



ELSEVIER

Journal of Experimental Marine Biology and Ecology,
214 (1997) 49–65

JOURNAL OF
EXPERIMENTAL
MARINE BIOLOGY
AND ECOLOGY

Use of seagrass *Zostera novazelandica* (Setchell, 1933) as habitat and food by the crab *Macrophthalmus hirtipes* (Heller, 1862) (Brachyura: Ocypodidae) on rocky intertidal platforms in southern New Zealand

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Received 2 February 1996; revised 22 October 1996; accepted 13 November 1996

Abstract

Along rocky reefs at Kaikoura, New Zealand, the crab *Macrophthalmus hirtipes* (Heller, 1862) constructs its burrows exclusively in patches of the intertidal seagrass *Zostera novazelandica* (Setchell, 1933). The occupation of seagrass patches is widespread, with 63% of patches having crab burrows. The number of externally visible burrows is highly correlated with the number of crabs inhabiting seagrass patches. Plaster casts of burrows revealed that burrows situated at the edge of seagrass patches differed from those away from the edge in having on average more entrances and passageways and, therefore, greater total burrow length. There was an average burrow density of $9.4 (\pm 1.04 \text{ S.E.})$ per m^2 of seagrass, but burrows were several times as numerous on the edges of patches, especially those that bordered tide pools. The diet of *M. hirtipes* was found to consist mostly of living seagrass ($50.4 \pm 3.40\%$ of foregut contents) and sediment ($39.2 \pm 3.11\%$ of foregut contents), with small amounts of isopods, amphipods and conspecifics also consumed. There were no intersexual or site-specific differences in diet. Ontogenetic differences in diet were found, with smaller crabs consuming more sediment and larger crabs consuming more seagrass. Crabs contributed significantly to erosion of seagrass patches. There was an average of $22.5\% (\pm 5.27)$ loss of patch area where crabs were present compared to $1.8\% (\pm 0.37)$ where crabs were absent from patches. Laboratory tests showed that burrow construction took around 250% longer in seagrass patches that had denser blade coverage. In the field, burrows persisted for up to 3 months, even if vacated by crabs. Their abundance at patch edges, combined with the loss of sediment and reduced binding of seagrass roots, accelerated erosion of seagrass patches. © 1997 Elsevier Science B.V.

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Keywords: Burrows; Crab; *Macrophthalmus hirtipes*; Seagrass; *Zostera novazelandica*

1. Introduction

Seagrasses are marine angiosperms that have successfully adapted to shallow coastal and estuarine environments, fulfilling several important ecological roles (Dawes, 1981; Duarte and Sand-Jensen, 1990). Because of their structural complexity, biodiversity and productivity, they have been described as the marine analog of tropical rainforests (Simenstad, 1994 in Dawes et al., 1995). Seagrasses form extensive continuous meadows, or individually discrete patches (Virnstein, 1995a), providing both a habitat and a source of food for a wide range of organisms including fishes, gastropods, crustaceans, and echinoderms (Kikuchi, 1974; Dawes, 1981; King, 1981; Den Hartog, 1987; Perez and Bellwood, 1988; Edgar, 1990; Wassenberg, 1990; Bishop, 1992; Rosas et al., 1994; Dawes et al., 1995; Greenway, 1995; Virnstein, 1995b). Seagrasses may also stabilise bottom sediments, improve water clarity (Ginsberg and Lowenstam, 1958; Dawes, 1981), aid in primary production (Dawes, 1981), and act as substrata for epiphytes (Humm, 1964; Philippart, 1995a,b).

In New Zealand, seagrasses are represented by the two species *Zostera capricorni* and *Z. novazelandica* (*muelleri*). Both species are usually found above or at the low tide mark of sheltered muddy tidal estuaries, river mouths and bay heads (Webb et al., 1990). *Zostera capricorni* is found only around the North Island of New Zealand, while *Z. novazelandica* is more widespread, occurring in all regions of the mainland (Webb et al., 1990).

Around the rocky exposed coastline of the Kaikoura Peninsula, *Z. novazelandica* occurs in isolated areas upon intertidal siltstone platforms. The seagrass patches initially form in sediment-laden tidal cracks, before expanding along cracks and over the siltstone to form discrete mats (Ramage, 1995). Although these seagrass patches range up to 10 m² in size, 75% of them are < 1 m² (Ramage, 1995), and do not form the extensive beds often seen in more sheltered habitats such as tidal estuaries. The intertidal platforms upon which *Z. novazelandica* occurs are frequently exposed to high energy oceanic swells and storm waves (Rasmussen, 1965), thus exposing the seagrass patches to physical disturbance.

The mud crab *Macrophthalmus hirtipes* (Brachyura: Ocypodidae) occurs within the patches of *Z. novazelandica* on the Kaikoura Peninsula. This crab is endemic to New Zealand, most commonly found below the mid-tide level of mud flats of harbours, lagoons and estuaries inhabiting temporary, water-logged burrows. It is in these habitats that such aspects of the biology of *M. hirtipes* such as burrowing behaviour, feeding, habitat preferences, population structure and reproduction have been investigated (Nye, 1974; Fielder and Jones, 1978; Simons, 1981; Simons and Jones, 1981; Hawkins and Jones, 1982; Jones and Simons, 1982; McLay, 1988). However, it is only through the presence of *Z. novazelandica* that *M. hirtipes* can populate the Kaikoura Peninsula, as seagrass patches are the only source of permanent sediment on the intertidal platforms.

