

Vulnerability of juvenile fish to piscivorous fish predators increases during nighttime in a seagrass bed in the central Seto Inland Sea, Japan

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To test the hypothesis that vulnerability to predation of small-sized fishes increases during nighttime, the fish species composition, abundance, biomass and stomach contents of potential predators, and the mortality rate during tethering experiments were compared between daytime and nighttime at a seagrass bed in the central Seto Inland Sea, Japan. A total of 494 fishes belonging to 30 taxa were collected using a round seine on 28 and 30 August 2007. Abundance and biomass of potential fish predators (piscivorous fish >82.5 mm in total length) were higher in nighttime than in daytime. *Sebastes cheni* juveniles and *Rudaris ercodes* were predated on by *Sebastes inermis* and *Lateolabrax japonicus*. Predation rate of juvenile *S. cheni*, a dominant species in the fish community, estimated from the ratio of the number of juveniles predated to that of population (sum of surviving and predated juveniles) during nighttime (1930–2100 h) was 5.1%. Tethering experiments for 6 h at the seagrass bed indicated that the mortality rate of juvenile *S. cheni* in nighttime was significantly higher than that in daytime. It is plausible that seagrass beds contribute as foraging habitats for piscivorous fish during nighttime although they are important nurseries for a variety of fish species.

Key words: seagrass bed, fish nursery, predation, day-night comparison, tethering experiment, Seto Inland Sea

Introduction

Production of fisheries resources and its economic value of coastal and estuarine ecosystems are among the highest of those of the world's ecosystems (Costanza et al., 1997). Vegetated habitats such as seagrass and macroalgae beds in estuarine and coastal waters serve as nurseries for a variety of fish species (Larkum et al., 2006). Analyses of spatio-temporal changes in habitat condition are indispensable for evaluation of the function of these habitats as fish nurseries since environmental conditions of coastal and estuarine ecosystems generally are highly variable within relatively small spatial and temporal scales.

Seagrass (mainly *Zostera* spp.) beds are widely distributed in estuarine and coastal waters of the world and have been referred to as nurseries for many fisheries resources as they serve as feeding grounds and refuges from predation for early life stages of various fishes (Fuse, 1962; Adams, 1976; Horinouchi et al., 1999; Heck and Orth, 2006). Although the role of seagrass beds as nurseries is an established ecological concept commonly accepted, the nursery-role concept has not been clearly defined. Recently,

juvenile fish production, but not the abundance of juvenile fish, has been suggested as a good index of the nursery function (Beck et al., 2001; Sano et al., 2008). However, information on fish production has been restricted (e.g. temporal changes in biomass of a cohort: Secor and Houde, 1995; Rooker et al., 1999; Shoji and Tanaka, 2007) while there are many observations on fish abundance in nurseries (e.g. comparison of fish abundance in seagrass bed with that in other habitats: Sogard, 1989; Hirai et al., 2009). Quantitative data on fish vital rates such as abundance, growth and mortality and resulting production and their temporal changes are needed to quantitatively evaluate the function of seagrass beds as fish nurseries.

To date, the majority of field observations for fish ecology have been conducted during the daytime. Difficulties in carrying out nighttime scuba-censuses and quantitative fish collections have held back progress in research on nighttime fish ecology. The majority of the observations and experiments to investigate fish assemblages and their predators in seagrass beds have been made during only the daytime in the previous studies (Fuse, 1962; Adams, 1976; Sogard, 1989; Heck and Orth, 2006; Larkum et al., 2006). On an annual scale ca. half of a day is composed of the nighttime. Therefore, information on the fish community structure and their vital rates during nighttime is indispensable in order to more accurately understand the function of

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seagrass habitats as fish nurseries. Recently, day–night changes in species composition and abundance of small-sized fishes and their predators have been reported in seagrass beds in Australian coastal waters (Hindell et al., 2000; Guest et al., 2003). However, there is no quantitative information on day–night difference in vulnerability of small fishes to predation in seagrass beds. Generally, vulnerability of fish early life stages to piscivorous predators in nighttime is higher than that in daytime since their swimming performance decrease in nighttime (Blaxter, 1968; Masuda, 2009).

