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PRIMARY RESEARCH PAPER

Effects of dead oyster shells as a habitat for the benthic faunal community along rocky shore regions

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Abstract Foundation species are crucial to understanding the mechanisms underlying faunal community structure. The present study aimed to clarify the habitat function of empty shells from dead oysters *Saccostrea kegaki* for the benthic faunal community of an intertidal rocky shore. We evaluated whether macroinvertebrates used the shells as a habitat. Results demonstrated that limpets (the dominant macroinvertebrates at the study site) did so more frequently than they inhabited live oysters, other sessile organisms, or rock surfaces. The dead oyster shells successfully functioned as a refuge from predation and as a nursery for limpets, because of their structural complexity (the presence of a depression on the inner side of the shell). Therefore, our study demonstrates the importance of dead *S. kegaki*, a shell-forming foundation species, and illustrates that the structural complexity of such species might result in habitat functions upon their death.

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Introduction

Foundation species provide habitats for other organisms through creating physical structures (Dayton, 1972; Fonseca et al., 1982). For example, mangroves, corals, oysters, and seagrasses are well-known foundation species groups inhabited by various marine communities (Stoner & Lewis, 1985; Ellison & Farnsworth, 1992; Reaka-Kudla, 1997; Minchinton & Ross, 1999). Their complex structures (e.g., mangrove roots, coral branches, and oyster shells) modify physical phenomena, such as flow velocity and sedimentation (Fonseca et al., 1982), as well as provide refuge, feeding grounds, and nurseries. Moreover, they determine species diversity, composition, and distribution (Hacker & Steneckd, 1990; Taylor & Cole, 1994; Alvarez-Filip et al., 2009; Fabricius et al., 2013). Therefore, identifying foundation species or species groups is crucial to studying the mechanisms underlying faunal community structure.

The dead bodies of foundation species commonly serve as habitats. For example, numerous species inhabit the calcareous branches of dead corals (Head et al., 2015). When dead foundation species retain habitat functions, they may support a community containing similar species composition as the one they supported while alive (Hauff & Jack, 2006; Kauffman & Cole, 2010). This pattern suggests that the species composition of communities associated with hard-structured foundation species should be resistant to disturbances. Although remnant structures are important in retaining the habitat functions of foundation species in marine and terrestrial ecosystems (Brokaw, 1985; Head et al., 2015), little is known about their exact functions.

Sessile organisms (e.g., oysters, mussels, and barnacles) are the major foundation species in the intertidal rocky shores that are ubiquitous from tropical to boreal regions (Tsuchiya & Nishihira, 1986). Their complex shells provide refuge from predation (Tsuchiya & Nishihira, 1985). Because predation is a process that alters species composition (Menge, 1995), oyster shells may play an important role in determining community structure. In particular, sessile organisms with calcified shells are likely to retain habitat functions because their shells persist after death (Gutiérrez et al., 2003; Summerhayes et al., 2009). Nevertheless, dead oyster shells in intertidal rocky shores have rarely been studied with the same detail as other shell-forming foundation species (Tsuchiya & Nishihira, 1985, 1986; Harley & O'Riley, 2011).

The present study aimed to examine the potential of empty shells as habitats for the benthic faunal community of an intertidal rocky shore. We conducted field observations to evaluate the abundance of macroinvertebrates inhabiting living and dead sessile organisms. Following the provision of empty oyster shells, we then registered the succession of species in these assemblages. Finally, we assessed the habitat function of dead oyster shells as refugia, measuring predation rates of carnivorous snails on limpets inhabiting dead oyster shells, live oysters, and bare substrates. The rugosity index was also determined as a measure of each habitat's structural complexity.

Materials and methods

Study site

Field surveys were conducted at the intertidal rocky shore of Nabeta, in southern Izu Peninsula, Shizuoka Prefecture, Japan (34°40′N, 138°56′E). At this site, the main sessile organisms are barnacles *Tetraclita japonica* (Pillsbry, 1916), mussels *Septifer virgatus* (Wiegmann, 1837), and oysters *Saccostrea kegaki* Torigoe & Inaba, 1981 (Appendix 1—Supplementary Material). This flat rocky shore is subjected to semidiurnal tides, with a tidal range of 0–1.8 m, and an annual water temperature ranging from 13 to 26°C. All field surveys were conducted during ebb tides, in May 2015.

