

Feeding preferences of two seagrass grazing monacanthid fishes

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Two seagrass grazing fishes, *Meuschenia freycineti* and *Meuschenia trachylepis* (Monacanthidae), were offered three choices of *Posidonia australis* seagrass blades of different epiphyte coverage and leaf age to determine whether these fishes exhibit a preference for epiphyte-covered seagrass blades. Both species removed significantly more biomass of the epiphyte-covered blades than of the two other blade types in multiple-choice tests. This clear preference for epiphyte-covered seagrass blades results in a preferred removal of older blades within the seagrass shoot of *P. australis*.

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Grazing on seagrass by fishes is a common phenomenon both in tropical and temperate habitats (Conacher *et al.*, 1979; Montague *et al.*, 1995; Mariani & Alcoverro, 1999; Valentine & Heck, 1999). Seagrass offers a fish grazer two potential food sources, epiphytes and the seagrass itself. If food value is obtained by the fishes from the seagrass leaves themselves, fishes would be expected to feed on young, growing leaves. Although these are potentially richer in defence chemicals, such as phenolic compounds (Agostini *et al.*, 1998), they contain lower amounts of structural components (and are therefore likely to be easier to digest) and are probably higher in nutrients than mature leaves (Alcoverro *et al.*, 1997; Hemminga & Duarte, 2000).

Temperate fishes grazing on seagrass are thought to select seagrass leaves and parts of leaves with a high abundance of epiphytes since epibiota (*i.e.* epiphytes and epifauna) are often more nutritious than the seagrass blade itself (Bell *et al.*, 1978; Alcoverro *et al.*, 1997; Tomas *et al.*, 2005). This is despite the fact that a wide range of species are capable of assimilating nutrients from seagrass itself and thus using it as a food source (Conacher *et al.*, 1979; Klumpp & Nichols, 1983; Havelange *et al.*, 1997; Carseldine & Tibbetts, 2005). The results from a recent experiment in *Posidonia oceanica* (L.) Delile,

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meadows indicated that grazing by the fish *Sarpa salpa* (L.) affected the epiphytic community to a much higher degree than the seagrass itself (Tomas *et al.*, 2005). A preference for epiphyte-covered seagrass blades, however, needs to be tested under controlled conditions. In previous studies, conclusions were either drawn from observations of grazing scars on seagrass and epiphyte removal in the field (Peirano *et al.*, 2001; Tomas *et al.*, 2005) or, in the majority of studies, from gut content analysis without quantifying the amount of bare seagrass *v.* seagrass with epiphytes attached consumed (Bell *et al.*, 1978; Edgar & Shaw, 1995).

The present study aimed to quantify feeding preferences of two monacanthid fishes on different types of seagrass blades by grazing fishes under controlled laboratory conditions. The species used were the six-spine leatherjacket *Meuschenia freycineti* (Quoy & Gaimard) and the yellow-finned leatherjacket *Meuschenia trachylepis* (Günther). Both species are endemic to Australia and adults occur on hard substrata such as rocky reefs while juveniles are temporary residents of *Posidonia australis* (Hook.f.) seagrass meadows. There they feed almost exclusively on the seagrass and its epiphytes, with seagrass constituting up to 60% of their diet (Bell *et al.*, 1978; Burchmore *et al.*, 1984). To test the hypothesis that fishes prefer epiphyte-covered blades over bare seagrass blades, independent of leaf age, the fishes were offered a choice of three blade types (young blades, mature blades without epiphytes and mature blades with epiphytes) and quantities of each blade type removed by fishes over 24 h were recorded.

Nine specimens of *M. freycineti* and 10 of *M. trachylepis* were collected in *P. australis* meadows in Botany Bay and Port Hacking (15 km and 35 km south of Sydney, Australia, respectively) using a seine net in September 2004. They were allowed to acclimatize to the tank environment in 200 l aquaria for 2 weeks. All specimens used in the experiments were juveniles, with total lengths (L_T) ranging from 100 to 120 mm. They readily fed on seagrass shoots after 1 day. This, and their general behaviour, indicated successful acclimatization. Trials were carried out with a single fish per tank in order to avoid a possible acceleration in grazing activity caused by aggregation of fishes (Supanwanid *et al.*, 2001). The bottom of each tank was covered with sediment to *c.* 2.5 cm depth and all experimental tanks were kept under a 12L:12D regime. Four of the five tanks were used as experimental tanks and the fifth as a control tank. A control treatment was necessary to obtain a correction factor for possible changes in seagrass biomass not caused by grazing. To test for feeding preferences in regard to seagrass morphology, the two fish species were offered a choice of three seagrass blade types. Each blade type represented a 'typical' part of the *P. australis* shoot as it would be accessible to the fishes *in situ* namely mature blades covered with epiphytes (epiphyte, E), mature blades without epiphytes (bare, B) and young, growing blades (young, Y). The leaves used in the experiments showed no previous grazing scars.

