

RESEARCH NOTE

MODE OF LIFE OF *ANOMIOSTREA CORALLIOPHILA* HABE, 1975 (OSTREIDAE): A SYMBIOTIC OYSTER LIVING IN GHOST-SHRIMP BURROWS

Ryutaro Goto¹, Ken Ohsuga² and Makoto Kato³

¹*Department of Marine Ecosystem Dynamics, Atmosphere and Ocean Research Institute, The University of Tokyo, 5-1-5 Kashiwa-no-ha, Kashiwa, Chiba 277-8564, Japan;*

²*1-108 Takano-Tamaoka-cho, Sakyo, Kyoto 606-8106, Japan; and*

³*Graduate School of Human and Environmental Studies, Kyoto University, Yoshida-Nihonmatsu-cho, Sakyo, Kyoto 606-8501, Japan*

Correspondence: R. Goto; e-mail: gotoryutaro@gmail.com

Most of the ocean bottom is covered by sediment, which is inhabited by various burrowing animals, including crustaceans, annelids and molluscs (MacGinitie & MacGinitie, 1968; Morton & Morton, 1983; Dworschak, Felder & Tudge, 2012). The burrows of these animals are often inhabited by small symbiotic animals, contributing to the biodiversity of the marine sedimentary habitat (Morton, 1988; Itani, 2004; Anker *et al.*, 2005; Kneer, Asmus & Vonk, 2008; Dworschak, Felder & Tudge, 2012). Symbiotic bivalves living in animal burrows are known from the three lineages Galeommatoidea, Myidae and Lucinidae (Lawly, 1978; Morton & Scott, 1989; Felder, 2001; Dworschak, Felder & Tudge, 2012; Goto *et al.*, 2012) and are often a major component of the diversity of burrow-associated symbionts (Itani, 2004; Anker *et al.*, 2005; Goto & Kato, 2012). In this study, we report that the bivalve *Anomioostrea coralliophila* Habe, 1975 (Ostreidae) lives symbiotically in the burrows of the ghost shrimp *Neocallichirus jousseaumei* (Nobili, 1904) (Callianassidae) (Fig. 1). To our knowledge, this is the first report of a tight symbiotic association between an ostreid bivalve and a burrow-dwelling crustacean. Although several individuals of the ostreid *Booneostrea subucula* (Jousseaume in Lamy, 1925) have been collected from an axiid shrimp burrow (Kneer *et al.*, 2013), it remains unclear whether it is a burrow-specific symbiont, because the sample size was small.

We surveyed the macrofauna associated with the burrows of *N. jousseaumei* (Fig. 1B) on the subtropical coast of Edateku (28°30'N, 129°21'E), Amami-Oshima Island, Kagoshima Prefecture, Japan, during spring low tides in May or June from 2005 to 2013. The habitat is the lower intertidal zone of a gravelly sandflat, with many embedded rocks (Fig. 1A). The burrows of *N. jousseaumei* are often constructed under rocks, so we looked for shrimp burrows by turning over the rocks. Animals associated with the burrows were collected and identified. Owing to obstruction by rocks, we could not dig up the lower parts of the burrows, so our observations were limited to the upper and middle parts. We examined at least 10 burrows in each year, in total more than 90 burrows over the course of 9 years. *Neocallichirus jousseaumei* constructs relatively spacious burrows (diameter 2–4 cm) that are branched in several places (Fig. 1C, D),

at which points the tunnels are wider than the other parts (Fig. 1D). The burrow wall is smooth and lined with fine brown mud (Fig. 1C–E).

During the 9-year survey, five symbiont species were found in the burrows of *N. jousseaumei* (Table 1): one ostreid bivalve (*A. coralliophila*) (Fig. 1C, D), two galeommatid bivalves (*Ephippodonta gigas* Kubo, 1996 and *Scintilla* sp.) (Fig. 1C, D), one tornid gastropod (*Teinostoma* sp.) (Fig. 1E) and one polynoid scale worm (Fig. 1F). Three symbiont species (*A. coralliophila*, *E. gigas* and a polynoid scale worm) were found in each year; *Scintilla* sp. was found every year except 2013, and *Teinostoma* sp. was found only in 2013. In our survey, these symbionts were never found outside the burrows in a free-living state or inside the burrows of other, sympatric invertebrates (e.g. *Neaxius* sp., *Ochetostoma* sp. and *Sipunculus nudus* Linnaeus, 1766).

