



Seagrass habitat complexity does not always decrease foraging efficiencies of piscivorous fishes

Masahiro Horinouchi^{1,*}, Naoki Mizuno², Yuka Jo², Masashi Fujita²,
Mitsuhiko Sano³, Yuzuru Suzuki²

¹Research Center for Coastal Lagoon Environments, Shimane University, 1060 Nishikawatsu-cho, Matsue, Shimane 6908504, Japan

²Fisheries Laboratory, Graduate School of Agricultural and Life Sciences, University of Tokyo, 2971-4 Bentenjima, Maisaka, Hamamatsu, Shizuoka 4310214, Japan

³Laboratory of Global Fisheries Science, Graduate School of Agricultural and Life Sciences, University of Tokyo, 1-1-1 Yayoi, Bunkyo-ku, Tokyo 1138657, Japan

ABSTRACT: The foraging efficiencies of predators in relation to seagrass density and microhabitat use patterns of prey during predator presence/absence were examined by laboratory experiments. The foraging efficiency of the permanent resident piscivorous sculpin *Pseudoblennius cottoides*, which employed ambush and stalk-and-attack tactics, was higher in the presence of seagrass, while that of the transient piscivorous gnomefish *Scombrops boops*, which employed chase-and-attack tactics, decreased in denser seagrass. When coexisting with gnomefish, juveniles of the prey goby *Gymnogobius heptacanthus* sometimes entered seagrass areas to avoid attacks by such predators. In the absence of gnomefish, however, goby juveniles almost always stayed outside the seagrass areas (instead inhabiting open areas adjacent to the outer seagrass edge), even when sculpin were absent. These phenomena suggested that dense seagrass may be characterized by a constant potential risk (for prey) resulting from permanent resident predators whose foraging efficiency was improved by the habitat structure. Accordingly, prey species lacking tactics to efficiently decrease risks from such predators may remain outside the seagrass habitat, although close enough to successfully retreat to it in response to acute temporal risks offered by transient chase-and-attack predators. Such differential habitat use patterns corresponding to different predator types may be at least partly responsible for the concentrations of small fishes sometimes observed in open areas adjoining the outer margins of natural seagrass habitats.

KEY WORDS: Permanent resident piscivorous fish · Foraging efficiency · Seagrass · Habitat complexity · Prey habitat choice

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INTRODUCTION

It is generally believed that seagrass habitats support large numbers of fish species and individuals and provide nursery habitats for juveniles of many species, whereas unvegetated bare substrata are usually characterized by fewer species and individuals (e.g. Kikuchi 1974, Sogard 1989, Edgar & Shaw 1995). The sheltering effect of habitat complexity against predators is sometimes considered as an especially important factor re-

sponsible for such differences, predation likely playing a significant role in generating habitat-specific patterns, either directly, by the removal of prey species, or indirectly, by inducing habitat selection in prey species. For small-sized fishes such as juveniles, this attribute is especially important because they are particularly vulnerable to predation (Sogard 1992) and, accordingly, sometimes select seagrass habitats in an apparent effort to reduce predation risks (e.g. Sogard & Olla 1993, Jordan et al. 1997, Gotceitas et al. 1997).

*Email: hori@soc.shimane-u.ac.jp

If predator-induced mortality is always higher in areas of lesser complexity (e.g. Heck et al. 2003, Heck & Orth 2006, but see also Horinouchi 2007a), such areas should almost always support fewer small fishes. However, such is not always the case in and around seagrass habitats (e.g. Uhrin & Holmquist 2003, Horinouchi 2007b). For example, in the temperate coastal region of Japan, larger numbers of small juvenile fishes, usually forming large shoals and/or schools, are often observed in open areas adjacent to the outer edge of seagrass habitats in spring, and fewer individuals are found within the dense seagrass (e.g. Horinouchi & Sano 1999, Horinouchi in press). To further clarify these observations, 2 hypotheses are tested in the present study: (1) the predation efficiency of small permanent resident piscivorous fish, seldom examined in the aforementioned studies, does not decrease in denser seagrass; accordingly, (2) dense seagrass is characterized by a constant potential predation risk induced by small permanent resident piscivorous fish, the prey remaining unaware of the former until attacked. Consequently, juveniles lacking effective tactics against such predators usually remain outside dense seagrass areas unless attacked there by transient predators.