Habitat use survey

Individuals were counted from each macroinvertebrate species inhabiting live and dead oysters, barnacles, mussels, and random bare surfaces (included as the control). Surveyed areas within each habitat were 5 cm × 5 cm ($n = 60$ per habitat), similar to the areas occupied by a single sessile individual. To guarantee independence, each habitat was separated by 1 m. The number of individuals per species per cm^2 (i.e., abundance) was calculated; macroinvertebrate abundances on and within biogenic habitats were compared to define habitat use patterns. In addition, the developmental stage of limpets (the most dominant taxon) was determined; individuals <8 mm were classified as juveniles, whereas >8 mm were classified as adults (Fletcher, 1984; Chambers & Mcquaid, 1994).

Differences in habitat use patterns were evaluated with the Steel–Dwass test, a non-parametric multiple comparisons analysis (Morley, 1982). The test compared overall average abundances between habitats and the abundance of several species between habitats. All statistical analyses were performed in R version 3.3.0 (R Core Team 2016).

Community composition and succession of macroinvertebrate species in empty oyster shells

Succession was evaluated through comparing community species composition and abundance at 1, 2, 7, 30, 60, 120, 150, and 210 days after the empty shells were provided. According to our survey, *S. kegaki* were the most common habitat. Thus, 40 individuals were sacrificed to count the number of inhabited shells and individuals of each associated species, after oyster top shells and flesh were removed at the study site. Species abundance on the dead oyster shells (determined under "Habitat use survey") was set as the control.

The Steel–Dwass test was used to compare the average abundances between species inhabiting dead oyster shells across the various days post-shell provision. The degree of similarity in species composition between periods was calculated with the Chao similarity coefficient, based on the individual numbers per species per period. The resultant similarity matrix was subjected to cluster analysis using group-average linkage.

Predation rates and rugosity per habitat

To assess the function of dead oyster shells as a shelter from predation, 45 of the dominant predator *Reishia clavigera* (Küster, 1960) and 60 *Cellana nigrolineata* (Reeve, 1854) were collected from the study site in December 2015. All individuals of both species were similar in size (less than 1.0 cm shell length in *C. nigrolineata* and 3.0 ± 0.5 cm shell height in *R. clavigera*) to prevent ontogenetic prey preference. Additionally, to prevent seasonal prey preference, sample collection and investigation were performed after the spawning season. Five predator (*R. clavigera*) and five prey (*C. nigrolineata*) individuals were distributed through nine perforated plastic cups (height, 4 cm; diameter, 8 cm), submerged in a plastic tank (50 cm × 30 cm × 10 cm) with continually flowing seawater. Each set of three cups corresponded to a different treatment. In one set, the lower part of an oyster shell was glued to the cup bottom using epoxy putty (Dead Oyster Shell). In the second set, the upper parts (lids) were glued to the bottom (Lidded Oyster Shell). The third set contained only a layer of epoxy putty at the bottom (Rock Surface). The number of prey individuals was counted on the seventh day of the experiment. Five individuals were placed into another set of Rock Surface cups to evaluate how epoxy putty affected limpet mortality. Again, the Steel–Dwass test was used to examine predation rates upon limpets (n/day/predator) across treatments.

To determine the structural complexity of dead oyster shells as a habitat, we compared their rugosity indices with those of living oyster shells and bare rock surfaces. Depression surface (T_r) and shell length (T_t) were measured in 40 habitats (live and dead oyster shells, plus 5 cm × 5 cm areas on bare rock surfaces), separated by more than 30 cm to guarantee independence. Measurements were taken in June 2015, using a string with a centimeter scale. The rugosity index (Ri) was defined as follows:

$$Ri = T_\mathrm{r}/T_\mathrm{t},$$

$Ri = 1$ denoted a flat surface, and Ri increased with increasing roughness (Trudgill, 1988). To analyze structural complexity, the mean and median rugosity indices across habitats were compared with the Steel–Dwass test.

