



The role of seagrass as preferred habitat for juvenile *Sillaginodes punctata* (Cuv. & Val.) (Sillaginidae, Pisces): habitat selection or feeding?

Rod M. Connolly

Department of Zoology, University of Adelaide, South Australia, 5005, Australia

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Abstract

Previous experiments have shown that the relationship between abundance of juvenile fishes and seagrass density is the result of habitat selection rather than direct predation, but have not distinguished between habitat selection and simple feeding. The simple feeding model, in which fish swim until they find food, eat it, and swim again, predicts that fish will be found where the most food is available regardless of the presence or density of seagrass. Food availability was manipulated in tanks in which juvenile *Sillaginodes punctata* (Cuv. & Val.) (King George whiting) were offered the choice of two habitats, live eelgrass (*Zostera muelleri* Irmisch ex Aschers.) or unvegetated sand. When food was available, fish were initially distributed in a way that strongly supported the feeding model, but once they were satiated, the distribution of fish fitted the predictions of neither model. In the absence of food, fish selected eelgrass habitat. At night, the distribution of fish showed that they took little account of food availability or habitat.

Keywords: Fish; Habitat selection; King George whiting; Predation; Seagrass; *Zostera*

1. Introduction

Seagrass meadows in many parts of the world support large numbers of juvenile fishes and provide a nursery habitat for many commercially important species (Pollard, 1984). Unvegetated areas adjacent to seagrass meadows have different fish assemblages, usually with fewer fishes and fewer species (Bell & Pollard, 1989). The two most common explanations for the greater abundance of fishes in seagrass have been (1) that seagrass provides greater protection from predators (often larger fish) and (2) that seagrass provides more food, not directly to grazing fishes but by supporting a diverse and abundant invertebrate fauna which can be consumed by carnivorous fishes.

Although many studies have shown a higher abundance of invertebrates associated with seagrass than with adjacent unvegetated patches (Howard et al., 1989), the role of seagrass in providing protection from predators is the model that has received most attention in recent times (Heck & Orth, 1980; and see review by Bell & Pollard, 1989).

Motile invertebrates, which show the same pattern of increased abundance in seagrass compared with unvegetated habitats, have been used in experiments to test the importance of seagrass. There is some evidence that amphipods can detect differences in canopy density, and that species that are more vulnerable to predation by fishes show a greater preference for dense seagrass (Stoner, 1980). Experiments investigating the importance of seagrass to invertebrates as a source of protection from predators have tested between the two factors, protection from predators and habitat selection. The behavioural mechanism of habitat selection is assumed to be a response to the habitat itself, but the underlying advantage might be in terms of any of several factors, including increased living space and food availability (Leber, 1985). Movement to find food is not the same as habitat selection, which may, however, result in occupation of habitat that supports more food. The selection of habitat and trade-offs between foraging and remaining safe from predators have also been studied in animals from non-marine systems. This work was traditionally aimed at elucidating rules governing decision-making in animals, and to a large extent is now based on optimality modelling (Krebs & Kacelnik, 1991).

Bell & Westoby (1986b) manipulated seagrass densities in field experiments and used predator exclusion cages to show that small fishes were more common in denser seagrass regardless of predator presence/absence. They showed convincingly that low fish numbers in patches with less dense seagrass cover were not due to increased predation, and concluded that small fishes select habitat. Bell & Westoby (1986b) suggested that predation may have been the ultimate selective agent resulting in habitat selection. The increased chance of finding food in denser seagrass is another possible agent.

As Bell & Westoby (1986a) point out, their results may be explained in ways other than habitat selection by fishes. Fishes might, for example, be attracted to more abundant food in denser seagrass. Food abundance was not measured by Bell & Westoby (1986a,b). A model not excluded by their results is that of small fishes simply swimming (with or without pattern) until they find food, at which time they pause to eat it, and continue swimming. Under this scenario, fishes would be found more often where there is more food, regardless of seagrass density. This contrasts with the prediction from the habitat selection model that fishes should be found in denser seagrass regardless of the amount of food available.