In the present study, we examined predator-prey interactions in relation to physically complex seagrass structures in a laboratory. The specific questions asked were: (1) Do foraging efficiencies of permanent resident or transient piscivorous fishes decrease with increasing habitat complexity? (2) Does a prey fish change its microhabitat use pattern in accordance with the presence/absence of permanent resident and/or transient predators?

MATERIALS AND METHODS

Experimental fishes. The blenniid *Pseudoblennius cottoides* (hereafter, sculpin) and the scombropid *Scombrops boops* (hereafter, gnomefish) were selected as resident and transient predators, respectively, and gobiid *Gymnogobius heptacanthus* juveniles as prey. In the temperate coastal region in Japan, including the present study site (Lake Hamana), sculpins reaching sizes of ca. 13 cm standard length (SL) reside in seagrass habitats (Nakabo 2000) throughout the year. In contrast, young gnomefish, usually forming small schools, sometimes utilize seagrass habitats while searching for prey in the spring, but rarely or never occupy seagrass habitats the rest of the year (e.g. Horinouchi in press).

Gymnogobius heptacanthus occupies the water column (Suzuki et al. 2004). Large numbers of juveniles occur in and around seagrass (*Zostera marina*) habitats

at Lake Hamana in spring (April through June), indicating that seagrass is one of the most important nursery habitats of this goby. *G. heptacanthus* usually form a group ranging in size from 2 to 100s of individuals. In particular, large groups of juveniles can be often observed in open areas adjacent to the outer edges of seagrass beds (Horinouchi & Sano 1999).

In the study area, *Pseudoblennius cottoides* were sometimes observed capturing juvenile *Gymnogobius heptacanthus* within seagrass, and young *Scombrops boops* were often observed actively chasing and sometimes successfully capturing *G. heptacanthus* around the seagrass habitats (M. Horinouchi pers. obs.). Horinouchi & Sano (2000) have reported that the main food items of both *P. cottoides* and *S. boops* were fishes including *G. heptacanthus* juveniles; young *S. boops* preyed mainly upon shoaling and/or schooling juvenile gobies including *G. heptacanthus*.

Collection and maintenance of experimental fishes.

Experimental fishes were collected with a small beach seine, hand nets or set nets in and around *Zostera marina* beds in Lake Hamana (a saltwater-influenced lake opening directly to the sea), Shizuoka Prefecture, Japan, from May to June 2008. Immediately after collection, they were transported to the Fisheries Laboratory, University of Tokyo, on Benten Island in Lake Hamana. A detailed map of the study site was given by Horinouchi (2008). In the laboratory, individuals of each species were maintained in continuous flow-through tanks supplied with filtered ambient seawater pumped from Lake Hamana. Prey and predators were fed ad libitum with cultured brine shrimp and wild live fishes, respectively. Similarly sized prey and predators (ca. 30–35 and ca. 70–100 mm total length [TL]) respectively, were used in all of the experimental trials to avoid possible size-related differences in predator-avoidance or prey-capture abilities. Experimental fishes were each used for a single trial only; further field sampling was conducted several times to obtain new experimental fishes. To decrease the incidence of natural mortality during the trials (i.e. not due to predation), only healthy prey juveniles were used. Just before being subjected to each trial, all prey juveniles were sufficiently fed with cultured brine shrimp.

Pre-experiment: quantity of prey required by individual predators. In the case of there being no difference in prey numbers eaten among treatments, it was necessary to establish that a lack of difference in foraging efficiency was responsible, rather than predator satiation. Therefore, the maximum numbers of prey individuals consumed by the experimental predators were determined in advance. After a 1 d starvation period in a holding tank, 1 sculpin or 3 gnomefish (because of their group-forming trait) were placed into a small aquarium (25 cm wide, 40 cm long and 25 cm

depth) supplied with filtered ambient seawater (21.8 to 23.6°C), which provided no means by which prey could avoid predation. Subsequently, 50 prey goby juveniles were introduced to the aquarium, and the number of survivors after 1 h was counted. Four trials were conducted for each predator type. Mean \pm SD prey numbers consumed by sculpin and gnomefish per hour were 15 ± 2.6 and 21.8 ± 4.9 , corresponding to prey mortality rates of 30 and 43.6%, respectively.

Expt 1: effects of seagrass complexities on foraging efficiency of predators. Artificial seagrass (green polypropylene) was used to simulate natural seagrass. Each unit of artificial seagrass was comprised of 2 leaves of 10 mm width, 0.5 mm thickness and 500 mm length. The length of the artificial seagrass corresponded to the mean \pm SD length of natural *Zostera marina* in Lake Hamana (49.2 ± 12.6 cm).

