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Effect of habitat complexity and predatory style on the capture success of fish feeding on aggregated prey

A.J. Flynn and D.A. Ritz*

School of Zoology, University of Tasmania, Box 252-05, GPO Hobart, 7001 Tasmania, Australia.
*To whom correspondence should be sent

When offered a choice between open water and a 'vegetated' area of an aquarium (artificial sea grass), mysid (*Paramesopodopsis rufa*) swarms always selected open water. In contrast, juvenile and adult sea horses, *Hippocampus abdominalis*, which feed by ambush predation, always selected vegetated areas even when their mysid prey occurred in the adjacent clear water. Lunging predators, Australian salmon (*Arripis trutta*), always preferred open water to vegetated regions of the tank. Increasing vegetation density, i.e. from low to medium habitat complexity had a positive effect on capture success of juvenile and adult sea horses feeding on mysid swarms. However, number of attacks by juvenile sea horses, but not adults, was significantly reduced in higher density vegetation. Number of attacks by Australian salmon decreased as vegetation density increased but capture success, nonetheless, increased. Density of vegetation did not significantly affect the number of unsuccessful attacks by adult sea horses. Whereas proportion of unsuccessful attacks increased with vegetation density for juvenile sea horses, it decreased for juvenile salmon. This result is thought to be due to the fact that high vegetation densities disrupt structure of the prey swarm, itself a defensive formation, leaving a large number of more vulnerable small groups. Cohesive escape responses of a large swarm are likely to be a more effective defence against a lunging predator than against an ambush predator whose strategy is to use stealth to avoid provoking escape responses. Dense vegetation will militate against this strategy.

INTRODUCTION

Numerous authors have reported a decrease in predator efficiency with increasing habitat complexity. For example, killifish, *Fundulus heteroclitus* (Heck & Thoman, 1981), largemouth bass, *Micropterus salmoides* (Savino & Stein, 1982; Gotceitas & Colgan, 1989), blennies, *Helcogramma medium* (Coull & Wells, 1983), pinfish, *Lagodon rhomboides* (Minello & Zimmerman, 1983) and damselfish, *Abudefduf sordidus* (Russo, 1987) suffer a reduction in, e.g. predation rate, number of prey consumed and foraging success with increasing habitat complexity. All of these studies concerned epiphytal or benthic prey such as amphipods and shrimp that either used vegetation for protection or had a physical association with the structure. The fish noted above are primarily pursuit hunters and a reduction in foraging success can probably be attributed to an increase in the number of visual barriers to the predator and prey refuges with increasing structural complexity. Little work has been conducted to examine the effect of habitat complexity on ambush predation and the effect of this factor on capture of aggregated prey has hardly been addressed. Several authors have suggested that structural complexity may improve the predation success of ambushers (or at least not inhibit it) by providing camouflage and reducing their visibility to prey (Coen et al., 1981; Howard & Koehn, 1985; Heck & Orth, 1980; James & Heck, 1994). In agreement with these predictions, the number of shrimp, *Hippolyte zostericola*, captured by the lined sea horse, *Hippocampus erectus*, was not influenced by increasing habitat complexities (James & Heck, 1994). Similarly, small pipefish that employ an ambush predation style did not respond to changes in habitat complexity when foraging on amphipods (Ryer, 1988).

The main objectives of this study were to answer the questions: does habitat complexity benefit prey or predator when the prey forms social aggregations; and secondly is foraging success influenced by predatory style? Foraging success of an ambush predator, the sea horse *H. abdominalis*, and a pursuit or lunging predator, Australian salmon *Arripis trutta*, when feeding on the swarming, epibenthic mysid, *Paramesopodopsis rufa*, are compared. *Paramesopodopsis rufa* occurs naturally above and between fronds of macroalgae in shallow water (Fenton, 1992), but unlike previous studies, there is no evidence whether this prey species uses vegetation as a refuge. On the other hand, *P. rufa* is known to gain protection by virtue of its swarming behaviour and active escape manoeuvres (O'Brien & Ritz, 1988). As a preliminary to these experiments, habitat preferences of both predators and prey were determined in laboratory tests.

MATERIALS AND METHODS

Experimental animals

Mysids (total body length ~13 mm) were collected in shallow water by snorkelling with a hand-held plankton net at Crayfish Point, Taroona (42°56′S 147°21′E) and in waters around the Kingston Beach Sailing Club (42°59′S

147°19′E) (both localities in south-east Tasmania, Australia). Animals were transferred from the net to a sealable plastic bucket that was filled to capacity to prevent damage due to splashing during transport. Mysids were held in a 158 l aquarium and fed ground fish pellets (formulated for Atlantic salmon), every 24 h. In all tanks, water quality was maintained using a filter (Eheim model 2213). Water temperature and salinity were stable at 12°C and 35 psu respectively.