Sillaginodes punctata (King George whiting) is the most important species in the commercial inshore scalefish catch in South Australia (Anonymous, 1992). Adults spawn offshore, and post-larvae settle in shallow coastal areas (Jones et al., 1990). As early juveniles, they are much more common over eelgrass (*Zostera muelleri*) than over adjacent unvegetated patches (Connolly, 1994). This tight association with eelgrass, which is similar to the *Zostera* habitat used by Bell & Westoby (1986b), makes early juveniles of *Sillaginodes punctata* ideal test animals for distinguishing between the predictions of the two models, habitat selection and simple feeding. Also, in an experiment

in which eelgrass was removed from large patches, *Sillaginodes punctata* numbers matched invertebrate production more closely than presence or absence of eelgrass (Connolly, unpubl. data). The responses of *Sillaginodes punctata* were therefore investigated in the laboratory, where food availability and vegetation could be controlled independently.

2. Materials and methods

Experiments were done in a tank, in which food availability was manipulated whilst fish were offered a choice between vegetated and unvegetated habitats. Half of the sandy bed of a 1 m diameter circular fibreglass tank was planted with eelgrass (*Zostera muelleri*) collected from the sublittoral fringe in Barker Inlet, South Australia (138° 30' E, 34° 45' S), a shallow marine-dominated estuary. Sediment was washed from the roots of the eelgrass to remove fauna prior to planting, leaving clean, intact plants, which were soaked for 8 h in freshwater. This soaking killed associated fauna, but did not damage the eelgrass. Eelgrass was then planted into sterilised sand and the tank filled with 350 l of filtered sea water. This stand of eelgrass was similar to that at the collection site with respect to shoot density and shape, size, colour, texture and flexibility of leaves. The remaining half of the tank was left as bare sand. The absence of motile invertebrates in the tank was confirmed using a 95 μm sweep.

Mean leaf length of eelgrass was 107 mm (SE 3.7) and water depth was 450 mm. This left a large volume of water above the eelgrass canopy, a space in which *Sillaginodes punctata* juveniles are often observed swimming in the field. Eelgrass appeared green and healthy throughout the study and was replanted in a different sector of the tank part way through each individual experiment. The tank was also rotated through a random number of degrees between trials within experiments.

Juvenile *Sillaginodes punctata* were collected from Barker Inlet using a 1-mm mesh seine net 2 days before the beginning of each experiment. Mean fish length of all fish used in experiments (measured after experiment) was 35.8 mm (SE 0.37). These fish were collected from an area with patches of eelgrass and unvegetated habitat. The fish were allowed to acclimate to laboratory conditions in five holding tanks, each with live eelgrass and unvegetated patches. Fish were fed frozen brine shrimp (*Artemia* sp.) for the first day and then live crustaceans (their normal diet) collected from Barker Inlet for the remainder of their time in the holding tanks.

For all experiments, each trial began by placing five fish, one from each holding tank, into a clean, opaque tank containing no food, eelgrass or sand. After 2 h, during which feeding was impossible, the five fish were released at the water's surface in the centre of the experimental tank. All fish immediately swam towards the bottom. In experiments requiring food, frozen brine shrimp were thawed and pipetted onto the sediment surface prior to fish release. For day experiments, an observer, motionless at the side of the tank on the boundary between the two habitats, recorded the habitat with which each fish was associated, every 5 min for the first 20 min, then every 15 min until 125 min after fish release. The height above sediment and distance to the side of the tank were also estimated. For night experiments, observations were made only at 10 and 60 min, by briefly illuminating the tank with a spotlight.

All fish from four trials (i.e. 20 fish) in the day and night experiments in which food was offered were preserved for later inspection of their stomachs for the presence of brine shrimp.

2.1. Design, and predictions from the models

Two designs were used to test between the models: (1) food offered only in the unvegetated habitat and (2) food offered in neither habitat. Predictions from the two models for both designs are shown in Table 1.