In the present study, in order to test the hypothesis that vulnerability to predation of small-sized fishes increases during the nighttime, fish sampling with a combination of tethering experiment using juvenile black rockfish *Sebastes cheni*, a dominant fish species in seagrass beds of the central Seto Inland Sea (Kamimura and Shoji, 2009), were conducted in summer at a seagrass bed in the central Seto Inland Sea, Japan. Species composition, abundance, biomass and stomach contents of potential predators, mortality rate during tethering experiments were compared between daytime and nighttime. There is a merit of the evaluation of nighttime predation in the dominant paradigm in seagrass ecology: seagrass beds have been considered as important nurseries for fish because of the low predation mortality based on the estimates mainly during the daytime. If predation mortalities on juvenile fish increase during nighttime, re-consideration of the function of seagrass beds as a predation refuge is necessary.

Materials and Methods

Field sampling

Biological and physical surveys were conducted on a seagrass bed off the eastern Ikuno Island, central Seto Inland Sea, Japan (Fig. 1). Ikuno Island has a population of about 30 without inhabitation on the eastern coast, which makes effect of human activities such as industrialization and fishing minimal in the seagrass bed. The vegetation of the seagrass bed is dominated by the seagrass *Zostera marina* and the mean shoot density around the sampling site fluctuates between 20 and 160 m⁻² within a year (Kamimura and Shoji, 2009). The sea bottom of the seagrass area is comprised of mud and sand.

Fish were collected using a round seine net (2 m in height, 30 m in length and 3 mm in mesh aperture: shown in Kamimura et al., 2011) in daytime (1300–1500 h: 28 August 2007) and nighttime (1930–2100 h: 30 August 2007), with tidal levels between 50–130 cm, when the edge of the seagrass bed was close to the shore. Three sides of a square (10 m in side length) were surrounded using the net, with another side facing into the shore (around the border of the seagrass bed). Fish sampling was carried out at four sepa-

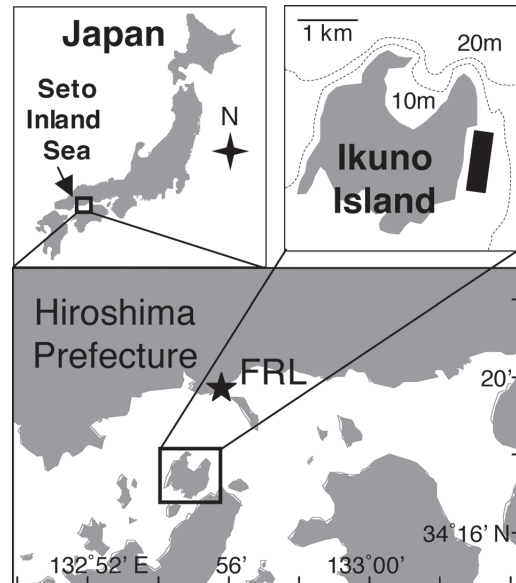


Figure 1. Map of southeastern Hiroshima Prefecture and central Seto Inland Sea, Japan, showing the seagrass bed (solid bar) off Ikuno Island where fish sampling and tethering experiment were conducted. Depth contours of 10 and 20 m are indicated as dotted lines. Tethering experiments in a tank were conducted at Fisheries Research Laboratory (FRL), Hiroshima University.

rate locations randomly selected within the seagrass bed during both the daytime and nighttime samplings. Fish collected were preserved in 10% formalin seawater solution. Water temperature and salinity were measured at around the middle of the seagrass bed.

Laboratory procedures

Fish were identified to the lowest possible taxon according to Nakabo (2002) and were measured in total length (TL, mm) and wet weight (g) in the laboratory. Mean fish abundance and biomass were expressed as the number and wet weight of fish 100 m⁻². Piscivorous fish >82.5 mm TL were considered as potential predators for the most numerically-dominant fish, black rockfish *S. cheni* (minimum TL: 55.0 mm) in the seagrass bed based on the relationships between body sizes of piscivorous fish predator and prey fish (predator body size is >150% of prey body size: Keast, 1985; Yamashita et al., 1993; Scharf et al., 1998). In order to detect evidence of predation on the juvenile rockfish in the seagrass bed, stomach contents of possible predators ($n=35$) were examined. Predation rate of the juvenile rockfish (number of juveniles predated 100 m⁻²/total abundance 100 m⁻²) was estimated.

