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Tests for artefacts in some methods used to study herbivory and predation in mangrove forests

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ABSTRACT: Ecologists have recently been cautioned about the potential for complex interactive artefacts to complicate the interpretation of field and laboratory experiments. This study in northern Australia tested for such effects in 2 methods commonly used to investigate herbivory and predation in mangrove forests: tethering and caging. There was no evidence that tethering leaves or propagules caused biases which would invalidate comparisons among habitats, but the method was likely to underestimate the intensity of feeding on propagules. There was also little evidence that cages had any effect on seedlings other than to reduce the intensity of herbivory. The results indicate that these methods are likely to provide useful, and non-problematic, information about the role of herbivory in mangrove forests.

KEY WORDS: Tethering · Caging · Artefact · Bias · Mangroves · Grapsid crabs · Herbivory · Predation

INTRODUCTION

Peterson & Black (1994) stated that current ecological practice 'implicitly assumes without requiring justification by proper test or compelling theory that the effects of artefacts of experimental intervention are constant across all treatments just because the intervention itself is identically applied to all treatments'. To illustrate this contention they reviewed studies in which tethered prey were used to determine if consumption varied among habitats (the 'treatments' in this case). They concluded that '(1) only 55% of the 22 studies even include discussion of artefacts of tethering; (2) only 9% acknowledge the possibility that the magnitude or direction of the between-habitat difference in predation... could be inaccurate if the artefactual enhancement of predation rate induced by tethering is not constant across habitats; and (3) no study actually tests the assumption that tethering artefacts are independent of habitat'. Of course, the problems which artefacts may create have been recognised for some time (e.g. Connell 1974, Dayton & Oliver 1980, Underwood 1986), especially, as Peterson & Black (1994) acknowledged, 'when the interventions required are grossly invasive and obvious'. Peterson & Black (1994) were, however, particularly concerned that ecologists did not appreciate that artefacts could interact with treatments in complex ways, rendering the results of simple controls misleading or worse.

Some of Peterson & Black's (1994) remarks were challenged. Aronson & Heck (1995) argued that their criticisms were 'overgeneralized' and 'inaccurate'. The latter observation was probably appropriate. For example, commenting on a study by Barshaw & Able (1990), Peterson & Black (1994) concluded that they 'failed to realize that the real significance of their study lies in its implication of a complex artefact'. In fact, Barshaw & Able (1990) had written 'The results of this study suggest that tethering to assess predation in different habitats should be evaluated for each new species under consideration because species-specific behavior patterns could create *habitat-specific tethering artefacts*' (my italics). The potential existence of such habitat-specific artefacts has also been recognised for some time. Virnstein (1978), for instance, discussing the problems potentially arising from the use of cages in soft sediment systems, indicated that the type and magnitude of artefacts could vary with environmental conditions (e.g. currents, sediment load, vegetation).

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Nonetheless, Peterson & Black (1994) provided a timely reminder that the artefacts introduced by experimental manipulations should be evaluated for each new method and situation, something which, despite Aronson & Heck's (1995) defence, ecologists have frequently neglected to do. Several of the studies Peterson & Black (1994) reviewed were, in fact, from one field in which this has frequently not been done: studies of the role of consumers in mangrove forests. Much interest at present centres on 2 questions (Robertson et al. 1992, Smith 1992): (1) How does predation on mangrove propagules affect the structure of the forest? and (2) How important are the various pathways for processing plant material in the forest? Two methods employed to address these questions are (1) the use of exclusion cages to determine the effects of herbivory and predation on the survival and growth of mangrove seedlings (e.g. Smith 1987a) and (2) the use of tethered food items to estimate the rate of consumption (e.g. Robertson 1986, Smith 1987b, Smith et al. 1989, McGuinness 1997a, b). (For the sake of convenience, the consumption of any plant material will be termed herbivory, although feeding on propagules is often referred to as predation.) In several studies there has been little or no mention of possible artefacts introduced by the experimental methods, or of the possibility that such problems may confound comparisons among different situations (e.g. habitats or sites; see Peterson & Black 1994 for examples).