Results

Habitat use survey

Macroinvertebrate use rates of live or dead oyster shells varied from 0 to 65.88% (Table 1). We could not determine habitat use rates on dead *S. virgatus* because they were washed away in the current. Dead *S. kegaki* shells were the most common habitat (Steel–Dwass, $P < 0.05$; Fig. 1), with nearly all studied macroinvertebrate species (Table 1) present in them (22/23 species). The primary inhabitants were limpets (Steel–Dwass, $P < 0.05$; Table 1), accounting for 57% of all counted organisms from dead oyster shells. In fact, some limpet species, along with mussels, muricid snails, and sea anemones, were found exclusively in dead oyster shells. All limpets observed were classified as juveniles (<5 mm).

Community composition and succession of macroinvertebrate species in empty oyster shells

Average macroinvertebrate and limpet numbers associated with each experimental period (±SD, $n = 40$ per period) were shown in Appendix 2—Supplementary Material. We observed no significant interspecific differences in the average number of individuals inhabiting empty oyster shells (Steel–Dwass, $P > 0.05$). Cluster analysis showed that communities could be divided into two major groups (per observation interval) that exhibit 50% dissimilarity (Fig. 2). Group I consisted of invertebrates detected during the initial (up to 30 days post-habitat provision) and the end of the experiment (210 days). Group II consisted of invertebrates from 60 days post-habitat provision until 150 days post-experiment start. Additionally, three distinct groups with 30% dissimilarity in their community composition were apparent: one during the experiment's first week, another on days 30 and 120, and third on days 60, 120, and 150.

Table 1 Average number of macroinvertebrates found within each habitat (±SD, n = 60 per habitat)

Macroinvertebrates	*Saccostrea kegaki*		*Tetraclita japonica*		*Septifer virgatus*		Rock surfaces
	Dead	Living	Dead	Living	Dead	Living	
Acanthopleura japonica (Lischke, 1873)	0.19 ± 0.45	0	0	0	–	0	0
Cellana nigrolineata (Reeve, 1839)	0.071 ± 0.26	0	0.031 ± 1.18	0	–	0.021 ± 0.15	0
Nipponacmea fuscoviridis (Teramachi, 1949)	0.059 ± 0.28	0.015 ± 0.12	0.063 ± 0.25	0.13 ± 0.54	–	0	0
Patelloida pygmaea form heroldi (Dunker, 1861)	0.18 ± 0.82	0	0	0	–	0.021 ± 0.15	0
Nipponacmea radula (Kira, 1961)	0.094 ± 0.30	0	0	0.065 ± 0.25	–	0.021 ± 0.15	0
Lottia kogamogai (Sasaki & Okutani, 1994)	0.047 ± 0.26	0	0	0.022 ± 0.15	–	0.021 ± 0.15	0
Siphonaria japonica (Donovan, 1824)	0.012 ± 0.11	0.015 ± 0.12	0.031 ± 0.18	0.043 ± 0.21	–	0	0
Cellana toreuma (Reeve, 1854)	0.012 ± 0.11	0	0	0	-	0	0
Cellana grata (Gould, 1859)	0.024 ± 0.15	0	0	0	-	0	0
Acmaea pallida (Gould, 1859)	0.012 ± 0.11	0	0	0	-	0	0
Patelloida saccharina form lanx (Reeve, 1855)	0.018 ± 0.13	0	0	0	–	0	0
Reishia clavigera (Küster, 1860)	0.094 ± 0.33	0	0.063 ± 0.25	0.022 ± 0.15	–	0	0
Nerita albicilla (Linnaeus, 1758)	0.024 ± 0.15	0	0	0	–	0	0
Nodilittorina radiata (Souleyet in Eydoux & Souleyet, 1852)	0.012 ± 0.11	0	0	0	–	0	0
Saccostrea kegaki Torigoe & Inaba, 1981	0.11 ± 0.35	0	0	0	–	0	0
Septifer virgatus (Wiegmann, 1837)	0.047 ± 0.21	0	0	0	–	0	0
Scaphopoda sp.	0.012 ± 0.11	0	0	0	–	0	0
Tetraclita japonica (Pilsbry, 1916)	0	0.044 ± 0.20	0.094 ± 0.30	0.13 ± 0.45	–	0	0
Fistulobalanus albicostatus (Pilsbry, 1916)	0.012 ± 0.11	0	0	0	–	0	0
Chthamalus challengeri (Hoek, 1883)	0.012 ± 0.11	0.015 ± 0.12	0.84 ± 2.4	0.20 ± 0.72	–	0	0
Pollicipes mitella (Linnaeus, 1758)	0.012 ± 0.11	0	0.094 ± 0.15	0	–	0	0
Anthopleura uchidai (England, 1922)	0.024 ± 0.15	0	0	0	–	0	0