Tethering experiments

In order to compare the vulnerability of juvenile black rockfish to predation in the seagrass bed between daytime and nighttime, tethering experiments were conducted. Prior

to the field experiment, control experiment was made in captive tanks to determine whether the juvenile could break free from their tethers. Juvenile black rockfish ($n=30$) were collected with the round seine net in the seagrass bed off Ikuno Island during the daytime on 16 August and were transported to the Fisheries Research Laboratory, Hiroshima University (FRL: Fig. 1). The fish were acclimated for 24 h in a 0.5-t tank. A transparent nylon monofilament line was passed through muscle tissue above the caudal vertebrae of 10 juvenile black rockfish (mean TL \pm standard deviation: SD=60.8 \pm 5.4 mm). Length of the tether was 1.0 m. Each fish was introduced into each 1.0-t tank (135 cm in diameter, 70 cm in water depth), with another tip of the tether attached to the circumference of the tank bottom. Each experiment (for 6 h) was started after confirming that all the fish were able to actively swim. Gentle aeration was used during each experiment. Water was replaced at a rate of about 100% day⁻¹. No observation was made during the experiment (0900–1500 h) in order to minimize any artifact effects caused by disturbance on the juvenile behavior.

In order to compare the vulnerability to predation of juvenile black rockfish to piscivorous predators, field experiments were conducted in the daytime (0900–1500 h) and nighttime (2100–0300 h) during 16–17 August in the seagrass bed off Ikuno Island. Experimental fish were collected from the seagrass bed off Ikuno Island at the same time as those used for the control experiment. Surface water temperature was 22.3°C in the daytime and 22.1°C in the nighttime and salinity 32.9 in the daytime and 32.6 in the nighttime at the start of each experiment in the middle of the seagrass bed. Ten fish for each of the daytime and nighttime experiments were tethered in the same manner as in the control experiment. Fish, with the other tip of the tether attached to an iron weight (1 kg), were introduced in the seagrass bed at an interval of >2 m. The water depth of the experimental area increased from ca. 100 to 260 cm (from low to high tide) during both daytime and nighttime experiments.

Results

Fish community in the seagrass bed

Water temperature and salinity were 25.9°C and 33.4 during the daytime sampling and 25.4°C and 33.2 during the nighttime sampling in the seagrass bed off Ikuno Island. Mean seagrass shoot density was 88 m⁻² (coverage rates: about 30–80%).

A total of 494 fishes belonging to more 30 taxa in 19 families were collected during the daytime sampling. *Rudarius ercodes* (35.7% in number), *S. cheni* (33.5%) and *Hypodytes rubripinnis* (10.5%) were numerically dominant and *S. cheni* (46.3% in weight), *H. rubripinnis* (25.2%) and *Ditrema temminckii pacificum* (5.5%) were dominant in