Five levels of seagrass density, i.e. 0, 25, 50, 75 and 100% of the natural Lake Hamana *Zostera marina* density, were employed, and each was assigned to a single transparent tank (1.0 m diameter, 0.8 m depth). Initially, 5 circular PVC base plates (1.0 m diameter, 1.0 cm thick) were prepared. As the mean interval between neighboring seagrass shoots was 6.8 ± 1.7 cm (corresponding to ca. 216 shoots m^{-2}) in the natural seagrass habitat, artificial seagrass was individually planted into holes made on each base plate at intervals of 7 cm for the 100% density treatment, 8 cm for 75%, 10 cm for 50% and 14 for 25%. For the 0% density treatment, no seagrass was planted. One experimental unit for each density treatment (5 units in total) was established, and each unit was placed on the bottom of its respective tank. Subsequently, a 3 cm thick layer of treated sediment was spread on the bottom of each tank so as to cover the base plate completely. The sediment was taken from the natural seagrass bed, and treated by washing out all organic matter via flowing freshwater. Each experimental tank was filled with filtered ambient seawater (21.5 to 23.5°C) to a depth of ca. 70 cm.

Fifty prey individuals were placed into a transparent cylindrical holder (20 cm diameter, 30 cm long), which was dipped into the surface water at the center of each tank. The bottom of the holder was then opened gently to release the juveniles within the tank, and the holder was then removed. One hour later, predators (either 1 sculpin or 3 gnomefish) were introduced into each experimental tank after a 1 d starvation period in a holding tank, and their subsequent foraging behaviour was observed. In each trial, the predators were allowed to feed for 1 h before removal from the tank and recovery of all surviving juveniles. Following each trial, each tank was washed and set up again following the above procedure, although the combination of tank and experimental unit was done randomly. The trials

were conducted between 07:00 and 18:00 h, providing a total of 6 replicates for each treatment for each predator type.

The mortality rates of the juveniles, i.e. foraging efficiencies of predators, were compared among different seagrass densities using 1-way ANOVA. In the case of significant differences, post-hoc Games-Howell tests were employed to check for differences between all pairs of seagrass densities.

Expt 2: prey microhabitat choice with predators absent/present. Three microhabitats of differential complexity, i.e. 0, 25 and 100% of natural seagrass density, were established in each experimental tank (1.0 m in diameter, 0.8 m depth). Circular PVC base plates (1.0 m diameter, 1.0 cm thick) were divided into three $\frac{2}{3}\pi$ radian circular areas, and artificial seagrass was individually planted in holes on the base at intervals of 7 cm (area 1 corresponding to 100% density) and 14 cm (area 2, 25%). The third area remained unplanted (0%). Four experimental units were established; the 0, 25 and 100% density areas were arranged in clockwise order on 2 experimental units and in anticlockwise order on the others. Each experimental unit was placed on the bottom of a single tank (4 tanks in total) and the base plate was covered completely by a 3 cm layer of treated sediment (see above). Each experimental tank was filled with filtered ambient seawater (21.5 to 23.5°C) to a depth of ca. 70 cm.

Prey microhabitat choices in the presence/absence of predators were examined; viz. both predators absent, sculpin present/gnomefish absent, sculpin absent/gnomefish present, and both predators present. For the 'both predators absent' treatment, 20 juveniles were placed into the transparent cylindrical holder, which was dipped into the surface water at the center of each tank. After recognition of group-forming in the holder, the juveniles were gently released and the holder was removed. One hour later, the position of the prey group in the tank was observed simultaneously from directly above and 3 sides of the tank. The seagrass density at the position of the group was regarded as having been selected for by the group. For 'predators present' treatments, one hour after releasing a juvenile group within the tank following the above procedure, 1 sculpin and/or 3 gnomefish, which had been starved for 1 d beforehand, were gently released at the center of the tank. Ten minutes later, observations commenced and fish positions and/or behavior were recorded for 10 min. Observations were conducted very carefully so as not to disturb the fishes. The seagrass density at the position where the surviving prey group spent the most time was regarded as having been selected for by the group. Predators' microhabitat-use patterns were also determined in the same manner. Twelve trials for each treatment were conducted between 07:00 and 18:00 h.

Contingency tables were created based on the number of times each seagrass density was selected by the prey juveniles. A chi-squared analysis was used to examine whether or not prey distribution patterns differed in the absence and/or presence of predators (Zar 1999).