Sea horses classed as juveniles were 75–140 mm total body length, from the tip of the snout to the tip of the extended tail. Those believed to be males exhibited only very early signs of brood pouch development. The distinctive mating behaviours, displayed by adults of the species, were not seen in these smaller animals and the conclusion was drawn that fish were juvenile. They were obtained from two sources. The first group (N=4) was donated by an aquarist and a second batch (N=5) was collected from the Tassal Ltd salmon farm at Killala (43°13′N 147°04′E) by farm divers or were collected as they fell onto the deck of farm vessels while nets were winched on board. No differences in behaviour of fish from the two sources were detected and they were kept together in holding tanks. Nine fish, readily identifiable by distinctive colour markings or crown tendril patterns, were used in experiments.

Adult *Hippocampus abdominalis* (N=9) were hand-collected using SCUBA under the jetties of the Royal Hobart Yacht Club in Sandy Bay (42°52′S 147°20′E). Once captured, adult sea horses were transferred to a sealed submerged bucket. All sea horses were kept in a 158 l holding aquarium in the laboratory. Again, nine fish that were easily distinguishable were used in experiments.

Juvenile salmon (nine individuals) ~70 mm total body length from the tip of the premaxilla to the fork of the caudal fin were caught using a beach seine at Pipeclay Lagoon and Cremorne Beach (42°58′S 147°32′E) after dark on a rising tide.

One salmon was placed in each of the nine compartments of a 173 l aquarium that was divided using mesh welded onto PVC brackets attached to the inside with silicone sealant. This system allowed water flow through the compartments and the maintenance of visual contact between fish while also keeping the experimental subjects identifiable.

Habitat complexity

The measure of habitat complexity used in this study was the number of artificial sea grass stems m^{-2}. Artificial sea grass was made from shredded green polyethylene sheet. Sea grass was tied in a random arrangement to plastic mesh of 1-cm^2 aperture with each tuft consisting of eight blades that were 30 cm long and ~0.8 cm wide. The mesh was anchored by ~3 cm of sand in a 60 l aquarium (75×30×35 cm). During experiments, artificial sea grass floated upright and occupied the entire water column. Densities of artificial sea grass represented conditions of no vegetation; low, 800; medium, 2400; and high, 3200 blades m^{-2} complexity. These values were quite similar to those used in a study of foraging in the sea horse *H. erectus* (James & Heck, 1994).

Habitat use experiments

Proportion of time spent foraging or sheltering was measured by filling one half of the aquarium (75×30×35 cm) with artificial sea grass of medium complexity (see above) in seawater of the same temperature and salinity as in the holding tanks. In this way, experimental subjects were offered a choice between an open water or vegetated area. Experiments lasted 10 min and the position of animals or swarms was recorded every 30 s. There were seven conditions, i.e. juvenile sea horse, adult sea horse, salmon, mysid swarm alone, or a combination of each predator and the prey. Each condition was replicated four times. Results were analysed using Chi-squared tests assuming the null hypothesis that predator and prey distribution was random (i.e. 5 min was spent in each half of the aquarium).

Foraging experiments

At the beginning of each experiment a swarm of 100 *P. rufa* was placed into the 60 l experimental aquarium at similar water temperature and salinity as the holding tanks. *Paramesopodopsis rufa* occurs naturally in relatively small swarms of between five and 1000 individuals (O'Brien, 1988). A submerged filter outlet provided a gentle current, promoting cohesive swarm structure. Behavioural equilibrium of the prey swarm was established in approximately 10 min after which time the filter was switched off. A single predator that had been starved for 24 h was gently introduced to the experimental aquarium and from the time when the first approach was initiated, the number of attacks, captures and misses were recorded by direct observation over a 10 min period. Each fish was used several times in the course of these experiments but only once on any given day. Number of replicate observations for each class of predator over the range of habitat complexities used were between 13–18 (juvenile sea horse), 20–27 (adult sea horse) and 18–36 (salmon). Both fish and mysids were changed for successive observations.

A sea horse approach was registered when the independent movement of both eyes associated with searching behaviour ceased and both eyes focused on a single mysid, or when the snout followed the escape path of a fleeing prey. An attack (or strike) was recorded when the sea horse performed a characteristic rapid upward movement of the snout (head-flick). A successful capture was recorded when the head-flick resulted in a prey item being sucked into the snout, even if the prey was later ejected. A miss was recorded when the head-flick was initiated, but the mysid intended for capture escaped.