Although early juvenile *Sillaginodes punctata* do not school strongly, the position of a fish in the tank could have affected the positions of other fish. To avoid potential dependence of counts within a tank, in each trial at each observation time the habitat containing the majority of fish scored a one and the other habitat a zero. These scores were summed for each time over the 25 trials of that experiment. Counts were then averaged over two periods (≤ 20 min and > 20 min) in which fish behaved quite differently in some experiments. The aim was to test the mean scores of each habitat (over the two periods) for departure from a 1:1 ratio. Data from night experiments were analysed using chi-square tests. Chi-square tests are valid only when based on counts drawn from a Poisson distribution (Kramer & Schmidhammer, 1992). Counts within each time were tested for departure from a Poisson distribution using a runs test with two nominal categories (Zar, 1984) and no departure from Poisson was detected in either of the experiments. It was possible to analyse data from day experiments using a *t*-test by using the multiple times to generate frequencies for each trial. This makes a more powerful test than the chi-square test (Kramer & Schmidhammer, 1992). A one-sample *t*-test was used to determine whether fish were more often over one habitat by testing whether the average number of times the majority of fish were over a habitat differed from the expected average (based on a 1:1 ratio).

Fish near the side of the tank (within 3 cm) may have been exhibiting thigmotaxis (the habit of positioning themselves near objects) and may not have been choosing between habitats. The scoring within trials was recalculated after excluding these fish. Where the same number of fish was found over both habitats, each habitat scored 0.5.

For both day experiments, the heights of fish over the two habitats were averaged in each trial over all times, so that for each trial there was one number for each habitat. The habitats were compared using the numbers from the 25 trials.

Table 1
Predicted results from the two models, habitat selection and simple feeding

Model	Design 1		Design 2	
	Eelgrass No food	Unvegetated Food	Eelgrass No food	Unvegetated No food
Habitat selection	++		++	
Simple feeding		++	○	○

++ = majority of fish on this side of tank; ○ = about half of fish on this side of tank.

3. Results

3.1. Design 1: Food in unvegetated habitat only

3.1.1. Day

Many fish spent the first 15–20 min feeding over the unvegetated habitat. After 20 min, fish fed much less frequently, and tended to be in or over the eelgrass. Significantly more fish were found over the unvegetated habitat during the first 20 min, but the number of fish over eelgrass after 20 min was not significantly greater (Fig. 1). The results over the first 20 min support the simple feeding model. Results from after 20 min fit the predictions of neither model.

The same patterns of fish behaviour and distribution were evident when fish close to the side of the tank were excluded from calculations (Fig. 1). Fish were closer to the side of the tank much more often over unvegetated habitat, and the effect of removing these from calculations was to increase the relative frequency of occurrence over eelgrass habitat.

3.1.2. Night

Fish were positioned differently during the night compared with the day. At both observation times there were no obvious patterns (Fig. 1). This evidence fits the pre-