Due to the isolated nature of individual seagrass patches, the habitat for *M. hirtipes* is

more restricted and marginal than that of mudflats in which it usually occurs. Given that previous studies of *M. hirtipes* occurring on mudflats have revealed it to be a deposit feeder (Beer, 1959; Fielder and Jones, 1978), the restriction of crabs to seagrass patches could affect the diet of *M. hirtipes*. In this study, we examine the previously uninvestigated use of *Z. novazelandica* as a resource by *M. hirtipes*, and the consequences of this to seagrass patches on rocky intertidal platforms.

2. Methods

2.1. Study sites

The study was done from May 1994 to July 1995 on the Kaikoura Peninsula on the central east coast of the South Island of New Zealand (43°25'S, 173°42'E). This area is at the northernmost position of the Subtropical Convergence (Heath, 1985) and is frequently exposed to high energy oceanic swells and storm waves. The range of annual sea temperatures is 8.5°C to 19°C (Ottaway, 1976). Two study sites, approximately 3 km apart on opposite sides of the peninsula, were used (Fig. 1). These two sites are the only locations on the Kaikoura Peninsula possessing significant concentrations of seagrass. Wairepo Flats has a northeasterly aspect and is composed of an extensive siltstone platform which gradually slopes down to a subtidal fringe of large brown algae such as *Cystophora* sp., *Corphophyllum maschalocypum* and *Macrocystis pyrifera*. Intertidally, extensive mats of turfing coralline algae and the fucallean alga *Hormosira banksii* are interspersed with seagrass patches and bare siltstone patches dominated by limpets and trochid gastropods. Mudstone Bay has a southerly aspect and is similarly composed of an extensive, gradually sloping siltstone platform. The algal and animal assemblages are similar to those at Wairepo Flats. More silt collects at Mudstone Bay, however, due to the shallower sublittoral bed nearby (Rasmussen, 1965).

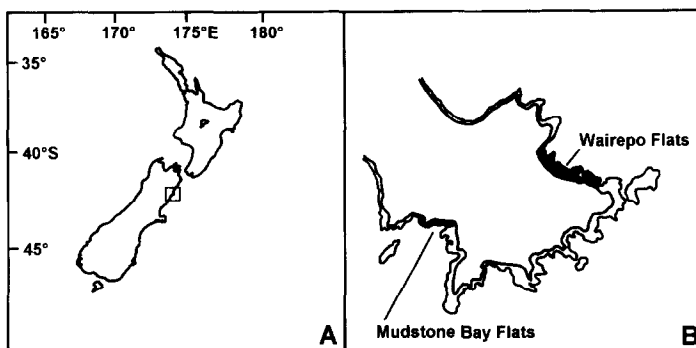


Fig. 1. Map of New Zealand showing the location of the Kaikoura Peninsula and the two study sites.

2.2. Sampling methods

Because of the sensitivity of seagrass to disturbance, and the apparent state of decline observed in a number of patches around Kaikoura (Ramage, 1995), a non-destructive method of quantifying use of seagrass as a habitat by *M. hirtipes* was necessary. Warren (1990) found that for another ocypodid crab, *Heloecius cordiformis*, inhabiting mangrove forests, counts of open burrows provided a quick and reliable estimate of apparent crab abundance. In May 1994, to determine whether the number of burrows visible on the surface of a patch of seagrass was a reliable indicator of the actual number of crabs inhabiting the seagrass, ten seagrass patches at each site were chosen at random for sampling. A 0.25 m² quadrat was randomly placed within each patch and the number of visible burrows was counted. The area within the quadrat was then rapidly dug out down to the bedrock and placed in a high-walled sieve (diameter of sieve = 60 cm, mesh size = 2 mm). The sediment was washed away from the seagrass and the number of crabs remaining was counted. The crabs collected were sexed to obtain an estimate of the sex ratio at each site. For ten of these 0.25 m² quadrats (five at each site), the vertical depth of a single burrow selected at random was determined by careful dissection of the seagrass before sieving, measured with a 1 m stainless steel rule and compared with the vertical depth of the seagrass itself.

In June 1994, transects were run perpendicular to the shore at both sites, from the mean high tide mark to mean low tide, at horizontal intervals of 4 m, along the entire area of each study site (Wairepo Flats = 900 m wide, Mudstone Bay = 450 m wide). The number of seagrass patches encountered 2 m either side of the transect and the presence or absence of burrows in these patches were recorded. To obtain an estimate of overall burrow density, 30 seagrass patches at each site were selected at random and a 1 m² quadrat placed at random within the patch. The number of burrows within each quadrat was then recorded.

The spatial distribution of burrows within seagrass patches was determined by randomly selecting ten large-sized (> 2 m²) patches at each site. For each patch, three 0.0625 m² quadrats were randomly placed and burrows were counted within each of four zones on a patch: 0–30 cm from the patch edge, 30–60 cm from the patch edge, 60–90 cm from the patch edge, and 90–120 cm from the patch edge. As large seagrass patches usually border tide pools along some of their perimeter, the sampling procedure was carried out on both tide pool, and non-tide pool regions of the patches. The percentage cover of seagrass blades was estimated from a grid placed in each quadrat.