An attacking salmon was recognizable by a behavioural change from a slow cruise to a burst of acceleration, achieved by the rapid movement of the caudal fin. An attack was recorded when jaw protrusion was accompanied by an expansion of the opercular and buccal cavities. A successful capture was registered when the targeted mysid was ingested. A miss was recorded when this sequence of events was performed but the mysid intended for capture escaped. Results from habitat complexity experiments were analysed using ANOVA in combination with multiple comparison tests.

Attack distances of sea horses were calculated by analysing digitized video footage of the sequence of the predator feeding on *P. rufa*. Starved sea horses of various known snout lengths (and therefore total body lengths) were placed in a 20 l aquarium in which a number of mysids had been allowed to acclimatize. For video analysis, mysids were stained for 4 h in neutral red (1% solution) in order to maximize their visibility in the recorded image. White painted walls placed inside the aquarium, further improved the resolution of the mysids. A mirror placed at an angle of 45° over the aquarium provided simultaneous plan and side views of the recorded image. Calibration scales visible in the recorded image were placed along the x, y and z axes. Two 20 W halogen lamps, one each side of the filming tank, provided illumination (intensity at the water surface was 19 μE m^{-2} s^{-1}). Sea horses were filmed using a Panasonic WV-BL600 colour video camera, with SVHS tape and a Panasonic FS 100 SVHS recorder. Analysis was achieved using an IBM compatible frame-grabber and MOCHA (Jandel Scientific) image analysis software (further details are described in Ritz et al. (1997)). By scanning the footage frame-by-frame, the instant before sea horses initiated the head-flick response could be located and digitized. The actual positions of the tip of the sea horse snout and a mysid could be expressed in terms of three coordinates and then translated to actual distances. These measurements were made for three juvenile and four adult sea horses.

RESULTS

Habitat use experiments

Results obtained from all combinations of predators and prey were very clear. Mysids spent 100% of their time in open water (i.e. <5% of swarm among fronds) when offered a choice between this and a vegetated area (χ^2, df=3, $P<0.001$). With or without prey present, both adult and juvenile sea horses spent nearly 100% of their time in the vegetated area (χ^2, df=3, $P<0.001$). With prey present in the open water nearby, sea horses would grasp a sea grass frond with their tails and lean into the mysid swarm, striking at peripheral individuals that were within range. Sea horses would sometimes detach from the sea grass and swim into the open water attacking mysids with poor success. It is worth noting that sea horses do not need to be attached to be able to feed (James & Heck, 1994; A.J.F., unpublished observations). Sea horses usually returned to the seagrass a short time after these visits. Regardless of whether prey were present, salmon spent 100% of their time in the open water habitat (χ^2, df=3, $P<0.001$).

Effects on foraging: sea horses

This experiment was designed to examine the effects of habitat complexity on the foraging behaviour and efficiency of juvenile sea horses, adult sea horses and salmon when feeding on a prey swarm of a particular size. However, it soon became clear that varying the density of artificial seagrass not only altered habitat complexity but also altered the swarm size and structure of *Paramesopodopsis rufa*. As habitat complexity increased, swarm structure became increasingly disrupted until in conditions of high complexity mysids occurred in many small groups (<10 individuals) whereas in no vegetation conditions they formed a single swarm. Therefore, increasing habitat complexity was inversely related to swarm size. Figure 1A illustrates the effect of habitat complexity on the number of attacks made and the percentage capture success (no. of captures/no. of attacks×100) achieved by juvenile sea horses.

Vegetation density had a highly significant inverse effect on the number of attacks performed by juvenile sea horses ($F_{3,24}=74.982$, $P<0.001$). Tukey tests revealed that the increase in habitat complexity from medium to high was the only increment not resulting in a significant fall in the number of attacks made by juvenile sea horses ($F_{1,8}=0.584$, $P>0.05$). Vegetation density had a positive effect on the percentage capture success of juvenile sea horses ($F_{3,24}=48.122$, $P<0.001$) (Figure 1). A Tukey test showed that the only significant improvement in capture success was due to the increase in habitat complexity from low to medium ($F_{1,8}=103.631$, $P<0.001$). The changes from no vegetation to low, and from medium to high complexities, had no significant effect on capture success ($F_{1,8}=1.746$, $P>0.05$; $F_{1,8}=0.432$, $P>0.05$, respectively).

In contrast to juveniles, habitat complexity had no significant effect on the average number of attacks made by adult sea horses ($F_{3,24}=1.368$, $P>0.05$) (Figure 1B). There was also no significant difference in the number of attacks ($F_{7,56}=0.966$, $P>0.05$) and capture success ($F_{7,56}=0.904$, $P>0.05$) achieved by male and female adult *Hippocampus abdominalis*. Thus the difference between adult and juvenile sea horses was not sex related.