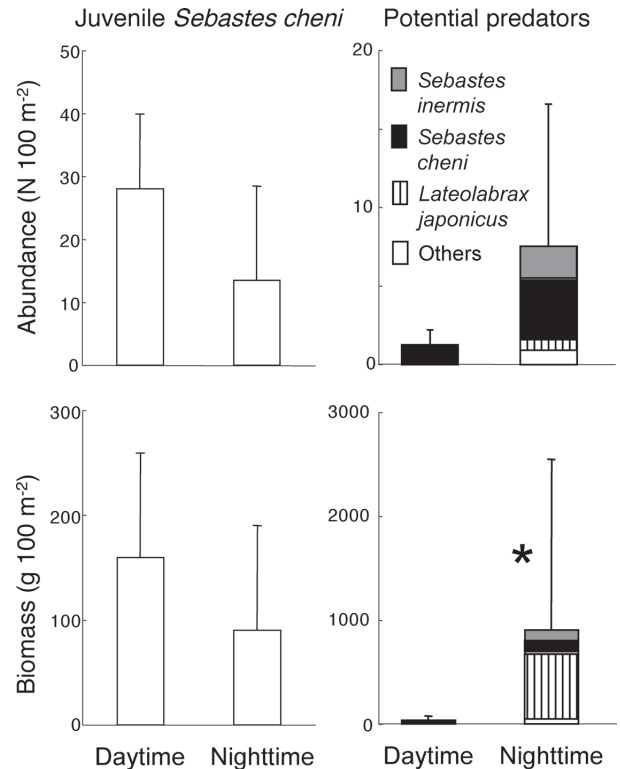


Figure 2. Abundance (number 100 m⁻², top) and biomass (g 100 m⁻², bottom) of juvenile *Sebastes cheni* (left) and potential piscivorous fish predators (right) in daytime and nighttime at the seagrass bed off Ikuno Island. Asterisk shows a significant difference in the predator biomass between daytime and nighttime (Wilcoxon test, $p < 0.05$).

weight in the daytime ichthyofauna. During the nighttime sampling, *S. cheni* (29.8% in number), *H. rubripinnis* (16.9%) and *Takifugu niphobles* (11.3%) were numerically dominant while *Lateolabrax japonicus* (50.1% in weight), *S. cheni* (12.2%) and *Sebastes inermis* (7.3%) were dominant in weight (Appendix 1).

Mean abundance and biomass of juvenile *S. cheni* during daytime were higher than those during nighttime although there was no significant difference (Fig. 2). *S. cheni* was the only potential predator collected in the daytime while potential predatory fish species were more diverse during the nighttime when *S. inermis*, *Sebastes hubbsi*, *L. japonicus*, *Hexagrammos agrammus* and *Pagrus major* in addition to *S. cheni* were collected (Fig. 2). *S. inermis* and *S. cheni* were dominant by number and *L. japonicus* was dominant by weight in nighttime. Mean abundance of potential predators in nighttime (7.5 \pm 9.1 100 m⁻²) was 6.0-fold higher than that in the daytime (1.3 \pm 1.0 100 m⁻²). Mean biomass of potential predators in nighttime (902.5 \pm 1640.9 g 100 m⁻²) was 23.3-folds of that in the daytime (38.7 \pm 30.6 g 100 m⁻²). There was a significant differ-

Table 1. Species name, number of individuals, total length (TL) of potential predators used for stomach contents analysis. A total of 35 potential predators collected during the daytime (D) and nighttime (N) samplings were analyzed. Species name and TL of fish prey are indicated.

Predator	Time period	N	TL range (mm)	Species name and TL (mm) of fish in stomach
<i>Sebastes inermis</i>	N	8	109–235	<i>Sebastes cheni</i> (60.2)
<i>Sebastes cheni</i>	D	5	118–128	
<i>Sebastes cheni</i>	N	14	105–164	<i>Sebastes cheni</i> (58.4), <i>Rudaris ercodes</i> (22.1, 31.4 and 42.9)
<i>Sebastes hubbsi</i>	N	2	134–140	
<i>Hexagrammos agrammus</i>	N	3	104–121	
<i>Lateolabrax japonicus</i>	N	2	430–700	
<i>Pagrus major</i>	N	1	170	

ence in biomass of potential predators between daytime and nighttime (Wilcoxon test, $p < 0.05$).

Predation

Of the 35 potential predators examined, three had fishes in their stomachs (Table 1). *S. inermis* (235 mm TL) ate a *S. cheni* (60.2 mm TL: juvenile), *L. japonicus* (430 mm TL) ate a *S. cheni* (58.4 mm TL: juvenile) and two *R. ercodes* (22.1 and 31.4 mm TL) and *L. japonicus* (700 mm TL) ate a *R. ercodes* (42.9 mm TL). Based on the ratio of abundance of predated *S. cheni* juveniles (0.5 ± 1.0 100 m⁻²) to total juvenile population abundance (9.8 ± 12.2 100 m⁻²) in the seagrass bed during the nighttime sampling (sum of the abundance predated and juveniles collected: 9.3 ± 11.2 100 m⁻²), predation rate of juvenile *S. cheni* was estimated to be 5.1%.

Tethering experiment

During the control experiment, no fish broke free from the tether and all fish survived for 6 h. During the field experiments, nine fish survived the daytime experiment in the seagrass bed and two fish survived the nighttime experiment. Numerical composition of juvenile *S. cheni* remaining at the end of the tethering experiment was significantly different between the daytime and nighttime trials (χ^2 -test: $\chi^2 = 19.06$, $p = 0.0008$).