RESULTS

Effects of seagrass complexity on foraging efficiency of predators

The permanent seagrass resident sculpin employed ambush or stalk-and-attack tactics when capturing prey. Sculpin usually remained still on a seagrass leaf or the substrate, capturing prey which came within striking range, although it sometimes moved gradually toward prey, with a final dash for capture. On the other hand, the transient piscivorous gnomefish employed chase-and-attack tactics. Gnomefish formed a group, swam toward the prey at high speed and then captured them.

The foraging efficiency of the sculpin (prey mortality) differed significantly among different seagrass densities (1-way ANOVA, $F = 4.40$, $p = 0.008$) (Fig. 1a), increasing in the presence of seagrass compared with seagrass absence, although post-hoc comparisons did not detect significant differences between the pairs except the 0 to 100% density pair (Fig. 1a). The foraging efficiency of gnomefish also differed significantly among different seagrass densities (1-way ANOVA, $F = 12.28$, $p < 0.001$) (Fig. 1b), decreasing with increasing density. Post-hoc comparisons detected significant differences between 0% and all other density levels, as well as the 25 to 100% density pair (Fig. 1b).

Prey microhabitat choice with predators absent/present

Seagrass density selection by prey juvenile group in the presence and absence of predators and predator microhabitat-use patterns of predators are shown in Fig. 2. In the absence of both predators, the prey group always stayed in the open area (0% seagrass density) adjacent to the outer edge of seagrass; prey juveniles kept single-group formation, and the group almost always remained motionless.

In the presence of one or both predators, most prey juveniles survived the trials. In the presence of gnomefish, which always occupied the open area, irrespective of sculpin presence, the distribution patterns of the prey group deviated significantly from the above. In some cases, prey stayed in seagrass areas of 25 or

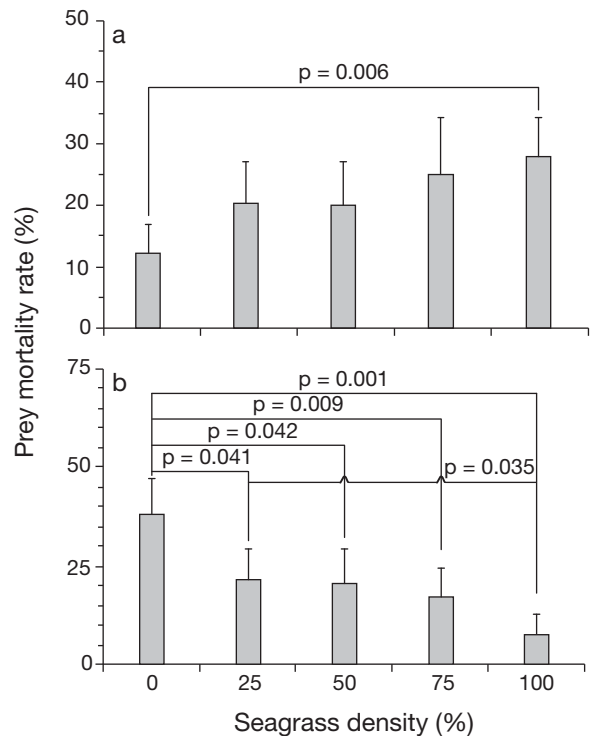


Fig. 1. *Gymnogobius heptacanthus*. Mortality rates of prey juveniles (%; mean \pm SD) induced by (a) sculpin *Pseudoblennius cottoides* and (b) gnomefish *Scombrops boops* in different seagrass densities. p-values indicate results of post-hoc Games-Howell test following ANOVA

100% densities (sculpin absence: $\chi^2 = 4.8$, $p < 0.05$; sculpin presence: $\chi^2 = 3.9$, $p < 0.05$) (Fig. 2); in others, prey occupied the open area, but exhibited group-manuevering when attacked by gnomefish. In the absence of gnomefish, the goby juveniles almost always occupied the open area adjacent to the outer edge of seagrass areas, the distribution pattern in the presence of sculpin being consistent with the pattern shown with both predators absent ($\chi^2 = 1.04$, $p > 0.90$) (Fig. 2). The prey group usually avoided the dense seagrass area (100% seagrass density) that sculpin preferred (Fig. 2).

