Fine-scale spatial and temporal variations in diets of the pipefish *Stigmatopora nigra* within seagrass patches

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Diets of the pipefish *Stigmatopora nigra* were analysed to determine if food availability was causing *S. nigra* to distribute according to habitat edge effects. Gut analysis found little difference in the diets of *S. nigra* at the edge and interior of seagrass patches, regardless of time of day or season. Fish diets did, however, vary with seagrass density: *S. nigra* in denser seagrass consumed more harpacticoid copepods and fewer planktonic copepods. The lack of difference in prey eaten by *S. nigra* at the edge and interior of patches suggests either that food was not determining *S. nigra* distribution patterns within patches or that differences in fish densities across patches meant that relative fish–prey densities were similar at edge and interior positions. Alternatively, any edge effects in diet might be masked by gradients in seagrass structure. © 2011 The Authors

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Key words: copepods; edge effects; gut analysis; *Heterozostera nigricaulis*; Port Philip Bay.

INTRODUCTION

The distribution of a species is governed by a variety of factors including resource allocation, species interactions and abiotic conditions. At habitat edges, changes in physical structure and subsequent changes in environmental variables can alter the distribution of resources (Murcia, 1995; Ries & Sisk, 2004). Changes in resource distribution at habitat edges can have direct (preferred habitat) and indirect (change in interactions) effects on the fauna (Murcia, 1995). Edge effects and how they affect the distribution of species are of fundamental interest to landscape ecologists, and, with increasing habitat fragmentation, greater understanding of edge effects is important for the management and conservation of communities (Ries *et al*., 2004; Hinchey *et al*., 2008).

Differences in food availability between the edge and the interior of habitat patches can cause shifts in the abundance of a species (Murcia, 1995; Ries *et al*., 2004).

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Optimal foraging theory predicts that a species will forage at locations providing the greatest benefit at the lowest energetic cost (Kotler *et al.*, 2010). If edges provide greater food availability, then in the absence of any costs such as predation or increased energy use, it would be expected that abundances would be greater at the edge of patches. Fish diets can reflect food availability (Hettler, 1989), and gut analysis has been used to assess diet variations across varying spatial and temporal scales (Hettler, 1989; Fell *et al.*, 1998; Hindell, 2006).

Wide-bodied pipefish *Stigmatopora nigra* Kaup 1856 are abundant in seagrass across southern Australia (Gomon *et al.*, 2008). Abundances of *S. nigra* are greater at the edge than interior of seagrass patches (Smith *et al.*, 2008), and this may be a result of greater food availability at the edge of patches (Macreadie *et al.*, 2009). *Stigmatopora nigra* use a prehensile tail to grasp seagrass blades within the canopy where they are camouflaged from predators and feed on plankton in the water column (Howard & Koehn, 1985; Jenkins & Sutherland, 1997; Kendrick & Hyndes, 2005). The congeneric spotted pipefish *Stigmatopora argus* (Richardson 1840) has been shown to move within patches according to the distribution of prey items (Macreadie *et al.*, 2010*a*).

The diet of *S. nigra* consists mostly of small crustaceans, which can include up to 91% planktonic copepods (Steffe *et al.*, 1989; Kendrick & Hyndes, 2005), suggesting that *S. nigra* depends on water movement for feeding opportunities. Seagrass structure alters water movement, reducing flow across seagrass patches (Peterson *et al.*, 2004). Decreasing water flow across seagrass beds is assumed to reduce the influx of planktonic copepods into the interior of patches, lowering food availability at the patch interior. Other prey items such as benthic crustaceans can also be more abundant at seagrass edges than further into patches depending on taxon and context (Tanner, 2005; Warry *et al.*, 2009; Murphy *et al.*, 2010; Macreadie *et al.*, 2010*b*). *Stigmatopora nigra* may be responding to a resource (copepod abundance) that itself is responding to patch edges, known as a 'cascading edge effect' (Ries *et al.*, 2004). Similarly, seagrass structure can alter abundances of prey items such as harpacticoid copepods, amphipods and ostracods (Connolly, 1995; Jenkins & Sutherland, 1997; Jenkins *et al.*, 2002), prey aggregations (Flynn & Ritz, 1999) and syngnathid foraging (Ryer, 1988; Flynn & Ritz, 1999), which may cause variation in *S. nigra* diet and may partially explain why *S. nigra* prefers long dense seagrass to short sparse seagrass (Steffe *et al.*, 1989).