All limpets were classified as juveniles, with shells <5 mm in length

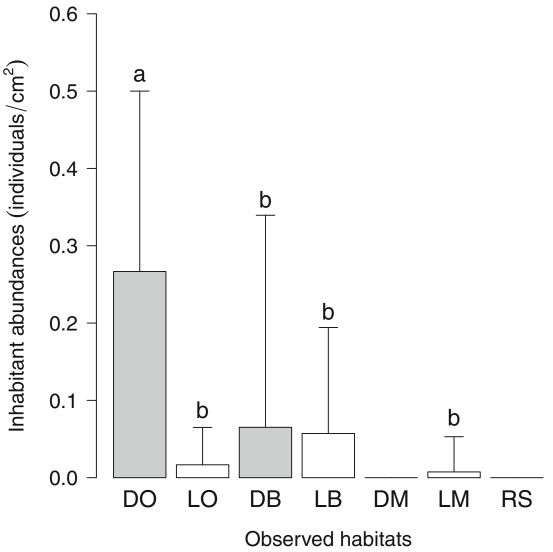

Fig. 1 Average number of macroinvertebrates in each habitat counted during May 2015 ($n = 60$). *DO* dead oysters, *LO* living oysters, *DB* dead barnacles, *LB* living barnacles, *DM* dad mussels, *LM* living mussels, *RS* rock surfaces. On average, DO contained more inhabitants than the other habitats (Steel–Dwass, $P < 0.05$). *Error bars* indicate standard deviation

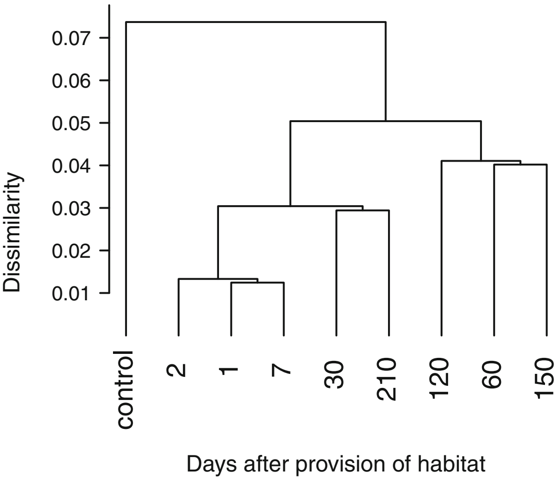

Fig. 2 Cluster analysis using the Chao similarity coefficient and the number of individuals per species inhabiting dead oyster shells, observed from May to December 2015. Assemblages could be divided into two major groups with 50% dissimilarity, or three major groups with 30% dissimilarity

Predation rates and rugosity per habitat

The predation rates of *C. nigrolineata* in each habitat were as follows: Dead Oyster Shell, 0.27 ± 0.12/day/predator; Lidded Oyster Shell, 0.80 ± 0/day/predator; Rock Surface with predators, 0.73 ± 0.12/day/predator; and Rock Surface without predators, 0/day/predator (Fig. 3). None of the limpets died in the "Rock Surface without predators" treatment; thus, the epoxy putty did not appear to significantly affect limpet mortality. The predation rate of *C. nigrolineata* in the "Dead Oyster Shell" group was significantly lower than in the "Lidded Oyster Shell" and "Rock Surface with predators" groups (Steel–Dwass, $P < 0.05$).