Several studies document the ways in which cages and tethers may create artefacts in some habitats. Among other things, the presence of cages in soft sediments may alter the sediment, the recruitment of organisms, the behaviour of consumers or prey, and the levels of light, oxygen and nutrients (Virnstein 1978, Peterson 1979, Dayton & Oliver 1980, Hulberg & Oliver 1980). Tethering food items may alter the ease with which they are detected, captured or consumed (Barshaw & Able 1990, Peterson & Black 1994, Aronson & Heck 1995, Micheli 1996). Any of these effects could vary among habitats or sites, if there are differences in environmental conditions or in the types of consumers present. The studies described here were done to test for potential artefacts in these 2 methods, and to examine if such artefacts varied among habitats. The specific aims were:

(1) To determine whether the presence of a tether affected herbivory on mangrove leaves or propagules (because these had to be marked in some treatments, a subsidiary aim was to test for biases introduced by the marking method);

(2) To determine whether the presence of a cage affected the survival of mangrove propagules, other than by reducing herbivory;

(3) To determine whether artefacts introduced by either method differed among habitats. Such differences would appear as interactions between habitats and the various treatments established to detect different kinds of artefactual effects.

MATERIALS AND METHODS

Study sites and species. Fieldwork was done in the mangrove forests at Ludmilla Creek (12° 25' S, 130° 51' E) and Elizabeth River (12° 32' S, 130° 59' E), Northern Territory, Australia. Ludmilla Creek is a small coastal estuary; the forest at this site has been described by McGuinness (1994, 1997a, b). Elizabeth River is a major estuary flowing into Darwin Harbour. Semeniuk (1985) and Woodroffe et al. (1988) described the forest at sites close to those studied here.

All studies were done in 3 types of habitat: tidal creek bank; tidal flat; and hinterland. Tidal creek banks occur along the edges of small creeks and channels flowing through the forest. This habitat is dominated by *Rhizophora stylosa*, although *Bruguiera exaristata*, *Avicennia marina* and *Ceriops tagal* may also be present (Semeniuk 1985, Woodroffe et al. 1988). The substratum is inundated by most low tides and the sediment is fine and loose. The tidal flat is the most extensive habitat in these forests. It is dominated by *Ceriops tagal*, which often forms dense mono-specific stands, but clumps of *B. exaristata* occur, as do scattered *A. marina* (Semeniuk 1985, Woodroffe et al. 1988, McGuinness 1994). The hinterland fringes the terrestrial edge of the forest. This habitat is inundated only by high spring tides and the sediment is firm. The forest is usually dominated by *Lumnitzera racemosa*, although *C. tagal* may occur (Semeniuk 1985, Woodroffe et al. 1988).

All experiments were done using propagules and leaves of *Ceriops tagal*. This species is common in northern Australia and is found across broad expanses of the intertidal zone (Hutchings & Saenger 1987, Wightman 1989). It produces numerous propagules over a period of a few months (Tomlinson 1986, Hutchings & Saenger 1987). From previous studies, these propagules appear to be moderately preferred by consumers (Smith 1987b, McGuinness 1997a), being taken more rapidly than those of species such as *Rhizophora stylosa*, but less rapidly than those of species such as *Avicennia marina*. The fallen leaves of this species are commonly taken by herbivorous crabs (Robertson & Daniel 1989, Micheli 1993).

