrell & Bell 1991; Edgar & Shaw 1993, 1995a,b; Hoss & Thayer 1993; Connolly 1994b; Eggleston et al. 1998; Jenkins & Wheatley 1998; Mattila et al. 1999; Hemminga & Duarte 2000; Spalding et al. 2003; Kwak & Klumpp 2004). As with invertebrate assemblages, there is great variability in fish species diversity and abundances among seagrass beds (Hemmiga & Duarte 2000). This variability is attributed to the vegetation structure of the beds and the extent of larval and juvenile settlement in the beds, as well as post-settlement mortality and migration processes, the location of the beds relative to other fish habitats and the physical-chemical environment of the beds. Seagrass beds may, therefore, vary considerably in terms of their value to fish assemblages.

There have, however, been very few studies on the significance of seagrass habitat to fish in New Zealand estuarine and coastal waters. Recent research in New Zealand has shown that seagrass, especially that which usually remains submerged at low tide, provides important nursery functions for a range of juvenile fish species, especially snapper (*Pagurus auratus*) (Morrison & Francis 2001a,b).

3.6.3 Habitat inter-linkages

A number of international studies have demonstrated that seagrass habitat does not exist in isolation and should not be viewed as separate, unconnected habitat, but rather is part of a habitat mosaic with other habitats (Irlandi & Crawford 1997; Micheli & Peterson 1999; Hemminga & Duarte 2000; Williams & Heck 2000; Wahl 2001; Spalding et al. 2003; Pittman et al. 2004; Van Elven et al. 2004; Bloomfield & Gillanders 2005). Seagrass habitat is a component of, and has a role in the functioning of, a wider suite of estuarine and coastal landscapes ('seascapes'), with linkages to both the surrounding unvegetated sand and mud, and other habitats (e.g. saltmarsh, mangroves, macroalgae and oyster reefs). These interconnections between ecosystem components are mediated through the transfer of organic matter and nutrients (Connolly et al. 2005), and animal movements: many marine animals have been found to move between different habitats on a daily or seasonal basis, or during various parts of their life-cycles (Orth & Van Montfrans 1987; Bell & Pollard 1989; Ferrell & Bell 1991; Sogard & Able 1994; Jenkins & Wheatley 1998; Hemminga & Duarte 2000; Linke et al. 2001; Nagelkerken & Van der Velde 2004). The spatial proximity of seagrass beds to other habitat types may have a significant effect on species diversity, abundance and distributions (Sogard 1989; Lipcius et al. 2005).

The effective management and conservation of seagrass habitat in New Zealand will require consideration of the relationships between seagrass and other components of the estuarine and coastal ecosystems of which it is a part. Understanding the functional roles of linkages between habitats in heterogeneous landscapes, and their effects on the structure and dynamics of estuarine and coastal communities, is essential if we are to manage entire ecosystems. Only by maintaining the total landscape to which seagrass belongs can we maintain the resilience of seagrass habitats and the diversity of associated communities (Virnstein 1995; Hovel & Lipcius 2001).

4. Seagrass distribution and abundance in New Zealand

Seagrass is predominantly intertidal in New Zealand, forming extensive monospecific beds or mosaics of discrete patches surrounded by unvegetated sediments on estuarine sand-flats at mid- to low tide levels (Turner et al. 1996, 1999; Van Houte-Howes et al. 2004). The beds may extend as subtidal fringes into the shallow subtidal areas of sheltered estuaries, and permanently submerged beds of seagrass have been recorded around offshore islands (e.g. Slipper Island and Great Mercury Island off the eastern Coromandel Peninsula) (Grace & Grace 1976; A-MS, pers. obs.). Seagrass beds also occur in association with sediment-filled crevices and tide-pools on open-coast intertidal platforms around the eastern coast of New Zealand (e.g. Te Angiangi Marine Reserve, Kaikoura Peninsula), where the seagrass is interspersed with algal beds and biological assemblages more characteristic of rocky, intertidal communities (Woods & Schiel 1997; Ramage & Schiel 1998, 1999). Spalding et al. (2003) estimated that there are 44 km^2 of seagrass habitat in New Zealand. This is small compared with other regions: for example, there is an estimated 71 400 km^2 in eastern Australia and 30 000 km^2 in Indonesia.

While *Zostera* is known to occur throughout the mainland coast of New Zealand, its distribution is not well documented. A recent review has suggested that while widespread, seagrass is likely to be a relatively uncommon habitat in most estuarine systems around New Zealand, particularly those that are shallow and turbid (Inglis 2003).

4.1 TRENDS IN SEAGRASS DISTRIBUTION, EXTENT AND CONDITION

Although seagrass systems are typically permanent over periods of years and decades, they can be highly dynamic, expanding into new areas and declining in others over relatively short timeframes (Clarke & Kirkman 1989; Olesen & Sand-Jensen 1994b; Turner et al. 1996; Spalding et al. 2003). Few studies have quantified temporal changes in the distribution, spatial extent (area) and condition of seagrass habitat in New Zealand in any detail, and there is a paucity of information on natural changes between years. In addition, in only a few instances has there been an evaluation of the contribution of different environmental factors and coastal processes to changes in seagrass distribution, extent and condition, and the ecological consequences of such changes have not been studied.

There have been few documented instances of seagrass loss in New Zealand. Available information suggests that seagrass habitat was once more widespread around New Zealand, and that both intertidal and subtidal areas of seagrass have declined at a number of localities, with the greatest losses occurring since the 1920s/1930s (MfE 1997; see Inglis 2003 for a review). Overall losses are

probably much greater than have been estimated to date. Historical information on seagrass distribution and extent is valuable for understanding the patterns of natural or human-induced (anthropogenic) change in an area, and is also useful for assessing the ecological significance of any new losses. However, the availability of reliable aerial photography and good quality field data limits the analysis of historical change to the last 40–50 years. This is an important limitation, as it is too short a time period to detect long-term cycles.

The causes of the documented decline in seagrass habitat around New Zealand are generally unclear, and have been variously attributed to a range of different human activities and natural events (MfE 1997; Inglis 2003). These include increased sedimentation and turbidity, the discharge of untreated sewage and industrial waste, and coastal development. Changes in sediment regimes (i.e. turbidity, sedimentation rates, or sediment textural characteristics), either as a result of land-based or coastal activities, have been identified as one of the most serious threats to the integrity of New Zealand's estuarine and coastal ecosystems (MfE 1997; Morrisey & Green 2000; Inglis 2003). Loss of *Z. capricorni* beds in eastern Australia, where up to 50% of the area of seagrass beds in numerous New South Wales estuaries has been reported as lost, has been attributed to smothering by sediment, light reduction, and dredging and construction (Walker & McComb 1992; Short & Wyllie-Echeverria 1996; Kirkman 1997; Seddon et al. 2000; Coles et al. 2003).

Even fewer studies have documented incidences where seagrass may have retained its historic coverage or increased in distribution, or the environmental conditions prevailing at any such localities. There are positive indications that seagrass beds are expanding in some New Zealand estuaries where they had formerly been reduced, as a consequence of improvements in water quality (Inglis 2003). However, there needs to be a better understanding of the requirements and potential for recovery after loss.

To effectively manage and conserve seagrass habitat, mapping and monitoring must be initiated. The relative paucity of information on the extent of natural changes in seagrass populations means that it is difficult to separate these from the impacts of anthropogenic activities.

4.2 EXAMPLES OF SEAGRASS DECLINE IN NEW ZEALAND

Comparisons of historical aerial photographs of Tauranga Harbour have shown that the total area of seagrass beds has declined from 4437 ha in 1959 to 2933 ha in 1996, which is a reduction of 34% over a period of less than 40 years (Park 1999a,b, 2001). The area of greatest decline has been in the enclosed upper reaches of the western margins of the harbour, where there has been a 69% reduction in the area of seagrass (Park 1999b, 2001). Subtidal areas have experienced the greatest loss: 90% of the subtidal beds in the whole harbour and 95% of those in the southern harbour have been lost (Park 1999b). Seagrass beds in the shallow subtidal areas and sub-estuaries with large catchments have been affected more than those in areas near the harbour entrance and in sub-estuaries with little catchment run-off (Park 1999a,b). The available information

indicates that sediment, and possibly nutrient loading, has played a major part in the documented changes in seagrass abundance in the harbour (Park 1999b, 2001). Other causes of seagrass loss in the harbour include reclamation of the seafloor and grazing by the introduced black swan (*Cygnus atratus*) (Park 1999a,b). Park (1999a,b) suggested that the decline in seagrass beds in the harbour may be slowing, and in some areas seagrass may be increasing in abundance. This is attributed to improvements in environmental practices, particularly the removal of point nutrient sources to the harbour (Tauranga sewage was discharged to the harbour until 1994) and reductions in the amount of land run-off and associated nutrients and sediments (Park 1999a,b).

Comparisons of historical aerial photographs of Whangamata Harbour (Coromandel Peninsula) indicate that the intertidal seagrass beds increased in extent from 79 ha in 1944 to 101 ha in 1965, an increase in area of 28% (Cawthron Institute 2000). The beds subsequently declined in spatial extent to 60 ha in 1998, a decrease of 41% (Cawthron Institute 2000). As well as a change in the total extent of seagrass beds in the harbour, the distribution of the remaining beds also changed over the same time period, declining in the upper reaches and increasing in the middle reaches of the estuary (Fig. 1). This decline in spatial extent and change in distribution has been attributed to the expansion of mud-flats, which has reduced the amount of suitable habitat for seagrass survival. Some of the areas where seagrass occurred historically have now been completely overgrown by mangroves (Fig. 1).
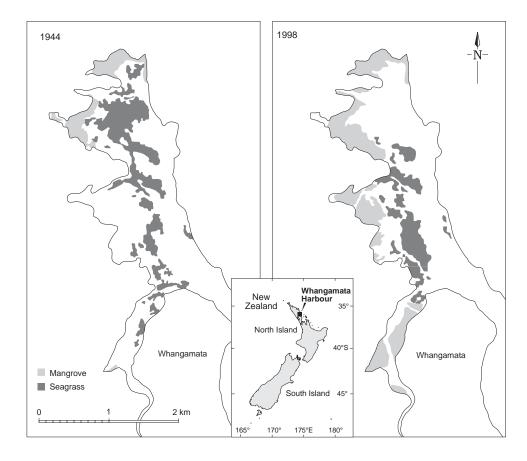

Figure 1. Changes in the distribution and extent of seagrass (*Zostera capricorni*) and mangrove habitat in Whangamata Harbour between 1944 and 1998. Based on aerial images from Cawthron Institute (2000).

5. Threats to seagrass

There have been no recent assessments of the overall condition of New Zealand's estuaries and therefore of the contemporary threats to seagrass habitats (Inglis 2003). The predominantly estuarine and near-shore coastal distribution of seagrass in New Zealand means that seagrass is likely to be particularly vulnerable to anthropogenic disturbance associated with catchment land-use activities and coastal development. In eastern Australia, estuarine seagrass communities are increasingly considered to be the most threatened of the seagrass habitats (Coles et al. 1989; Lee Long et al. 1996; Coles et al. 2003).