DISCUSSION

The present study revealed that the foraging efficiency of the permanent resident sculpin *Pseudoblennius cottoides*, which employed ambush and stalk-and-attack tactics, was improved by dense seagrass, thereby contrasting with the generally-held notion of lower efficiency in a more structurally complex seagrass habitat (e.g. Heck & Orth 2006). However, results obtained for the transient chase-and-attack predator

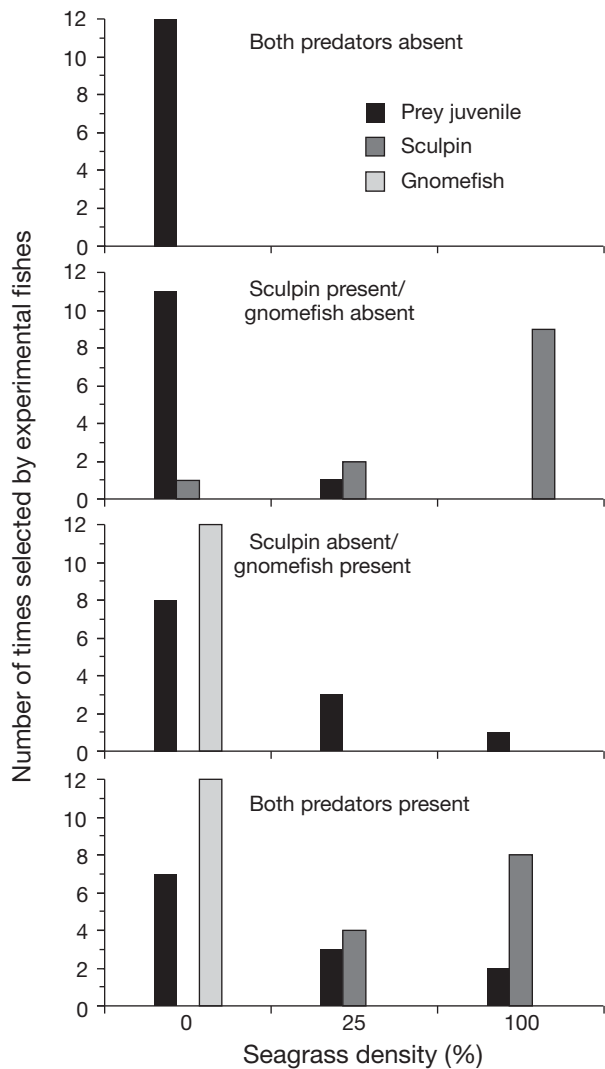


Fig. 2. Seagrass densities (0, 25 and 100% of natural seagrass density) selected by prey juveniles *Gymnogobius heptacanthus* in the presence and absence of predators (sculpin *Pseudoblennius cottooides* and gnomefish *Scombrops boops*) and by predators in the treatments. Twelve trials were conducted for each combination

gnomefish *Scombrops boops* were consistent with this notion.

Several hypotheses can be advanced for the high efficiency shown by sculpin in dense seagrass. Early recognition of a predator, beyond that predator's strike range or at an early attack stage, may enable prey species to employ anti-predator behavior successfully (e.g. FitzGibbon 1989, Lingle & Wilson 2001). In a complex habitat, however, prey vision is obstructed, which sometimes leads to a delay or failure in detecting the presence and/or approach of predators, and results in subsequent prey capture. In fact, during the present study, prey juveniles often showed no response to

sculpin until they were captured, probably due to view obstruction by the seagrass. Laurel & Brown (2006), who examined experimentally the foraging efficiency of an ambush predator *Myoxocephalus scorpius*, suggest that predators likely take advantage of the visual impairment of prey by seagrass. In addition, increased habitat complexity may provide more sites from which predators may attack (Janas 1985), thereby increasing the profitability of ambush tactics. Stalk-and-attack tactics may also be favored in complex habitats. Prey capture may be more successful due to the use of seagrass as a cover while stalking; predators may be able to move closer to the prey without being detected. Denser seagrass may therefore improve the foraging efficiency of sculpin employing ambush and stalk-and-attack tactics. Several studies of other vegetation systems have also provided results which support this view (e.g. Savino & Stein 1989b, Eklöv & Diehl 1994, Willis & Anderson 2003, Hawkins et al. 2005). In addition to cryptic body coloration, sculpin are also characterized by a small body size with a slender cylindrical trunk, enabling freedom of movement even in dense seagrass and efficient capture of prey. Accordingly, the foraging efficiency of such small permanent resident predators may be further enhanced in dense seagrass.