Temporal changes in prey availability can affect species' abundance (Thayer & Sydeman, 2007). Distribution of *S. nigra* may change according to copepod abundances which can vary both seasonally (Hall & Bell, 1993) and diurnally (Walters & Bell, 1986). *Stigmatopora nigra* is a visual predator (Howard & Koehn, 1985) and may feed more effectively during the day than the night, and this could affect their dietary composition.

In a previous study (Smith *et al.*, 2010), abundances of *S. nigra* were greater at the edge than the interior of seagrass patches during the day in autumn, but not at any other time. In this study, it was hypothesized that if food availability was causing edge effects for *S. nigra*, abundances of prey in *S. nigra* guts would be greater at the seagrass edge than the middle in autumn, assuming diet reflects food availability (Hettler, 1989). By determining the gut contents of *S. nigra*, this study aimed to assess: (1) differences in feeding between the edge and the middle of seagrass

patches, (2) changes in feeding over diel cycles or seasons and (3) the relationship between feeding and seagrass structure.

MATERIALS AND METHODS

FIELD SAMPLING

Fish were sampled from seagrass patches at Blairgowrie on the south-eastern coast of Port Phillip Bay, Victoria, Australia (38° 21′ 46″ S; 144° 47′ 21″ E). At Blairgowrie the seagrass *Heterozostera nigricaulis* grows in patches of varying size in shallow (<1 m) water. Gut analysis was done on a sub-sample of *S. nigra* collected by Smith *et al.* (2010) who investigated the importance of patch size on the within-patch distribution of fishes. Briefly, *S. nigra* were caught using a push net (0·5 m × 1 m, with 1 mm mesh), pushed for 5 m in seagrass parallel to, and, within 1 m of the seagrass−sand interface (edge) and for 5 m at the middle of each of the 10 patches. Samples were taken on 4 days and 4 nights during autumn (May) and spring (October) 2006. Fish were anaesthetized in 200 mg l^{-1} benzocaine and preserved in ethanol. At each sampling period, four seagrass samples were taken at both positions in each patch to determine seagrass density. Seagrass samples were collected by cutting all seagrass within a 0·25 m^2 quadrat. Smith *et al.* (2010) concluded that there was little difference in *S. nigra* abundances at the edge and the middle of small patches, therefore only the six largest patches (461−5934 m^2) were used for gut analysis.

LABORATORY METHODS

Under a dissecting microscope, *S. nigra* guts were removed, opened and contents emptied onto a drop of glycerol on a microscope slide. Dietary items within guts were identified to the lowest taxonomic group possible and the number of individual prey items from each group counted. Copepod prey were divided into two groups: the general planktonic calanoid and cyclopoid copepods (planktonic copepods) and the general benthic harpacticoid copepods (harpacticoid copepods). Fish standard length (L_S) was measured to the nearest mm.

DATA ANALYSIS

Data were checked for normality and homogeneity of variance using box plots and log_{10} transformed where required and reassessed (Quinn & Keough, 2002). Differences in prey abundance in *S. nigra* guts at the edge and the middle of seagrass patches were assessed using a repeated measures ANOVA design. Season (autumn and spring) and time of day (day and night) were treated as fixed factors; position (edge and middle) was treated as a repeated measure. Gut contents were averaged over patches to ensure there were no sampling times or positions where fish were not sampled and sampling occasions (4 × 2 time of day × 2 season = 16) were used as replicates. Abundances of total prey, harpacticoid copepod prey, planktonic copepod prey and L_S were analysed.

Analysis of seagrass density between positions and season was done using a repeated measures model using season as a fixed factor and position as the repeated measure, with seagrass patches used as replicates. Additionally, the relationship between gut contents (total prey, benthic prey and planktonic prey), and both L_S and seagrass density, was assessed separately using linear regression. Abundances were averaged over sampling days (n = patch 6 × position 2 × season 2 × time of day 2 = 48) and treated as dependant variables in regression analyses.

RESULTS

The guts of 350 *S. nigra* were analysed; 179 from the edge of seagrass patches and 171 from the middle. Copepods were the most frequently occurring prey in guts

TABLE I. Percentage of *Stigmatopora nigra* guts containing prey items pooled across position, season and time of day, and mean ± S.E. prey items per gut at the edge and middle of seagrass patches pooled across season and time of day