While the number of attacks made by adult sea horses did not change, the effect of habitat complexity on percentage capture success was significant ($F_{3,24}=358.799$, $P<0.001$). As in the case of juveniles, the improvement observed in adult sea horse capture success between the low and medium conditions could explain the total variation and was the only significant increase ($F_{1,8}=4254.5$, $P<0.001$).

Salmon

Juvenile salmon performed significantly fewer attacks on *P. rufa* as habitat complexity increased ($F_{3,24}=147.887$, $P<0.001$) (Figure 1C).

A Tukey test revealed that only the complexity change from medium to high did not result in a decrease in the number of attacks ($F_{1,8}=4.539$, $P>0.05$). A significant increase in the percentage capture success of salmon was recorded at every increase in habitat complexity ($F_{3,24}=215.965$, $P<0.001$) (Figure 1C).

Comparisons between fish species: number of attacks

Both adult and juvenile sea horses foraged in an attached fashion for most of the time given any density of sea grass, and always foraged in an ambush mode. However, juveniles were characterized by more energetic swimming and were often moving quite rapidly through the sea grass using their tails as holdfasts and levers.

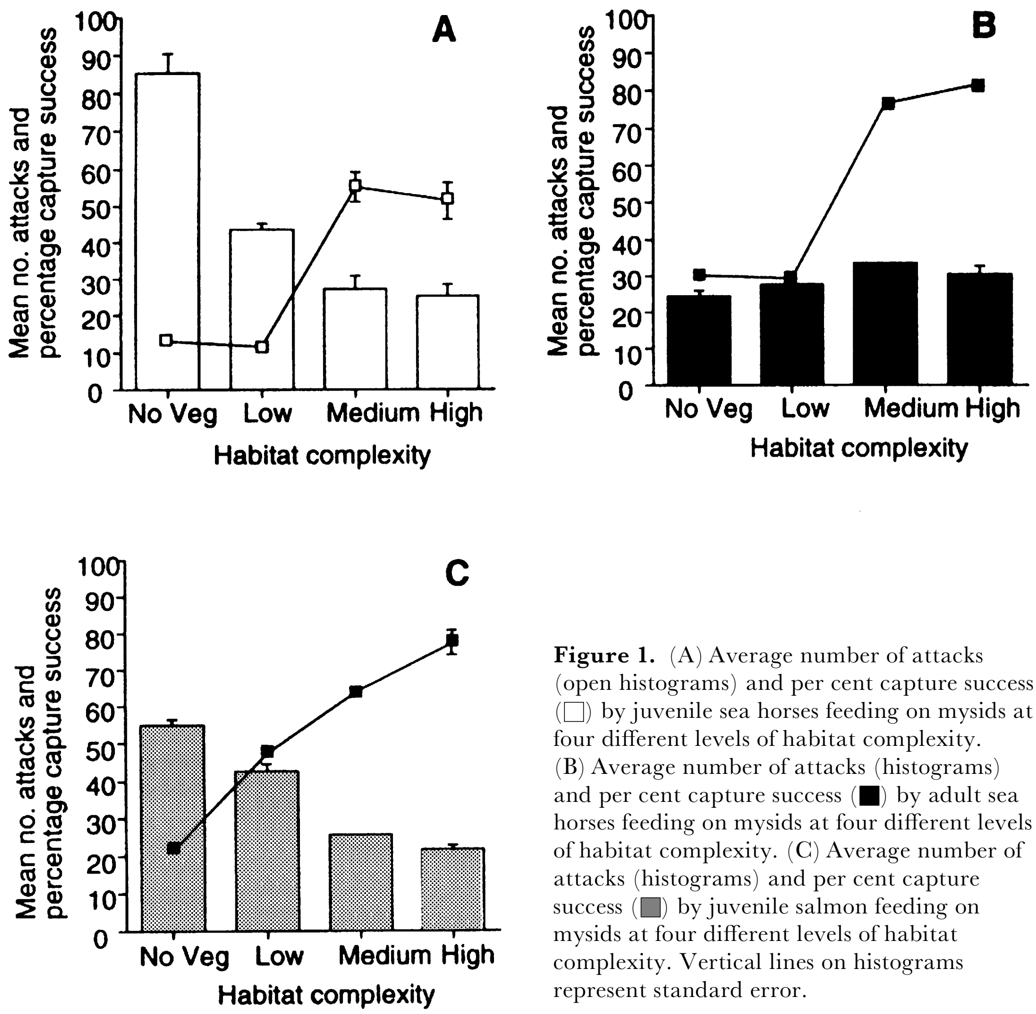

Figure 1. (A) Average number of attacks (open histograms) and per cent capture success (□) by juvenile sea horses feeding on mysids at four different levels of habitat complexity. (B) Average number of attacks (histograms) and per cent capture success (■) by adult sea horses feeding on mysids at four different levels of habitat complexity. (C) Average number of attacks (histograms) and per cent capture success (▨) by juvenile salmon feeding on mysids at four different levels of habitat complexity. Vertical lines on histograms represent standard error.