Declines in seagrasses have been occurring worldwide, with increasing frequency during recent decades (Walker & McComb 1992; Short & Wyllie-Echeverria 1996; Hemminga & Duarte 2000; Duarte 2002; Green & Short 2003). International studies have demonstrated that seagrass beds are subject to a variety of natural and anthropogenic disturbances, such as storm damage, grazing by herbivores and disease, as well as threats caused by point and non-point sources of pollution, decreasing water clarity, excessive nutrients, increased sedimentation and direct mechanical damage (e.g. dredging and propeller scarring). In many cases, several factors interact to make the process of loss more complex, and natural disturbances may be exacerbated by interactions with anthropogenic perturbations (Pulich & White 1991; Burkholder et al. 1992; Walker & McComb 1992; Van Lent et al. 1995; Short & Wyllie-Echeverria 1996; Kirkman 1997; Livingston et al. 1998; Moore & Wetzel 2000; Spalding et al. 2003; Walker 2003; Ibarra-Obando et al. 2004).

The most ubiquitous and pervasive cause of seagrass decline is reduction in the amount of photosynthetically available radiation. There are three major factors that can cause a reduction in light availability:

- Chronic increases in dissolved nutrients, leading to the proliferation of phytoplankton, macroalgae or algal epiphytes on seagrass leaves and stems (eutrophication)
- Chronic increases in suspended sediments, leading to increased turbidity and potentially increased sedimentation
- Pulsed increases in suspended sediments and/or phytoplankton, which cause a dramatic reduction in light penetration for a limited time (Walker & McComb 1992; Walker 2003)

The run-off of nutrients and sediments into estuarine and coastal areas as a result of human activities on land is considered to represent the greatest threat to seagrasses worldwide (Hemminga & Duarte 2000; Coles et al. 2003; Green & Short 2003; Walker 2003).

Relatively short-term stressful conditions, especially during critical periods, can have long-term consequences for seagrasses, even after environmental conditions have improved. Therefore, it is necessary to consider the impacts of pulsed or extreme events as well as changes in average conditions when determining the threats to seagrass survival (Moore et al. 1997; Longstaff & Dennison 1999).

5.1 ANTHROPOGENIC PROCESSES

Seagrasses are particularly susceptible to anthropogenic disturbances, including coastal developments, such as jetty, marina and harbour construction; land reclamation; industrial pollution and storm-water run-off along shorelines; run-off from catchment activities; boat moorings and dredging; and various recreational and commercial activities (Kemp et al. 1983; Cambridge & McComb 1984; Shepherd et al. 1989; Walker & McComb 1992; Nienhuis et al. 1996; Hemminga & Duarte 2000; Kendrick et al. 2002; Green & Short 2003; Walker 2003; Duarte et al. 2004). The frequency of these activities and their effects on seagrasses are likely to increase with increasing human populations and use of estuaries and coastal areas.

5.1.1 Increases in sediment loading

The growth and productivity of seagrasses relies significantly upon the amount of photosynthetically available radiation that penetrates the water column to reach submerged leaves (Kenworthy & Haunert 1991; Dennison et al. 1993). When sediment loading becomes excessive, there is increased turbidity in the water column overlying the seagrasses and reduced light penetration through the water, resulting in reduced photosynthesis and growth, and ultimately declines in seagrass survival (Cambridge & McComb 1984; Larkum et al. 1989; Shepherd et al. 1989; Giesen et al. 1990; Onuf 1994; Moore et al. 1997; Vermaat et al. 1997; Bach et al. 1998; Hall et al. 1999; Longstaff & Dennison 1999; Hemminga & Duarte 2000; Ingram & Dawson 2001; Coles et al. 2003; Spalding et al. 2003; Walker 2003). Seagrass species vary widely in their tolerance to light deprivation, and the nature of the response (e.g. physiological or morphological responses) is dependent on the intensity and duration of light reduction, as well as the influence of other environmental conditions (Longstaff & Dennison 1999).

In extreme cases, excessive sediment loads may result in the actual smothering and burial of seagrasses, especially in low wave-energy environments, where fine sediments are deposited (Kirkman 1978; Shepherd et al. 1989; Duarte et al. 1997; Manzanera et al. 1998; Terrados et al. 1998). Layers of sediment that settle on top of the plants can have the same effect as increases in turbidity, by preventing light from reaching the plants. Most seagrasses can survive moderate inundations of sediment, with mortality occurring beyond a given threshold of sediment accretion (Fonseca 1996; Duarte et al. 1997; Vermaat et al. 1997; Manzanera et al. 1998). The effects of sediment smothering are dependent on the properties of the sediment, the duration of sediment inundation, the volume of sediment and the depth to which the plant is smothered, as well as the morphology of the species involved (Clarke & Kirkman 1989). Fonseca (1996) reported that *Zostera* beds only suffered significant shoot mortality when 50% of the plant's height was buried under sediment for c. 3 weeks. Vermaat et al. (1997) found that Mediterranean *Zostera noltii* was able to redirect the horizontal rhizome to survive burial, and that plants successfully grew through a sediment layer of 2 cm in 4 months; they recommended, as a practical range, that for the maintenance of seagrass beds, short-term sedimentation occurring over time spans of < 2 months should not exceed

5 cm. Further studies are needed to predict the capacity of New Zealand *Zostera* to respond to changes in sedimentation patterns.

Once an initial decline has begun, further losses may follow due to feedback effects. For example, sediments will no longer be stabilised and thus will erode more quickly, resulting in the loss of more seagrass, reduced recolonisation by seagrasses and increased burial of plants (Shepherd et al. 1989; Giesen et al. 1990; Walker & McComb 1992). The turbidity resulting from the increased sediment loads in the water can also lead to further degradation of the beds.

Catchment land-use activities, such as land clearance for coastal developments, forestry and agricultural purposes, are generally considered to be the primary causes of increases in the rates of soil erosion and consequently in sediment transport into estuarine and coastal waters (MfE 1997; Morrisey & Green 2000). It is currently difficult to know what effect catchment practices have had on seagrass in New Zealand, although it is likely that poor catchment practices have increased the stresses on seagrass communities, and contributed to their overall decline in a number of areas (Park 1999a,b, 2001; Inglis 2003).

5.1.2 Increases in nutrient loading (cultural eutrophication)

Increases in nutrient loading, particularly nitrogen, may arise from land-based point (e.g. sewage effluent and urban/stormwater outfalls) and non-point (e.g. groundwater seepage from septic systems and agricultural run-off) sources entering estuarine and coastal waters. In some cases, where seagrass growth is limited by available nutrients, localised increases in nutrient levels may be favourable for seagrasses (Orth 1977a; Harlin & Thorne-Miller 1981; Fourqurean et al. 1995; Udy et al. 1999). More often, however, increased nutrient loading is cited as a major cause of the decline, or lack of recovery, of seagrass beds (Nienhuis 1983; Orth & Moore 1983; Cambridge et al. 1986; Neverauskas 1987b; Shepherd et al. 1989; Burkholder et al. 1992; Lapointe et al. 1994; Short & Burdick 1996; Short et al. 1996; Hemminga & Duarte 2000; Deegan 2002; Kendrick et al. 2002; Spalding et al. 2003; Walker 2003; Hale et al. 2004).

A variety of detrimental effects associated with increases in nutrient levels have been identified. Increases in nutrient loading in estuarine and coastal waters can promote the growth of phytoplankton, epiphytic algae and bottom-living and free-floating macroalgae (eutrophication) (Harlin & Thorne-Miller 1981; Bulthuis & Woelkerling 1983a,b; Borum 1985; Cambridge et al. 1986; Silberstein et al. 1986; Neverauskas 1987a; Shepherd et al. 1989; Lapointe et al. 1994, 2004; Onuf 1996; Frankovich & Fourqurean 1997; Valiela et al. 1997; Walker 2003). This enhanced growth will reduce the amount of light reaching seagrass beds through either direct shading or increases in water-column turbidity, which will in turn reduce the plants' photosynthetic capability and thus deplete storage materials, with negative impacts on seagrass growth, productivity and distribution (Harlin & Thorne-Miller 1981; Van Montfrans et al. 1984; Borum 1985; Silberstein et al. 1986; Shepherd et al. 1989; Walker & McComb 1992; Short et al. 1996; Cardoso et al. 2004; Irlandi et al. 2004). In addition, the increased growth of epiphytes can have other impacts on seagrasses, such as reducing the diffusion of gases and nutrients to seagrass leaves (Borowitzka & Lethbridge 1989; Shepherd et al. 1989; Walker 2003; Irlandi et al. 2004).

The inter-relationship between grazing invertebrates and epiphyte abundance on seagrasses may also contribute to seagrass loss. In the presence of grazers there may be a substantial reduction in epiphyte biomass, with concomitant effects on the maintenance of growth, productivity and depth distributions of seagrasses (Howard & Short 1986; Shepherd et al. 1989; Hemminga & Duarte 2000; Hughes et al. 2004; Frankovich & Zieman 2005; Hays 2005). However, in the absence of grazing invertebrates, or where there is a rapid accumulation of nutrients leading to growth rates of epiphytes that are too high to allow control by grazers, there may be a reduction in seagrass growth rate and productivity.

Eutrophication may not only result in a reduction in light availability, but also an increased loading of sediments with organic matter and the development of highly reducing conditions in the sediment, anoxia of bottom waters, and an increase in nutrient concentrations to potentially toxic levels, each of which can have a negative effect on seagrass functioning (Hemminga & Duarte 2000).

The magnitude of nutrient loading is largely unknown for most of New Zealand's estuarine and coastal areas. However, continued increases in nutrient loading may result in long-term and/or irreversible effects on estuarine and coastal ecosystems, including seagrasses, as has been reported elsewhere (Howarth et al. 2002; Seitzinger et al. 2002). Specific examples include Moreton Bay, Queensland (Abal et al. 2003; Tarte 2004) and Chesapeake Bay, Virginia (Batiuk et al. 2000). The well-documented and negative responses of seagrasses to nutrient enrichment elsewhere in the world suggest that management action to restrict the release of nutrients from point and non-point sources to coastal waters in New Zealand would be warranted.

5.1.3 Direct physical habitat disturbance and mechanical damage

Activities such as the construction of bulkheads, groynes, breakwaters, piers, docks, pipelines and other hard structures, land reclamation, infilling, dredging, and the disposal of dredged spoil for coastal developments have been widely recognised as the major anthropogenic disturbances contributing to the immediate loss of seagrass habitat (Cambridge & McComb 1984; Larkum & West 1990; Loflin 1995; Burdick & Short 1999; Hemminga & Duarte 2000; Kendrick et al. 2002; Green & Short 2003; Spalding et al. 2003; Walker 2003). While seagrass loss due to direct physical disturbance is generally relatively localised in extent when compared with the more widespread changes associated with sediment and nutrient inputs, it may nevertheless be significant.