To assess quantitatively the burrow occupancy of each symbiont species, we recorded the numbers of symbionts observed in 13 *N. jousseaumei* burrows on 25–26 May 2013 (Table 1). *Anomioostrea coralliophila* was found in more than 75% of the burrows examined (Table 1) and multiple individuals were often clustered at the wider junctions of the tunnels (Fig. 1C, D). *Ephippodonta gigas* was found in c. 30% of the burrows observed (Table 1). *Scintilla* sp. was not found in the 2013 survey, although it was found at a similar frequency to *E. gigas* in the other years. One species of polynoid scale worm was found in c. 15% of the shrimp burrows and was always solitary (Table 1). One individual of *Teinostoma* sp. was found in the 2013 survey, but in no other year.

Since its description (Habe & Kosuge, 1966; Habe, 1975), *Anomioostrea* has been an enigmatic genus of the family Ostreidae. Its ecology is unknown and it includes only the type species, *A. coralliophila*. Our results suggest that this bivalve is a burrow-specific symbiont. Its occupancy of a cryptic habitat is probably the main reason that its ecology has remained unresolved for such a long period. In contrast, *E. gigas* is known to be a burrow associate of a thalassinidean shrimp (Lützen & Nielsen, 2005). We previously identified the host shrimp as *Callianidea typa* H. Milne Edwards, 1837 (see Goto *et al.*, 2012), but correct this to *N. jousseaumei* in this study. Species of *Scintilla* bivalves, tornid