Adults employed a practically motionless mode of predation. This lowered level of activity in adult sea horses is reflected in the lower number of attacks made by adult sea horses in comparison to juvenile sea horses and salmon in the no vegetation ($F_{1,8}$=93.125, $P<0.001$; $F_{1,8}$=225.9, $P<0.001$) and low complexity ($F_{1,8}$=37.041, $P<0.001$; $F_{1,8}$=38.583, $P<0.001$) conditions, where the most unobstructed space was available (Figures 1A–C). In the medium and high complexity conditions, there was no significant difference between the number of attacks made by juvenile sea horses, adult sea horses and salmon ($F_{1,8}$=1.7, 5.108, 1.12, all $P>0.05$).

Capture success

Despite performing a lower number of attacks, adult sea horses achieved a higher percentage capture success than juveniles in all habitat complexities ($F_{1,8}$=33.99, 20.876, 32.014, 25.094, all $P<0.001$) (Figures 1A,B). One possible reason for the reduced capture success of juvenile sea horses compared to adults is the greater number of attacks resulting in a miss for the former in all levels of habitat complexity ($F_{1,8}$=8.978, 10.868, 22.402, 13.424, all $P<0.05$) (Figure 2). In this figure, percentage unsuccessful attacks are defined as no. misses/no. attacks×100. Although adult sea horses attacked fewer mysids, they were more accurate.

Juvenile sea horses suffered a significant increase in the number of misses recorded in the high complexity condition as compared to that when foraging in no vegetation ($F_{3,24}$=3.881, $P<0.05$) (Figure 2). The percentage of unsuccessful attacks for adult sea horses did not vary significantly over the range of habitat complexities used in this study ($F_{3,24}$=2.136, $P>0.05$).

Salmon missed a higher proportion of mysids than juvenile and adult sea horses in the no vegetation condition ($F_{1,8}$=39.41, 1330.174, all $P<0.001$) and low complexity treatments ($F_{1,8}$=20.261, 241.907, all $P<0.001$) (Figure 2). However, the accuracy of salmon was improved by the presence of more complex structure and a significant reduction in the number of misses in the medium and high complexity conditions was recorded ($F_{3,24}$=27.334, $P<0.001$). The decline in failure rate provides a possible explanation for the increase in capture success of *Arripis trutta* in these two treatments (Figure 1C).

Sea horse attack distance

The difference in the number of misses made by juvenile and adult sea horses can be partly explained by the difference in the distance needed to approach a mysid before initiating the head-flick. Image analysis of video footage, although being performed on a small sample size (N=7 individuals), revealed a clear correlation between

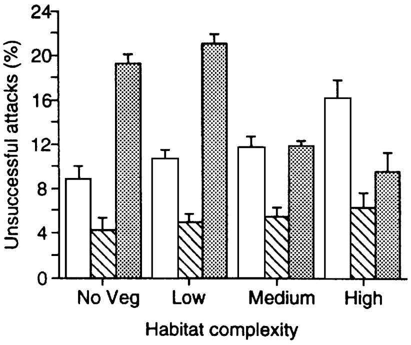

Figure 2. Percentage of unsuccessful attacks by juvenile sea horses (□), adult sea horses (▨) and juvenile salmon (■) feeding on mysids at four different levels of habitat complexity. Vertical lines on histograms represent standard error.

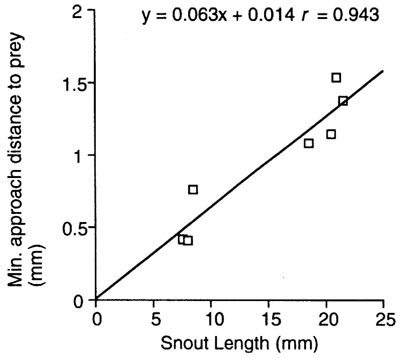

Figure 3. Relationship between snout length and minimum distance sea horses need to approach their mysid prey before initiating the head-flick used in capture.

snout length (as measured from the centre of the eye to the tip of the snout) and the distance needed to approach a prey item before attempting a capture (r=0.943) (Figure 3). Since snout length was found to be linearly related to total body length (r=0.905) (Figure 4), juveniles need to get closer to a mysid than adults for successful capture.