The dominant consumers of plant material in many tropical mangrove forests, including those in Australia, are the resident sesarmid crabs (Smith 1987b, Robertson & Daniel 1989, Smith et al. 1989, 1991, Micheli 1993, Steinke et al. 1993), although other species may play some role (Camilleri 1989, Robertson & Daniel 1989). Several sesarmids are common in the Darwin region, and at Ludmilla Creek, including *Metopograpsus frontalis, M. gracilipes, M. latifrons, Sesarma semperi* and *S. meinerti* (R. Hanley & F. Perrett pers. comm., author's pers. obs.). *S. meinerti*, in particular, is known to feed on the leaves and propagules of *Ceriops tagal* and other mangroves (Steinke et al. 1993) and appears to be one of the dominant consumers in local forests (McGuinness 1997a, b). Some intertidal molluscs may feed on this material (Smith et al. 1989), but the only local species known to do this, *Terebralia palustris* (T. Crowe pers. comm.), is not abundant, particularly at these sites. Agile wallabies *Macropus agilis* are common in and around the Ludmilla Creek mangroves and do feed on established seedlings (Smith 1987a, author's pers. obs.); they have not, however, been observed to take material from the forest floor. I know of no reports of subtidal species feeding on mangrove material *in situ* in Australian forests.

Tethered propagules and leaves. Sesarmid crabs usually remove propagules or leaves to their burrows to consume them (Robertson & Daniel 1989) and the main bias created by tethering these items is likely to result from interference with this process. It should be possible to estimate the magnitude of this bias by varying the length of the tether; propagules on long tethers should be more easily taken down burrows than propagules on very short tethers (comparison of Treatments 3, 4 and 5 in Table 1). It is possible that the presence of tether itself may interfere with the normal manipulation of the food item but this problem is likely to be minimal when the point of attachment is small relative to the size of the food item, as is the case with the leaves and propagules of *Ceriops tagal*. Three lengths of tether were used: 5 cm, 50 cm and 100 cm. The latter is the longest length which is likely to be generally practical and this, and 50 cm, have been used in previous studies (e.g. Smith 1987b, Smith et al. 1989, McGuinness 1997a, b). Tethered propagules were attached to 6 cm roofing nails pushed into the sediment.

Even long tethers may, however, introduce some bias. There may be no simple way to estimate this, but in some circumstances it may be possible to show that it is *not* important. If the rate of loss of propagules on long tethers (Treatment 5) is similar to that of untethered propagules (Treatments 1 and 2), then, either there is no bias, or the bias is similar to the rate of tidal removal; the latter does not seem likely. These untethered propagules had, however, to be marked in order to distinguish them from 'natural' items falling or washing into the area but this procedure introduced a second potential bias. The marking procedure involved painting one end of the propagule or leaf and it is possible that this would either discourage consumers or make the items more easily visible. A test for effects of marking was done using tethered unmarked and marked propagules (Treatments 5 and 6). Untethered propagules marked with only a small spot of paint (Treatment 1) were included as an additional test of this bias but, since these might be much harder to find than more obvious untethered, half-painted propagules (Treatment 2), this comparison is potentially confounded.

Table 1. Treatments used to examine bias in estimates of herbivory on *Ceriops tagal* leaves and propagules. See text for further explanation of treatments

Treatment	Tether	Marking	Tether bias	Marking bias
1: Small-mark	None	Small spot	None	Small
2: Large-mark	None	Half painted	None	Great
3: Short-tether	5 cm	None	Largest	None
4: Medium-tether	50 cm	None	Intermediate	None
5: Long-tether	100 cm	None	Least	None
6: Marked-long-tether	100 cm	Half painted	Least	Great

For each treatment, 2 replicates were established in 5 × 5 m plots and 10 propagules, or leaves, were tethered or placed in each plot (only 2 replicates could be done because of limited space in the hinterland). The tidal creek bank and tidal flat habitats were on the Elizabeth River, but the hinterland sites were at Ludmilla Creek. This arrangement was required because there was insufficient hinterland at Elizabeth River, and space in the other habitats at Ludmilla Creek was limited (where other studies were underway). The experiment with propagules began on 4 January 1995 and was sampled after 5, 20, 40 and 57 d. The experiment with leaves was started on 14 March 1995 and was sampled after 7, 17 and 37 d. On each occasion the number of propagules or leaves remaining undamaged (intact) was recorded.