The direct and immediate effects of dredging through or near seagrass beds include physical disturbance and removal of the beds, as well as seagrass mortality from excessive burial. However, the indirect effects of dredging activities are equally important. Indirect losses often arise from the disturbance of sediments during dredging operations, which results in increased turbidity and suspended sediment loads in the water column (Quammen & Onuf 1993; Onuf 1994). While periods of reduced water quality may be temporary and may not have long-term impacts on seagrasses, if construction or dredging activity affects the hydrodynamic characteristics of a site (such as depth profile, current direction or velocity), the long-term survival of seagrass beds may be threatened (Cambridge et al. 1986; Giesen et al. 1990; Larkum & West 1990; Onuf 1994; Ingram & Dawson 2001); for example, the loss of seagrass in Stanley Bay,

Auckland Harbour, is believed to be linked to the construction of tide deflectors, which caused the formation of a tidal stream (Hounsell 1935, cited in Dromgoole & Foster 1983). Dredging activity may also alter sediment dynamics, resulting in the mobilisation of sediment contaminants, and modification of sediment chemistry and nutrient availability (Duarte et al. 2004). In addition, dredging may result in sedimentation of rich organic material; the decomposition of this, combined with reductions in plant productivity (i.e. small root-zone oxygen flux), can result in toxic concentrations of sulphide in the root-zone, which has negative impacts on seagrass biomass and survival (Eldridge et al. 2004).

One of the most direct adverse effects on seagrass beds is the damage caused by recreational boating activities (e.g. cutting by propellers, propeller wash, anchor and mooring damage, and boat groundings) which may result in significant, localised impacts on the physical integrity of seagrasses (Zieman 1976; Walker et al. 1989; Hastings et al. 1995a,b; Dawes et al. 1997; Creed & Filho 1999; Francour et al. 1999; Spalding et al. 2003; Milazzo et al. 2004). For example, propeller scarring can create a continuous line of seagrass damage that fragments the seagrass bed and increases the bed edge, which is vulnerable to erosion; this results in further scouring and deepening of the scoured area (Zieman 1976; Walker et al. 1989). As a consequence of increased bed fragmentation and bed-edge habitat, there may also be effects on associated animal communities (see Irlandi 1997; Eggleston et al. 1999; Frost et al. 1999; Bell et al. 2001; Bologna & Heck 2002; Hovel & Lipcius 2002). The potentially long-term negative impact of recreational boating activities on seagrass habitat has long been recognised internationally (Zieman 1976; Walker et al. 1989), and the cumulative impacts of such events can lead to the large-scale loss of seagrass beds from heavily trafficked areas (Francour et al. 1999). However, there is little information regarding the extent of any effect of recreational boating activities in New Zealand, and the areas of greatest potential impact have not been identified.

Other activities relating to boat operations have also been reported to impact on seagrasses, including the construction of docks, which shade the seafloor and prohibit light penetration (Loflin 1995; Burdick & Short 1999; Shafer 1999).

Some fishing activities may also impact on seagrass beds (Fonseca et al. 1984; Peterson et al. 1987; Meyer et al. 1999; González-Correa et al. 2005; Neckles et al. 2005). For example, harvesting of scallops by trawling or dragging through submerged seagrass beds may disturb the beds either through direct removal of seagrass or through increased turbidity.

Intertidal seagrasses are vulnerable to damage by activities such as trampling by humans and stock, horse riding, and off-road driving (Miller 1998; Ramage & Schiel 1999).

5.1.4 Pollutants

Pollution of coastal environments, either from point or diffuse sources, can result in significant changes in water and sediment quality, which in turn can influence seagrass beds. There is little or no information about the effects of toxic compounds on the growth and survival of seagrass in New Zealand estuarine and coastal areas. The relatively limited information available from

international studies suggests that heavy metals, antifoulants and organic booster biocides, oil and chemical oil dispersants, organic pollutants, and herbicides are all potentially harmful (Cambridge et al. 1986; Ward 1989; Short & Wyllie-Echeverria 1996; Bester 2000; Hemminga & Duarte 2000).

A number of recent studies have assessed the toxicological impacts of pollutants (including herbicides, heavy metals and petrochemicals) on *Z. capricorni* in coastal areas of eastern Australia. Results have indicated that anthropogenic pollutants have the capacity to impact on seagrass physiology (e.g. photosynthetic potential and amino acid content), even in acute exposure events (e.g. Haynes et al. 2000; Prange & Dennison 2000; Macinnis-Ng & Ralph 2002, 2003, 2004).

5.1.5 Introduced species

The introduction of exotic marine species, either deliberately or via ships' hulls or ballast water, presents a potential threat to seagrasses. Introduced species may become established and encroach upon local seagrass communities, with potentially significant negative effects on ecological function and biodiversity.

While there appears to be no information available about the effects of introduced species on seagrass in New Zealand, international studies have demonstrated that effects may occur. For example, seagrasses in Lindisfarne National Nature Reserve in north-east England have declined through a combination of a change in sedimentation pattern and encroachment by cord-grass (*Spartina anglica*) (Percival et al. 1998). In California, the Asian mussel (*Musculista senhousia*) has been shown to have variable effects on *Z. marina*, with dense mats of the bivalve impeding rhizome growth and vegetative propagation, but possibly enhancing leaf growth by pseudofaecal deposition (Reusch 1996; Reusch & Williams 1999; Williams & Heck 2000).

Die-back within beds of the seagrass *Posidonia oceanica* in the Mediterranean has been associated with invasion by the 'tropical' strain of the green seaweed *Caulerpa taxifolia*, which exhibits rapid vegetative growth, increases organic matter deposition, and produces toxic secondary metabolites that inhibit interspecific competitors (De Villèle & Verlaque 1995); this species is included in the Ministry of Fisheries' list of unwanted organisms, and has been identified as potentially causing serious problems should it invade New Zealand's marine environment (Ministry of Fisheries n.d.).

5.1.6 Global climate change

The effects of long-term climate change on seagrasses are not straightforward to predict, but they are likely to be significant. Potential impacts are likely to arise from rising sea levels, leading to longer submergence periods; changing tidal regimes, which have implications for light availability, exposure at low tide and water column turbidity; increased coastline regression and sediment erosion associated with sea-level rise; temperature increases, which could reduce growth and productivity, resulting in die-back of species at the upper limits of their thermal tolerance, and favouring conversion of seagrass areas to mangrove communities and enhancing the growth of algae and phytoplankton; localised decreases in salinity; damage from enhanced levels of ultraviolet radiation; and

unpredictable impacts from changes in the distribution and intensity of extreme events, which may result in an increase in direct physical disturbance of seagrass beds as well as an increase in sediment delivery to estuarine and coastal areas (Short & Neckles 1999; Hemminga & Duarte 2000; Duarte et al. 2004). In contrast, an increase in atmospheric carbon dioxide could lead to higher concentrations of carbon dioxide in seawater, which in turn could increase the productivity and depth range of seagrass.

5.2 NATURAL PROCESSES

5.2.1 Meteorological events

Threats to seagrasses are not limited to anthropogenic factors. Storms, heavy or prolonged rains, and floods are examples of natural disturbances that can affect seagrass beds, especially if there is significant sediment resuspension and redistribution (Patriquin 1975; Birch & Birch 1984; Kirkman 1985; Shepherd et al. 1989; Kirkman & Kuo 1990; Larkum & West 1990; Fletcher & Fletcher 1995; Preen et al. 1995; Reusch & Chapman 1995; Hemminga & Duarte 2000; Cabello-Pasini et al. 2002; Coles et al. 2003; Kendall et al. 2004). Increased turbidities are often associated with increased sediment loads following periods of intense rainfall and sediment resuspension by wind- and tide-driven water turbulence. Natural disturbances may be exacerbated by interactions with anthropogenic disturbances, so that exact causal factors are difficult to ascertain; for example, catchment land-use practices may exacerbate the effects of natural catastrophic events through increased soil erosion and nutrient run-off (Preen et al. 1995).

Water motion, generated from tides and winds, may also have a measurable effect on the growth and distribution of seagrasses by scouring the seafloor and eroding sediments, and damaging or uprooting seeds and mature plants (Patriquin 1975; Spalding et al. 2003).

Extensive losses of shallow subtidal and intertidal seagrasses have also been documented following the extreme conditions associated with hot El Niño summers (Seddon et al. 2000).

5.2.2 Grazing and bioturbation

Grazing by waterfowl, herbivorous fish and invertebrates, and in tropical systems by turtles, dugongs and manatees, is another form of disturbance that may result in reduced leaf cover or loss of whole plants, causing natural fluctuations in seagrass populations (Ogden 1976; Jacobs et al. 1981; Cambridge et al. 1986; Klumpp et al. 1989; Larkum & West 1990; Valentine & Heck 1991; Rose et al. 1999; Hemminga & Duarte 2000; Spalding et al. 2003). Extensive intertidal seagrass beds in New Zealand estuaries provide important grazing areas for waterfowl. For example, the black swan is one of the primary direct grazers on seagrass in New Zealand. The swans may crop only the leaves, or they may uproot the plants and create bare patches in the bed that are up to 1 m across (Byrom & Davidson 1992; Sagar et al. 1995; Israel & Fyfe 1996; Ismail & Israel 1997; Park 1999a,b; Ismail 2001).

Bioturbation, as a result of the activities of animals (e.g. burrowing, locomotion and feeding) in seagrass beds, may also reduce seagrass cover or slow down spread and colonisation (Orth 1975; Suchanek 1983; Philippart 1994; Valentine et al. 1994; Philippart & Dijkema 1995; Townsend & Fonseca 1998; Hemminga & Duarte 2000; Dumbauld & Wyllie-Echeverria 2003; Spalding et al. 2003). For example, birds, crabs and rays may disturb roots and rhizomes, and can tear apart seagrass leaves as they forage for buried food. In addition, the elevated levels of biologically enhanced sediment transport can reduce the light available for photosynthesis or physically smother seagrasses. The destabilisation and loss of patches of *Zostera* on intertidal platforms on the Kaikoura Peninsula may have been exacerbated by the mud crab *Macrophthalmus hirtipes*, which burrows into the sediment of patches, particularly along edges bordering tide-pools, and feeds on seagrass plants (Woods & Schiel 1997).

It is rare for grazing and bioturbation activities to disrupt seagrass beds over large areas (Spalding et al. 2003).

