7. Tidal Flats as Habitat for Endangered Benthic Animals: Importance of Animal Burrows for Symbiotic Species

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1. Tidal Flats as Habitats for Endangered Species

In inner bays and estuaries, tidal flats of various sizes are formed (Figure 1). Tidal flats are an extremely productive area: abundant benthic diatoms grow on the sand and mud particles; salt marshes in the temperate zone and mangrove forests in the tropical zone often develop; seagrass meadows are spread out in the offshore area. In such a productive area, a wide variety of animals can live there: abundant filter feeding benthos contribute to the removal of suspended particles, playing a major role of water purification function; some molluscans and crustaceans are very populous, making them important species for fishery[1,2]. Some large fish species also spend time at tidal flats as feeding grounds as adults and/or nursery grounds. In addition, tidal flats have other ecological services, such as coastal protection, erosion control, carbon sequestration, tourism, recreation, and education[1, 2]. However, tidal flats are heavily used by human globally; especially in Japan, 40% of the tidal flat area was lost due to land reclamation during the 40 years from 1945[3].

Wada et al. (1996) were the first to warn that the benthos of Japan's tidal flats were in a critical condition[4]. However, in Japan, the Red List by the Ministry of Environment, Government of Japan was first created for terrestrial species, and the Marine Life Red List[5] was created only in 2017. Japanese Association of Benthology (2012) has published a Red Data Book of animals living in tidal flats, ahead of the Ministry of Environment, and designated 651 species (462 mollusks, 138 arthropods, 21 polychaetes and 30 other invertebrates) as threatened benthic animals[6]. Henmi et al. (2014) analyzed the characteristics of 651 species of the RDB[6] and found the following[7]. First, the highest numbers of RDB species (about 15% of the total) were recorded on the Ryukyu Islands (south-western Japan); second, the main reasons for the listing of RDB were habitat degradation and population decline; and third, the relatively high percentage of parasitic and symbiotic RDB species (10.4% of mollusks, 18.1% of arthropods, and 14.3% of polychaetes). The last point is particularly important when considering the conservation of endangered species; that is, the conservation of not only endangered species but also their host species would be essential.

Symbiotic relationships in tidal flats are mainly found in animal burrows; most of the symbiotic animals listed in the RDB by the Japanese Association of Benthology[6] live associated with burrowing animals in tidal flats (following Ross (1983)[8], the term "symbiotic" is used literally in the sense of "living together" in this paper). Host burrowing animals include annelid worms (especially echiurans and chaetopterid polychaetes)