Data were analysed by 2-factor analyses of variance (ANOVA) on the results at each time, with the factors 'Habitat' and 'Treatment', both fixed. Although there were only 2 replicates of each treatment, the test for the Habitat × Treatment interaction had 10 and 18 degrees of freedom, suggesting that the experiment would have moderate power. This was confirmed by power analysis: the probability of detecting a difference of 25% among the treatments ranged from 9 to 70%, depending on the exact form of the alternate hypothesis and the error variance at the different times.

Caged propagules. For cage effects, 5 treatments were established (Table 2): (1) no cage (control), (2) full cage (caged), (3) cage with no roof (fenced), (4) open-sided cage (a cage with 2 facing sides missing) oriented with the prevailing water flow (open-with), and (5) open-sided cage oriented against the prevailing flow (open-against). One of the potential artefacts created by cages are alterations to the flow regime (Virnstein 1978), resulting in sedimentation or erosion and other effects. The last 2 treatments (Treatments 4 and 5 in Table 2) were designed to test for these: any alterations to flow should produce greater effects in the open-against plots. Previous experience with cages in these habitats suggested that other artefacts, although possible, were unlikely (e.g. organisms did not colonise cages and light levels under the mangrove canopy are very low). These points are considered later (see 'Discussion').

If there were no effects of flow, then comparisons could be done to test for effects of crabs (Treatments 1 vs 3, and 2 vs 4 and 5) and wallabies (Treatments 2 vs 3, and 1 vs 4 and 5). If there were effects of flow, then tests for effects of crabs and wallabies could still be done (Treatments 2 vs 5, and 2 vs 3, respectively); but these are less reliable because there is doubt as to the extent to which (a) the fences limit the access of large crabs and (b) the open-against and open-with treatments limit the access of wallabies.

Experimental plots were 0.5 × 0.5 m and were replicated 3 times in each habitat at Ludmilla Creek. Cages were 40 cm high, constructed of 1 cm welded metal mesh and designed to exclude the larger crabs, primarily *Sesarma meinerti*, likely to feed on propagules. Areas containing *S. meinerti* burrows, distinguishable by size (usually >5 cm) and shape, were avoided, although some individuals subsequently invaded cages in the hinterland (see 'Results'). No attempt was made to alter the initial densities of small crabs inside experimental plots because it would have been impossible to do this without severely disturbing the habitat. The direction of flow was checked by anchoring small pieces of flagging tape inside each plot and observing their location after a series of high tides had inundated the area.

In each plot, 20 propagules were planted on 5 December 1994 and the position of each was marked with a short bamboo skewer. On 10 subsequent occasions the numbers of propagules surviving and growing were recorded. At 2 of these times, the numbers of crab burrows per plot in 2 size categories, ≤5 cm (small burrows) and >5 cm (large burrows), were counted.

Data were analysed by 2-factor ANOVA on results at 1, 8 and 30 wk (selected simply to represent the start, middle and end of the experiment) with the factors 'Habitat' and 'Treatment' both fixed. There were 3 replicates of each treatment, so the test for the Habitat × Treatment interaction had 8 and 30 degrees of freedom, suggesting that this experiment would also have moderate power. This was again confirmed by power analysis: the probability of detecting a difference of 25% among the treatments ranged from 14 to 77%, depending on the exact form of the alternate hypothesis and the error variance at the different times. Given the objectives of the study, it is, nonetheless, important to interpret the results of this and the previous experiment cautiously.