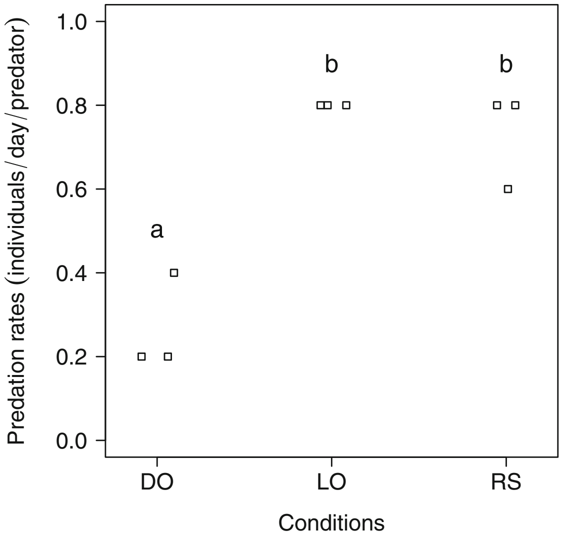

Fig. 3 Abundance of consumed limpets consumed under each experimental condition ($n = 3$). *DO* dead oyster shell, *LO* lidded oyster shell, *RS* rock surfaces. The number of consumed limpets in the DO group was the least among the conditions tested (Steel–Dwass, $P > 0.05$)

The mean and median values of the rugosity index calculated for each habitat were as follows: Dead Oyster Shell, 1.33 ± 0.19, 1.3; Live Oyster Shell, 1.04 ± 0.06, 1.0; and Rock Surface, 1.20 ± 0.32, 1.0 (Fig. 4). The rugosity index of dead oyster shells was higher than that of any of the other habitat (Steel–Dwass, $P < 0.05$), likely due to a surface covered with depressions.

Discussion

Along the studied intertidal rocky shore, more macroinvertebrate species were found in dead oyster shells than in living oyster shells or bare rocks. Moreover, dead oyster shells were an effective refuge from predation for limpets. As all counted individuals

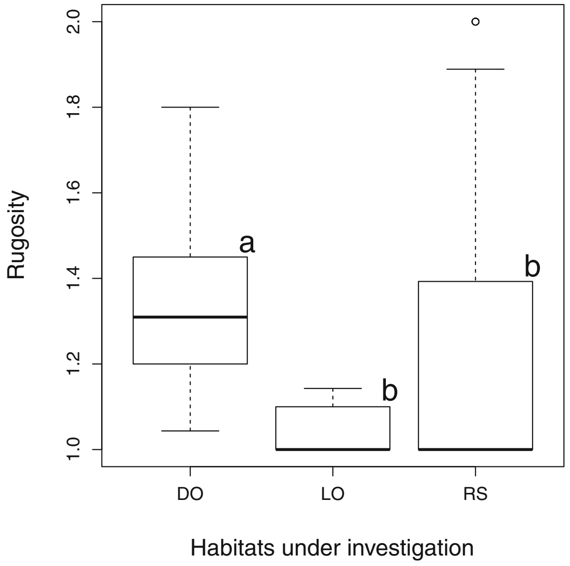

Fig. 4 Rugosity index of each habitat ($n = 30$). *DO* dead oyster shell, *LO* living oyster shell, *RS* bare rock surface. Each *box* represents an interquartile range, and the *horizontal line within the box* indicates the median. The *whiskers* extend to the lowest and highest values, below and above the first and third quartiles, respectively, excluding outliers. *Circles* represent outliers between 1.5 and 3.0 times the interquartile range. Dead oyster shells had the most complex structure among studied habitats (Steel–Dwass, $P < 0.05$)

were juveniles, this habitat may also serve as a nursery.

Although living oysters are thought to be an important habitat in many regions, e.g., Minchinton & Ross (1999), dead *S. kegaki* shells comprised the most used habitat in this study. In addition, some species exclusively occupied dead oyster shells, including limpets, mussels, barnacles, and sea anemones, with limpets being dominant (Table 1). Grazing by limpets can alter micro- and macroalgae abundance and community structure directly or indirectly (Jenkins & Hartnoll, 2001; Jenkins et al., 2001; Wada et al., 2013), for instance, by interfering with the settlement of sessile organisms (Menge et al., 2010). Therefore, by dominating dead oyster shells, limpets could constitute an important factor determining species composition along the intertidal rocky shore. A similar pattern has been reported in other oyster communities (Miller & Carefoot, 1989; Tuckwell & Nol, 1997; Minchinton & Ross, 1999), suggesting that limpets may selectively use dead oyster shells.