Prey type	Guts with prey (%)	Mean ± S.E. prey items per gut	
		Edge	Middle
Total prey	96·3	87·63 ± 8·63	88·11 ± 6·16
Planktonic copepod prey	89·1	72·50 ± 7·98	68·2 ± 5·82
Harpacticoid copepod prey	89·4	12·17 ± 2·31	17·50 ± 2·32
Gammarid amphipods	56·9	2·32 ± 0·34	1·29 ± 0·12
Unidentified worms	12·9	0·36 ± 0·12	0·54 ± 0·35
Ostracods	9·4	0·09 ± 0·03	0·29 ± 0·08
Shrimp larvae	5·7	0·08 ± 0·03	0·15 ± 0·06
Isopods	3·4	0·07 ± 0·04	0·06 ± 0·03
Caprellid amphipods	3·7	0·03 ± 0·01	0·07 ± 0·03
Unidentified prey	2·0	0·01 ± 0·01	0·04 ± 0·02
Gastropods	0·9	0·01 ± 0·01	0·01 ± 0·01
Crab larvae	0·3	0·01 ± 0·01	0·00 ± 0·00
Tanaids	0·3	0·00 ± 0·01	0·01 ± 0·01
Cumaceans	0·3	0·01 ± 0·01	0·00 ± 0·00

(Table I), with harpacticoid and planktonic copepods present in 89·4 and 89·1% of individual *S. nigra* guts sampled, respectively. Planktonic copepods were the most abundant prey observed in *S. nigra* guts averaging 70·4 prey items per gut. Other prey items included amphipods, tanaids, ostracods and isopods (Table I).

POSITION, SEASON AND TIME OF DAY

The abundance of prey in *S. nigra* guts did not vary significantly between the edge and the middle of seagrass patches (Table I), time of day or season for total prey, harpacticoid or planktonic copepods, except that harpacticoid copepods were more abundant in the diet in spring than autumn (Table II and Fig. 1). The L_S of *S. nigra* were significantly longer in spring (mean ± S.E. = 84·1 ± 1·3 mm) than autumn (mean ± S.E. = 68·1 ± 0·8 mm) and a 4·1 mm difference in L_S between the middle (mean ± S.E. = 76·8 ± 1·1 mm) than the edge (mean ± S.E. = 72·7 ± 1·3 mm) of seagrass patches (Table II). Seagrass density did not vary statistically between the edge and the middle of patches or between seasons (repeated measures, season d.f. = 1,10, $P > 0.05$, position d.f. = 1,10, $P > 0.05$, season × position d.f. = 1,10, $P > 0.05$).

PREY RELATIONSHIP WITH *S. NIGRA* L_S AND SEAGRASS DENSITY

Regression analysis comparing *S. nigra* L_S and prey items showed that abundances of harpacticoid copepod prey items increased with *S. nigra* size (linear regression, d.f. = 1,43, $P < 0.05$; Fig. 1) but there was no relationship with total prey abundance (linear regression, d.f. = 1,43, $P > 0.05$), planktonic copepod prey abundances (linear regression, d.f. = 1,43, $P > 0.05$) or seagrass density (linear

TABLE II. Results of repeated-measure ANOVA, assessing *Stigmatopora nigra* L_S, total prey abundance, harpacticoid copepods and planktonic copepods between positions (edge and middle), seasons (autumn and spring) and time of day (day and night)

Source	d.f.	L_S		Total prey		Harpacticoid copepods		Planktonic copepods	
		F-ratio	*P*	*F*-ratio	*P*	*F*-ratio	*P*	*F*-ratio	*P*
Between subjects									
Season	1	24·9	<0·001	0·4	>0·05	7·1	<0·05	2·7	>0·05
Time of day (TOD)	1	0·5	>0·05	2·1	>0·05	1·0	>0·05	1·9	>0·05
Season × TOD	1	0·9	>0·05	1·5	>0·05	0·1	>0·05	0·5	>0·05
Error	12								
Within subjects									
Position	1	5·9	<0·05	0·2	>0·05	0·7	>0·05	0·7	>0·05
Position × season	1	0·2	>0·05	0·6	>0·05	1·4	>0·05	0·1	>0·05
Position × TOD	1	0·1	>0·05	0·1	>0·05	1·0	>0·05	4·0	>0·05
Position × season × TOD	1	0·1	>0·05	0·2	>0·05	0·2	>0·05	0·4	>0·05
Error	12								

L_S, standard length.

regression, d.f. = 1,43, $P > 0.05$). Seagrass density was significantly correlated with *S. nigra* gut contents. As seagrass density increased, the abundance of harpacticoid copepod prey increased (linear regression, d.f. = 1,43, $P < 0.05$), but planktonic copepods decreased (linear regression, d.f. = 1,43, $P < 0.05$; Fig. 1). There was no relationship between seagrass density and total prey items (linear regression, d.f. = 1,43, $P > 0.05$).