Table 2. Treatments used to examine artefacts of caging on rates of herbivory on *Ceriops tagal* propagules and their potential effects. Effects with a '?' may be questionable. For example, open cages with flow may interfere with water flow to some extent. See text for further explanation of treatments

Treatment	Water flow	Crab herbivory	Wallaby herbivory
1: Control	Normal	Normal	Normal
2: Cage	Reduced	Reduced	Reduced
3: Fence	Reduced	Reduced?	Normal
4: Open cage with flow	Normal?	Normal	Reduced?
5: Open cage against flow	Reduced	Normal	Reduced?

RESULTS

Tethered propagules and leaves

Analyses of the percentage of propagules which remained intact revealed significant differences among treatments which persisted to the end of the study (Table 3, Fig. 1). Tukey's HSD test indicated that after 5 and 57 d the small-mark and large-mark treatments had a similar percentage of intact propagules, which was less than the percentage intact in the other treatments; the latter were all equal. Tukey's tests could not separate means at the intervening times.

All leaves were gone from all treatments in the tidal flat by the first sampling time, but most survived in the tidal creek bank and hinterland, except in the small-mark and large-mark treatments (Fig. 2). This caused significant interactions between Habitat and Treatment at the first 2 sampling times (Table 3). At the first sampling time, all tidal flat treatments, and the small-mark and large-mark treatments in the tidal creek bank and hinterland, had a significantly smaller percentage of leaves remaining than did other treatments (Tukey's tests). Over time the percentage of leaves intact in the other treatments at the tidal creek bank and hinterland declined towards zero. Tukey's tests could not separate means at the last 2 times.

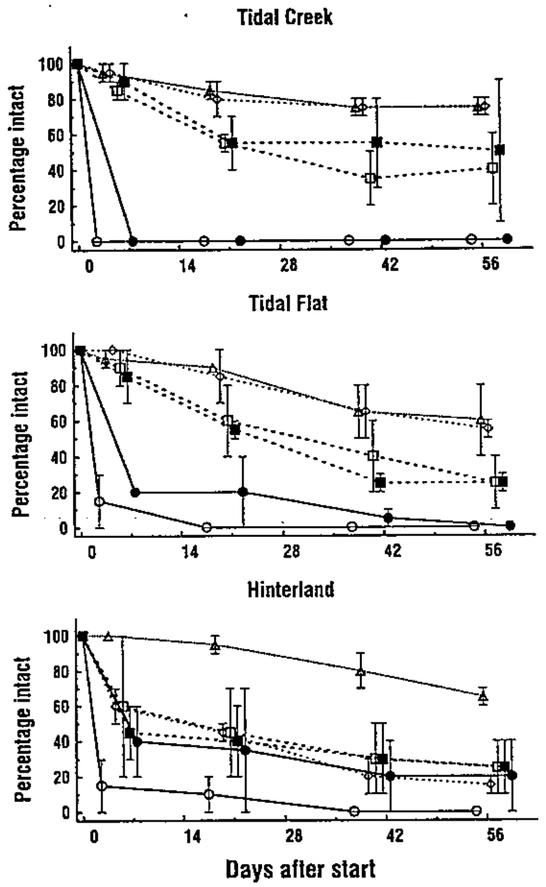

Fig. 1. Mean percentage of propagules intact at different times in the tether study. (○) Small-mark; (●) large-mark; (△) short-tether; (◇) medium-tether; (□) long-tether; (■) marked-long-tether. Error bars show ± 1 SE