To examine the morphological characteristics of the burrows constructed by *M. hirtipes*, casts were made of 30 burrows from different patches, 15 at each site. Patches were selected at random, then a random allocation was made as to whether a burrow at the edge (0–30 cm from edge) or a non-edge (> 30 cm from edge) burrow would be cast. The casts were made when the patches were exposed at low tide using FFFF casting grade Plaster of Paris. Prior to casting, water within the burrows was extracted using a 50 ml syringe with flexible tubing attached which was inserted as far as it would go into the burrow. A liquid slurry of plaster was then poured into the burrows, and the burrows marked with a white upright plastic marker pushed into the seagrass and left for 24 h before the hardened caste was carefully dug out and extracted from the seagrass. Once extracted from the seagrass, the following measurements and observations were

recorded for each burrow: greatest vertical depth, total burrow length (length of all entrances and passageways combined), number of crabs per burrow as well as each crabs' sex and size, average burrow diameter (mean taken from diameter measured at burrow entrance, mid-point and end-point), number of entrances, and finally, number of passageways per burrow.

The persistence of crab burrows was determined by placing a 0.25 m² quadrat within each of ten randomly selected patches at each site. The quadrats were marked with plastic corner stakes. A gridded quadrat (100 × 5 cm squares) was laid within the marked area and the position of all existing burrows was mapped. Every 7 d for a further 11 weeks, the marked areas were examined and all burrows were mapped.

In August 1994, the effect of blade density on burrowing was determined by selecting 15 sections (approximately 35 cm × 18 cm × 10 cm deep) which were carefully dug out intact from large seagrass patches (> 1 m²). Five sections had approximately 100% seagrass blade cover, five had 50% blade cover, and five had no blade cover. Once dug out, these sections were immediately transferred to the laboratory and placed in aquaria (35 cm × 18 cm × 18 cm), covered with 5 cm of fresh seawater, and provided with a bubbled air supply. One crab was placed into each aquarium and the time from initiation of burrow construction to time of burrow completion was recorded.

To determine the effect of crabs on the rate of patch erosion, each of five patches possessing crab burrows at each site had a white upright plastic marker placed in the centre in December 1994. Five compass bearings were randomly selected, and the distance from the plastic marker to the edge of the patch along each of these compass bearings was measured. The total number of crab burrows present in the patch was recorded, and blade density of the patch was estimated using a 0.25 m² gridded quadrat. After 6 months, the distance along each compass bearing from the plastic marker in centre of each patch to the edge of the patch was measured, and number of burrows and blade density were recorded. This treatment included a range of burrow densities from 1–48 crab burrows per patch. For comparison, five patches that did not possess crab burrows at each site were treated as above.

Sixty crabs were collected from each site for gut content analysis from May to June 1994. Upon capture, crabs were immediately placed in 10% formalin and taken to the laboratory where they were sexed and the carapace width was measured using vernier callipers (± 0.1 mm). The foregut of each crab was dissected out, opened along the mid-ventral line, and the contents washed out into a gridded (100 × 4 mm² squares) petri dish. Foregut contents were estimated as the percent volume each different type of food item contributed to the total volume of the foregut contents as estimated by the total number of 4 mm² squares covered by the foregut contents.

3. Results

3.1. Occupation of seagrass patches by crabs

The number of crab burrows visible at the surface of seagrass patches was positively correlated with actual number of crabs present, both at Wairepo Flats ($r_g = 0.954$, $P < 0.001$), and at Mudstone Bay ($r_g = 0.853$, $P < 0.01$). For the rest of the study a 1:1

crab to burrow ratio was assumed. The sex ratio of male to female crabs was 1:1.1 both at Wairepo Flats ($n = 31$) and at Mudstone Bay ($n = 19$), which do not vary significantly from an even ratio ($\chi^2 \approx 0.04$, n.s.). The depth of burrows was related to the depth of seagrass patches ($r_8 = 0.90$, $P < 0.001$), which in large patches can reach 36 cm between the surface of the patch and the hard reef below it.

A total of 2141 seagrass patches around the Kaikoura Peninsula were examined, 1349 (63%) of which possessed crab burrows. At Wairepo Flats, 65.8% of seagrass patches were occupied by crabs compared to 57.7% at Mudstone Bay. The occupation of burrows was not dependent on site ($\chi^2 = 13.7$, $P > 0.05$). There was no relationship between the number of crab burrows and seagrass patch size ($r_{28} = 0.15$, $P > 0.05$) or patch depth ($r_8 = 0.34$, $P > 0.05$). However, there was a negative correlation between the number of burrows and the density of seagrass blades on patches ($r_{28} = -0.64$, $P < 0.01$). The overall density of crab burrows per m^2 was 9.73 (± 1.24) at Wairepo Flats and 9.1 (± 1.7) at Mudstone Bay.

3.2. Variation within seagrass patches

An ANOVA with the factors Site (Wairepo vs Mudstone), Pool (adjacent or not adjacent to tide pool), Distance (four zones within seagrass patches), Patches within Sites, and all interactions, was used to analyse crab abundances and the percent cover of seagrass blades. Patches within Sites was treated as random. The abundance of crab burrows varied within seagrass patches (Fig. 2), with the majority of burrows occurring in the sides of patches associated with tide pools (Fig. 2A, B; $F_{1,18} = 28.9$, $P < 0.001$). There was no difference between sites ($F_{1,18} = 0.61$, $P = 0.44$), and no interactions of Site with the other factors were significant. Crab burrows decreased in abundance towards the centres of patches ($F_{3,54} = 18.1$, $P < 0.001$), but the magnitude of this effect depended on whether or not patches were associated with tide pools ($F_{3,54} = 21.8$, $P < 0.001$).