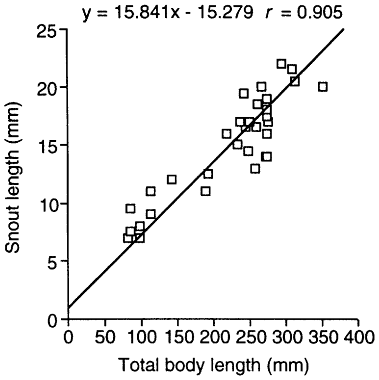

Figure 4. Relationship between snout length and total body length in sea horses.

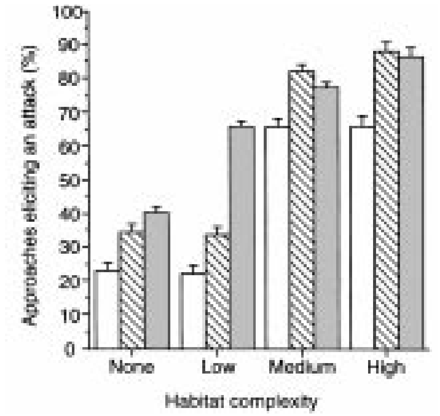

Figure 5. Percentage of attacks that resulted in a strike by juvenile sea horses (□), adult sea horses (▨) and juvenile salmon (■) feeding on mysids at four different levels of habitat complexity. Vertical lines on histograms represent standard error.

Approaches and attacks

Curves for percentage of approaches which elicited an attack for adult and juvenile sea horses (Figure 5) are similar in shape to those for percentage capture success (Figures 1A,B). Again the only increment that caused a significant increase in the attack rate was between the low and medium complexities ($F_{1,8}$=237.636, 102.805, all $P<0.001$). There was no improvement in the attack rate between no vegetation and low complexity ($F_{1,8}$=0.178, 0.069, all $P>0.05$), or between medium and high complexity conditions ($F_{1,8}$=1.933, 0.116, all $P>0.05$) (Figure 5).

It is possible that salmon were able to achieve a greater capture success than juvenile sea horses, despite performing less approaches and recording more misses because they followed up a greater percentage of their approaches with attacks (Figure 5). Post hoc tests confirmed that at all complexity conditions the attack rate of juvenile sea horses was significantly lower than that of adult sea horses ($F_{1,8}$=16.532, 7.136, 10.549, 10.692, all $P<0.05$) and salmon ($F_{1,8}$=23.403, 231.905, 6.734, 10.17, all $P<0.05$). The increase in the attack rate of *A. trutta* also mirrored the increase in percentage capture reported earlier (Figure 1C). At all increases in habitat complexity there was a significant increase in the percentage of approaches eliciting an attack ($F_{1,8}$=173.376, 28.989, 20.8, all $P<0.001$).

DISCUSSION

Habitat use study

Both age-classes of *Hippocampus abdominalis* displayed a preference for vegetated habitat over open water in habitat use experiments regardless of whether prey were present. According to the results above, this would serve to maximize their prey capture efficiency and coincidentally assist in remaining concealed from their own predators. Prey capture efficiency of sea horses foraging in vegetation may be improved in terms of an increase in the number of successful captures and/or in terms of the minimization of energy expended in order to capture prey. Note that it is not essential for sea horses to be attached in order to catch prey. Our observations suggest that hungry individuals preferred to forage freely while those approaching satiation adopted an attached mode (Ocken, 1994).

Despite recording a heightened capture success in vegetated as opposed to open water habitats, *A. trutta* always occupied open water when offered a choice between the two. Thus predatory success cannot always be used to predict predator distribution. Salmon naturally occur in social groups that would lack structure and coordination in vegetation. Reports of juvenile *Arripis trutta* schooling over sea grass beds (Hutchins & Swainston, 1986; Kuiter, 1993) might have more to do with seeking protection from predators than attempting to improve capture success.

When offered a choice between an open water and a vegetated habitat, *Paramesopodopsis rufa* swarms occupied open water for the duration of all experiments, regardless of whether predators were present. This result strongly suggests that the cohesive swarm affords greater protection and is the preferred anti-predator refuge. These data may also suggest that the sensory mechanism by which swarm structure is maintained and escape responses initiated is, at least in part, visual.

A preliminary field study of sea horse distribution (unpublished observations) revealed that adults occupied seagrass habitats roughly corresponding to low–medium complexity (as defined above). *Paramesopodopsis rufa* has not been recorded from sea grass habitats in Tasmania. Complexity of macroalgal habitats could not easily be equated to artificial laboratory habitats but sea horses were usually present in such locations and mysids (including *P. rufa*) were present in the vicinity, usually in open water above or between clumps. Juvenile salmon are reported to move over 'dense' sea grass flats as the tide rises in order to feed (Robertson, 1982), though it is not clear whether they actually penetrate habitats of highest complexity. Both sea horses and salmon have been reported to feed on mysids in Tasmania (unpublished observations; Fenton, 1996).