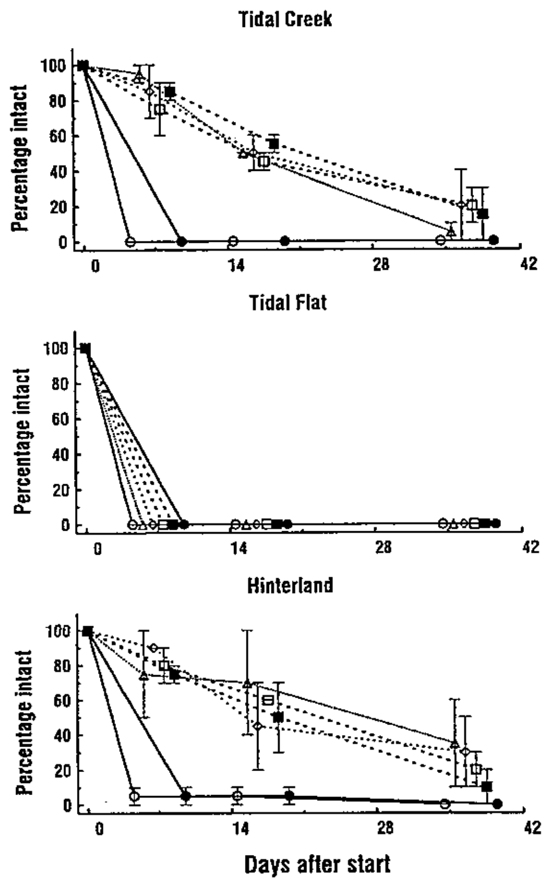

Fig. 2. Percentage of intact leaves in the tether study. Symbols and error bars as in Fig. 1

Caged propagules

The numbers of propagules remaining and growing were always highly correlated (mean $r = 0.92$, $n = 45$), so analyses were only done on the percentage remaining. There were significant interactions between Habitat and Treatment in all analyses (Table 4). In the tidal creek bank, the percentage of propagules remaining declined over time, but the means of the 5 treatments did not differ greatly (Fig. 3) and Tukey's tests could not separate them. In the tidal flat, clear differences, which persisted to the end of the study, developed among the treatments. The percentage of propagules remaining in the control, open-with and open-against treatments declined rapidly to zero, but most propagules in the fenced and caged treatments survived (Fig. 3). Tukey's tests detected differences between the caged/fenced plots and the other 3 treatments at 8 wk, but not at the other times. Results in the hinterland were similar. The percentage of propa-

Table 3. Summary of ANOVA on percentage of propagules and leaves remaining intact in the tethering experiment. All data were arcsin transformed; Cochran's test was non-significant at all times. Values in the table are the mean squares from the ANOVA at each time. *Significance at $p < 0.05$

	df	Propagules				Leaves		
		5 d	20 d	40 d	57 d	7 d	17 d	37 d
Habitat	2	0.136	0.033	0.025	0.079	2.698*	1.399*	0.294*
Treatment	5	1.628*	1.247*	0.924*	0.832*	0.895*	0.415*	0.118
H × T	10	0.141	0.070	0.065	0.061	0.236*	0.115*	0.048
Residual	18	0.092	0.082	0.054	0.060	0.042	0.042	0.050