A previous study suggested that the settlement of sessile organisms on a particular surface provides more attachment area (Gutiérrez et al., 2003). Since the number of inhabitants increased from live to dead shells, we found clear evidence of oysters acquiring habitat function after death. This improved habitat function of dead oyster shells occurs because they have no lids, and the underside of the shell has a larger area than the lid. Thus, these shells exhibit greater species abundance and richness than other habitat options. However, bare rock surfaces have even more surface area than dead oyster shells, yet very few macroinvertebrates attached to them (Table 1). This outcome suggests that factors specifically provided by dead oyster shells and other sessile organisms (e.g., predation refuge) might be more important than large attachment areas. For example, dead corals continue to support abundant and diverse fish populations, as long as the complex structure of their calcareous branches persists (Lindahl & Marcus, 2001).

Limpet predation rates when attached to dead oyster shells were lower than rates on lidded (living) oyster shells (Fig. 4). Moreover, the rugosity index of dead oyster shells was the highest among all habitats (Fig. 3), an outcome observed when the shell lid was detached post-death, exposing the inner depression. Thus, these results imply that dead oyster shells act as refuge from predation, and that this habitat function is likely attributable to the depressions on their inner surfaces. Indeed, because limpets attach firmly to depressions as their primary escape mechanism, dead oyster shells are more suitable habitats than bare rock or other, flatter surfaces (Lam, 2002). Although previous studies have suggested that only the complex structures of foundation species groups such as corals and mangroves are maintained beyond their lifetime (Ellison & Farnsworth, 1992; Head et al., 2015), our results showed that the shells of sessile organisms can increase in complexity and thus are also maintained after death (Tsuchiya & Nishihira, 1985, 1986; Minchinton & Ross, 1999). Though our results are promising, we should note that the present results were demonstrated only in the lab and with a limited sample size. However, these data will serve as a baseline for further research, including field enclosure experiments to verify findings under artificial conditions.

Our succession experiment demonstrated that limpets were among the main pioneer species. After empty shells were provided, limpets were dominant during the initial experimental period (one to seven days), and remained so throughout the subsequent ones. We had originally expected succession in dead oyster shells to take a long time, because limpets are competitive, bulldozing through competing sessile species and directly interfering with their settlement (Menge et al., 2010). However, our results suggest that succession only spans approximately one month. Specifically, within 30 days after shell provision, sampled communities were contained within the same 50% dissimilarity cluster (Fig. 2), whereas those sampled after 30 days were contained in another 50% dissimilarity cluster. This succession rate is higher than the six-month period reported for barnacle and mussel beds (Dürr & Wahl, 2004). Such disparities could be attributed to competitive exclusion. Dominant juvenile limpets grazed on other juvenile sessile organisms attempting to colonize the same habitat, affecting faunal community alternation. Consequently, limpets bulldozing is the likely factor driving community development patterns on oyster shells.

The species composition survey and the succession experiment demonstrated that all individuals belonging to *Patelloida* spp. and *Cellana* spp. inhabiting dead oyster shells were juveniles. At least for the studied limpets, dead oyster shells thus seem to be important nursery grounds. Both nursery and predation refuge are the same functions of tidal pools for limpets (Heck, 1997; Delany et al., 1998; Heck et al., 2003). Together, current and previous results suggest that habitats acting as a refuge from predation might contribute to high juvenile survival rates in nurseries. The lack of adult limpets could be attributed to oyster shell size, which were insufficient for adult use as a predation refuge; *Cellana* spp. and *Patelloida* spp. shells typically grow larger than 2 cm, or around the length of an oyster shell (Iwasaki, 1993; Liu & Morton, 1998).

In the present study, the succession experiment started just after the limpet settlement season (Delany et al., 1998). Thus, the experimental results should reflect the juvenile limpets' use of if dead oyster shells as a nursery. Indeed, juvenile limpets dominated communities. The lack of juveniles from other sessile organisms may be that they were too small for field observation. Moreover, their settlement seasons (Menge et al., 2010) were not taken into consideration here. Future studies will likely observe greater numbers of species such as mussels and sea anemones if the experiment period is extended to include the settle seasons of various organisms.

In conclusion, dead oyster shells were crucial habitats functions for the benthic faunal community along an intertidal rocky shore, highlighting oysters as foundation species that acquire additional habitat functions upon death. It was also apparent that the habitat functions of dead species may be overlooked if the living organisms (e.g., oysters, mussels, and barnacles) are not already being used as habitats (Tsuchiya & Nishihira, 1985; Minchinton & Ross, 1999). Therefore, researchers should focus on both living and dead foundation species to clearly understand the effects of their habitat functions on the associated communities.

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