5.2.3 Wasting disease

Pathogenic micro-organisms can also impact seagrass populations. A wasting disease caused by the marine slime mould *Labyrinthula zosterae* is widely considered to have contributed to extensive damage to North Atlantic populations of *Z. marina* during the 1930s, and to a more localised and less severe epidemic along the eastern coast of North America in the 1980s (Den Hartog 1996). While there is some evidence that *Labyrinthula* is often present in *Z. marina*, and that it plays a part in the initial decomposition of aged plants (Den Hartog 1996), recent investigations have clearly demonstrated that *Labyrinthula* is not only a secondary infection of senescent leaves or an indication of decomposition in *Z. marina* but is also a primary pathogen of this species (Ralph & Short 2002). Under light and temperature stress, it can develop precociously in younger plant parts, causing the symptoms of wasting disease (Den Hartog 1996). It is now widely believed that a decline in the health of seagrasses as a result of adverse environmental conditions or anthropogenic stresses such as nutrient loading, light attenuation and physical disturbance, may increase the susceptibility of seagrasses to the disease (Den Hartog 1987, 1996; Short et al. 1987, 1988).

In the late 1950s/early 1960s, widespread die-off of *Zostera* in a number of harbours around New Zealand following symptoms of wasting disease was linked to the presence of *L. zosterae* (Armiger 1964; Armiger 1965, cited in Inglis 2003). Subsequent studies have reported the occurrence of *Labyrinthula* in other seagrass populations around New Zealand. For example, winter senescence and the abscission of older leaves in patches of *Zostera* on intertidal platforms on the Kaikoura Peninsula may have been exacerbated by infection by *Labyrinthula* (Ramage & Schiel 1999). Inglis (2003) suggests that occasional recurrent outbreaks of wasting disease are likely in New Zealand *Zostera* populations, and that further study is required to understand the epidemiology of these outbreaks and whether they are exacerbated by human activities.

6. Consequences of loss or degradation of seagrass

Although seagrass losses have been well documented internationally, the consequences of this loss are generally less well understood.

With the loss of the seagrass root-rhizome system, sediments are more easily resuspended, resulting in an increased turbidity and reduced light availability (Shepherd et al. 1989; Larkum & West 1990; Kenworthy & Haunert 1991; Walker & McComb 1992; Rose et al. 1999; Morris & Virnstein 2004; Newell & Koch 2004). The loss of seagrasses may also be accompanied by changed patterns of sediment erosion and accumulation (Christiansen et al. 1981; Cambridge & McComb 1984; Shepherd et al. 1989; Thayer et al 1994; Fonseca 1996; Newell & Koch 2004). These secondary conditions may exacerbate the impacts of seagrass loss, and may result in a reduction in the recovery process in areas where there has been widespread seagrass loss.

Loss of seagrass habitat will mean loss of estuarine and coastal ecosystem productivity. The consequences for secondary production under conditions of seagrass decline are generally not well understood, but there is the potential for declines in species abundances and loss of species diversity of seagrass-associated flora and fauna, and consequently changes in community structure and ecosystem functioning (Cambridge & McComb 1984; Bell & Pollard 1989; Edgar et al. 1994; Thayer et al. 1994; Tolan et al. 1997; Eggleston et al. 1998; Terrados et al. 1998; Matheson et al. 1999; Rose et al. 1999; Asmus & Asmus 2000; Deegan 2002; Vanderklift & Jacoby 2003; Cardoso et al. 2004; Bloomfield & Gillanders 2005). The significance of the loss of seagrasses will be dependent on site-specific relationships between fauna and seagrasses.

7. Seagrass recovery

The nature, intensity and the frequency, timing and/or duration of a disturbance event will influence both the extent of seagrass loss and the timing of recovery. With increasing anthropogenic pressures on coastal ecosystems, and their negative effects on seagrass communities, an understanding of the recovery process is essential in developing strategies to deal with potential disturbances.

Seagrass loss can often occur rapidly, with large changes in distribution and abundance over time-scales of as little as weeks or months (Kirkman 1978; Nienhuis 1983; Clarke & Kirkman 1989; Shepherd et al. 1989; Thayer et al. 1994; Short et al. 1996; Longstaff et al. 1999; Seddon et al. 2000; Frederiksen et al. 2004a; Morris & Virnstein 2004). While recovery can similarly be relatively rapid when suitable environmental conditions are present (Clarke & Kirkman 1989; Kirkman & Kuo 1990; Creed & Filho 1999; Rasheed 1999; Plus et al. 2003;

Spalding et al. 2003; Cunha et al. 2004; Frederisksen et al. 2004b; Morris & Virnstein 2004), in some instances it may take years for seagrass beds to recover (Clarke & Kirkman 1989; Kirkman & Kuo 1990; Philippart & Dijkema 1995; Rollon et al. 1999; Hemminga & Duarte 2000; Meehan & West 2000; Bryars & Neverauskas 2004; Cunha et al. 2004; Frederiksen et al. 2004a; Whitfield et al. 2004; González-Correa et al. 2005; Neckles et al. 2005).

While the disturbance and loss of seagrasses is well documented, the mechanisms of recovery and the factors that influence recovery are generally less well understood. Seagrasses rely to varying degrees on vegetative (asexual) or sexual reproduction for the maintenance of existing beds, with vegetative propagation known to be an important mechanism for seagrass recovery and spread (Patriquin 1975; Williams 1990; Thayer et al. 1994; Dawes et al. 1997; Rasheed 1999; Rollon et al. 1999; Meehan & West 2000; Cunha et al. 2004; Kendall et al. 2004). Colonisation of new, unvegetated areas, or recolonisation of disturbed areas that may be spatially separated from existing beds, will depend on species-specific dispersal capabilities and the success of recruitment. Seagrass recovery is most often dependent on the presence of water and sediment of a quality suitable for seagrass growth and survival.

Rasheed (1999) found that small-scale disturbances (0.25 m², i.e. the size of disturbance corresponding to anchoring damage, propeller scars, grazing or burrowing) in beds of *Z. capricorni* at sites in Cairns Harbour, Queensland, recovered in terms of above-ground biomass and shoot density within c. 12 months through vegetative propagation from surrounding rhizomes. There was no significant recovery by sexual means, although flowering and fruiting were observed; seeds stored in the sediment played no role in recovery.

Where large-scale losses of seagrasses occur and there are few adult plants remaining, or when the below-ground root and rhizome system suffers damage or the environmental conditions are unsuitable over a protracted period, the ability of the plant to produce new growth is severely impacted, and, depending on the species concerned, seagrass recovery may take extended periods, especially if recovery is dependent on recolonisation by propagules (Zieman 1976; Birch & Birch 1984; Fonseca et al. 1987; Peterson et al. 1987; Clarke & Kirkman 1989; Shepherd et al. 1989; Walker et al. 1989; Dawes et al. 1997; Hawkins et al. 1999; Rasheed 1999; Coles et al. 2003; Olesen et al. 2004; Neckles et al. 2005). In Tauranga Harbour, for example, disturbance of an area of seagrass bed caused by the laying of a pipeline was still evident some 20 years later (Park 1999a). In some cases, the seagrasses may never be able to recover. For example, an area of *Z. capricorni* beds in Cairns Harbour, Queensland, which was dredged in 1982 to depths greater than the limit of the seagrass light requirements, has shown no recovery to date (Rasheed & Roelofs 1997, cited in Rasheed 1999).

8. Considerations for management of seagrass

The shallow-water coastal and estuarine areas around New Zealand are subject to increasing pressures as a result of population growth and increased demands for coastal developments (e.g. marine farms and marinas) and increased development in the surrounding catchments (e.g. forestry, agriculture and urban development). As human pressure grows in these areas and their surrounding catchments, the degradation and loss of the remaining areas of seagrass habitat is likely to continue. Land-use practices and coastal management will require careful consideration to minimise the adverse impacts of increasing population and development pressure. The challenge is to effectively co-ordinate seagrass management and conservation actions, and to reduce the increasing pressures on these valuable components of estuarine and coastal ecosystems.

This report has focused on seagrass; however, the management of seagrass is inextricably linked with the management of estuaries and coastal ecosystems. Seagrass is one component of a wider system of communities and habitats; therefore, there needs to be a holistic, ecosystem-based approach to the management of estuarine and coastal systems and their catchments, which will address the issues of seagrass as well as other sensitive and valuable estuarine and coastal communities.

8.1 THE LEGISLATIVE FRAMEWORK

The Resource Management Act 1991 (RMA) is the principle legislation governing the management of natural and physical resources, including the coastal environment, with the exception of fisheries. The key themes underpinning the RMA are the sustainable management of natural and physical resources, the integrated management of resources, and the control of adverse effects of activities on the environment.

Under the provisions of the RMA, the Minister of Conservation and the Department of Conservation, Regional Councils and Territorial Local Authorities jointly manage the coastal environment. The Minister of Conservation is required to prepare a New Zealand Coastal Policy Statement (DOC 1994), which states the policies that have been developed to achieve the purpose of the RMA in relation to the coastal environment. Seagrass does not receive specific reference in the Coastal Policy Statement. However, the protection of areas of significant indigenous vegetation is identified as a national priority for the preservation of the natural character[1] of the environment. This is to be achieved through the protection of ecosystems that are unique to the coastal environment and vulnerable to modification

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[1] Natural character refers to the natural qualities of the coastal environment, including natural elements of ecological, physical, spiritual, cultural or aesthetic values.

(including estuaries and coastal wetlands), and by minimising the disturbance to other areas of predominantly indigenous vegetation. The protection of the integrity, functioning and resilience of the coastal environment, in terms of the dynamic processes and features arising from the natural movement of sediments, natural movement of biota, natural substrate composition, natural water quality, natural biodiversity, productivity and biotic patterns, as well as the intrinsic values of ecosystems, is also identified as a national priority for the preservation of natural character of the coastal environment. The maintenance and enhancement of water quality is identified in the Coastal Policy Statement as one of the matters to be considered with regard to the preservation of the natural character of the coastal environment. All of these provisions have the potential to provide for the protection of seagrass habitat in the coastal marine area.

Regional Councils are required to prepare Regional Coastal Plans that set out how they will carry out their resource management responsibilities in the coastal marine area of the region. In the coastal marine area, Regional Councils, in conjunction with the Minister of Conservation, have responsibility for land and associated natural and physical resources, the occupation of space and the extraction of material, any actual or potential effects of the use, development or protection of land, and the discharge of contaminants. Regional Councils have only limited management responsibility for the use of land. Control may be exercised for the purpose of soil conservation and the maintenance and enhancement of the quality of water in water bodies and coastal water. The principal functions of Territorial Local Authorities relate to the control of the effects of land-use and subdivision of land. Integrated management of natural and physical resources is a primary function of Regional Councils and Territorial Local Authorities.