The percent cover of seagrass blades showed a reverse trend (Fig. 3A, B). A greater cover of seagrass blades occurred in the sides of patches not associated with tide pools

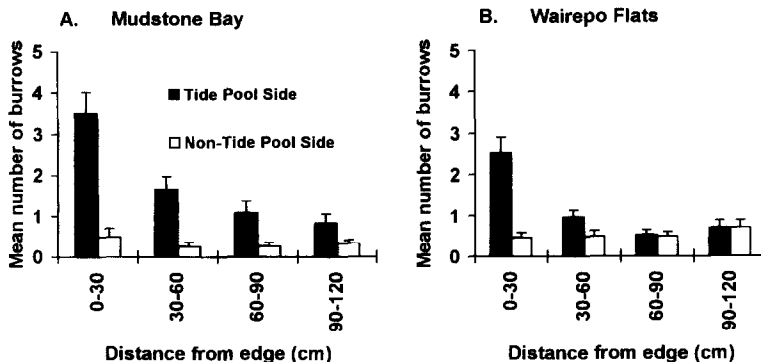


Fig. 2. The abundance (mean \pm 1 S.E.) per 0.0625 m^2 of crab burrows within patches of seagrass at (A) Mudstone Bay and (B) Wairepo Flats.

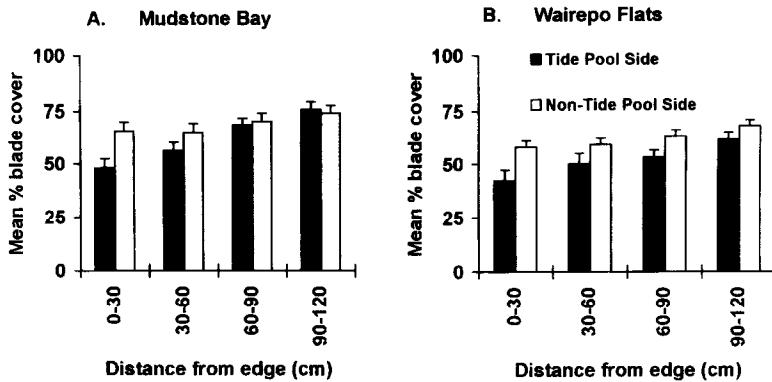


Fig. 3. Percent cover (mean \pm 1 S.E.) of seagrass blades in patches of seagrass at (A) Mudstone Bay and (B) Wairepo Flats.

($F_{1,18} = 8.2$, $P = 0.01$), but this effect varied among patches within sites ($F_{18,320} = 66.8$, $P < 0.001$). There was a significant increase in blade cover towards the centre of patches ($F_{3,54} = 26.8$, $P < 0.001$), but this effect also depended on whether the patches were associated with tide pools ($F_{3,54} = 4.9$, $P = 0.005$). Overall, the percentage cover of seagrass blades varied inversely with the number of crab burrows ($r_{478} = -0.38$, $P < 0.001$).

3.3. Burrow construction

From a total of 30 burrows originally cast, 21 of the plaster casts were found to have filled all possible entrances and passageways upon extraction. Of these burrows (eight from Wairepo Flats and 13 from Mudstone Bay), several burrow characteristics were seen. In cross section, the burrows were slightly dorso-ventrally flattened and could descend at a steep angle deeply into the seagrass, remain nearly parallel with the surface at a shallow depth, spiral slightly, or run straight. The number of burrow entrances and passageways also varied (Fig. 4A, B, C).

Morphological measurements made of the 21 intact burrows (Table 1) showed no significant differences in burrow characteristics attributable to site (all ANOVAs, $P > 0.05$). Similarly, there was no significant difference in the depth to which burrows ran that was attributable to location of the burrows within the seagrass patches. However, the total length of burrows varied significantly within patches ($F_{1,20} = 5.03$, $P < 0.05$); burrows located at the edges of patches had a mean length of 18.5 ± 3.35 cm, while burrows away from the edges averaged 13.1 ± 1.25 cm in length. This difference can be attributed to the significantly greater ($F_{1,20} = 14.03$, $P < 0.01$) number of passageways that burrows located at the edges of patches (mean = 1.9 ± 0.26) possessed when compared with non-edge burrows (mean = 1 ± 0). Burrows located at the edges of patches also had significantly ($F_{1,20} = 4.9$, $P < 0.05$) more entrances (mean = 1.8 ± 0.15) than non-edge burrows (mean = 1.3 ± 0.14).

In those burrows which were found to contain crabs upon careful shattering of the

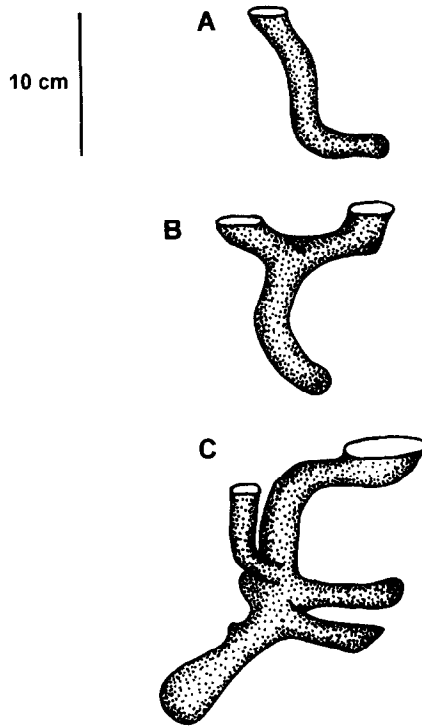


Fig. 4. Types of burrow construction of the crab *Macrophthalmus hirtipes* in seagrass patches: (A) single entrance and single passageway (B) double entrance and single passageway, and (C) double entrance and triple passageway. Burrow entrance is at the top of each passageway.

casts, there was only ever one crab per burrow. Crab size (carapace width) was significantly correlated with average burrow diameter ($r_{19} = 0.88$, $P < 0.001$) and was always larger than the average diameter of the burrow that the crab inhabited. This is indicative of ocypodid crabs as they burrow sideways. The sex ratio of crabs found in the burrows was exactly 1:1.

