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Abstract—Information on behavioral variation among sympatric congeneric species is important for understanding the mechanisms that enable their coexistence. The aim of this study was to elucidate the characteristics of diurnal vertical distribution of congeneric *Sebastes inermis* and *S. ventricosus* through observations during laboratory experiments in 2011. When 25 individuals of each species were accommodated in a 1-kL tank, *S. inermis* stayed mainly at the bottom, whereas *S. ventricosus* actively swam 0–60 cm above the bottom. At various intraspecific densities, *S. inermis* were similarly distributed at the bottom, *S. ventricosus* were distributed more widely, and the frequency of individuals in the upper layers of water in the tank increased with density. These results indicate that the different behaviors of the 2 species make their coexistence possible without severe competition for microhabitats.

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Interspecific differences in the vertical distribution patterns of *Sebastes inermis* and *S. ventricosus*

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The genus *Sebastes* is widely distributed, mainly in temperate to Arctic waters throughout the North Pacific (Hyde and Vetter, 2007), and many *Sebastes* species are important in fisheries. *Sebastes* species are often segregated between habitats, possibly because of interspecific competition (Larson, 1980) or an interspecific difference in habitat preference (Richards, 1986). Nonetheless, some congeneric *Sebastes* species do coexist (Matthews, 1990; Benestan et al., 2021). Ecological differences would enable such closely related species to coexist (Love et al., 2002), but studies that focus on behavior between coexisting species have seldom been conducted (Tolimieri et al., 2009). Understanding of the mechanisms underlying species distribution is important for conservation and fisheries management (Williams and Ralston, 2002; Frid et al., 2018).

Three species, *Sebastes inermis*, *S. ventricosus*, and *S. cheni*, which are widely distributed in the coastal waters of Japan, had long been regarded as a single species owing to their morphological similarities (Kai and Nakabo, 2008; Mohri et al., 2013). They were classified into 3 species in 2008 on the basis of morphological and genetic differences (Kai and Nakabo, 2008). *Sebastes inermis* has a higher dependence on shrimp as food (Akeda et al., 2012) and a slower growth rate (Kamimura et al., 2014) than the other 2 species. These differences could possibly be attributed to interspecific behavioral differences. Local fishermen have suggested that the 3 species use different habitats, but so far the interspecific habitat variation has not been studied.

The aim of this study was to clarify the behavioral characteristics of *S. inermis* and *S. ventricosus* under laboratory conditions, by gaining insights into their habitat utilization and overlap. These 2 species are common in the Seto Inland Sea, in southwestern Japan, and the catch of these 2 species is usually much greater than that of *S. cheni*. We explored the following 2 hypotheses: 1) the behavioral patterns or layers of vertical distribution differ between species and 2) the behavioral characteristics of each species do not change under various intraspecific densities.

Materials and methods

Preparation and rearing methods

The individuals of both species, *S. inermis* and *S. ventricosus*, used in the experiments of this study were caught with a small set net (known as *Tsubo-ami*) in coastal areas from depths of approximately 5–8 m off Okino Island (34°09′13″N, 132°26′6″E) from March through May in 2010 and 2011. Approximately 500 fish, with total lengths of 130–160 mm, were captured. The fish were initially kept in a 5-kL tank in the laboratory and fed commercial dry pellets (Otohime EP4[1], Marubeni Nisshin Feed Co. Ltd., Tokyo, Japan) in the amount of 0.5% to 1% of the total mass of fish per day until December 2011.

Before the experiments, we identified the species of caught individuals on the basis of their external characteristics (e.g., pectoral fin length, differences in body color, and the presence or absence of reddish irregular stripes and dots in the interorbital region; see Suppl. Fig. 1) (Kai and Nakabo, 2008; Nakabo and Kai, 2013). The species identification was validated on the basis of meristic characters that were counted for 50 individuals (25 individuals for each species) after the experiments were completed. The numbers of anal fin rays, pectoral fin rays, gill rakers, and pored lateral line scales are usually 7, 15, 35, and 40 in *S. inermis* and 7 or 8, 16, 37, and 46 in *S. ventricosus*, respectively (Kai and Nakabo, 2008).