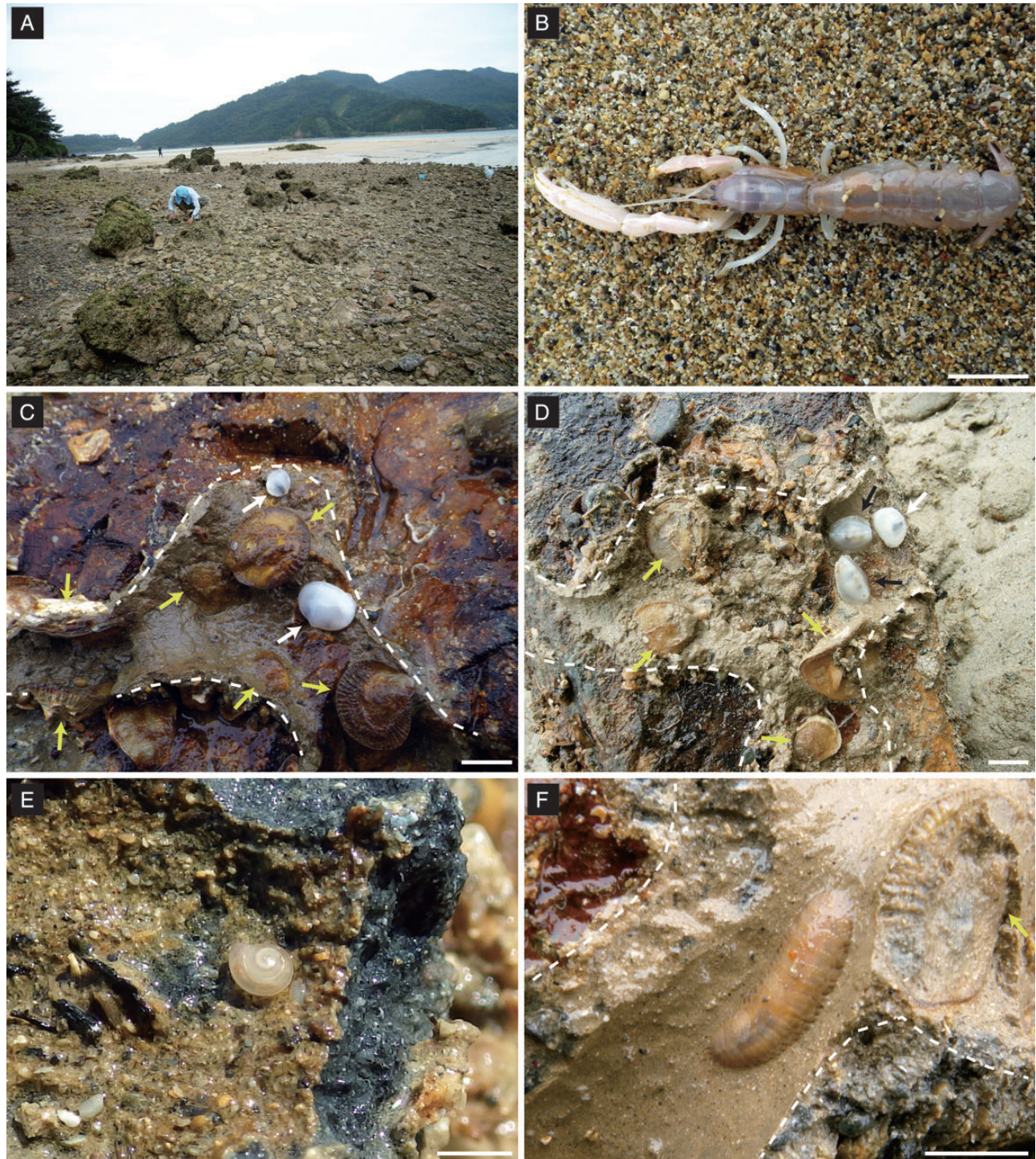


Figure 1. *Neocallichirus jousseaumei*, its symbiotic macrofauna and habitat. **A.** Gravel beach adjacent to a sand flat in Edateku, Amami-Oshima Island, Kagoshima Prefecture, Japan. **B.** *Neocallichirus jousseaumei*. **C, D.** *Anomiosrea coralliophila* (yellow arrows), *Scintilla* sp. (white arrows) and *Ephippodonta gigas* (black arrows) in burrows of *N. jousseaumei*. **E.** *Teinostoma* sp. on burrow wall. **F.** Polynoidae sp. on burrow wall. The burrow wall is visible as the areas between the two broken white lines. Scale bars: **B, C, D, F** = 1 cm, **E** = 5 mm.

snails and polynoid scale worms have sometimes been reported as burrow associates of marine benthic invertebrates (Morton, 1988; Eckelbarger, Bieler & Mikkelsen, 1990). Therefore, we infer that *Scintilla* sp., *Teinostoma* sp. and the one species of polynoid scale worm that we found in the *N. jousseaumei* burrows are also burrow-specific symbionts.

Anomiosrea coralliophila firmly attaches its left valve by cementation to the rocks embedded in the burrow wall (Fig. 1C, D).

Several small individuals were attached to the right valves of larger ones (Fig. 2B). The shell of *A. coralliophila* is inequivalve and its left valve is deeply concave, forming a cup shape, with radial ribs on its surface (Fig. 2A). The right valve is thin and lid-shaped (Fig. 2B, C) and forms part of the burrow wall (Fig. 1C, D). The surface of the right valve is flat and smooth, with only weak radial ribs (Figs 1C, D, 2C), which may be an adaptation to reduce its friction with the host shrimp. The

outlines of both the left and right valves are variable, adjusting to the shape of the substrate or the burrow wall (Fig. 1C, D). Figure 3 shows the relationship between shell height and shell

Table 1. List of symbiotic invertebrates observed in the burrows of *Neocallichirus jousseaumei*, showing the results of a quantitative survey in 2013: burrow occupancy rates (i.e. number of burrows with symbionts divided by the total number of burrows), the mean number of individuals per burrow with standard error (SE) and the maximum number of individuals per burrow.

Species	Family	Burrow occupancy rate (%)	Mean \pm SE per burrow	Maximum N per burrow
<i>Anomiostrea coralliophila</i>	Ostreidae	76.9	2.2 ± 0.48	5
<i>Ephippodonta gigas</i>	Galeommatidae	30.8	0.5 ± 0.24	3
<i>Scintilla</i> sp.*	Galeommatidae	–	–	–
<i>Teinostoma</i> sp.	Tornidae	7.7	0.08 ± 0.08	1
Polynoidae sp.	Polynoidae	15.4	0.15 ± 0.15	1

**Scintilla* sp. was not found in the 2013 survey, but was found in all other years.

width in *A. coralliophila*, based on 49 specimens collected at the study site between 2005 and 2013. The shell height increases faster than the shell width in the early stage of growth, meaning that it first grows horizontally and then vertically relative to the substrate (Figs 2, 3). The shell growth of *A. coralliophila* probably modifies the structure of the burrow of *N. jousseaumei*.