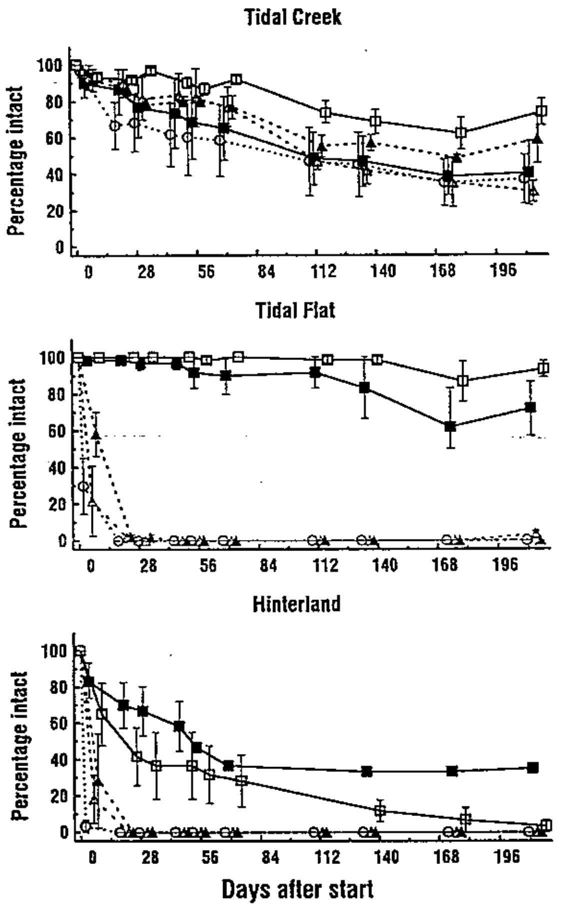

Fig. 3. Percentage of propagules surviving in the cage study. (○) Control; (□) fence; (■) cage; (△) open-with; (▲) open against. Error bars show ± 1 SE

gules surviving in the control, open-with and open-against treatments again dropped rapidly to zero, while survival in the caged and fenced treatments appeared higher (Fig. 3). In this case, survival was greatest in the caged plots, although Tukey's tests were unable to separate means at any time. There was an increase between the second to last and last sampling times in the number of propagules in some

Table 4. Summary of ANOVA on percentage of propagules remaining intact in the cage experiment. All data were arcsin transformed; Cochran's test was non-significant at all times. Values are the mean squares from the ANOVA at each time. *Significance at $p < 0.05$

Source	df	1 wk	8 wk	30 wk
Habitat	2	2.126*	2.748*	1.501*
Treatment	4	0.844*	1.380*	0.842*
H × T	8	0.340*	0.473*	0.364*
Residual	30	0.088	0.071	0.059

treatments in the tidal creek bank and tidal flat (Fig. 3). This was caused by the loss of several skewers, resulting in confusion between planted and naturally established propagules.

The number of small crab burrows differed among habitats at both sampling times (ANOVA on log-transformed data, both $p < 0.001$), with significantly more in plots in the tidal creek bank (mean of both times = 21.5) than in the tidal flat or hinterland (means = 2.4 and 2.3, respectively). Large burrows were present only in plots in the hinterland at the first sampling time. At this time, the percentage of propagules surviving was negatively correlated with the number of large crab burrows ($r = -0.42$, $p < 0.05$, $n = 45$).

DISCUSSION

Tethered propagules and leaves

The effects of the different lengths of tethers differed between leaves and propagules. There was little evidence that the length of the tether affected the rate of loss of leaves. There was, however, considerable evidence that propagules on longer tethers were lost more rapidly. Although multiple comparisons tests could not separate means for the 3 lengths of tether, short-tethered propagules were lost more slowly than long-tethered propagules in all 12 sets of observations (3 habitats by 4 times). The difference in results between leaves and propagules may result from differences in the species consuming these 2 types of items. The major consumer of propagules in local forests, *Sesarma meinerti*, occurs at low densities. McGuinness (1997b) found an average of only 0.1 large burrows m^{-2} (likely to be occupied by *S. meinerti*) in mid-shore regions at Ludmilla Creek. In contrast, the mean density of smaller burrows was 23.0 m^{-2} (although note that burrow counts may give a biased estimate of abundance; Warren 1990). Leaves are likely to be taken by a wider range of these smaller and more common species (Camilleri 1989, Robertson & Daniel 1989), so leaves on even short tethers may be close to the burrow of a potential consumer, whereas tethered propagules may have been some distance from the nearest *S. meinerti* burrow. Crabs attempting to take propagules on short tethers may have been frustrated by being unable to carry them to their burrows (also see Micheli 1996).

Tethering leaves, therefore, seems likely to provide valid estimates of the activity of herbivores. The only bias is likely to be due to the leaves being available for a longer period, particularly low on the shore. This is important to consider when estimating the amount of material removed from different habitats by consumers (see Robertson 1986). It should, however, be less important for comparisons of the activity of herbivores. In this study, because there was no interaction between habitat and length of tether, a similar conclusion applies to propagules. The tether probably did, however, interfere with some attempts at herbivory on propagules, so the true rate of consumption may be higher than observed, a conclusion also reached by McGuinness (1997b) on the basis of different evidence.