3.4. Effect of seagrass density on burrowing

The laboratory-based experiments showed that seagrass blade density had no effect on the time it took crabs to initiate burrow construction ($F_{2,12} = 0.11$, $P = 0.9$), or on the number of attempts at burrowing ($F_{2,12} = 0.46$, $P = 0.6$). However, burrow construction took about three times longer at 100% blade cover than at 0% and 50% blade cover (Fig. 5; $F_{2,12} = 3.9$, $P = 0.05$). Crabs in patches of 100% blade cover took 416 (± 110.6) min to complete burrow construction, while at blade covers of 50% and 0% they took 171 (± 45.4) and 145 (± 54.2) min respectively.

Table 1
Morphological characteristics of casts of crab burrows taken from seagrass patches

Site	Location	Vertical burrow depth (cm)	Total burrow length (cm)	Number of crabs	Crab sex	Crab size (mm)	Average burrow width (mm)	Number of entrances	Number of passageways
Wairepo Flats	Edge	12.6	27.2	1	Male	23.5	17.87 ± .87	2	1
	Edge	19	38	1	Male	24.6	19.2 ± 1.46	2	3
	Edge	9.2	11.5	0			11.87 ± .26	2	2
	Non-edge	18.7	20.1	1	Female	18.2	16.9 ± .26	1	1
	Non-edge	8.3	12.9	1	Female	14.6	13.57 ± .21	2	1
	Non-edge	9.9	12	1	Male	16.2	15.83 ± .22	1	1
	Non-edge	15.5	19.2	1	Male	22.6	22.03 ± 1.15	2	1
	Non-edge	7.4	8.2	1	Male	14.9	13.6 ± .36	1	1
Mudstone Bay	Edge	12.6	26.1	0			15.83 ± .38	2	3
	Edge	9.9	13.6	1	Female	17.4	17.63 ± .24	2	2
	Edge	10.5	17.3	0			15.5 ± .40	2	1
	Edge	9.2	16.4	1	Male	21.1	21.2 ± 1.03	2	2
	Edge	6.4	7.3	1	Female	16.9	14.9 ± .1	1	1
	Non-edge	11.2	14.6	0			15.63 ± .28	2	1
	Non-edge	5.2	6.4	1	Female	12.6	11.8 ± .31	1	1
	Non-edge	7.3	8.9	1	Male	15.2	14.87 ± .13	2	1
Non-edge	Non-edge	14.6	17.8	1	Female	17.3	16.83 ± .09	1	1
	Non-edge	9.6	12.9	1	Male	16.3	14.73 ± .56	1	1
	Non-edge	12.8	14	1	Female	12.5	12.33 ± .18	1	1

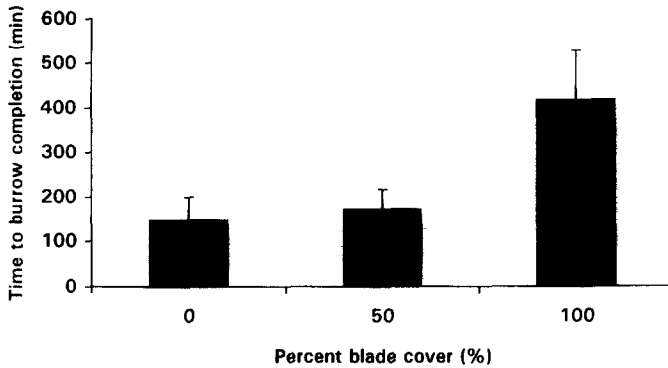


Fig. 5. Time in minutes (mean \pm 1 S.E.) taken to complete burrow construction in laboratory-based experiments using seagrass of 0, 50 and 100% blade cover.

3.5. Persistence of burrows and effects of crabs on patch erosion

The occupation of burrows is not permanent and over time burrows become filled in with loose sediment except when the edges of patches have been eroded away exposing some portion of the burrow, allowing water movement to flush the burrows clear of sediment. Following each high tide period, crabs in occupied burrows were observed to clear away sediment that had begun to fill in their burrows. At both sites, mapped burrows disappeared gradually over time (Fig. 6). After 3 months, five of the original 30 burrows (17%) at Wairepo Flats, and seven of the original 36 burrows (19%) at Mudstone Bay remained occupied by crabs, as indicated by plumes of expelled sediment at burrow entrances.