Habitat complexity and foraging

Declining predation success with increasing habitat complexity is a common theme in the literature on the predatory behaviour of fishes. The present study has demonstrated that conclusions drawn from results of past work on predator–prey interactions may not apply where the predator is attacking social, aggregated prey that are capable of active coordinated escape manoeuvres. Contrary to several reports of declining predation success by fish as habitat complexity increases (Heck & Thoman, 1981; Savino & Stein, 1982; Gotceitas & Colgan, 1989; Coull & Wells, 1983; Minello & Zimmerman, 1983; Russo, 1987), adult and juvenile sea horses, experienced an increase in capture success with increasing habitat complexity. In both age-classes of sea horse, the nature of this increase in capture success was stepwise. There was no increase in capture success between the no vegetation and low complexity but increasing blade density from low to medium resulted in a significant improvement. Further increases in habitat complexity from medium to high did not affect capture success. In James & Heck's (1994) study of another ambush predator, sea grass blade density had no effect on foraging success of *H. erectus* when feeding on shrimp, *H. zostericola*.

Habitat complexity and prey behaviour

Relationships between capture success and habitat complexity for both sea horses and salmon are probably due as much to the behaviour of the prey as to that of the predator. The swarming behaviour of *P. rufa* protects individuals against predators (O'Brien & Ritz, 1988; Ritz, 1994). Breakdown in the size or coordination of mysid swarms can: (1) reduce the degree to which the swarm is able confuse a predator; (2) decrease the effectiveness of anti-predator manoeuvres; and (3) reduce the predator-detecting capabilities of individuals (probably a function of swarm size) rendering individuals more vulnerable to predation. An explanation for the non-linear increase in capture success by *H. abdominalis* may thus lie in the decline in *P. rufa* swarm size and collapse of structure with increasing habitat complexity observed in this study. Sparse vegetation caused a relatively minor disruption of swarms usually resulting in the swarm splitting into two. On the other hand, medium levels of vegetation resulted in a more severe breakdown in mysid swarm size and structure, with formation of many small groups. The fact that swarm breakdown was not markedly more severe in highly complex situations may account for the stepwise pattern of increase in sea horse capture success.

That the presence of vegetation is detrimental to the structure of social aggregations is supported by the reported breakdown in school formation of bluegills, *Lepomis macrochirus*, when subject to medium and high vegetation densities (Savino & Stein, 1982) and inverse relation between group size of perch (*Perca fluvitilis*) and vegetation density (Eklov, 1997). *Lepomis macrochirus* was able to avoid predators in high vegetation densities by leaving the school and dispersing among the plant stems. This alternative means of protection is an option not adopted by *P. rufa* as this species is an obligate swarmer (Ritz, 1994).

Capture success by sea horses

At all levels of habitat complexity, adult sea horses achieved a greater capture success than juveniles, despite the former sometimes performing fewer attacks. In his discussion of optimal searching methods, Hughes (1980) predicted that because metabolic requirements of an organism usually decrease with an increase in body weight, small predators should use more costly searching tactics than large animals, particularly when eating prey of similar size. This prediction appeared to hold true in this study. Juvenile *H. abdominalis* foraged in a more active, energetically expensive fashion than adults, performing more attacks in the no vegetation and sparse conditions. A possible explanation for how adult sea horses were capable of achieving a greater capture success than juveniles lies in the difference in the percentage of unsuccessful attacks for the two age-classes. In all treatments, juvenile *H. abdominalis* made more unsuccessful attacks than adults. The poor success rate of juvenile sea horses may be related to the distance required to approach a mysid before initiating the head-flick response. Small *H. abdominalis* needed to approach mysids more closely than large individuals before attempting a capture. Presumably, the closer to a mysid that a sea horse needs to be prior to performing a strike, the more likely that the prey will detect the predator and make a successful escape. Alternatively capture success rate may simply be a function of experience.

Juvenile sea horses missed more *P. rufa* in the high complexity condition than in all others. This is an unexpected result considering that mysids in highly complex environments had little space in which to perform escape responses and swarm structure was disturbed to its highest degree. Perhaps, in the high complexity treatment, vegetation structure became a hindrance to the movement of juvenile sea horses and sea grass blades may have served as a visual barrier between predator and prey. The presence of structure, therefore, can potentially offer protection to swarming prey. However, *P. rufa* were still captured more efficiently by juvenile sea horses in vegetated conditions. It remains unclear whether this improvement of predatory capabilities came about as a result of the morphological and behavioural adaptations of the sea horse enabling them to hunt effectively in vegetated conditions, or as a result of the breakdown of swarm cohesion in such circumstances. A combination of the two seems likely.