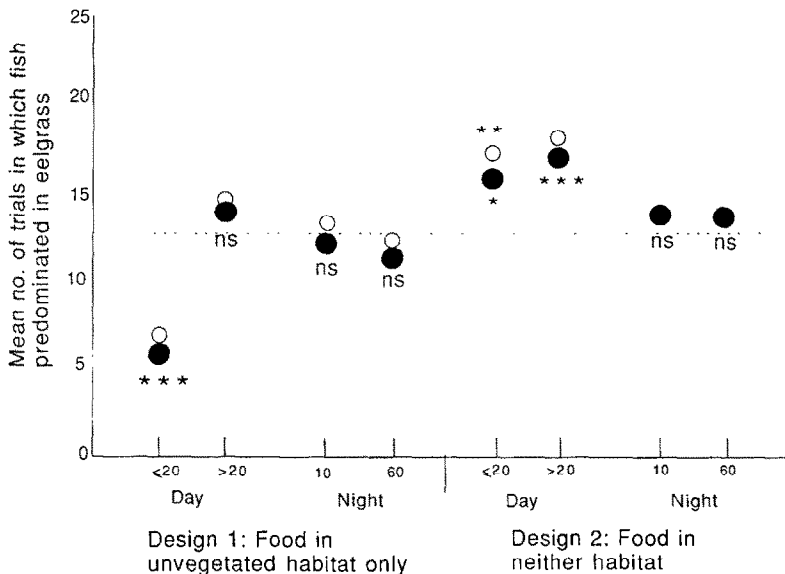


Fig. 1. Mean number of trials in which fish predominated in eelgrass habitat. Circles are means for the periods shown as numbers in min on x-axis. ●, all fish; ○, fish near side of tank excluded. Dashed line shows number of trials expected (12.5) under 1:1 relationship between eelgrass and unvegetated habitats. Statistical significance is shown by probabilities: ns > 0.05, * < 0.05, ** < 0.01, *** < 0.001, based on chi-square tests for night data and *t*-tests for day data, as explained in text. Probabilities are the same for ○ and ● except for Design 2. Day, ≤ 20 min, as shown.

dictions of neither of the models and does not distinguish between them. Results were changed very little when fish close to the side of the tank were excluded from calculations (Fig. 1).

3.2. Design 2: Food in neither habitat

3.2.1. Day

Fish were consistently more common in eelgrass habitat than over unvegetated habitat over both periods, and the differences were significant (Fig. 1). No marked difference in fish behaviour was observed before and after 20 min. These results support the habitat selection model.

When fish close to the side of the tank were excluded, the relative frequency of occurrence in eelgrass was increased. The pattern was the same as when all fish were included (Fig. 1), again supporting the habitat selection model.

3.2.2. Night

As for Design 1, no departure from a 1:1 ratio was found at either 10 or 60 min (Fig. 1). The evidence supports the simple feeding model as a departure from a 1:1 ratio was not shown (Table 1). This support is, however, logically weak, being a situation in which a negative (non-significant) result supports a positive conclusion (support for a model) (Toft & Shea, 1983); the result is more useful after consideration of statistical power. Power calculations for the tests on fish positions are the same for both times. From observed values 14:11, which is an effect size of about 0.1 (Cohen, 1988; Eq. 7.2.1), and with $\alpha = 0.05$, power = 0.1. If we require equal probabilities for Type I and II statistical errors ($\alpha = \beta = 0.05$, and power = 0.95), with $n = 25$, the minimum detectable effect size is 0.7, which equates to a departure from 1:1 of at least 21:4. The low power of the test limits the support that the result provides for the simple feeding model.

Results were the same when fish close to the side of the tank were excluded from calculations.

3.3. Stomach analysis

Sixteen of the 20 fish from the Day, Design 1 experiment had brine shrimp in their stomachs. In the night experiment, eight fish had brine shrimp in their stomachs. The stomachs of several of the fish from the day experiment were full to the point of being distended, a condition not observed by the author during the analysis of hundreds of stomachs from *Sillaginodes punctata* juveniles feeding in the wild (unpubl. data).

3.4. Distance above sediment

In both the Day, Design 1 experiment and the Day, Design 2 experiment fish were significantly higher above the sediment in the eelgrass than on the unvegetated side (Design 1: eelgrass, mean 56 mm (SE 1.7), unvegetated 28 mm (0.9), $p < 0.001$; Design 2: eelgrass 64 mm (1.4), unvegetated 32 mm (0.9), $p < 0.001$). The mean height in

eelgrass was less than the top of the canopy, and only a few fish were observed above the canopy.

4. Discussion

The daytime distribution of *Sillaginodes punctata* did not completely support either of the two models, habitat selection or simple feeding. Rather, the results show that after fish had been unable to feed for a short period their distribution could be explained by the simple feeding model if food was present. Once satiated, however, fish showed no preference for either habitat, and neither model was supported. In the absence of food, their distribution could be explained by the habitat selection model.