Experiment on behavior during coexistence

To observe the distribution and behavior of *S. inermis* and *S. ventricosus* when they were allowed to coexist, we conducted an experiment in which individuals of the 2 species were accommodated in a 1-kL transparent tank and kept without feeding for 2 successive days (herein called the *coexistence experiment*). Twenty-five fish of each species (a total of 50 individuals) were accommodated in the tank. The experiment was carried out twice in 2011, on 28–29 July (first trial) and 23–24 August (second trial). The fish used in the first trial were replaced with other individuals for the second trial. The tank was filled with filtered seawater to a depth of 80 cm, and water was exchanged at a rate of 3.6 L/min. The water temperature ranged from 24.2°C to 25.6°C and from 25.2°C to 26.0°C in the first and second trials, respectively. The intensity of illumination above the water surface ranged from 37 to 40 lx, and the current velocity was <0.01 m/s in the tank during the period of the experiment. The depth of seawater in the tank was marked with white insulating tape every 20 cm from the bottom, and depth layers of seawater in the tank were defined, for the purposes of assessing vertical distribution, as surface (0–20 cm), subsurface (20–40 cm), medium (40–60 cm), and bottom (60–80 cm).

The behavior of the fish was recorded during the experiment by using a digital video camera (NV-GS70, Panasonic Holdings Corp., Kadoma, Japan, and DCR-PC350, Sony Group Corp., Tokyo, Japan). The recordings were made 9 times for a total of 90 min each day, with 10-min recordings from 3 viewing angles over the following 3 time periods: 0900–1000, 1300–1400, and 1700–1800 (Suppl. Fig. 2, Suppl. Video). A total of 18 video images per trial were used to count the number of individuals of each species distributed in each layer (Suppl. Fig. 1). The number of individuals of each species at each layer was counted 5 times at each angle. Additionally, individuals distributed in the bottom layer with part or several parts of their body (e.g., caudal, pelvic, or anal fin or other ventral regions) in contact with the bottom of the tank were regarded as demersal individuals.

Experiment on behavior at different densities

To test whether or not the distribution pattern of each species changed at different densities, an experiment was conducted by using individuals of each species after being kept without feeding for 3 d (herein called the *density experiment*). For each species, 10 individuals (low density), 25 individuals (medium density), and 50 individuals (high density) were accommodated in 3 circular 500-L tanks for observation. We used smaller tanks than those used in the coexistence experiment to make it easier to count the number of fish present. This strategy also accounted for the fact that none of the fish in the coexistence experiment appeared in the surface layer of their tanks. The tanks were filled with filtered seawater to a depth of 60 cm. The water conversion rate and illumination conditions were the same as those used in the coexistence experiment.

The experiment on *S. inermis* was carried out twice in 2011 for 2 consecutive days, on 21–22 November (first trial) and 24–25 November (second trial), with fish selected randomly for each trial. Similarly, the experiment on *S. ventricosus* was carried out in 2011 on 28–29 November (first trial) and 1–2 December (second trial). The water temperature ranged from 17.2°C to 18.7°C during the experiment. A line was drawn horizontally with a marker every 20 cm from the bottom of each tank to divide the tank into 3 depth layers: surface (0–20 cm), medium (20–40 cm), and bottom (40–60 cm). The layers where fish were distributed were observed visually, without the use of video recordings. These observations were recorded during 2 time periods: 1100–1200 and 1300–1400. In each of the 3 tanks, fish were counted for each layer 5 times at approximately 2-min intervals during each time period.

Data analyses

To compare the distribution patterns between species, nested multivariate analysis of variance (MANOVA) was performed by using the percentage of individuals at each depth layer. The data were arcsine square-root transformed. In the coexistence experiment, the initial explanatory variables were *species* and *time of day*, and *trial*

[1] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

and *date* were used as random variables. In the density experiment, the initial explanatory variables were *species* and *density*, and *trial* was used as a random variable. Additionally, in the coexistence experiment, the proportion of demersal individuals in contact with the bottom was compared between species for each time period of each day by using Fisher's exact test (Fisher, 1925). We conducted statistical analyses using R, vers. 4.1.0 (R Core Team, 2021).