The RMA requires the assessment of any actual or potential environmental effects of particular activities that are the subject of resource consent applications. This includes assessment of the effects of a proposed activity or development in the coastal marine area that may affect a seagrass bed, and the ways in which any adverse effects may be mitigated. The Fourth Schedule of the RMA sets out the matters to be included in an environmental assessment, including any actual or potential environmental effects of the proposed activity; possible alternative locations or methods for undertaking the activity if it will result in any significant adverse effect on the environment; a description of the mitigation measures (safeguards and contingency plans) to be undertaken to help prevent or reduce the actual or potential effects; and how effects will be monitored in areas where the scale or significance of the activity's effects are such that monitoring is required. Measures to help prevent or reduce the actual or potential effects and to protect seagrass functions and values can typically include buffer zones to maintain distance between the seagrass habitat and the works being undertaken; design modifications to reduce impacts; scheduling of works that increase turbidity to periods when baseline turbidity is naturally high or to particular current directions or tidal phases; scheduling of works to avoid ecologically important periods; and rehabilitation of the habitat after the completion of works (Coles & Fortes 2001). If a consent authority decides to

grant consent for an activity, it may do so subject to conditions (undertakings required of the applicant). These may include a requirement for a financial contribution, which under the RMA includes a contribution of money, land, works (including the protection or enhancement of any natural or physical resource) or services for purposes specified in the relevant plan, including the purpose of ensuring positive effects on the environment to offset any adverse effects; a bond in respect of the performance of any one or more of the conditions of the consent; and a requirement to undertake a programme of monitoring. With respect to the discharge of contaminants, the consent authority may require the adoption of the best practicable option, or other alternatives, including a condition requiring the observance of minimum standards of environmental quality, to prevent or minimise any actual or likely adverse effect on the environment. Regulatory authorities may require the development of environmental management plans for developments. These plans could include limits on measurable environmental parameters, such as light loss, turbidity and water flow, and identify changes that if exceeded act to trigger a management action or even cessation of the work to protect seagrass (see Coles & Fortes 2001).

Other agencies also have responsibilities for managing aspects of the coastal environment. This includes, for example, the Minister of Fisheries and Ministry of Fisheries, which are responsible for the maintenance of the sustainable use of fisheries resources and fisheries habitat management; and the Maritime Safety Authority, which is responsible for dealing with marine pollution prevention.

In the context of the effective management and conservation of seagrass habitat there are a number of key issues that need to be considered by management agencies. These are discussed in the following sections.

8.2 INTEGRATED CATCHMENT MANAGEMENT

High water quality is essential to the health of seagrass. The key focus for the management of seagrass should therefore be a comprehensive approach to maintaining and improving estuarine and coastal water quality, specifically by reducing inputs of sediment and nutrients. Improved management of catchment land-use practices and catchment run-off is critical for achieving a sustained improvement in estuarine and coastal water quality by ensuring that erosion and contaminant (sediments and nutrients) run-off from catchments and rivers is minimised.

Management needs to focus on better integration of land, stream and estuary-based activities, thereby recognising and accommodating the interdependence of terrestrial, freshwater, coastal and marine systems. This will require better integration between management agencies and their respective responsibilities to ensure a co-ordinated, cross-sectoral and ecosystem-based approach to managing the coastal environment. Integrated catchment management programmes are likely to be one of the best management measures for successful seagrass protection, given that seagrass is at the downstream end of catchment run-off.

8.3 MANAGEMENT OF ACTIVITIES IN THE COASTAL MARINE AREA

In-water and shoreline developments (e.g. marinas, canal developments and causeway construction), works such as the dredging of navigational channels, and boating activities need to be carefully managed to minimise direct physical impacts on seagrass habitat. Seagrass beds outside the immediate footprint of developments may also be affected by changes in water quality and sediment transport patterns; therefore, there needs to be adequate consideration of potential off-site effects. Proper management of seagrass habitat requires a greater awareness and understanding of the consequences of alterations to, and activities within, estuarine and coastal systems.

The distribution and extent of seagrass habitat and the ecosystem values of that habitat represent the basic information required by resource managers to aid planning and development decisions that will minimise impacts on seagrass habitat (Coles & Forte 2001; Coles et al. 2003). To adequately assess the effects of a development proposal on seagrass, resource managers require a detailed understanding of the site-specific significance of the seagrass habitat, which includes consideration of ecological, social, cultural and economic significance, and the implications of any loss or degradation should the development proceed. Such understanding is generally not available.

Walker et al. (2001) recommend that assessments of seagrass significance should include:

- Identification of the ecological functional roles of seagrass in the area of the proposed development site
- Quantification of the loss of ecological functional roles resulting from any historical seagrass losses in the area
- Determination of the amount of loss of seagrass that can be sustained without significantly impairing the ecological functional role of seagrass in the area
- Quantification of the loss of ecological functional role in the area resulting from previous activities
- Quantification of the loss of ecological functional role that can be potentially replaced by mitigation

Such assessments need to be undertaken within the context of natural changes in the area and distribution of seagrass, and not just the anthropogenic losses of seagrass beds. The relative significance of seagrass habitat is likely to vary considerably within and between estuarine and coastal systems, further complicating management decisions.

Identification and quantification of the significance of seagrass habitats, and the costs associated with loss or degradation of these habitats, is critical if resource managers are to be better informed about the consequences of management decisions. Generic arguments that seagrass habitat is important are often insufficient to convince potential developers and other users that their protection is warranted. Monetary valuation techniques can be used to provide an economic basis for seagrass protection. However, many of the values associated with the benefits of seagrass habitat are indirect or non-use, cannot

readily be quantified, and are thus rarely assigned any monetary value. This is in contrast to the benefits of development proposals, which are more easily quantified by developers and are recognised as they yield commercial gains and revenues. As a consequence, the total costs of a development in terms of the loss of ecosystem services (i.e. loss of indirect or non-use benefits) often go largely unacknowledged and are frequently underestimated by resource managers.

8.4 WATER-QUALITY MANAGEMENT

The focus for a number of international seagrass management responses has been on improving water quality by controlling sediment and nutrient loads from catchments to achieve water-quality standards that correlate with healthy seagrass beds (e.g. Johansson & Greening 2000; Batiuk et al. 2000; Morris et al. 2002; Orth et al. 2002; Biber et al. 2003a,b). The underlying assumption is that if water quality is maintained or enhanced, the seagrass habitat will persist.

In Tampa Bay, Florida, for example, local, state and federal agencies working co-operatively through the Tampa Bay National Estuary Program have agreed to adopt nitrogen-loading targets for the Bay, based on the water-quality requirements for seagrass species (Johansson & Greening 2000). A long-term goal to restore 95% of the seagrasses observed in 1950 has been identified, which will require preservation of c. 10 400 ha of seagrasses present in the Bay in 1992 and restoration of an additional 5000 ha. Field measurements indicated that 20%–25% of surface irradiance would be required for sustained growth of the seagrasses, and models were used to estimate the nitrogen-loading rates and associated water-column chlorophyll-*a* concentrations required to maintain irradiance levels at the maximum depth of seagrass growth in 1950. To achieve the long-term seagrass restoration goal, a 7% increase in nitrogen loading associated with a projected 20% increase in the watershed human population over a 20-year period will need to be offset. Stakeholders involved in the Program have identified and committed to specific nitrogen load reduction projects to ensure nitrogen management targets and seagrass restoration goals are met. In the Indian River Lagoon, Florida, the goals of the seagrass restoration programme include efforts to maintain and enhance the water quality necessary for seagrass health (Morris et al. 2002). The minimum light requirement of seagrasses in this lagoon is 25% of surface light. This light requirement is compared with the amount of light reaching a target depth for seagrass restoration of 1.7 m (15%); the difference indicates the level of water-clarity improvement that is required to ensure the sustainability of seagrasses to the target depth. The minimum light requirements for seagrasses will be used to establish pollution-load reduction guidelines.

The 'Australian and New Zealand Guidelines for Fresh and Marine Water Quality' (ANZECC & ARMCANZ 2000a) promulgates a water-quality management framework that could be utilised to protect seagrass in estuarine and coastal ecosystems in New Zealand. The framework includes a requirement for the identification of 'environmental values', which are particular values or uses of the environment (e.g. aquatic ecosystems, recreation and aesthetics,

cultural and spiritual) that require protection from the effects of contaminants and inappropriate land management practices. Once the environmental values to be protected have been identified, the level of protection required to maintain the environmental or water quality needs to be determined. Management goals that reflect the specific threats to the established values, the desired levels of protection for aquatic ecosystems, and the key attributes of the resource that must be protected can then be formulated; for example, a management goal could be to improve seagrass habitat condition and productivity. Management goals should be achievable and measurable, and represent the key objectives that should be achieved through management plans.

Associated with each environmental value are guidelines or 'trigger values' for substances that might potentially impair water quality (e.g. nutrients, sediments and pollutants). These are recommended numerical concentration levels or descriptive statements that will support and maintain the designated environmental value of a particular water body. If these values are exceeded, which is indicative that there may be a potential environmental problem, they may be used to trigger or initiate further investigation or some form of management response. 'Water quality objectives' are numerical concentration levels or descriptive statements that are specific or detailed targets agreed between stakeholders or set by local authorities, and which become the indicators or measures used by resource managers to measure and report on performance.

The 'Australian and New Zealand Guidelines for Fresh and Marine Water Quality' (ANZECC & ARMCANZ 2000a) include default low-risk guideline trigger values for a number of physical and chemical stressors (e.g. chlorophyll-a, nutrients, turbidity and suspended particulate matter) for estuaries and marine ecosystems around Australia. However, none of these have currently been identified for New Zealand estuarine and marine ecosystems.

Additional research and evaluation is needed to develop regional or local minimum water-quality guidelines to sustain seagrass growth and survival—particularly with respect to optical water quality (e.g. chlorophyll, which is indicative of nutrient loading, clarity and turbidity) (cf. Wazniak et al. 2005; Western Australian Environmental Protection Authority 2005). This will require information on the responses of seagrass to natural and human impacts (particularly the physiological and biochemical responses of seagrass plants to reduced light conditions), and identification of the current status and trend of seagrass distribution, including determination of acceptable levels of change in seagrass distribution and the environmental conditions that may cause these changes. Seagrass trigger values will need to be scientifically defensible; objective, explainable and understandable; ecologically achievable; incorporate natural variability; incorporate both maximum (ideal) and minimum acceptable levels; and incorporate statements for protecting seagrass diversity and functional integrity.

8.5 CUMULATIVE ENVIRONMENTAL IMPACTS

While the impacts on seagrass associated with any individual activity or disturbance may be relatively insignificant, the cumulative impacts of gradual, incremental increases in catchment run-off, point-source discharges, and direct physical damage, which are associated with growing population pressure on the coast and increasing coastal development, present a serious threat to the long-term survival of seagrass around New Zealand. Incremental increases in impacts associated with population and development pressures must be managed if some of the losses that have been reported internationally are to be avoided.

There needs to be greater consideration of the cumulative environmental impacts that can result from 'small' environmental decisions, by incorporating an ecosystem-based approach to resource management decision-making. If a seagrass bed is already stressed (e.g. due to non-point source run-off affecting water quality), the dredging of a new channel or increased boat traffic to a new marina may drive the nearby seagrass population beyond its physiological limits, resulting in its degradation and, ultimately, potential loss.