On the other hand, the foraging efficiency of gnomefish, a chase-and-attack predator, decreased with increasing seagrass density. Several studies have provided explanations for the lower foraging efficiency of such predators in habitats of higher structural complexity (e.g. Savino & Stein 1989a,b, Gotceitas & Colgan 1989, Lima & Dill 1990, Eklöv & Diehl 1994, Almany 2004). Essentially, visual acuity, essential for chasing and capturing prey successfully, is obstructed by complex structures. Additionally, weaving speedily through seagrass after prey is apparently more difficult in denser seagrass for a predator with a relatively large body size.

Five levels of seagrass density were employed in the present study. A specific threshold at which predator efficiency starts to decrease rapidly, however, was not detected, although the existence of such has been anticipated in several earlier studies (e.g. Nelson 1979, Gotceitas et al. 1997, Bartholomew et al. 2000). For chase-and-attack gnomefish, such a threshold, if it exists, may be between 0 and 25% of natural seagrass density, because the foraging efficiency (prey mortality rate) in 25% density was significantly lower than that in 0% density, decreasing to ca. half of the latter. This suggests that even sparse seagrass sometimes serves as an efficient shelter against chase-and-attack predators, which may explain, at least in part, the relatively large numbers of juvenile fishes sometimes occurring in sparser seagrass (e.g. Horinouchi & Sano 1999). That is, such juveniles may have retreated to

sparser seagrass in order to avoid chase-and-attack predators. In the present microhabitat-choice experiment, for example, prey juveniles sometimes entered the area of 25% seagrass density in the presence of gnomefish.

Although the spatial scale of the microhabitat-choice experiment was small, the experimental fishes exhibited the same microhabitat-use patterns at the larger natural seagrass habitats (see Horinouchi & Sano 1999, Horinouchi in press). In the absence of gnomefish, irrespective of sculpin presence/absence, prey juveniles usually occurred in the open area (0% seagrass density) adjacent to the outer edge of the seagrass. Such a phenomenon, in addition to the high foraging efficiency of the permanent resident predator in dense seagrass, suggests that for prey fishes, dense seagrass is likely to be characterized by a constant potential predation risk from permanent resident piscivores. Therefore, goby juveniles may tend to stay outside dense seagrass because they do not usually employ anti-predator tactics such as cryptic coloration or solitary and inactive behavior which effectively decreases their chances of detection or encountering an ambush. Prey juveniles, however, sometimes utilized seagrass areas in the presence of chase-and-attack predators, suggesting that in apparently acute situations they sometimes enter seagrass cover where the efficiency of the former predator decreases significantly, although anti-predator tactics such as group-maneuvering in the open remains an option for avoiding predation. Such differential habitat use patterns corresponding to different predator types may be responsible for the concentrations of small fishes sometimes observed in open areas adjoining the outer margins of natural seagrass habitats (e.g. Horinouchi in press).

It is clear that no single factor can explain fish distribution patterns. Food availability also sometimes strongly influences fish distribution patterns. The dominant food item of *Gymnogobius heptacanthus* juveniles is zooplankton (Horinouchi & Sano 2000), large swarms of the latter often being observed in the open areas adjoining natural seagrass habitats and also in sparser seagrass, although seldom in dense seagrass (M. Horinouchi unpubl. data). In addition, feeding upon small zooplankton may be easier in less complex microhabitats. Such food availability patterns, in addition to predation, are likely to contribute to the microhabitat preferences of juvenile fishes. The amount of the among-shoot space may also be one of the factors influencing juvenile distribution patterns. Dense seagrass may be unfavorable for prey juveniles because the limited among-shoot space prevents them from forming larger groups (Horinouchi & Sano 1999). Further studies are needed to clarify the relative importance of predation, food availability, the amount of

among-shoot space and other factors, such as current velocity, in determining the distribution patterns of juvenile fishes.

Acknowledgements. We are grateful to T. Takami, K. Urushibata, A. Kurata, J. Miyajima, all staff of the Fisheries Laboratory, University of Tokyo, and H. Hoshikawa for their generous assistance with fieldwork. Constructive comments on the manuscript from G. S. Hardy, Y. Nakamura, A. Yoshizawa and anonymous reviewers were much appreciated. We thank the fishermen's unions in Lake Hamana for their permission to collect experimental fish.

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*Editorial responsibility: Charles Birkeland,
Honolulu, Hawaii, USA*

*Submitted: August 1, 2008; Accepted: December 1, 2008
Proofs received from author(s): February 21, 2009*