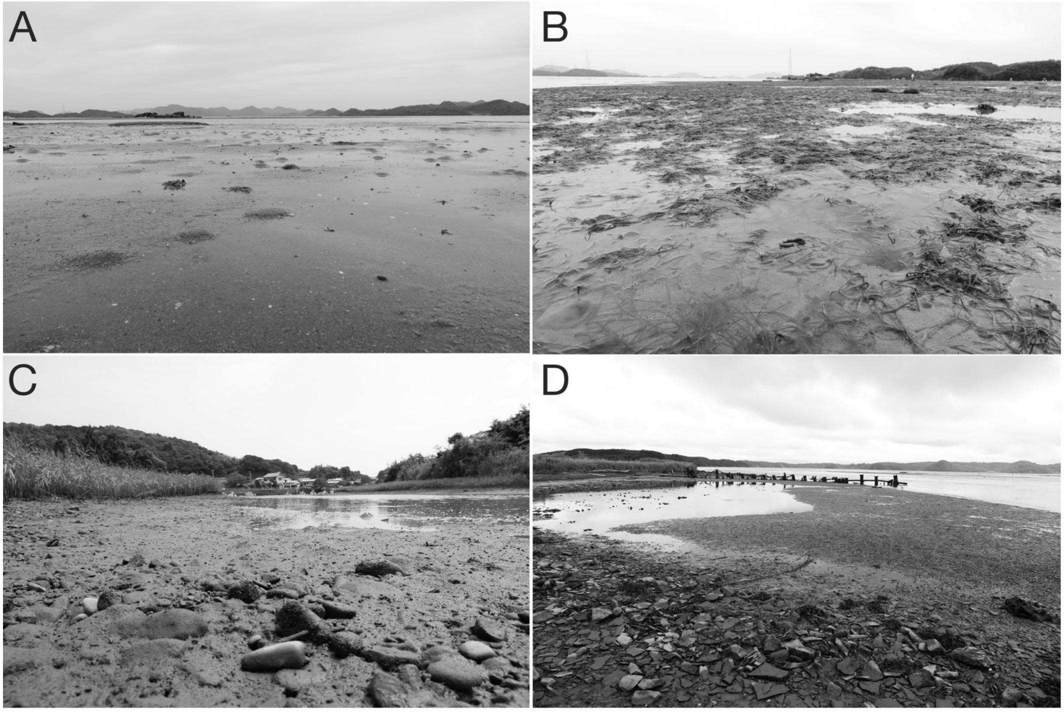

Figure 1 Various tidal flats in Japan. A) Sandy-mud tidal flat with invertebrate mound. Hachi, Takehara City, Hiroshima, Japan. B) *Zostera* seagrass meadow. Hachi, Takehara City, Hiroshima, Japan. C) Salt marsh. Takeshima-gawa, Shimanto City, Kochi, Japan. D) Northern temperate tidal flat. Akkeshi lake, Akkeshi, Hokkaido, Japan.

and shrimps (especially callianassids, upogebiids, and alpheids). In this chapter, recent behavioral and ecological studies of symbiotic relationships in shrimp burrows are shown. For research of symbioses in annelid burrows, many papers and reviews have already been published[9, 10, 11, 12, 13.]

2. Symbioses in Burrows of Alpheid Shrimp

Alpheus shrimps of the family alpheidae usually construct their own burrows in soft sediments, but some species live under rocks or dead corals[14]. Such burrows provide living space for symbiotic animals such as crabs, shrimps, and gobies[15, 16.] The goby-alpheid shrimp association in subtidal coral reefs is one of the best studied cases of marine mutualism. In such relationships, the shrimp constructs and maintains the burrow that the goby also lives in; the goby warns the shrimp of danger through tactile communications[15, 17]. In terms of habitat for endangered species, an endangered estuarine goby *Apocryptodon punctatus,* listed as VU on the Red List by the Ministry of the Environment, Government of Japan[18], is suggested to live symbiotically with *Alpheus* sp. (as *A. richardsoni*) and *A. dolichodactylus* in temperate muddy flats in Japan[19]. The burrow morphology of *Alpheus* sp. (= *A. richardsoni*) was complicated and stratified, with many short cul-de-sac branches and looped structures[20] (Figure 2A, B). More studies are needed to elucidate how *A. punctatus* uses such a complicated shrimp burrow.

Taking into account the use of alpheid shrimp burrows by endangered gobies, another important species is *Acentrogobius* sp. 2 (sensu Akihito et al., 2013[21]) living in temperate tidal flats. Although *Acentrogobius* sp. 2 is not listed on the Red List[18], several congeneric species distributed in subtropical estuaries are listed on the Red List and some ecological characteristics might be common among these species. Kirihara et al. (2020) surveyed the surface activity of *Acentrogobius* sp. 2 around the burrows of the snapping shrimp *A. brevicristatus* by quantitative observation on a tidal flat in Japan. *Acentrogobius* sp. 2 used shrimp burrows as a refuge, but used the area in front of the burrow entrance for only about 30% of the observation period[22], which is much shorter than the known cases of obligate mutualistic gobies, i.e. 85% in *Nes longus*[23]. Henmi et al. (2020) confirmed the facultative non-mutualistic nature of *Acentrogobius* sp. 2 - *A. brevicristatus* relationship by mesocosm experiments. The burrow morphology of *A. brevicristatus* is relatively simple and shallow with long tunnels and several burrow openings[14] and most burrow dimension are positively correlated with the shrimp size, suggesting that the burrow size was optimal for the shrimps[24]. However, such positive correlations disappeared when *Acentrogobius* sp. 2 was added to the mescosm tank. Smaller burrows may not be suitable for shrimp, and larger burrows require more energy to construct and maintain, suggesting that symbiosis with *Acentrogobius* sp. 2 is costly to shrimp[24]. These studies showed that alpheid shrimp burrows in tidal flats are used as refuges for several goby species that do not have the well-known mutualistic relationship with shrimp.