Current decision-frameworks for managing coastal systems do not adequately incorporate this ecosystem-based approach. As a consequence, there is the potential for numerous relatively small-scale impacts on seagrass beds to be occurring without any protection and mitigation to offset the cumulative losses. Until an ecosystem-based perspective is taken, such cumulative losses are likely to continue.

The absence of accurate inventories of seagrass habitat makes it difficult to accurately assess the cumulative impact of human activity on them. Monitoring changes in seagrass distribution and condition should enable early identification of areas that may be under threat due to cumulative influences.

8.6 SEAGRASS HABITAT IS NATURALLY VARIABLE

Seagrass communities are naturally spatially and temporally dynamic features of estuarine and coastal ecosystems (Larkum & West 1983; Clarke & Kirkman 1989; Kirkman & Kuo 1990; Hemminga & Duarte 2000; Frederiksen et al. 2004b; Krause-Jensen, Almela et al. 2004). The distribution and abundance of seagrass undergoes extensive natural fluctuations due to variable growth conditions; for example, there may be significant declines following storm events. Future efforts to manage and conserve seagrass will be dependent on a comprehensive understanding of the natural patterns and scales of variability and the causes of these changes, so that anthropogenic impacts on the seagrass can be fully assessed.

8.7 PROTECTION OF SEAGRASS HABITAT

Total protection from and avoidance of any impact is the best strategy to ensure the persistence of seagrass habitat and its continued ecosystem value. Limited areas of New Zealand seagrass habitat are provided with some measure of protection under national legislation. For example, Farewell Spit in the north west of the South Island, which includes extensive areas of intertidal seagrass beds, is listed under the Ramsar Convention on Wetlands and is managed as a Nature Reserve under the Reserves Act 1977. Whanganui (Westhaven) Inlet, which is also in the north west of the South Island, and Te Angiangi in the Central Hawke's Bay, are both designated as Marine Reserves under the Marine Reserves Act 1971, and include areas of seagrass habitat.

Regional Coastal Plans may identify different types of management areas in recognition of the different values (e.g. ecological, cultural, scenic and historical) associated with them[2]. When considering applications for resource consents within these areas, Regional Councils may give priority to avoiding adverse effects on the values associated with any area, and seagrass habitat may receive some level of protection within these areas. For example, Kawhia and Aotea Harbours on the west coast of the North Island have extensive areas of seagrass habitat that are identified as specific values in designated 'Areas of Significant Conservation Value' in the Waikato Regional Coastal Plan (Environment Waikato 2001).

Where identified values for a specific management area include seagrass habitat, there may need to be some further assessment of the relative importance or value of different areas of seagrass habitat in terms of functional differences, as not all are likely to be of equivalent ecological value. This might include consideration of factors such as plant age, population structure, patch and bed formation, location (e.g. whether a seagrass bed near the mouth of an estuary has the same functional value as a seagrass bed near the head of an estuary), and inter-linkages with adjacent habitats. In the absence of knowledge and understanding of the different conservation, productivity, and other values for each different area of seagrass habitat, management agencies assessing the impacts of development and catchment run-off are likely to make uninformed, and possibly inappropriate, assessments of which developments may occur.

In the future, a greater level of protection needs to be afforded to seagrass habitat. Seagrass habitat should be set aside or incorporated into reserves or other protected areas to ensure the long-term protection of some seagrass habitat in a natural state. It will be important to ensure that there is adequate representation of the full range of variation in seagrass communities in any network of marine reserves, and to identify areas of seagrass habitat that are of particular ecological significance or that may be considered particularly unique

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[2]   New Zealand coastal policy statements may contain policies relating to areas in the coastal marine area that have significant conservation value. The 1990 and 1992 draft New Zealand Coastal Policy Statement (DOC 1990, 1992) included reference to the identification and protection of significant conservation values, but this was not included in the final Coastal Policy Statement (DOC 1994). Nevertheless, some Regional Councils have included these areas, either as 'areas of significant conservation value' or by some other name, in their plans. For example, the Waikato Regional Council identifies a number of areas of significant conservation values (ASCVs) in its Regional Coastal Plan (Environment Waikato 2001).

or rare. These might include, for example, the remaining areas of subtidal seagrass habitat, areas of very large intact seagrass beds (e.g. Farewell Spit) and the seagrass habitat found in some of the fiords (G. Inglis, NIWA, pers. comm. December 2003). There has been very little study of these seagrass habitats, and they could have quite different functional significance from the intertidal estuarine seagrass habitat, which has largely been the focus of studies in New Zealand to date.

While seagrass may be protected within the boundaries of marine reserves or other protected areas, this is to little avail if the adjacent waters are inadequately managed. Many of the threats to seagrass come from remote sources (e.g. catchment run-off), and there are currently limited mechanisms available for dealing with activities that may affect sites but occur outside the reserve boundaries. This reinforces the importance of adopting a cross-sectoral approach to the management of seagrass habitat. It is also important to identify and implement performance indicators against which to measure the success (or otherwise) of the protection management (Leadbitter et al. 1999; Coles & Fortes 2001).

8.8 ENHANCEMENT, RESTORATION AND MITIGATION

Once lost, seagrass may not readily recover naturally. The plants require specific environmental conditions that are often lost with the decline of the seagrass, and locations that once supported abundant seagrass beds may become unsuitable as habitat for seagrass. As a consequence of the recognised importance of seagrass habitats and their associated communities and the significance of their loss, opportunities for seagrass enhancement, restoration and mitigation have been receiving increasingly greater attention internationally (Fonseca 1992; Kirkman 1992; Fonseca et al. 1998; Lord et al. 1999; Hemminga & Duarte 2000; Christensen et al. 2004).

It is important to define what is understood by enhancement, restoration and mitigation:

- Enhancement is the improvement, augmentation or rehabilitation of a degraded or affected area, with the expectation that it will result in the return of seagrass, improve the condition of existing seagrass, and improve ecosystem function

- Restoration is the return from a disturbed or totally altered condition to a pre-existing natural or altered condition

- Mitigation is the actual restoration, creation or enhancement of functionally equivalent seagrass habitat to compensate for seagrass habitat loss as a result of development activities, or more broadly to provide some form of compensatory effect (Turner 2000)

There is no one method by which seagrass restoration is undertaken, and a variety of trials have been carried out internationally with varying degrees of success (Kenworthy & Fonseca 1992; Davis & Short 1997; Balestri et al. 1998; Harwell & Orth 1999; Lord et al. 1999; Orth et al. 1999; Calumpong & Fonseca

2001; Balestri & Bartini 2003; Peralta et al. 2003; Christensen et al. 2004). Conventional planting and transplanting techniques that have been used for terrestrial plants are not successful with seagrasses, and while planting seagrass is not technically complex, seagrass habitat restoration is an inherently complicated process that has not yet been shown to offset net habitat losses. Successful seagrass restoration is contingent on good water quality, as well as appropriate site selection, planting techniques, monitoring and the implementation of appropriate corrective actions when a project is not progressing towards clearly defined goals (Thorhaug 1985; Fonseca et al. 1987, 1988, 1994, 1998; Fonseca 1989a, 1992; Thom 1990, 2000; Hawkins et al. 1999; Lord et al. 1999; Kentula 2000; Short et al. 2002).

Attempts at restoration are unlikely to be successful if environmental conditions are unfavourable, and the success of any seagrass restoration will be dependent on a physical environment that will not only ensure initial establishment, but will also support long-term growth and survival. The parameters of the restoration site must also closely match those of the donor site if restoration is to be successful (Fonseca et al. 1998; Christensen et al. 2004). Programmes to improve water quality and habitat conditions (e.g. sediment characteristics, depth and site hydrodynamics), thereby enhancing the processes of natural recolonisation, should be central components in any restoration effort. Excess sediment accretion or loss must be rectified to prevent transplants from being smothered or washed away and high sediment levels in the water column, which would inhibit photosynthetically available radiation. The transplants may also be smothered by epiphytes if there are high concentrations of nutrients in the water column. While the restoration of seagrasses is at the stage where technologies are available, overcoming inadequate water-quality conditions is the greatest obstacle to seagrass restoration worldwide (Spalding et al. 2003).

The focus of many restoration efforts has been largely on restoring persistent vegetative cover; there needs to be a shift in emphasis towards restoring ecological functions, especially those perceived as ecosystem services (Cairns 2000; French-McCay & Rowe 2003; Peterson & Lipcius 2003). Provision of physical habitat structure does not necessarily guarantee the return of normal function (functional equivalency), and even where there is recovery, the rate of return of function may lag structural restoration by many years (Fonseca et al. 1994, 1998; Fonseca, Kenworthy et al. 1996; Fonseca, Meyer et al. 1996; Sheridan 2004). Many seagrass restoration efforts have not consistently restored full functionality equivalent to that which has been lost (Homziak et al. 1982; McLaughlin et al. 1983; Smith et al. 1988; Fonseca et al. 1990; Bell et al. 1993; Brown-Peterson et al. 1993; Race & Fonseca 1996; Williams & Davis 1996; Sheridan 2004). Seagrass restoration efforts often result in the development of seagrass communities that have limited productivity, sparser growth and lower diversity, in areas where conditions are inadequate for the successful establishment of the intended community. Designing seagrass beds to maximise functional equivalency requires a detailed knowledge and understanding of the mechanisms that result in a particular community and levels of secondary productivity (Williams & Heck 2000). Furthermore, there is often a net loss in functional seagrass habitat or, at best, a trade-off involving the exchange of an existing system with that of an ecologically dissimilar one, often not even on a

1:1 spatial scale (Fonseca 1992; Fonseca et al. 2000). Restoration of seagrass habitat should not, therefore, be seen as a viable alternative to management actions focusing on avoidance and minimisation of seagrass-bed impacts.

Where development that will result in the loss of seagrass habitat proceeds, there should be a requirement for compensatory mitigation to offset unavoidable impacts on seagrass that remain after all appropriate and practicable avoidance and minimisation. This should not necessarily mean the substitution of naturally unvegetated areas for vegetated habitat, as this typically creates only a transient seagrass bed, and does not necessarily improve existing habitat functions. Instead, a mitigation programme may consider enhancing other components of the estuarine habitat to preserve some of the identified ecosystem values provided by the seagrass habitat under threat. Mitigation programmes need to be carefully and thoroughly planned, incorporate clearly defined ecological goals and objectives within an adaptive management framework, and be systematically evaluated against scientifically robust performance criteria (Pastorok et al. 1997; Hackney 2000; Kentula 2000; Short et al. 2000; Thom 2000; Kirsch et al. 2005; Thom et al. 2005). Seagrass restoration projects that lack clearly defined goals and objectives are less likely to be successful, and in many cases it may be impossible to gauge success in the absence of clearly defined performance criteria. The low success rate of international mitigation projects has been attributed to failures in the planning process as much as to any other causes (Fonseca et al. 1998).