Night experiments gave conflicting results. In Design 1, neither model was supported, as fish were evenly distributed in the tank. In Design 2, the same even distribution fits the predictions of the simple feeding model. The support is weak, however, because the test had little power to detect a departure from a 1:1 ratio. Even if a 1:1 ratio had been demonstrated, the simple feeding model is not the only explanation of an even distribution of fish. Taken together with the evidence from the Design 1 experiment, it seems that at night, although some of the fish ate food, they generally took little account of habitat or food.

Much of the rationale for the current experiments comes from the work of Bell & Westoby (1986a,b), especially the discounting of predation as the proximate cause of lower fish abundance in less dense seagrass. However, Bell & Westoby compared fish densities of dense and sparse eelgrass, unlike the present comparison between eelgrass and unvegetated habitat. Their overall model has two parts relevant to the present study: (1) fish larvae settle into seagrass beds, regardless of the density of seagrass, in much greater abundance than into adjacent unvegetated areas, and (2) juvenile fishes then select dense in favour of sparse seagrass within the seagrass bed. Although *Sillaginodes punctata* juveniles and the eelgrass beds of Barker Inlet are similar to the fishes and eelgrass worked on by Bell & Westoby, in Barker Inlet fishes move in over tidal flats on each tide, necessarily choosing anew each tide between eelgrass and unvegetated habitat. In this system, comparisons both of differing densities of eelgrass and of eelgrass with unvegetated habitat are relevant. In the model of Bell & Westoby, both parts described above can possibly be explained by the simple feeding model, since there is more food (invertebrates) in denser eelgrass than in sparser eelgrass, and more food also in sparser eelgrass than adjacent bare patches (Connolly, unpubl. data).

The models of habitat selection, simple feeding and protection from predators need not apply exclusively to all animals in seagrass. In tests comparing the importance of predation and habitat selection for invertebrates, different species gave different results (Leber, 1985). Rozas & Odum (1988) concluded that both protection from predation and better feeding were important for the fishes they studied in freshwater marshes, although the mechanism resulting in more fishes being in vegetated patches was not determined. In tank experiments offering a choice between artificial seagrass and unvegetated substratum, juvenile walleye pollock (*Theragra chalcogramma*) were found more often over unvegetated habitat, except when fish were exposed to a predator

model, when fish moved to the artificial seagrass (Sogard & Olla, 1993). Sogard & Olla (1993) took no account of food availability.

The daytime responses of juvenile *Sillaginodes punctata* differed depending on whether or not food was present. Even in the presence of abundant food, however, behaviour differed as time spent exposed to food increased, presumably resulting in a decreasing degree of hunger. In optimality modelling terms, responses depended on an environmental variable but also on the internal state of animals (Krebs & Kacelnik, 1991). An appropriate further step in experimentation with *Sillaginodes punctata* would be to examine the trade-offs fish make in deciding, for example, whether to search and where to search for food. The current experiments could also be combined with exposure to predators. Fish should be offered choices not only between seagrass and unvegetated habitats but also between dense and sparse seagrass.

The experiments presented here were done in the laboratory because there is no way of presenting food independently of vegetation in the field. A feature of these experiments is that live eelgrass was used in the tank. However, several other factors may be importantly different from field conditions. The density of *Sillaginodes punctata* in Barker Inlet ranges up to 2.5 fish/m², whereas in the tank the density was 7.1 fish/m². The size of the tank was small relative to the size of patches worked on by Bell & Westoby (1986b) and Connolly (1994). The observations that generated the models tested in this paper may not hold for patch sizes as small as those in the tank. An alternative explanation for the increased abundance of fish in eelgrass in the tank is that, because water circulation was less vigorous than in the field, dissolved oxygen levels may have been higher on the eelgrass side during the day. Oxygen levels were not measured during the experiments.

Habitat selection by fishes may be innate or learned. These two possibilities have not been separated here, since fish were collected after exposure to an area with eelgrass and unvegetated patches, and concomitant abundances and distributions of predators and prey. Also, fish were briefly exposed to the habitats and prey distribution of holding tanks.