Over a 6 month period, seagrass patches that had crab burrows suffered a greater proportional loss of patch area due to erosion of patch edges compared to patches that were free of crab burrows ($F_{1,16} = 17.8$, $P < 0.001$; Fig. 7). This result did not vary

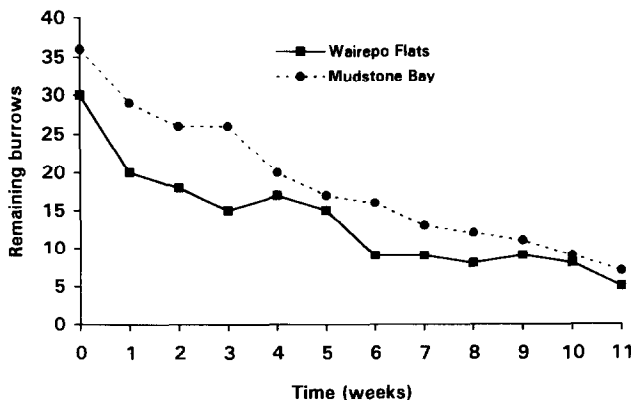


Fig. 6. The number of marked crab burrows remaining through time at Wairepo Flats and Mudstone Bay.

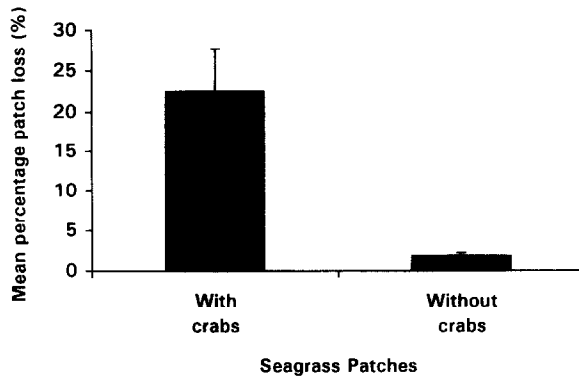


Fig. 7. Mean (± 1 S.E.) percentage patch loss after 6 months in seagrass patches with and without burrows of the crab *Macrophthalmus hirtipes*.

between sites ($F_{1,16} = 2.2$, $P = 0.16$). Patches with crab burrows had a mean loss of 22.5% (± 5.27) of the original size over 6 months, while patches without crab burrows lost 1.8% (± 0.37) of their surface area during the same time. There were no site-specific differences in proportional patch loss over this time ($F_{1,16} = 2.2$, $P = 0.16$).

3.6. Diet of crabs within seagrass patches

Of the 120 crabs examined (65 male, 55 female), 106 (88%) contained material in their foreguts. The main contents of the foreguts of *M. hirtipes* were living seagrass

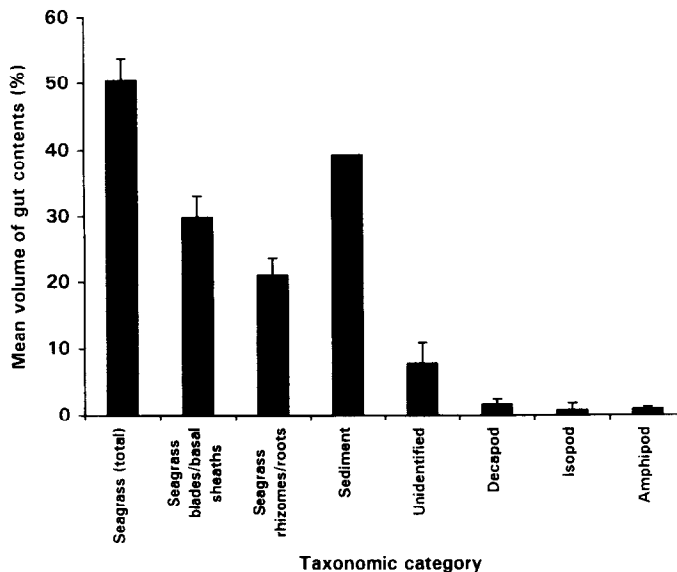


Fig. 8. Mean (± 1 S.E.) percent volume of foregut contents of all crabs examined from both study sites.

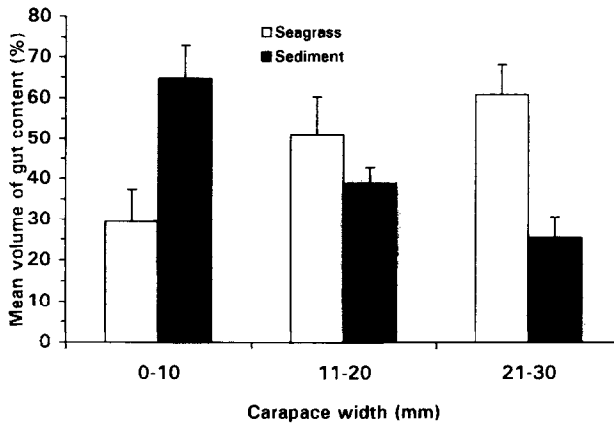


Fig. 9. Mean (\pm S.E.) percent volume of seagrass and sediment in foreguts of *Macrophthalmus hirtipes* of three size classes.

($51 \pm 3.4\%$ S.E.) and sediment ($39 \pm 3.1\%$; Fig. 8). Both aerial portions (blades and basal sheaths) and subterranean portions (rhizomes and roots) of seagrass were present in the guts, accounting for 30% (± 2.2), and 21% (± 2.6) of foregut contents respectively. Less abundant were decapods ($1.6 \pm 1.07\%$), amphipods ($0.9 \pm 0.64\%$) and isopods ($0.7 \pm 0.34\%$). There were no intersexual ($F_{1,101} = 0.09$, $P = 0.77$) or site ($F_{1,101} = 0.98$, $P = 0.32$) differences in diet. There were, however, differences in diet among different sized crabs (Fig. 9). Larger crabs (i.e., 11–20 mm and 21–30 mm carapace width) ate more seagrass than did smaller crabs (i.e., 1–10 mm carapace width) ($F_{2,102} = 3.6$, $P < 0.029$; SNK test: 1–10 < 11–20 = 21–30 mm CW). Conversely, smaller crabs had a greater relative volume of sediment than did larger crabs ($F_{2,102} = 7.3$, $P = 0.001$; SNK test: 1–10 > 11–20 = 21–30 mm CW).