One approach to offsetting the degradation or loss of seagrass habitat that has been adopted internationally but not yet in New Zealand is the application of mitigation banking (Turner 2000). Mitigation banking is a system whereby the benefits attributable to the restoration, enhancement or creation of ecosystems or habitats are quantified, and the agency or group producing them receives mitigation credits from the appropriate regulatory authority (Etchart 1995). These credits are then placed in a mitigation bank account, from which withdrawals can be made. Thus, when a project is proposed that involves unavoidable losses, these losses or debits are quantified using the same method that was used to determine credits, and a withdrawal equal to that amount can be debited against the mitigation bank account. This system is controversial, and not without limits and risks. However, while existing natural ecosystems or habitats should not be traded indiscriminately for the construction of artificial systems in order to allow use and development to proceed, mitigation banking does have the potential to create a form of tradable permit, which is in accordance with the philosophy of utilising economic instruments as a means of achieving the purpose of the RMA (Turner 2000).

While restoration should not be considered as an option over preservation, restoration techniques for areas once supporting seagrass growth should be further developed and encouraged in order to augment available habitat. There have been few direct attempts to restore seagrass systems in New Zealand, and they have been small-scale and of limited success in terms of seagrass survival (e.g. Turner 1995). Further research is needed to address issues central to successful restoration projects. This should include site selection and preparation, including the rehabilitation of environmental conditions that existed prior to seagrass loss; appropriate planting methodologies, and methods

to accelerate natural recruitment processes; selection of donor stocks to maximise chances of success and minimise damage to donor beds; methods to improve the long-term survival, growth and coverage rates of seagrass; and the ecological function of restored seagrass habitat. It is important that any experimental or pilot-scale seagrass restoration projects should be monitored and their performance evaluated to enable testing of the efficacy of the proposed restoration; this can then be followed by full-scale implementation of the most successful technique.

9. Considerations for monitoring seagrass

Monitoring is an important aspect of managing any natural ecosystem. There is a need to regularly assess and quantify the status and trends of seagrass distribution, extent, abundance and condition in estuarine and coastal areas on a national, regional and local basis on both seasonal and inter-annual time-scales. This requires the development of appropriately designed and implemented long-term monitoring programmes for the measurement of key parameters to assess changes in seagrass distribution, extent, abundance and condition. An understanding of the natural range of and patterns of variation in seagrass parameters in both space and time is essential for distinguishing anthropogenic change from the natural background levels of change. Without this understanding, it will not be possible to interpret changes in the system and assess the need for management, or reach decisions on an appropriate and robust management response. Resource managers need information on what levels of change are likely to be ecologically significant. Monitoring methods must be capable of detecting and estimating the sizes of realistic levels of change against the background of natural spatial and temporal variability, at an appropriate scale and with documented reliability and precision.

Monitoring enables early detection of change, thereby enabling resource managers to adjust management practices and/or take remedial action earlier for more successful results. Monitoring also allows resource managers to evaluate the success of policies and rules that have been made to mitigate or avoid adverse effects. While there is no formal programme in place for monitoring long-term changes in seagrass distribution, extent, abundance and condition, the Ministry for the Environment has proposed that the extent and condition of seagrass beds be monitored as one of the national environmental performance indicators for the marine environment (MfE 2001). Limited monitoring of seagrass is also undertaken as part of resource consents.

Various methods are available to monitor changes in seagrass distribution, extent, abundance and condition, but the limitations of each method need to be understood, and they should only be used to answer well-defined questions. A variety of monitoring methods are well documented in a number of readily available publications (Phillips & McRoy 1990; Coles et al. 1996; Kirkman 1996;

Lee Long et al. 1996; English et al. 1997; Thomas et al. 1999; Short & Coles 2001; Borum et al. 2004).

SeagrassNet is a global monitoring initiative that was established in 2001 to investigate and document the worldwide status of seagrass resources (SeagrassNet n.d.). The programme started with an ongoing pilot study in several countries in the western Pacific. Since then, a globally applicable monitoring protocol and web-based data reporting system have been established. The ultimate aim of the programme is to increase knowledge and public awareness of the importance of seagrasses and coastal management issues, and to develop community participation and ownership, as well as long-term, broad-scale monitoring of seagrass habitat, seasonal patterns, condition and trend data (McKenzie & Campbell 2002).

The intent of this report is not to provide coverage of the full range of monitoring methods for seagrass, but to identify some of the key considerations in the development, implementation and interpretation of a programme for monitoring seagrass. The appropriate seagrass parameters to be monitored at a particular site will be project-specific and dependent on why and where the monitoring is being conducted, as well as by whom. Sampling designs for seagrass monitoring programmes, as well as the location and number of sites, etc., should be tailored to the question being asked of the data, the precision required and the parameters of the habitat being monitored, with due consideration of cost-benefit, logistical and safety issues. To develop an effective monitoring programme, intensive data collection is likely to be required in baseline studies, to provide initial estimates of spatial variability. Monitoring programmes need to be based on a sound understanding of variability and incorporate sufficient levels of sample replication to enable changes that are ecologically meaningful to be detected with reasonable statistical power. It is also important to identify the amount of change, or to define any persistent trends (e.g. change in one direction over a number of successive sampling periods) that will be used to initiate a management response (Lee Long et al. 1996). Simultaneously, data should be collected on physical parameters that are important to seagrass growth and survival and which may also be useful in interpreting changes in seagrass (e.g. light (turbidity and depth), sediment characteristics and nutrient levels).

Careful consideration needs to be given to the development of a suitable quality-assurance process to ensure consistent sample collection, handling and processing protocols. Standardised data recording and database management procedures are also important to ensure that all the data generated are accurate, compatible and representative of the actual samples, and that estimates of error and reliability accompany each seagrass parameter measured. Consideration should also be given to the presentation, including techniques of integrating spatial and temporal data, and the processing, analysis, interpretation, storage and archiving of data. This should include the generation of associated procedural information (metadata).

9.1   ISSUES OF SCALE

The spatial arrangement of seagrass habitat varies over scales ranging from millimetres to kilometres (Robbins & Bell 1994; Turner et al. 1996). 'Seagrass-landscapes', extending over kilometre-wide scales and often containing important topographic heterogeneity, are made up of seagrass patches and beds at the scale of metres to tens of metres. At the centimetre to millimetre scale, individual shoots are composed of multiple blades of contrasting sizes, ages, epiphytic populations, etc. In addition, seagrass can change in different ways both spatially and temporally. There may be changes in bed location, depth distribution, area or shape, shoot density, biomass, plant productivity, or a change in the associated flora or fauna; or there may be a combination of any or all of these at small or large spatial or temporal scales (Coles et al. 1996; Lee Long et al. 1996). These changes may occur naturally and on a regular seasonal or annual basis.

Seagrass can be monitored at a range of spatial and temporal scales. For example, spatial scales ranging from less than 1 m^2 to greater than 10^9 m^2 and temporal scales ranging from minutes to decades may provide meaningful information depending on the question being asked. The scale of the approach (i.e. the spatial and temporal scales adopted) will depend on the question of interest, as no single scale is appropriate or sufficient for all approaches to seagrass monitoring and management, and no one approach is applicable over all scales (Virnstein 1995, 2000). For example, the question of 'How much seagrass is present in the area?' would require different approaches depending on whether the question was in relation to a national scale, regional scale, estuary or sub-estuary scale, a particular bay in an estuary, or to a particular seagrass patch. There is no reason to expect that patterns found at any one scale are transferable to other scales. For example, the dynamics of seagrass beds (e.g. growth, grazing, biomass development and flowering) cannot be examined by extrapolating processes examined at small scales (< 1 m^2) to the entire bed (Duarte & Kalff 1990; Vidondo et al. 1997). Effective management requires accurate and timely information at varying scales. If adequate consideration of scale is not incorporated into the design of a seagrass monitoring programme, then errors of measurement, inappropriate techniques for assessment, implementation of wrong solutions and a lack of understanding of the system under study can result (Virnstein 2000).

Often a hierarchy of information is required. There are at least four scales of approach in seagrass monitoring programmes, from the 'broad-scale big picture' to the 'finer scales with more detail' (Virnstein 2000).

Landscape (macro)-scale approaches provide information on large-scale changes (many kilometres) over multi-year time frames. Examples of large-scale questions include 'What is the total area of seagrass in the area of interest at a given time?' and 'How has the total area of seagrass changed over time?' For these types of questions, remote-sensing mapping methods are generally appropriate, which involve satellite imagery or aerial photography, on-site ground-truthing surveys, photo-interpretation and the delineation of seagrass areas (e.g. Israel & Fyfe 1996; Wyllie et al. 1997; Kendrick et al. 1999, 2002).

Such landscape-scale maps provide powerful tools for presenting large-scale patterns and detecting long-term changes in abundance and distribution. These maps can be used to help identify 'healthy' areas that may deserve special protection efforts and potential 'problem' areas that may require further investigations and may be of management concern. However, these maps cannot be scaled down to finer scales, and they provide no basis for attributing any observed change to a specific impact (Lee Long et al. 1996).

The scale of the mapping is important and will be dependent on the objectives of the project and the detail to be shown. Scale is a compromise between resolution of the different ground signatures, coverage of the study area, including land features sufficient for horizontal control, and cost (Dobson et al. 1995). The minimum mapping unit is quite large (e.g. 0.1–0.2 ha with 1:24 000–1:10 000 scale photographs). From aerial photographs, it is difficult to map features less than a few metres in size or to accurately locate the edge of seagrass beds or map very sparse beds (Environment Waikato n.d.). These methods are not, therefore, suitable for detecting local or short-term changes, as these are indistinguishable from locational and interpretative errors.

Medium (meso) approaches provide information on medium-scale changes (tens or hundreds of metres) over shorter time-scales (months). An example of a medium-scale question is 'What is the percentage cover of seagrass in a selected area of seagrass bed at a given time?' For these questions, repeated monitoring of fixed transects positioned across a seagrass bed, using standardised quantitative techniques, can detect local changes in factors such as tidal elevation, percentage cover, shoot density, biomass and canopy height over short time-scales (e.g. Carruthers & Walker 1999; Kirkman & Kirkman 2000; Morris & Virnstein 2004). This provides an early indication of whether the condition of the seagrass bed is stable, improving or declining, and the magnitude of any change.

Although fixed transects are powerful for monitoring change within part of a bed, the results from a single transect cannot be scaled up to represent changes over the whole bed or for comparisons among beds. While it is invalid to extrapolate from a line to an area, the power of spatial inference increases with multiple transects (Kirkman 1996; Virnstein 2000; Duarte & Kirkman 2001). For example, if a section of an estuary or seagrass bed is sampled with multiple randomly located transects, then generalisations can be made about the wider area. However, there must be sufficient replication to give good estimates of the particular variables the study wants to estimate, or to give powerful tests if it is a hypothesis-testing study.