In conclusion, the responses of early juvenile *Sillaginodes punctata* support the simple feeding model when fish have not fed for a short time, but support the habitat selection model in the absence of food. *Sillaginodes punctata* took little account of food availability or habitat type at night.

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References

- Anonymous, 1992. Catch, effort and value of production of South Australian fisheries. *Safish*, Vol. 17, p. 25.
- Bell, J.D. & D.A. Pollard, 1989. Ecology of fish assemblages and fisheries associated with seagrasses. In,

- Biology of seagrasses*, edited by A.W.D. Larkum, A.J. McComb & S.A. Shepherd, Elsevier, Amsterdam, pp. 536–564.
- Bell, J.D. & M. Westoby, 1986a. Variation in seagrass height and density over a wide scale: effects on common fish and decapods. *J. Exp. Mar. Biol. Ecol.*, Vol. 104, pp. 275–295.
- Bell, J.D. & M. Westoby, 1986b. Abundance of macrofauna in dense seagrass is due to habitat preference, not predation. *Oecologia*, Vol. 68, pp. 205–209.
- Cohen, J., 1988. *Statistical power analysis for the behavioural sciences*. Lawrence Erlbaum Associates, New Jersey, second edition, 567 pp.
- Connolly, R.M., 1994. A comparison of fish assemblages from seagrass and unvegetated areas of a southern Australian estuary. *Aust. J. Mar. Freshwater Res.*, Vol. 45 (in press).
- Heck, K.L. & R.J. Orth, 1980. Seagrass habitats: the roles of habitat complexity, competition and predation in structuring associated fish and motile invertebrate assemblages. In *Estuarine perspectives*, edited by V.S. Kennedy, Academic Press, New York, pp. 449–464.
- Howard, R.K., G.J. Edgar & P.A. Hutchings, 1989. Faunal assemblages of seagrass beds. In *Biology of seagrasses*, edited by A.W.D. Larkum, A.J. McComb & S.A. Shepherd, Elsevier, Amsterdam, pp. 536–564.
- Jones, G.K., D.A. Hall, K.L. Hill & A.J. Staniford, 1990. The South Australian marine scalefish fishery. *Green Paper, South Australian Department of Fisheries*, January, 1990.
- Kramer, M. & J. Schmidhammer, 1992. The chi-squared statistic in ethology: use and misuse. *Anim. Behav.*, Vol. 44, pp. 833–841.
- Krebs, J.R. & A. Kacelnik, 1991. Decision-making. In *Behavioural ecology. An evolutionary approach*, edited by J.R. Krebs & N.B. Davies, Blackwell Scientific Publications, Oxford, third edition, pp. 105–136.
- Leber, K.M., 1985. The influence of predatory decapods, refuge, and microhabitat selection on seagrass communities. *Ecology*, Vol. 66, pp. 1951–1964.
- Pollard, D.A., 1984. A review of ecological studies on seagrass-fish communities, with particular reference to recent studies in Australia. *Aquat. Bot.*, Vol. 18, pp. 3–42.
- Rozas, L.P. & W.E. Odum, 1988. Occupation of submerged aquatic vegetation by fishes: testing the role of food and refuge. *Oecologia*, Vol. 77, pp. 101–106.
- Sogard, S.M. & B.L. Olla, 1993. The influence of predator presence on utilization of artificial seagrass habitats by juvenile walleye pollock, *Theragra chalcogramma*. *Environ. Biol. Fish.*, Vol. 37, pp. 67–65.
- Stoner, A.W., 1980. Perception and choice of substratum by epifaunal amphipods associated with seagrasses. *Mar. Ecol. Prog. Ser.*, Vol. 3, pp. 105–111.
- Toft, C.A. & P.J. Shea, 1983. Detecting community-wide patterns: estimating power strengthens statistical inference. *Am. Nat.*, Vol. 122, pp. 618–625.
- Zar, J.H., 1984. *Biostatistical analysis*. Prentice-Hall, New Jersey, second edition, 718 pp.