Results

Coexistence experiment

Almost all the *S. inermis* were distributed in the bottom layer, whereas *S. ventricosus* were distributed not only in the bottom layer but also in the medium and subsurface layers (nested MANOVA: $F_{1,68}$=18.1, P<0.001) (Fig. 1). No individuals of either species were observed in the surface layer. Time of day did not have a significant effect on where the fish were distributed ($F_{2,68}$=2.0, P=0.07). The proportion of demersal individuals in the bottom layer was significantly greater for *S. inermis* (818 of 1080 individuals counted) than for *S. ventricosus* (61 of 1300 individuals counted) (Fisher's exact test: P<0.001, for all cases). *Sebastes ventricosus* swam actively, and a few individuals exhibited aggressive behavior toward other conspecific individuals. In contrast, *S. inermis* mostly lay on the bottom without moving and did not have aggressive behavior. Aggressive behavior of *S. ventricosus* toward *S. inermis* was rarely observed.

Density experiment

Regardless of the density of fish in their tank, *S. inermis* were distributed almost exclusively in the bottom layer, and few individuals were found at the medium and surface layers (Fig. 2). In contrast, *S. ventricosus* were distributed more widely in the medium and surface layers, with a significant difference observed between species (nested MANOVA: $F_{1,236}$=578.7, P<0.001). The proportion of *S. ventricosus* distributed at the medium and surface layers was higher under greater densities, and the effect of density was also significant ($F_{2,236}$=13.3, P<0.001).

Discussion

This study is the first to clarify the behavioral difference between *S. inermis* and *S. ventricosus*. When these 2 species were accommodated in the same tank, *S. ventricosus* clustered farther from the bottom and swam more actively than *S. inermis*. This tendency was commonly observed in the intraspecific density experiment, although the proportion of individuals of *S. ventricosus* at the medium and

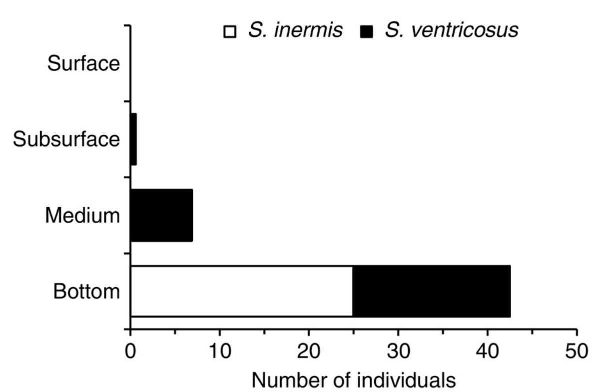

Figure 1

Average number of individuals of *Sebastes inermis* and *S. ventricosus* observed in each layer of seawater in a 1-kL tank during 2 trials of an experiment conducted at the Fisheries and Ocean Technologies Center of the Hiroshima Prefectural Technology Research Institute in 2011: 28–29 July (first trial) and 23–24 August (second trial). In this coexistence experiment, 25 individuals of each species were placed in the same tank. To assess vertical distribution of fish, 4 depth layers of seawater in the tank were defined as follows: surface (0–20 cm), subsurface (20–40 cm), medium (40–60 cm), and bottom (60–80 cm). The data presented are the averages from both trials.

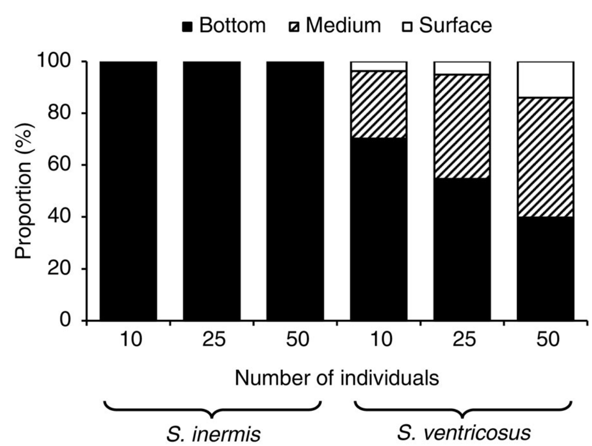

Figure 2

Proportions of fish observed in layers of seawater in three 500-L tanks, each with 10, 25, or 50 individuals of *Sebastes inermis* or *S. ventricosus*, during an experiment conducted at the Fisheries and Ocean Technologies Center of the Hiroshima Prefectural Technology Research Institute in 2011. The density experiment was carried out in 2 trials for each species: *S. inermis* on 21–22 November and 24–25 November and *S. ventricosus* on 28–29 November and 1–2 December. To assess vertical distribution of fish, 3 depth layers of seawater in the tanks were defined as follows: surface (0–20 cm), medium (20–40 cm), and bottom (40–60 cm), The data presented are the average proportions from both trials.

surface layers increased with increasing density. These results indicate that both species have species-specific behavioral patterns, regardless of the presence of the other species or the density of the same species. Therefore, the results support the 2 hypotheses.