Site-specific (micro)-scale approaches typically provide information on small changes (metres to tens of metres). An example of a site-specific scale question is 'What are the processes governing the establishment, maintenance and mortality of patches at a site?' These approaches typically involve mapping of sites within one bed or a small number of beds that are separated by distances of metres or tens of metres, and include the study of the dynamics of seagrass patches across a small area of seafloor or the study of the spread of seagrass by rhizome growth at the edge of the beds. For example, Olesen & Sand-Jensen (1994b) studied seagrass patch dynamics in 120-m² permanent plots to evaluate recruitment and rates of expansion and mortality of patches. Fonseca & Bell

(1998) mapped seagrass coverage within 50 m × 50 m permanent study sites, which were chosen to represent a wide range of seagrass coverage, ranging from continuous to widely dispersed, discrete patches in the seagrass landscape. Spatially explicit data on seagrass presence/absence was produced by direct field observations in 1-m² areas centred on each intersection of 1-m² grids positioned on the 50 m × 50 m study site (2500 grid-points).

Process-based approaches involve studies of relationships between plant physiology (e.g. chlorophyll-*a* content, carbon:nitrogen:phosphorus ratios and carbohydrate composition) and plant productivity and demography (e.g. leaf growth, rhizome growth, photosynthetic potential, shoot density and biomass), as well as the environmental parameters that affect the condition and distribution of seagrass (e.g. light, turbidity, depth, temperature, salinity and sediment nutrients) (Kennedy et al. 2004; Krause-Jensen, Marbà et al. 2004). Examples of process-based questions include 'How is the photosynthetic capacity of seagrass shoots influenced by different levels of nutrient enrichment?' and 'How do larval movement, water flow and seagrass structural characteristics interact to determine the patterns of animal distribution in seagrass beds?'

9.2   THE MONITORING PARADIGM

Many seagrass monitoring programmes focus on establishing long-term trends in factors such as seagrass cover and biomass; consequently, they tend to focus on the seagrass as an end in itself. In addition, the seagrass parameters quantified in these programmes often tend to be based on convenience, rather than any analysis of the ecological determinants of seagrass distribution or the ecological role of seagrass habitat (Thomas et al. 1999). While this information may serve to alert resource managers to large-scale or long-term changes in seagrass distribution and condition, any subsequent management response (e.g. policy development) will usually depend on more detailed, process-orientated studies, which require a more conceptual understanding of seagrass systems. In a recent review of seagrass monitoring programmes in Australia, Thomas et al. (1999) reported that few monitoring programmes identify specific management actions associated with the programme, and although situations could be identified where management action had taken place following a decline in seagrass cover, in most cases monitoring had been instigated as part of a management response.

Thomas et al. (1999) have advocated the need to base monitoring programmes on a conceptual understanding or models of the system being monitored, and they suggest that a more conceptual approach to the design of monitoring programmes can demonstrably add value to resource management. The development of such conceptual models serves to clearly identify the individual components and the links between seagrass and other components of the system (e.g. major external driving forces; stressors; ecological effects caused by the stressors; the ecological elements or attributes of the system; and critical pathways or ecological linkages) (Thomas et al. 1999; Lee Long & Thom 2001).

These models assist in identifying variables that are important to monitor, as well as variables for which information is lacking or for which more extensive monitoring is required, thus helping to clarify the monitoring needs. Equally importantly, the process may result in the elimination of some potential monitoring variables from a monitoring programme, for example if they are shown to be too variable to be useful. The development of conceptual models also allows more meaningful interpretation of the results of a monitoring programme. Information on change in seagrass distribution, abundance, growth patterns, productivity, morphology or nutrient content is of limited value without an understanding of the likely influencing factors (Lee Long et al. 1996).

The 'Australian Guidelines for Water Quality Monitoring and Reporting' (ANZECC & ARMCANZ 2000b) also advocate the development of conceptual process models as part of the development of monitoring programmes. These models enable identification of the key processes of the system to be monitored and help to define relationships such as 'cause-and-effect' and 'how the system works', as well as the 'why' questions. These models may be as simple as a box diagram illustrating the components and linkages in the system to be monitored.

9.3 SEAGRASS AS AN INDICATOR OF BIOLOGICAL HEALTH OF ESTUARINE ECOSYSTEMS

Seagrasses have relatively high light requirements (15%–25% of light at the water surface) compared with other estuarine primary producers (e.g. phytoplankton and algae; typically < 5%), and are therefore susceptible to low light stress (Dennison et al. 1993). Seagrasses are thus potentially sensitive indicators of declining water quality in estuaries (e.g. increased light attenuation as a consequence of increased turbidity and/or increased phytoplankton biomass as a consequence of increased nutrient loading) and have been proposed as 'canaries' or 'barometers' of estuarine change, providing an early warning of decline in estuarine health (Biber n.d.; Dennison et al. 1993; Biber et al. 2005). Generally, the presence of healthy seagrass communities (and, implicitly, healthy seagrass plants) can be considered to be a useful measure of the condition of estuarine and coastal ecosystems (MfE 2001; Biber et al. 2005). However, the decline or loss of seagrass reflects lethal stress levels and indicates that estuarine water quality has degraded to a point that there is unlikely to be sufficient time for corrective action (Biber n.d.; Hemminga & Duarte 2000; Biber et al. 2003b, 2005). Therefore, early detection of sub-lethal stress thresholds in seagrass plants is important for the effective management and protection of seagrass. There has been considerable interest internationally in developing measures of seagrass health that reliably show measurable and timely responses to environmental factors that cause sub-optimal seagrass growth (e.g. light attenuation), as predictive indicators of ecosystem condition and function (Kenworthy & Haunert 1991; Dennison et al. 1993; Neckles 1994; Durako 1995; Longstaff & Dennison 1999; Wood & Lavery 2000).

Biber et al. (2003a,b, 2005) have proposed a suite of potential predictive indicators of seagrass health over a range of hierarchical levels:

- Bio-optical models of water quality in relation to habitat requirements (Biber et al. n.d., 2003a,b, 2005; Gallegos 1994, 2001; Gallegos & Kenworthy 1996; Kenworthy & Fonseca 1996; Zimmerman 2003).

- Growth measurements and morphological parameters (e.g. plastochrone interval, plant morphometrics, shoot demographics, and shoot and rhizome apical densities) (Durako 1995; Lee et al. 2004; Turner & Schwarz in press; ST, unpubl. data).

- Biochemical markers of stress (e.g. amino acid composition, carbohydrate concentrations, altered chlorophyll-*a*:chlorophyll-*b* ratios, and chlorophyll fluorescence (e.g. Fourqrean at al. 1997; Beer et al. 1998; Ralph 1999; Beer & Björk 2000; Durako & Kunzelman 2002; Enríquez et al. 2002; Biber et al. 2003a,b, 2005; Lee et al. 2004; Turner & Schwarz in press).

Further work is necessary to provide management-relevant information on the selection and usefulness of a robust suite of indicators, in the context of how stress regimes influence parameter values, variability and confidence limits. The goal should be to produce regionally explicit subsets of these indicators to address the particular management question of local or regional interest in the most appropriate way.

The successful management and conservation, and ultimately restoration, of *Zostera* in New Zealand will depend on the accurate assessment of seagrass condition and an understanding of the complex causal relationships between site characteristics and seagrass health and persistence. In ten estuaries around the central North Island, a suite of potential indicators of sub-optimal health of intertidal *Zostera* beds have been investigated, including photosynthetic capacity, biomass, shoot density, plant morphology and nutrient content (A-MS & ST, unpubl. data). The aim was to assess whether it is possible to detect sub-optimal health before a given seagrass bed begins to undergo an irreversible decline. Preliminary results show that photosynthetic capacity, total biomass and shoot density are correlated in a consistent manner across the ten estuaries, and that on the basis of these three parameters the estuaries could nominally be separated into high, intermediate and reduced health categories. Further work is required to relate these one-off measures to changes in environmental conditions and to the trajectory of the seagrass response over a range of time-scales. This work complements other studies in New Zealand (e.g. Schwarz 2004; Turner & Schwarz in press), including the establishment of criteria for defining healthy seagrass habitat, understanding how seagrass may be employed as an indicator of environmental health, the assessment of their ecosystem role and an assessment of the potential for restoration.

10. Information and education

The management of seagrass in New Zealand would benefit from appropriately targeted information and advice on the role and importance of seagrass habitat, the critical issues affecting seagrass, the need for effective management and conservation, the range of damaging activities, and the actions that can be taken to prevent or minimise such damage (see Coles & Fortes 2001; Lee Long & Thom 2001).

Public education activities could usefully focus on what individuals can do to reduce the impacts on seagrass from human disturbances. For example:

- Water quality: Coastal residents can prevent pollutants from entering storm-water drains by not putting petrol, paints, solvents and garden chemicals down storm-water drains. They can also reduce the non-point source pollution reaching coastal areas, and seagrass beds in particular, by following directions on lawn and garden products, and not over-using fertilisers, pesticides or herbicides. Farmers can carefully manage farm effluent and grazing to prevent run-off into waterways.

- Stream-edge management: Land-owners can plant a buffer strip of plants or leave vegetation along streams and at the edge of estuaries to help stabilise the banks, reduce sediment erosion and trap nutrients.

- Boating: Boat users should know the water-depth requirements of their boat's design, and if they observe seagrass in the prop-wash they should stop the motor and drift or pole into deeper water. Boat users should avoid anchoring in seagrass beds, as the anchoring of boats can cause significant damage to seagrass.

- Physical disturbance: People should use caution when wading in shallow water and avoid walking through seagrass beds, as this can damage the root-rhizome system. Stock should be fenced out, so that they do not graze or trample seagrass beds.

In recent years, the heightened interest in mangroves in northern New Zealand estuaries and discussion of the advantages and disadvantages of this native estuarine ecosystem component (Green et al. 2003) has highlighted the need to increase public appreciation of the importance of estuarine and coastal vegetation. Promotion of a sense of community stewardship and responsibility for the conservation of estuarine ecosystems (Green et al. 2005) will ultimately include considered management of seagrass. One international initiative to foster such stewardship has been the establishment of community Seagrass-Watch programmes in Queensland (McKenzie et al. 2000). Seagrass-Watch is a community-based monitoring programme involving a partnership between community groups and various government agencies, which developed out of the recognition that limited resources made it logistically impossible for government agencies alone to address state-wide enquiries about seagrass issues. The programme has captured the interest of coastal communities concerned about the condition and loss of seagrasses in their areas, and has

motivated communities to play a primary information-gathering role by working in partnership with government agencies. Seagrass-Watch collects data about the condition and trend of near-shore seagrasses throughout Queensland and provides an early warning of major changes in seagrass abundance, distribution and species composition.

The potential for increased threats and pressures to New Zealand seagrass systems presents a serious risk to their long-term survival. Greater education, awareness and involvement in improving catchment land-use practices and minimising the direct impacts of development in the coastal environment will help to minimise impacts on seagrass. The protection of New Zealand's seagrass habitat will depend on improved community awareness, regional and long-term planning, and active changes in catchment land-use practices to contain overall downstream impacts and stresses.

11. Acknowledgements

12. References

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