DISCUSSION

A variety of prey were consumed by *S. nigra* at the edge and middle of seagrass patches. *Stigmatopora nigra* prey items in this study were similar to those reported in other studies where copepods were the main food source (Steffe *et al*., 1989; Kendrick & Hyndes, 2005). There was, however, little difference between *S. nigra* prey at the middle and edge of patches regardless of season and time of day. It was hypothesized that greater *S. nigra* abundances at the edge during the day in autumn in Smith *et al*. (2010) would be reflected as greater gut prey abundance at the edge during this time, if food availability was causing *S. nigra* edge effects. This hypothesis was therefore not supported.

Optimal foraging theory predicts that species will forage where benefits are greatest and costs are lowest (Kotler *et al*., 2010). Edges can facilitate or restrict movement of prey into and out of patches enhancing or reducing benefits to predators and consequently altering species abundances at habitat edges (Ries & Sisk, 2004). Seagrass
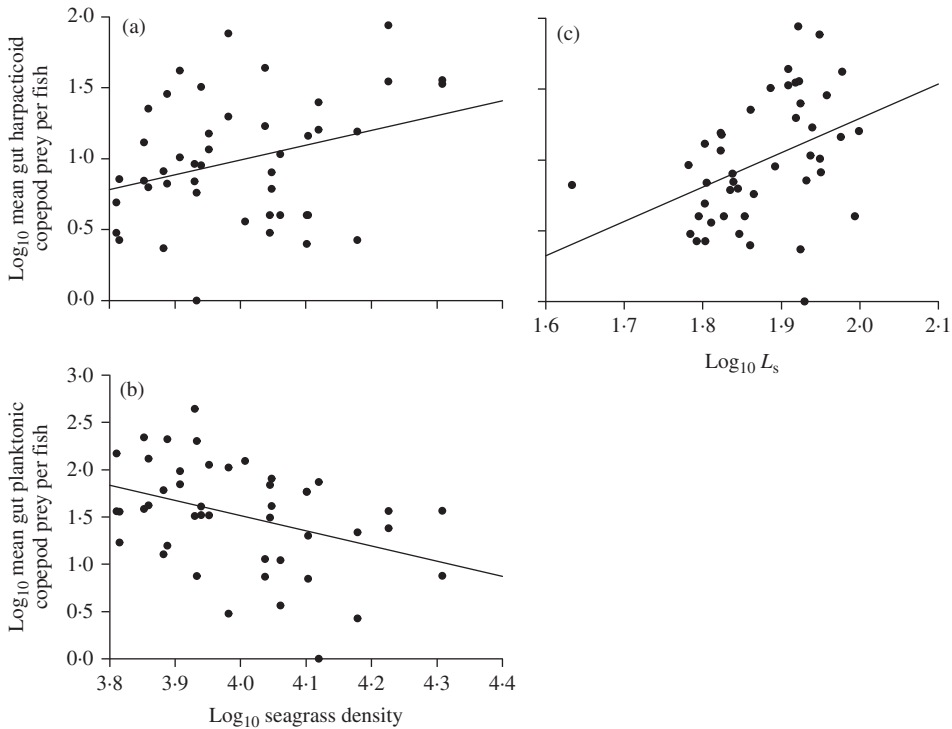
FIG. 1. Relationship between seagrass density and mean (a) harpacticoid and (b) planktonic copepod prey items in *Stigmatopora nigra* guts, and (c) *S. nigra* standard length (L_S) and mean harpacticoid copepod prey items in *S. nigra* guts. The curves were fitted by: (a) $y = 1.045x - 3.888$ ($r^2 = 0.10$), (b) $y = -1.605x + 7.932$ ($r^2 = 0.14$) and (c) $y = 2.421x - 3.549$ ($r^2 = 0.16$).

structure at the seagrass edge affects water currents (Peterson *et al.*, 2004), which are thought to alter abundances of meiofauna and plankton (Bell *et al.*, 2001; Warry *et al.*, 2009), prey of many seagrass animal species. Food availability is thought to play an important role in determining edge effects in seagrass beds (Connolly & Hindell, 2006) and has been suggested to be causing edge effects for polychaetes (Bell *et al.*, 2001) and *Stigmatopora* sp. (Smith *et al.*, 2008; Macreadie *et al.*, 2009). Irlandi & Peterson (1991), however, found growth of the clam *Mercenaria mercenaria* to be greater at seagrass edges but could not attribute increased growth to greater food availability. Using *S. nigra* gut prey abundance as a proxy for food availability, this study found little evidence to support food availability as an underlying cause of edge effects. Recent work by Macreadie *et al.* (2010*a*), however, showed that the distribution of *S. argus*, a conspecific of *S. nigra*, within artificial seagrass patches, was caused by the distribution of prey. Therefore, the importance of food availability in determining edge effects should not be discounted.