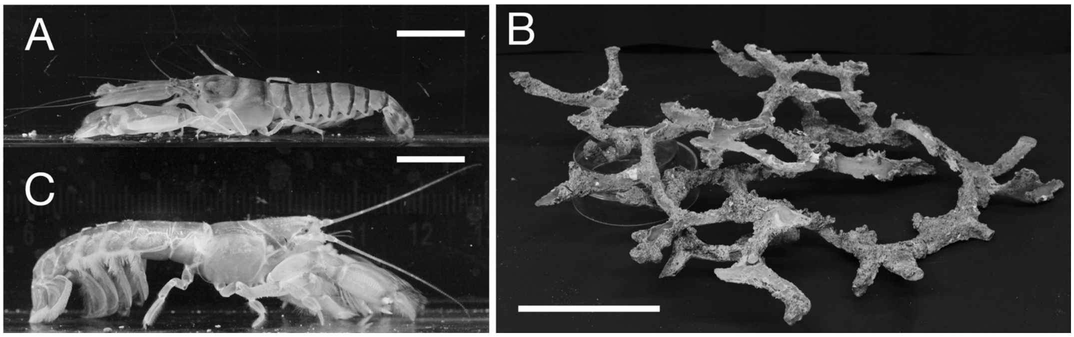

Figure 2 Burrowing crustaceans. A) Alpheid shrimp *Alpheus* sp. (= A. *richardsoni*). B) Burrow morphology of *Alpheus* sp. (see Kirihara et al. 2021). C) Upogebiid shrimp *Upogebia yokoyai*. Scale bar = 10 mm (A, C); 10 cm (B).

3. Symbioses in the Burrows of Upogebiid Shrimp

Upogebiid shrimps (Figure 2C) construct Y-shaped burrows in sandy or muddy sediment all over the world[25]. They are suspension feeders, creating water currents by beating their pleopods and filtering suspended matter in the burrow[26]. Owing to the feeding behavior, the burrow is well oxygenated and a variety of symbiotic animals, such as bivalve, scale worms, crabs, shrimps, and gobies, are known to live in the upogebiid shrimp burrows[9, 26, 27, 28.] However, most of the records of such co-existence were snapshots, and little is known about the ecology of the symbionts, such as whether they are always in the burrows of their hosts, and how often they move in and out of the burrows.

The goby, *Eutaeniichthys gilli*, listed as NT on the Red List[18], was studied in aquaria to quantify the use of