Capture success by salmon

Unlike that recorded for *H. abdominalis*, the increase in capture success and attack rate of *A. trutta* with increasing habitat complexity was linear in fashion. This suggests that *A. trutta* is more sensitive to changes in the swarm size and cohesion (and therefore protective qualities) of *P. rufa* swarms that occurred as a result of the presence of vegetation. *Arripis trutta* missed more mysids than juvenile and adult *H. abdominalis* in the no vegetation and low complexity treatments. Unlike the sea horse that attempts to conceal its predatory intent until the last instant, the Australian salmon utilizes a lunging style of predation that advertises predatory intent in the early stages of attack. Swarming mysids sensing an attack in its early stages presumably have time to take evasive action, which would contribute to the relatively poor success of salmon in no vegetation and low complexity conditions. The number of failed attacks made by salmon decreased significantly in the medium and high complexity conditions, casting doubt on the proposal that vegetation enhances the escape capabilities of prey.

Comparison between fish

The number of attacks made by juvenile sea horses and salmon declined with increasing habitat complexity, although the change from medium to high complexity had no significant effect. Juvenile sea horses and salmon may have intentionally suppressed the energetically costly process of attacking *P. rufa* because they were able to achieve a greater capture success. Alternatively, these predators may have suffered an enforced decline in attacks due to the limited amount of movement possible in medium and highly complex environments. If this was the case, then juvenile sea horses and salmon could have still recorded an increase in capture success, in spite of this restriction in movement, due to the heightened vulnerability of *P. rufa*.

In his study of pipefish foraging, Ryer (1988) asserted that some degree of behavioural plasticity is important for predators to cope with changing conditions. Indeed, *Micropterus salmoides* was found to switch predatory tactics from searching to ambushing when faced with an increase in plant density, thereby maintaining a similar capture rate over all densities (Savino & Stein, 1982). In the same study, northern pike, *Esox lucius*, employed an ambush foraging mode in all plant densities and experienced no change in capture rate with increasing habitat complexity.

Making use of their prehensile tail, juvenile sea horses attached themselves to artificial sea grass when present rather than actively swimming. *Hippocampus abdominalis*, with its upright swimming posture and modified swimming fins, is capable of manoeuvring through structurally complex situations and was able to capture mysids successfully in even the most complex treatment. That adult sea horses in particular attempt to forage optimally in changing habitat complexities is supported by these predators recording no change in the number of attacks or the percentage of unsuccessful attacks over the range of habitat complexities. In low vegetation conditions where a high degree of movement is possible, adult *H. abdominalis* minimized their swimming activity, making few attacks. By only targeting mysids that came into reach, adult sea horse attacks were highly accurate.

The lower capture success of juvenile sea horses, the higher number of attacks, high activity and failure rate suggests that when feeding on the same prey, adult *H. abdominalis* are more efficient predators than juveniles. However, ontogenetic dietary shifts are likely to occur due to gape-limitation in these fish. No information is available on the diet preferences of juvenile sea horses. The inefficiency of juvenile sea horse foraging could also be due to fish collected from the field having not yet encountered the size range of *P. rufa* used in these experiments. Due to their small gape, juveniles in the field may choose to forage on smaller prey as these are probably captured and handled with greater efficiency. It is possible that adult sea horses have had more exposure to the prey, further contributing to their success.

Care must be taken before drawing conclusions as to the relative effectiveness of ambush and lunging predation when feeding on *P. rufa* in vegetation. The behavioural repertoire of sea horse foraging was not disturbed by the presence of vegetation. The typical ambush and head-flick observed in open water was performed by sea horses in vegetation, possibly with higher efficiency, aided by the utilization of camouflage and suppression of swimming. However, salmon were required to modify their attack sequence from a long distance lunge initiated a great distance from the prey swarm in open water to a short-scale 'picking' style in vegetation. It should be noted that our unpublished observations show that juvenile salmon forage more successfully in groups when attacking aggregated prey, though this would presumably be hindered by vegetation.

The stealthy approach of *H. abdominalis* toward the prey swarm could be said to have been benefited by the presence of cover in the form of artificial sea grass. This, in conjunction with the morphological adaptations of sea horses to life in structurally complex habitats, suggests that *H. abdominalis* is a more effective predator than *A. trutta* in vegetated conditions. The higher capture success of *A. trutta* recorded in this study was most likely an artefact of the heightened vulnerability of *P. rufa* in vegetation as opposed to open water.

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