4. Discussion

The exposed coastline of the Kaikoura Peninsula is dominated by rocky intertidal platforms which normally would not be inhabited by burrowing mud crabs. The occurrence of the burrowing crab *Macrophthalmus hirtipes* is enabled only by the presence of the intertidal seagrass *Zostera novazelandica*. Because this seagrass occurs along the platforms in hundreds of discrete patches, most of which are $< 1 \text{ m}^2$ in surface area and around 10 cm deep (Ramage, 1995), it provides a fragmented and spatially restrictive habitat in comparison to the waterlogged sediments of mudflats, lagoons and estuaries which *M. hirtipes* usually occupies. The seagrass also provides an alternative source of nutrition for these crabs which are normally deposit feeders. The distribution of crabs around the Kaikoura Peninsula exactly matches that of *Z. novazelandica*, with 63% of patches having crab burrows.

The nearly 1:1 sex ratio of crabs and their densities in seagrass patches are typical of those occurring in mudflats (Nye, 1974; Simons and Jones, 1981). For example, Simons

and Jones (1981) reported crab densities ranging between 11–41 per m² in an estuary in southern New Zealand, and Stephenson (1970) reported crab densities of 11 per m² in a central NZ mudflat. At our study sites, the overall densities were around 9 per m², but the greatest densities reached >40 per m² on the tide pool side of seagrass patches.

According to Beer (1959); Fielder and Jones (1978), *M. hirtipes* is mainly a deposit feeder that uses its hair-lined chelipeds to sieve through the sediment and concentrate organic matter before it is transferred to the mouthparts. It is unable to maintain prolonged recirculation of branchial fluid when exposed to air (Hawkins et al., 1982; Hawkins and Jones, 1982). It seems likely, therefore, that crabs construct their burrows along patch edges bordering tide pools because it allows them to remain submerged within tide pools when the seagrass patches and surrounding bedrock are exposed to air during low tide. Indeed, the only crabs observed foraging during low tide at Kaikoura were found in the tide pools bordering seagrass patches (personal observation). On mudflats and estuaries, however, *M. hirtipes* has been observed feeding on the surface exposed to air at low tide (Fielder and Jones, 1978; Williams et al., 1985).

An influencing factor in the abundance of crabs in the tide pool edges of seagrass patches is the reduced density of seagrass blades along the margins of tide pools. The laboratory-based experiments showed that crabs can burrow into these areas of reduced blade cover 2–3 times faster than into the areas of patches with a dense cover of seagrass blades. Blade cover and crab abundance clearly interact, however, because seagrass forms a major component of the diet of crabs.

The burrowing behaviour of *M. hirtipes* in seagrass in the field and laboratory, the occupation of burrows by single crabs, and the physical characteristics of burrows are very similar to those described by Nye (1974) in a mudflat habitat. Crab burrows were usually simple in construction with a single entrance, a passageway with no elaborate galleries, and were occupied by only one crab. In branching burrows, at least one of the branches was found to open into tide pools at the edge of the seagrass patch. Except for deep (>30 cm deep) seagrass patches, the depth to which crab burrows extended was restricted to the depth to which the seagrass ran before meeting the underlying bedrock. At our study sites burrow depth averaged 11.5 cm (± 4.1 S.D.), compared to 6 cm (± 1.5) in mudflats (Nye, 1974). Once the bedrock was encountered, the subsequent path the burrow took depended on the contours of the bedrock.

The burrows of *M. hirtipes* in seagrass patches lasted longer than the transient burrows in mudflats. Nye (1974) found that, for burrow entrances on mudflats, only 11% were in the same position one day later, while none was in the same position one week later. Relatively nomadic in nature, *M. hirtipes* does not have a strong affinity to a burrow and will sometimes wander away to construct a new one, even though it may have just defended its previous burrow (Beer, 1959). In contrast, the seagrass burrows of *M. hirtipes* were relatively persistent, some being in their original position after 3 months. This implies that crabs have a longer residence time in seagrass, perhaps because of the lesser amount of suitable habitat available coupled with the energetic cost of burrow construction.

Burrows are constantly being filled in with waterborne sediment or with sediment loosened from the walls of the burrow interior. This requires regular expulsion of sediment to maintain a clear passageway (Nye, 1974; Fielder and Jones, 1978; Jones and

Simons, 1982). The difference in burrow persistence between seagrass patches and mudflats may arise because the interconnecting rhizomes and roots reduce cave-ins of burrow walls. Although the maintenance of burrows by crabs may be reduced, the burrowing activity is to the detriment of seagrass patches. Crabs affect patch stability by reducing the binding effects of the interweaving rhizome/root network. In our study, this was shown to accelerate the erosion of occupied seagrass patches by a factor of 12 compared to patches that were free of crabs. Studies elsewhere have shown similar effects. In the northern Gulf of Mexico, for example, stone crabs (*Menippe spp.*) had a similar detrimental effect on the turtlegrass *Thalassia testudinum* (Valentine et al., 1994). Over a 7 month period, twice as much recession of seaward edges of turtlegrass occurred where stone crabs had constructed their burrows.