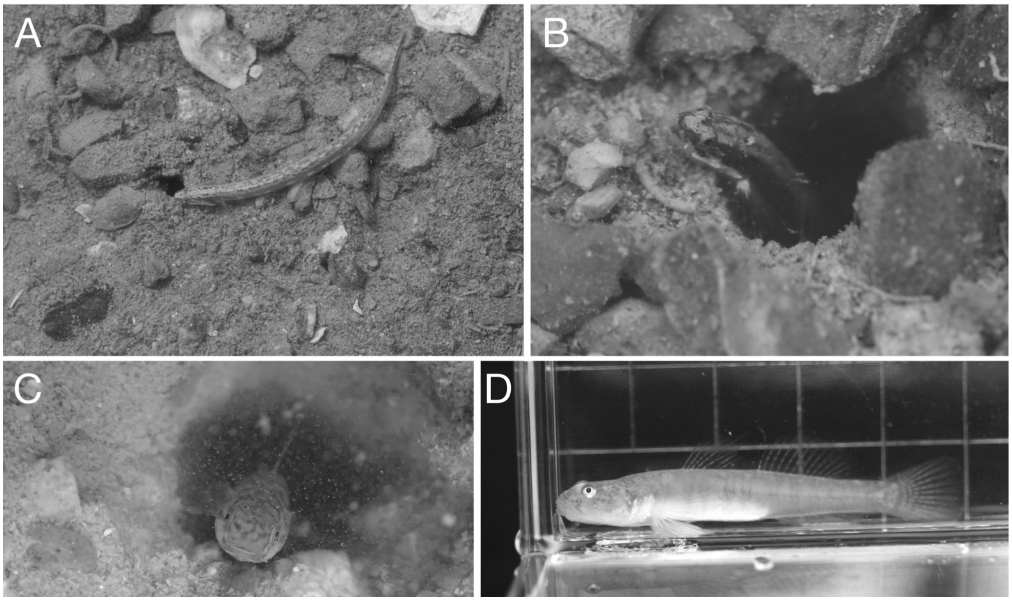

Figure 3 Symbiotic gobies. A) *Eutaeniichthys gilli*, listed as NT in the Red List (Ministry of the Environment, 2020). B) *Eutaeniichthys gilli* coming out of the *U. yokoyai* burrow. C) Free-living *Mugilogobius abei*, occasionally using shrimp burrow. D) *Gymnogobius macrognathos*, listed as VU on the Red List (Ministry of the Environment 2020), collected from the burrows of *U. major* in Akkeshi, Hokkaido.

the *Upogebia yokoyai* burrow[29]. The goby frequently entered and exited the shrimp burrows with bout durations of several seconds to several minutes and spent in the burrows for about 25% of the observation time in total. *E. gilli* was suggested to feed on small crustaceans and other organic matter on the surface of the mud, frequently using shrimp burrows for possible predator avoidance[29] (Figure 3AB). Two species of free-living gobies were tested for the use of *U. yokoyai* burrows in the same experimental set-up; *Favonigobius gymnauchen* never used shrimp burrows, but *Mugilogobius abei* spent about 3% of the observation time[29, 30]. Field surveys showed that *M. abei* occasionally used crustacean burrows as shelter in the habitat where few surface structures were available[30] (Figure 3C). Biotic and abiotic habitat analyses have shown that four species of the endangered *Gymnogobius* goby species can use *Upogebia* and/or callianassid *Neotrypaea* shrimp burrows as shelter[31]. These studies have shown the importance of shrimp burrows for both symbiotic and free-living gobies.

Shrimp burrows are also used as a spawning nest by *Gymnogobius* gobies (Figure 3D); *G. cylindricus*, listed as EN in the Red List[18], uses *Upogebia* shrimp burrows as a spawning nest[32], while *G. macrognathos*, listed as VU in the Red List[18], uses *Neotrypaea* shrimp burrows as a spawning nest[32, 33]. Henmi et al. (2017) have elucidated that *G. macrognathos* elaborately widens the shrimp burrows as spawning nests[33].

Sestrostoma toriumii, listed as NT on the Marine Life Red List[5], is a varunid crab that is associated with upogebiid burrowing shrimps in intertidal mud flats[34] (Figure 4A). Laboratory experiments by Henmi and Itani (2014) confirmed that *S. toriumii* spends 60~80% of the observed time in burrows of *U. yokoyai*[35]. Some of the experimental crabs stayed in burrows throughout the observation period, whereas others left and reentered burrows. Occasionally, *S. toriumii* was expelled from a burrow following agonistic behavior by the host[35], but *S. toriumii* sometimes avoided hostile responses of the host species through escape and pass-under behavior[36]. *Sestrostoma* sp., listed as EN on the Marine Life Red List[5], is another crab species symbiotic in *Upogebia* burrows[34]. Long-term video recordings in aquaria showed that this crab was always clinging under the abdomen of the shrimp and can molt without detaching from the shrimp body[37]. When the host shrimp molted, the crab detached from the shrimp body for some minutes and reattached to the body[37]. In the case of the symbiotic bivalve *Peregrinamor ohshimai*, listed as NT on the Red List[18], the bivalve can walk on the surface of the host's body and reattach to the body when the host shrimp molt[38].