Discussion

In the present study, comparison of fish assemblages and survival rates of juvenile *S. cheni* during the tethering experiments between daytime and nighttime indicated that vulnerability of the juveniles to predation increased during the nighttime in the seagrass bed. In addition, the seagrass bed off Ikuno Island is suggested to contribute not only as important nurseries for juvenile fish but also as foraging habitat for predatory fish especially during nighttime. Generally piscivorous fish predators are possibly eat prey multiple times within one night since predated organisms are digested and evacuated from the stomach in several hours after feeding (Nashida and Tominaga, 1987; Buckel and Conover, 1996; Shoji and Tanaka, 2005). Therefore, it is

plausible that the total predation rate of juvenile fish by piscivorous fishes in the seagrass bed during the whole nighttime (from sunset to sunrise) would be higher than that estimated in the present study: 5.1% as a “snap-shot” estimate of the predation in the present study (1930–2100 h).

Nocturnal feeding of piscivorous fishes on juvenile fishes would be more effective since probability of capturing juvenile fishes is expected to increase during nighttime due to lower swimming performance of juvenile fish (Blaxter, 1968; Masuda, 2009). The evidence that seagrass beds contribute to production of piscivorous predators in addition to juvenile fishes in the present study suggest that ecosystem services of seagrass beds are higher than those estimated in the previous study (Costanza et al., 1997), in which production of the predatory fish was not estimated. Quantitative estimation of provisioning services including production of the predatory fishes (or role as feeding ground for predatory fishes) as well as those of small fishes would improve the future re-evaluation of total ecosystem services of seagrass bed.

Tethering experiments have been widely applied for relative comparisons of predation rates between fish habitats with different structures of the bottom and vegetation although there seems to be various artifacts associated with the technique (Shulman, 1985; Nakamura and Sano, 2004). In the present study, the nighttime predation rate of tethered juvenile *S. cheni* (80%: two of ten survived for 6 h) was significantly higher than the instantaneous predation rate estimated from the stomach contents analysis (5.1%). It is possible that the tethered rockfish juveniles with reduced mobility were more easily captured by piscivorous fishes than they were without tethering. The results from the tethering experiment, together with those from abundance, biomass and stomach contents analysis for fish predators, support the conclusion that susceptibility of juvenile *S. cheni* to predation by piscivorous fish increase in nighttime in seagrass bed.

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瀬戸内海中央部のアマモ場における稚魚に対する魚食性魚類による捕食圧は夜間に増大する

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瀬戸内海中央部のアマモ場において小型魚類への捕食圧が夜間に高まるという仮説を検証することを目的として、魚種組成、稚魚の潜在的捕食者の個体数、バイオマスおよび胃内容物、さらに糸つなぎ実験によって得られた稚魚の生残率を調べて昼夜で比較した。アマモ繁茂期（2007年8月28日と30日）に巻き網を用いて合計494個体（30分類群）の魚類を採集した。夜間には日中に比べて魚食性魚類（全長>82.5mm）の個体密度、バイオマスが大きく、アカメバル *Sebastes inermis* およびスズキ *Lateolabrax japonicus*

の胃内容物からシロメバル *Sebastes cheni* 稚魚、アミメハギ *Rudaris ercodes* が認められた。捕食された稚魚の個体数と藻場に現存する個体数の比から試算した優占種シロメバル仔稚魚の夜間（1930–2100h）の被食率は5.1%であった。シロメバル稚魚を用いたアマモ場での糸つなぎ実験（6時間）による生残個体の割合は日中よりも夜間に有意に低かった。以上の結果から、稚魚のゆりかごと呼ばれているアマモ場は、夜間には一部の魚食性捕食者の摂餌場としての役割も果たしていることが示唆された。

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Appendix 1. Total number (N), biomass (W), composition in number (N%) and biomass (W%) and rank in number and biomass of fish collected during the daytime (August 28, 2007) and nighttime (August 30, 2007) samplings (four trials each) at a seagrass bed off Ikuno Island in the central Seto Inland Sea, Japan.