The association between *A. coralliophila* and the host shrimp appears to be a commensal one. Living in the shrimp burrow probably provides protection for *A. coralliophila* from predation pressure and environmental stresses (e.g. high temperatures). The bivalve may also benefit from the water currents created by the host's activity, if they are rich in oxygen and/or food particles. It is likely that the presence of *A. coralliophila* neither benefits nor harms its host shrimp. However, mutualism is still a possibility. The shells of *A. coralliophila* may increase the stability of the burrow by forming part of the tunnel wall as a more substantial material than sand or rubble, and this could reduce the time and energy the shrimp must spend on burrow maintenance (see also Kneer *et al.*, 2013). The filter-feeding of *A. coralliophila* may also generate water currents, improving the circulation in the burrow (see also Kneer *et al.*, 2013).

It has been suggested that active mobility is essential for burrow associates because they must accommodate changes in the burrow environment (e.g. tunnel collapse or abandonment

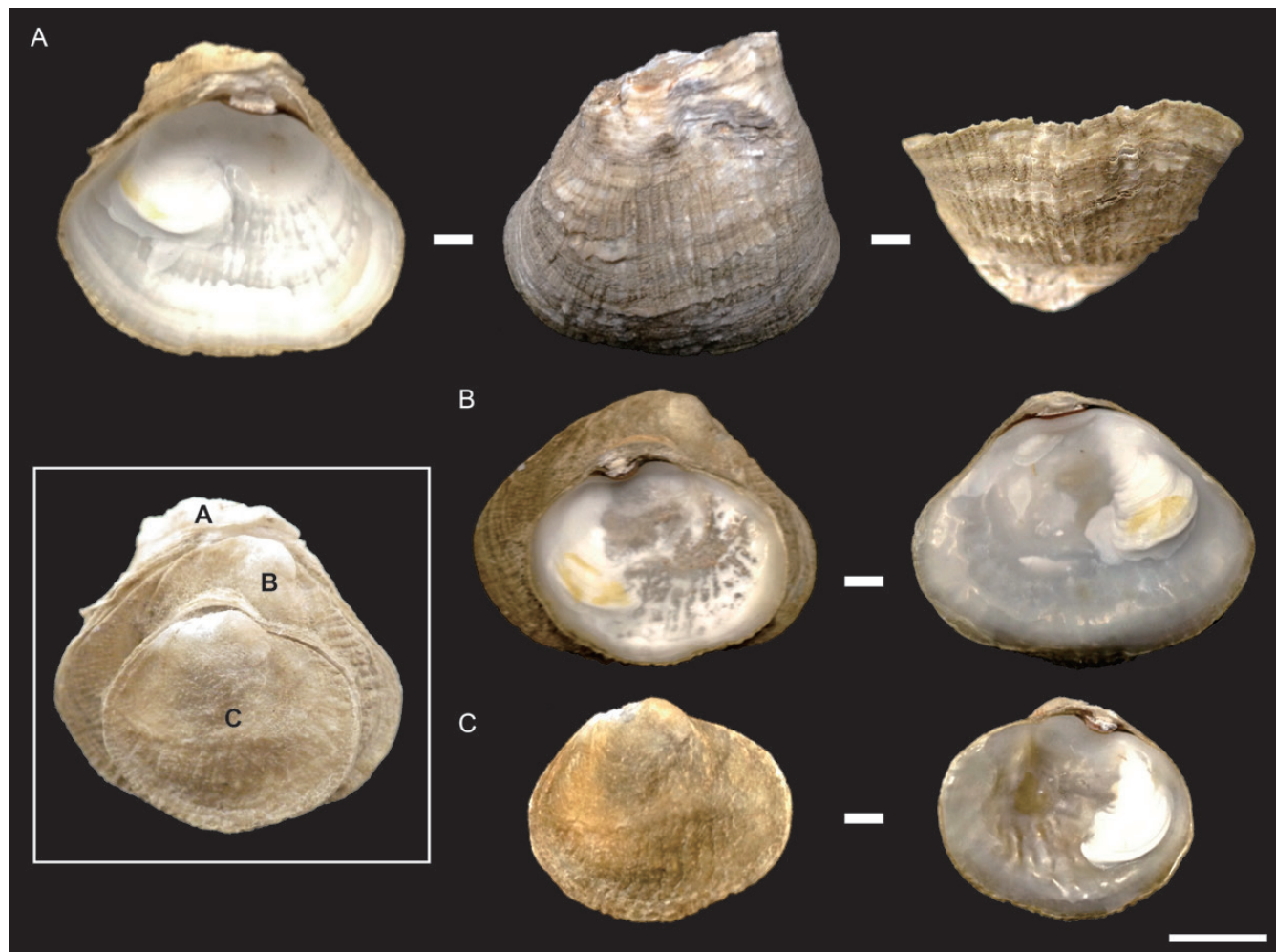


Figure 2. The shell of *Anomiostrea coralliophila*. **A.** Left valve of individual 1. **B.** Right valve of individual 1, which is attached to by the left valve of individual 2 (smaller). **C.** Right valve of individual 2. Scale bar = 1 cm.

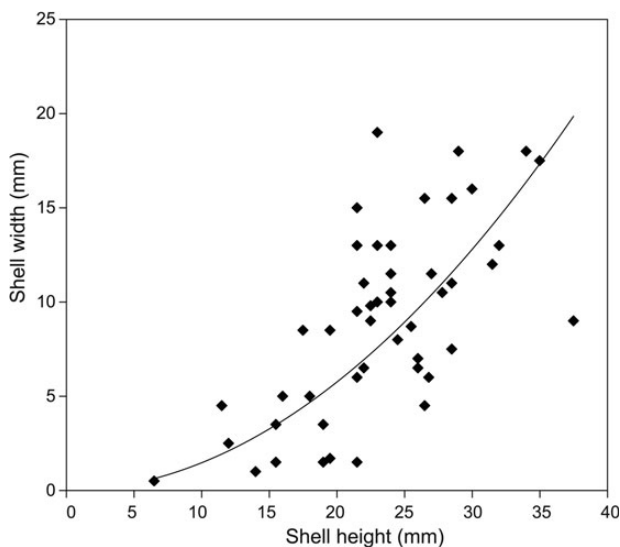


Figure 3. Relationship between shell height and shell width in *Anomiotrea coralliophila*. Regression curve: $y = 0.0156x^{1.9725}$ ($R^2 = 0.55$).