These relatively simple results are probably explicable in terms of the biology of the organisms involved. Leaves and propagules are, of course, inanimate, so tethering does not interfere with escape or defence behaviour (as in, e.g. Barshaw & Able 1990, Barbeau & Scheibling 1994, Zimmer-Faust et al. 1994). Tethering might conceivably affect the orientation of propagules, by constraining them to lie flat against the substratum, but the majority of naturally occurring *Ceriops tagal* propagules are in this position (McGuinness 1997b).

The only difference among habitats was that consumption of propagules and leaves was greater in the tidal flat than in the tidal creek bank at Elizabeth River (comparisons with the hinterland would not be meaningful in this instance because these observations were made at a different site). Osborne & Smith (1990) found greater predation on *Aegiceras corniculatum* propagules tethered high on the shore, a result they attributed to the longer foraging time available. Frusher et al. (1994) found *Sesarma brevipes* and *S. messa* to be much more abundant in high shore regions; the latter species at least is a major consumer of leaves (Robertson 1986, Micheli 1993).

Finally, it is worth noting that there was little evidence that marking propagules and leaves with paint affected the rate of loss. There were no significant differences in loss between painted and unpainted leaves and propagules, whether or not they were tethered. In some situations, the numbers of painted propagules recovered appeared to be greater, but these differences were never significant and decreased over time. Micheli (1993) used a different method to assess the affect of marking leaves and also found no effect on their rate of removal by crabs.

Caged propagules

In contrast to the results for tethers, there was always an interaction between caging treatment and habitat. There was, however, little evidence of artefacts. The means of the 5 treatments in the tidal creek bank did not differ significantly, although there was a tendency for propagules in the fenced and open-against treatments to have slightly greater survival. This might result from some naturally-occurring propagules being retained in these plots and mistaken for those planted. In the tidal flat, more seedlings survived in the caged and fenced plots than in any of the other treatments. Results in the hinterland were similar, although Tukey's test could not separate means at any time. These results can be attributed to the activities of herbivores; a conclusion supported by the negative correlation between the survival of seedlings and the numbers of large crab holes in the experimental plots. Agile wallabies were probably responsible for the reduced survival of seedlings in control and fenced plots in the hinterland.

While artefacts are common in caging experiments in soft-sediment systems (Virnstein 1978, Peterson 1979, Hulberg & Oliver 1980, Summerson & Peterson 1984), they are not always present (e.g. Mahoney & Livingston 1982, Quammen 1984, Raffaelli & Milne 1987). As discussed by Virnstein (1978), the type and magnitude of these artefacts will depend on the extent to which the cage modifies the environment and the activity of non-target species. The results of this study suggest that such effects in mangrove forests may often be minor. Rates of flow and sedimentation may be too low for the hydrodynamic effects of the cages to be important. At Ludmilla Creek, minor erosion occurred around some fences and cages in the tidal creek bank but this had no apparent effect on seedling survival. There is also usually little light under the canopy (Smith 1987a, McGuinness 1997a), so the cages probably did not provide significant shelter from physical stress. And, at least in the habitats studied here, no other organisms colonised the surfaces of the cages. There was also no evidence that the cages affected the behaviour of mobile organisms, most of which seek refuge by burrowing. A possible exception was *Sesarma meinerti*, which burrowed in some experimental plots in the hinterland, perhaps in response to the availability of food.

Conclusions

These results suggest that tethering and caging food items are appropriate methods for examining the roles of herbivory and predation in mangrove forests. Artefacts or biases were relatively minor and could be overcome by the use of suitable controls and careful interpretation. The recommendations of Peterson & Black (1994) should, however, always be heeded to avoid wasted effort or erroneous conclusions. In particular, studies should always incorporate appropriate controls designed with reference to the natural history of the species likely to be present.

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