There are a variety of factors that may explain the lack of difference in *S. nigra* diets between the edge and the middle of patches. Differences in *S. nigra* abundances between the edge and the middle of patches were only recorded during one of four sampling periods (Smith *et al.*, 2010), which may have restricted the chances of supporting the hypothesis if some factor was masking the effect of food availability

on *S. nigra* during this one sampling period. Alternatively, in small patches, there may not be any differentiation between edge and interior habitats in water movement and subsequent prey availability. Abundances of copepods and other *S. nigra* prey, however, have been shown to decrease at only short distances into seagrass patches (<5 m; Tanner, 2005; Warry *et al.*, 2009), suggesting that even in small patches there will be some decrease in prey availability at the patch interior. Foraging at the edge may present danger from predators inhabiting habitats adjacent to seagrass habitats (Connolly & Hindell, 2006) resulting in little difference between gut content of animals sampled at the edge and middle of patches. Finally, there may have been no difference in *S. nigra* gut content between the edge and the middle of patches if *S. nigra* were moving between the edge and the middle of patches.

Another explanation for the lack of difference in diet between edge and inner positions might be that differences in fish densities across patches result in relative fish–prey densities that are similar at edge and interior positions. This possibility is worth following up in future studies. In addition, although fish diets can reflect food availability (Hettler, 1989), it is acknowledged that food availability may not be reflected in diets. For example, if prey densities are greater at the edge than interior but dietary needs can be fulfilled at each position, then greater prey abundances at the edge will not be reflected in diets. Furthermore, if species show prey preference or certain prey have greater energy value, species distribution will be determined by that specific prey. The composition of *S. nigra* diets varied little between the edge and the middle of patches; however, without a measure of prey availability, *S. nigra* prey preference is unknown.

Variation in fish lengths can affect the amount of prey eaten (Edgar & Shaw, 1995). Harpacticoid copepods were more abundant in *S. nigra* guts as fish L_S increased. Similar to other pipefish species such as hairy pipefish *Urocampus carinirostris* Castelnau 1872, *S. nigra* L_S were greater in spring (Howard & Koehn, 1985), which may be related to recruitment to seagrass patches during autumn. Greater *S. nigra* L_S in spring coincided with greater abundances of harpacticoid copepods in fish guts, which may partly explain the relationship between L_S and harpacticoid abundance. The L_S of *S. nigra* were greater in the middle of seagrass patches than the edge, but were unlikely to be masking any differences in diet because there was no relationship between L_S and gut content, and size differences between positions were only small.

Seagrass structure can affect *S. nigra* abundances (Steffe *et al.*, 1989) but are unrelated to *S. nigra* distribution between the edge and the middle of patches (Smith *et al.*, 2008, 2010). The findings of this study are similar to those of Steffe *et al.* (1989), who found that seagrass density did not affect total gut content, but can affect the type of prey *S. nigra* eats. Abundances of benthic harpacticoid copepods in gut samples increased as seagrass density increased, while abundances of planktonic copepods decreased as seagrass density increased. The relationship between seagrass density and *S. nigra* prey items could be attributed to prey availability. Harpacticoid abundance increases with increasing seagrass density (Jenkins *et al.*, 2002; Murphy *et al.*, 2010), explaining greater harpacticoid abundances in *S. nigra* guts in dense seagrass and greater planktonic copepod prey in sparse seagrass. Alternatively, changes in seagrass density could affect the foraging efficiency of *S. nigra*. Syngnathid foraging behaviour can change according to seagrass structure (Ryer, 1988; Flynn & Ritz, 1999), which may facilitate harpacticoid copepod capture in dense seagrass and restrict planktonic copepod capture. Seagrass structure, by changing prey availability

or foraging behaviour, is therefore probably more important than seagrass edges in determining the types of prey eaten by *S. nigra*.

In summary, little difference was found in gut prey abundances between fish sampled at the edge and middle of patches, although prey types eaten differed depending on seagrass density. Lack of difference between gut content at the edge and middle of patches suggests that food availability is not causing a habitat edge effect in *S. nigra* populations. Factors such as fish movement, distribution and seagrass patch size, however, may also influence patterns in gut prey abundances.

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