by the host) (Yonge, 1951). Indeed, most symbiotic bivalves living in animal burrows can move actively using their muscular feet (e.g. Yonge, 1951; Goto, Hamamura & Kato, 2011). However, *A. coralliophila* is firmly attached to the substrate, embedded in the burrow wall by cementation. This suggests that the burrow of *N. jousseaumei* is a very stable environment, where the burrow routes rarely change. If *A. coralliophila* benefits the host shrimp in some way, the host shrimp may construct the burrow to include the bivalves inside it.

The type specimen of *A. coralliophila* was collected in the Philippines (Adams & Reeve, 1848) and it has since been recorded in various places in the Indo-West Pacific, from the Red Sea to Borneo (Huber, 2010). The host shrimp *N. jousseaumei* has also been recorded widely in the Indo-West Pacific, from the Red Sea to French Polynesia (Dworschak, 2011). The large overlap in their distributions suggests that the symbiotic association of these two species occurs widely in the Indo-West Pacific. No other host of *A. coralliophila* has yet been reported. Considering that *A. coralliophila* has a relatively large shell (Fig. 3), possible hosts are limited to animals that construct large burrows. The other axiidean shrimp that constructs relatively spacious burrows, *Neaxius* sp., often coexists with *N. jousseaumei* at our study site. However, we did not observe any of the symbionts of *N. jousseaumei*, including *A. coralliophila*, in the burrows of *Neaxius* sp. This suggests that host burrow size is not the sole determinant of host specificity of these symbionts.

This study provides a new example of a burrow associate from the family Ostreidae. Apart from *A. coralliophila*, several other ostreids have symbiotic associations with other animals. For example, *Cryptostrea permollis* (Sowerby, 1871) is known to live in sponges (Forbes, 1966). An intriguing question is how these symbiotic species evolved in this family. To answer this question, we are now analysing the molecular phylogeny of this bivalve group.

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