For B and E blade types, only blades other than the innermost blade of a shoot were used. For B, epiphytes were scraped off the blades using a microscope slide. Microscopic examination revealed that scraping did not cause any physical damage to the blades. For E, blades or parts of blades which were completely covered with epiphytes on both sides were used. No quantitative assessment of the epiphytic community was made, however, qualitative observations

indicated that the epibiotic community in this study was similar to that reported from Western Australian *P. australis* meadows (Trautmann & Borowitzka, 1999). The main algae present were encrusting coralline algae as well as genera such as *Ceramium*, *Entocladia*, *Cladophora* and *Ulva*. Algal cover was very dense (*i.e.* 100% of the seagrass blade was covered). The epifaunal community consisted mostly of hydroids (genus *Plumularia*), polychaetes (genus *Spirorbis*) and bryozoans. The experimental 'shoots' of each of the choices consisted of two blades which were held together at one end by two metal staples.

For Y, the short innermost blades of a shoot were used which grow between two to three longer, mature, blades. In the experiment, the short blades were covered on both sides by artificial blades made of PVC ribbons to offer the fishes the same access to the blades, as they would have in the field. All three blades were held together at one end by two metal staples. Three experimental 'shoots' were attached in random order to a lead weight (*i.e.* each weight contained a range of combinations of the three food types) using rubber bands at the stapled end. For each trial four such lead weights were buried closely together at a random location in each tank, mimicking the shoot density in a dense *P. australis* meadow (300 shoots m^{-2}). Each fish was allowed to feed on them for 24 h and were not starved prior to the beginning of an experiment. Due to the great difference in mass between the blades with epiphytes and the two other blade types it was not possible to offer equal amounts of biomass of all three choices. Instead, overall blade length was equal in order to control for the effect of food quantity available per choice. Control tanks received the same amount of shoots but did not contain any fishes.

All shoots were blotted dry prior to being weighed before the start of each trial. Y blades were weighed without the artificial blades. Mean \pm S.E. wet mass of shoots offered in all trials was 2.8 ± 0.0 g for B, 5.7 ± 0.1 g for E and 2.1 ± 0.0 g for Y shoots. After 24 h, shoots were blotted dry and weighed again and bite marks on B and Y blades were recorded. Due to the extensive seagrass biomass removal from E blades it was not possible to count individual bite marks on this blade type. Since the absolute mass varied among blade types, the change in biomass was then converted into a per cent change in biomass for each blade type. Subsequently, the quantities eaten of each type by each fish in three replicate trials were calculated by subtracting the biomass after 24 h from the biomass initially provided. Correction factors for mass gain or mass loss of each blade type obtained in the control experiments were applied prior to data analysis. The corrected quantities were then used to calculate an overall mean \pm S.E. of each blade type eaten.

Each fish was used in three consecutive trials (each trial being separated by 3 days) and the average biomass removal in all three trials was then used for statistical analysis. Thus data (*i.e.* fishes were replicates) met the assumption of independence (Sokal & Rolf, 1995). Consecutive trials were employed because it was assumed that an individual fish's feeding motivation could differ from day to day due to, *e.g.* state, feeding motivation, disturbance and availability of shoots (*e.g.* blades could have become detached at various stages throughout the experiment) (Colgan, 1986; Salvanes & Hart, 1998). Preference ranks for the three blade types were calculated for each individual fish using Manly's α (second model) since biomass consumed during a trial could not be replaced

(Krebs, 1989). The rank distribution for each species was compared using an Anderson's test (Brockhoff *et al.*, 2003).

Fishes were observed to inspect all shoots before they started feeding and did not feed on blades which had become detached (*i.e.* bitten off) and were lying on the bottom of the tanks. On average *M. freycineti* consumed $73.0 \pm 3.3\%$ of the E blades, removing both epiphyte and seagrass biomass, $8.8 \pm 1.7\%$ of the B and $2.8 \pm 0.6\%$ of the Y blades (Fig. 1). In all trials, fishes removed all epiphytic material from the blades with epiphytes as well as consuming most of the blade itself, while B and Y blades did not receive more than four bites on average overall. Preference rankings concurred with mean food type consumption with E ranking one in all individuals, B ranking second in all individuals and Y third. The distribution of rank preferences differed significantly (Anderson's test, $n = 9$, $P < 0.001$).

The mean \pm s.e. consumption of E by *M. trachylepis* ($41.0 \pm 4.0\%$) was lower than by *M. freycineti* but fishes also consumed all epiphytic material and a large part of the seagrass blade itself. Both B and Y were only consumed in very small amounts ($2.4 \pm 0.4\%$ and $2.6 \pm 0.6\%$, respectively, by blade type; Fig. 1) and did not receive more than three bites in any single trial. E was ranked first by fishes in all individual preference rankings, Y second in 80% of individual trials and third in 20%. Rank preferences were not randomly distributed (Anderson's test, $n = 10$, $P < 0.001$).