The difference in behaviors of *S. inermis* and *S. ventricosus*, with *S. inermis* being bottom dwelling and far less active in comparison to the constantly swimming *S. ventricosus*, may be related to their feeding habits. Both *S. inermis* and *S. ventricosus* are highly selective for shrimp; however, high selectivity for amphipods and mysids has been reported for *S. ventricosus* (Akeda et al., 2012). Such prey may be more available for off-bottom individuals because the prey often appears in the water column (Sudo and Azeta, 1992). On the west coast of North America, *Sebastes* species that are distributed near the bottom of the seafloor mainly feed on benthic animals, whereas those distributed in the water column mainly feed on zooplankton (Brodeur and Pearcy, 1984; Hallacher and Roberts, 1985).

Notably, *S. inermis* were less active and consumed less energy than *S. ventricosus* in our study. The amount of food intake may largely differ between the 2 species because *S. inermis* grow slower than *S. ventricosus* (Kamimura et al., 2014). Faster growth in *S. ventricosus* would require greater food consumption than that of *S. inermis*, and shoaling behavior, which has been observed only in *S. ventricosus*, may be advantageous for foraging efficiency (Pitcher et al., 1982). Additionally, it has been hypothesized that the swim bladder is more developed in *S. ventricosus* for hovering because the swim bladder is essential for buoyancy maintenance and, therefore, reduces the energy consumption of actively swimming fish (Schwebel et al., 2018). However, we could not detect any differences in the size of the swim bladder between the 2 species, on the basis of photographs of 5 individuals for each species (Suppl. Fig. 3) taken with a soft X-ray apparatus (MI100F, Haitex, Inc., Nagoya, Japan). As a result, we are unable to provide support for the previously mentioned hypothesis regarding swim bladder development.

Johnson et al. (2003) observed the behaviors of 14 *Sebastes* species in Alaska, using a remotely operated vehicle, and found that most species were not demersal and swam actively or hovered near the bottom. In our study, *S. inermis* exhibited demersal behavior, chiefly resting at the bottom. It should be noted that many species of the genus *Sebastes* have different distribution or swimming patterns during the day and night (Green and Starr, 2011; Hannah and Rankin, 2011). For example, *S. cheni* exhibit active swimming and vertical movement to the bottom and surface of the water column only at night (Sakurai et al., 2013). *Sebastes inermis* move to eelgrass beds at night and exhibit active feeding behavior (Shoji et al., 2017). Moreover, habitat use may change ontogenetically (Rooper et al., 2007). Future studies are expected to reveal the diel changes in habitat use, feeding activity, and behavioral patterns of *S. inermis* and *S. ventricosus*.

Resumen

La información sobre las variaciones en el comportamiento entre especies congéneres y simpátricas es importante para comprender los mecanismos que permiten su coexistencia. El objetivo de este estudio fue elucidar las características de la distribución vertical diurna de las especies congéneres *Sebastes inermis* y *S. ventricosus* mediante observaciones realizadas durante experimentos de laboratorio en 2011. Cuando se alojaron 25 individuos de cada especie en un tanque de 1 kL, *S. inermis* permaneció principalmente en el fondo, mientras que *S. ventricosus* nadó activamente a 0–60 cm por encima del fondo. A distintas densidades intraespecíficas, *S. inermis* se distribuyó de forma similar en el fondo, *S. ventricosus* se distribuyó más ampliamente, y la frecuencia de individuos en las capas superiores del agua del tanque aumentó con la densidad. Estos resultados indican que los diferentes comportamientos de las 2 especies hacen posible su coexistencia sin una competencia severa por los microhábitats.

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