Family	Species	Daytime						Nighttime					
		Total			Total			Total			Total		
		N	N%	Rank	W	W%	Rank	N	N%	Rank	W	W%	Rank
Clupeidae	<i>Etrumeus teres</i>	0	0.0		0.0	0.0		1	0.8		20.2	0.5	
Hemiramphidae	<i>Hyporhamphus sajori</i>	0	0.0		0.0	0.0		9	7.3	4	63.4	1.4	10
Aulorhynchidae	<i>Aulichthys japonicus</i>	1	0.3		0.7	0.1		0	0.0		0.0	0.0	
Syngnathidae	<i>Syngnathus schlegeli</i>	14	3.8	4	17.5	1.3	8	1	0.8		2.2	0.0	
	<i>Urocampus nanus</i>	1	0.3		0.3	0.0		0	0.0		0.0	0.0	
	<i>Hippocampus coronatus</i>	7	1.9	6	5.8	0.4		1	0.8		5.4	0.1	
Scorpaenidae	<i>Sebastes inermis</i>	0	0.0		0.0	0.0		4	3.2	7	321.0	7.3	3
	<i>Sebastes cheni</i>	124	33.5	2	636.9	46.3	1	37	29.8	1	538.4	12.2	2
	<i>Sebastes oblongus</i>	4	1.1		12.7	0.9		1	0.8		4.3	0.1	
	<i>Sebastes hubbsi</i>	0	0.0		0.0	0.0		3	2.4	9	100.3	2.3	7
Tetrarogidae	<i>Hypodytes rubripinnis</i>	39	10.5	3	346.5	25.2	2	21	16.9	2	193.8	4.4	5
Platycephalidae	<i>Platycephalidae</i> sp.	1	0.3		0.1	0.0		0	0.0		0.0	0.0	
Hexagrammidae	<i>Hexagrammos agrammus</i>	1	0.3		17.3	1.3	8	6	4.8	6	76.8	1.7	8
Cotiidae	<i>Pseudoblennius cottoides</i>	1	0.3		1.6	0.1		1	0.8		9.3	0.2	
Percichthyidae	<i>Lateolabrax japonicus</i>	0	0.0		0.0	0.0		2	1.6		2660.0	60.1	1
Sillaginidae	<i>Sillago japonica</i>	5	1.4	9	5.0	0.4		4	3.2	7	3.2	0.1	
Haemulidae	<i>Plectorhinchus cinctus</i>	0	0.0		0.0	0.0		2	1.6		7.2	0.2	
Sparidae	<i>Acanthopagrus schlegelii</i>	0	0.0		0.0	0.0		2	1.6		11.0	0.2	
	<i>Pagrus major</i>	0	0.0		0.0	0.0		1	0.8		70.0	1.6	9
Embiotocidae	<i>Ditrema temminckii pacificum</i>	6	1.6	7	75.5	5.5	3	3	2.4	9	4.4	4	
Labridae	<i>Halichoeres poecilopterus</i>	4	1.1		69.9	5.1	4	0	0.0		0.0	0.0	
Gobiidae	<i>Pterogobius elapoides</i>	1	0.3		5.4	0.4		2	1.6		11.9	0.3	
	<i>Favonigobius gymnauchen</i>	3	0.8		1.7	0.1		7	5.6	5	8.4	0.2	
	<i>Mugil cephalus cephalus</i>	6	1.6	7	13.9	1.0		0	0.0		0.0	0.0	
Siganidae	<i>Siganus fuscescens</i>	5	1.4	9	3.8	0.3		1	0.8		1.1	0.0	
Monacanthidae	<i>Rudarius ercodes</i>	132	35.7	1	47.1	3.4	6	0	0.0		0.0	0.0	
	<i>Thamnaconus modestus</i>	2	0.5		24.7	1.8	7	0	0.0		0.0	0.0	
Tetraodontidae	<i>Takifugu pardalis</i>	2	0.5		10.3	0.7		0	0.0		0.0	0.0	
	<i>Takifugu poecilonotus</i>	9	2.4	5	17.5	1.3	8	1	0.8		2.1	0.0	
	<i>Takifugu niphobles</i>	2	0.5		61.6	4.5	5	14	11.3	3	122.0	2.8	6
	Total	370	100.0		1375.9	100.0		124	100.0		4425.9	100.0	