Feeding preferences for *P. australis* blades with epiphytes were clearly evident in both fish species. The actual biomass loss of the seagrass leaves was higher with epiphytes than without since fishes of the size used in the experiment generally consume epiphytes by biting off half moon shaped pieces from the seagrass (*pers. obs.*). Although the unequal amounts of biomass offered to the fishes might have biased the results, it is unlikely that the highly significant results obtained were just a consequence of bias towards the epiphyte choice. Moreover, gut content analysis of both *M. freycineti* and *M. trachylepis* feeding

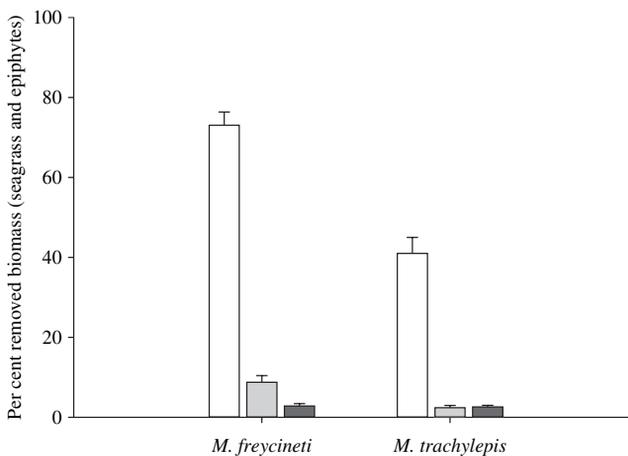


FIG. 1. Mean \pm s.e. per cent biomass of seagrass removed in multiple-choice feeding experiments by *Meuschenia freycineti* ($n = 9$) and *Meuschenia trachylepis* ($n = 10$). Choices are mature leaves with epiphytes (□), mature leaves without epiphytes (▒) and young leaves without epiphytes (■).

in situ showed that they consumed significantly more seagrass with epiphytes attached than bare seagrass, and stable isotope analysis revealed that the epifauna and, to a slightly lesser extent, the epiphytes of *P. australis* are the main food source of the two grazers (Wressnig, 2006).

Similarities in the diet of the two species have been reported in several earlier studies (Bell *et al.*, 1978; Fisheries, 1981) and are not surprising since the two species are closely related (*i.e.* congeners) and live in the same habitat as juveniles. The difference in overall consumption of seagrass between the two species observed in this experiment might be due to inherent differences in daily seagrass consumption. The daily ration of *P. australis* with attached epibionts consumed *in situ* by *M. freycineti* has been found to be twice as high as that of *M. trachylepis* (Wressnig, 2006).

In this experiment, the young, soft, nutrient-rich seagrass blades (Y) were only consumed in approximately the same amounts or smaller amounts than the mature bare blades, possibly because of the presence of high concentrations of feeding deterrents such as phenolic compounds. Young growing leaves of *P. oceanica* have been found to contain the highest concentrations of phenolic compounds with concentrations decreasing with increasing leaf age (Agostini *et al.*, 1998). In the Mediterranean Sea, herbivore attacks of *S. salpa* (Sparidae) on *P. oceanica* have been shown to be highest in the oldest leaves of the shoot and to decrease with decreasing leaf age. This might at least partly be due to the presence of high concentrations of phenolic compounds in young leaves (Alcoverro *et al.*, 1997). In the present study, a potentially confounding effect could have arisen from the removal of epiphytes from mature leaves since injuries caused by scraping could have led to the release of feeding deterrent chemicals. Microscopic examination, however, revealed that the surface of scraped leaves did not differ from that of 'naturally' epiphyte-free leaves and that scraping did not cause any observable physical damage. Therefore, leaf scraping is unlikely to have confounded the results of the experiment.

This study was conducted in winter when the overall species numbers of algae are reduced, while the numbers of erect colonies increase (Trautmann & Borowitzka, 1999). Nevertheless, a change in epiphytic community structure towards summer is unlikely to impact the feeding preference of the two grazers to a great extent since it was found that *P. australis* epiphytes and epifauna constitute the main dietary component of both fish species during winter and summer (Wressnig, 2006).

The results of this preference experiment confirm the findings of several previous studies which suggested that fishes grazing on seagrass prefer the epiphytes growing on the seagrass blades (Conacher *et al.*, 1979; Cebrian *et al.*, 1996). Since epiphyte growth increases with leaf age a preference for epiphyte-covered blades by the two grazers ultimately results in a preferred removal of older blades within the seagrass shoot.

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