The burrowing of *M. hirtipes* along the margins of seagrass patches probably exacerbates patch erosion more so than if burrows were mainly constructed within the interiors of seagrass patches. The edges of seagrass patches are most prone to erosion through water movement over reef platforms (Ramage, 1995). Once patches begin to decline along their edges, the interiors of burrows are soon exposed. This creates a greater surface area for further erosion and the area immediately surrounding the burrow is rapidly undermined and torn away by water movement.

Along with a variety of other organisms such as echinoids, limpets, gastropods, parrot fish, turtles, water fowl, dugongs and manatees that use seagrasses as a source of food (King, 1981; Greenway, 1995), some crabs have also been identified as grazers of seagrasses. For example, Caine (1980) found that out of 21 specimens of the crab *Pugettia producta* collected from San Juan Island, Washington, USA, living seagrass (*Zostera marina*) blades accounted for 23% of foregut contents while Perez and Bellwood (1988) found small quantities of seagrass in the foregut of the crab *Matuta lunaris*. In our study, *M. hirtipes* was both a deposit feeder and a grazer of seagrass, eating aerial and sub-surface portions. Since about 20% of its food is comprised of seagrass rhizomes and roots, much of the feeding activity of *M. hirtipes* probably occurs within its burrows. This may be related to the maintenance of burrows, which are free of protruding rhizomes and roots.

In contrast to studies on mudflats, where deposit feeding is the main source of food for *M. hirtipes* (Beer, 1959; Fielder and Jones, 1978), the amount of inorganic material consumed by crabs in our study was second to seagrass consumption. In the field and in the laboratory, *M. hirtipes* showed both the deposit-feeding behaviour described by Fielder and Jones (1978) and active grazing of seagrass blades. Crustaceans, such as amphipods, isopods, and conspecifics formed only minor parts of the diet. Although necrophagy may contribute to its feeding, *M. hirtipes* is capable of active predation and has been observed capturing the isopod *Isocladus armatus* in the field (pers. obs.).

The blade coverage of seagrass patches affects invasion by crabs. Patches with a dense cover of seagrass blades have sediments below them that are firmly consolidated by rhizomes and roots. Laboratory experiments showed that this combination considerably lengthens the time it takes crabs to construct burrows. Few of the robust and healthy-looking patches have crabs inhabiting them. However, patches are temporally variable in size and blade cover, which provides suitable times for invasion by crabs. Harrison (1987) found that when established plots of the seagrass *Zostera marina* were denuded in summer on Roberts Bank, south-west coast of British Columbia, Canada, the

burrowing shrimp *Callinasa californiensis* was able to burrow into the sediment of the seagrass plots from which they had previously been excluded because of the blade coverage. The density of the blade cover of seagrass patches at Kaikoura varies seasonally, with the lowest density in winter (July–August). This coincides with the period of most severe wave action when patch mortality is greatest and when the major erosion of patches occurs (Ramage, 1995). Therefore, the majority of patches have at least a few months per year when they are susceptible to invasion by crabs. This invasion probably occurs laterally from patches already occupied with crabs, or from larval settlement (newly settled juveniles around 2–3 mm carapace width were occasionally observed hidden under shell fragments and detritus on the surface of seagrass patches). Invasion probably does not occur from subtidal sources, as snorkelling and SCUBA dives did not reveal any subtidal populations.

Furthermore, many patches are affected by a wasting disease reportedly caused by the myxomycete *Labyrinthula macrocystis* Cienk, as seen across Europe and North America in the 1930s (Armiger, 1964). *Labyrinthula* was seen in the seagrass around the Kaikoura Peninsula (Ramage, 1995) and on another platform in southern New Zealand (personal observation). *Labyrinthula* may be a normal secondary composer present in healthy seagrasses (Den Hartog, 1987) and not primarily responsible for the deterioration of seagrass patches. Patches often recover with the growth of new blades, but the overall effect is that for several months of the year blade cover is drastically reduced and patches are more vulnerable to possible invasion by crabs and, consequently, to severe erosion.

The physical and biotic factors leading to patch erosion are compounded by anthropogenic influences, which can be great along accessible intertidal platforms. Foot and vehicular traffic such as motorbikes and four wheel drive vehicles were seen to damage patches, which can take years to recover. For example, in another study Zieman (1976) found that seagrass damaged by boat propellers took 2–5 years to recover.

The crab *M. hirtipes* is an opportunist in rocky intertidal seagrass patches, extending its range into the only sediment-filled and relatively stable habitat available on rocky platforms. It is probably the most important animal affecting seagrass patch dynamics on rocky platforms in southern New Zealand. Although crabs do not inhabit the smallest patches forming in shallow tide pools or tidal cracks, they occupy a high proportion of established patches on the rocky platforms. There was no discernible effect of crabs in the recruitment of new patches, but their major influence in seagrass dynamics is the destabilisation and partial mortality of established patches. While patches are healthy, with a dense cover of seagrass blades, the crab probably has little effect on them. However, during times of physical or biotic stress the crabs can contribute significantly to patch deterioration, primarily through the disruptive effect their burrows have on seagrass patch stability.

Acknowledgments

Thanks to J. vanBerkel for assistance, to the Zoology Department and Edward Percival Marine Station, University of Canterbury, for facilities. The research was possible through the Public Good Science Fund of New Zealand, grant numbers UOC

318 and UOC 412; we gratefully acknowledge their support. Thanks also to two anonymous reviewers for helpful comments.

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