Alpheid shrimps from well over 15 genera are known to live symbiotically in animal burrows[39]. Using aquarium observation, Henmi and Itani (2021) described and compared the behavior of *Stenalpheops anacanthus*, listed as NT on the Marine Life Red List[5], and *Athanas japonicus*, living symbiotically in the burrows of *U. yokoyai*[39] (Figure 4BC). The average time taken for *S. anacanthus* to enter the burrow for the first time was much shorter (1 min) than that of *A. japonicus* (13 min). Subsequently, *S. anacanthus* made longer use of the burrow (80% of the observation period) than *A. japonicus* (49%). The frequency of tail-first exit, which may indicate a sudden expulsion from the burrow by the host, was more frequent in *A. japonicus* (25%) than in *S. anacanthus* (7%). The benefit to alpheids is probably finding refuge from predators and the acquisition of detritus that flows into the host’s burrow, as suggested for burrowing symbiotic crabs[9, 40]. Judging by the observation that alpheids were often expelled from the host’s burrow, the host may receive little benefit from the association. Another symbiotic alpheid *Betaeus jucundus* has a possible negative effect on the behavior of host callianassid shrimp[41].

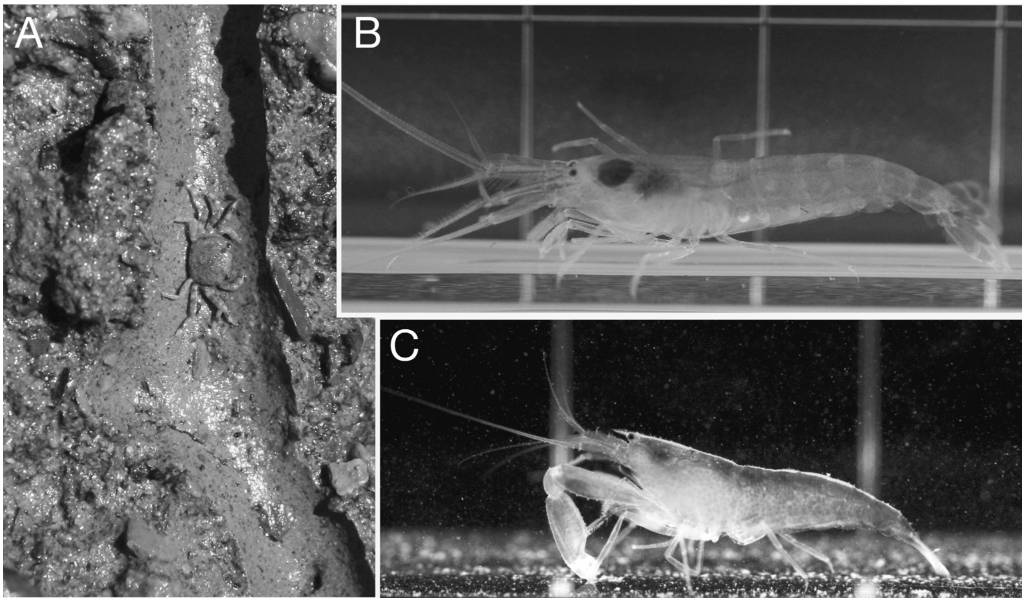

Figure 4 Symbiotic crustaceans. A) *Sestrostoma toriumii*, listed as NT on the Red List (Ministry of Environment, 2017), in the *U. yokoyai* burrow. B) *Stenalpheops anacanthus*, listed as NT on the Red List (Ministry of the Environment, 2017). C) *Athanas japonicus*.

4. Summary

In this chapter, we have presented the importance of shrimp burrows as a shelter or permanent home for endangered gobies and crustaceans. Although these shrimp species are a common and least concerned species, their burrows are very important to maintain and create biodiversity. It is necessary to preserve tidal flats where there may be a variety of burrowing benthos.

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