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Mucus-net feeding behavior by the sessile gastropod *Thylacodes adamsii* (Gastropoda: Vermetidae)

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Abstract. Vermetid gastropod *Thylacodes adamsii* secrete a mucus net for feeding. We observed a feeding behavior of *T. adamsii* in the intertidal zone of Shirahama, the coast facing the Pacific Ocean. *Thylacodes adamsii* spread its mucus net within 20 minutes of submergence. Creating a network of mucus threads immediately after submergence may be important for efficient feeding when *T. adamsii* is distributed in the intertidal zone. Additionally, we investigated the organisms trapped in the mucus net, because identifying the species from the stomach contents of *T. adamsii* was difficult. The organisms trapped on *T. adamsii* mucus nets in Shirahama included Dinophyta, Nematoda, Annelida, Arthropoda, Gastropoda, Chordata, and particles of seaweeds. By contrast, the most frequently trapped organisms in Maizuru, the coast facing the Sea of Japan, were diatoms. The difference between organisms trapped in Shirahama and Maizuru is probably due to the different vertical distribution of *T. adamsii* at the two locations.

Keywords: feeding cycle, Mollusca, intertidal, subtidal, Shirahama, Maizuru

1. Introduction

Many marine organisms use mucus for their vital processes. Molluscs secrete mucus for movement (e.g., Denny, 2008), defense (e.g., Ocaña, 2003), and feeding (e.g., Kamimura and Tsuchiya, 2004). Some species, including *Patella pellucida*, use mucus threads like a sail to drift within water currents (Vahl, 1983). These sail-like mucus threads are highly effective in aiding the dispersal of young *Mytilus edulis* (Lane et al., 1985). *Siphonaria pectinata*, meanwhile, produce a thick, white toxic mucus in order defend against predation (Ocaña, 2003). Some gastropods are suspension feeders. They trap suspended particles through mucus feeding, ciliary feeding, and filter feeding, using all three methods separately or together (Declerck, 1995). The family Vermetidae, Ampullariidae, Olividae, and Trimusculidae spew mucus nets for feeding (Declerck, 1995). For other examples, *Batillaria zonalis* forms a mucus 'food cord' to entangle particulate materials, which are subsequently ingested (Kamimura and Tsuchiya, 2004). *Trimusculus conicus* (as *Gadinalea nivea*) secretes the mucus net as a curtain in front of the head, extending outwards from the mantle margin, and ballooning out with the current from behind (Walsby et al., 1973). Pelagic tunicates of the genus *Oikopleura* also produce mucous structures termed 'houses' in order to suspension feed (Flood et al., 1992).

Multiple studies examine the feeding habits of vermetid gastropods: *Ceraesignum maximum* (Hughes and Lewis, 1974; Kappner et al., 2000; Gagern et al., 2008); *Thylacodes natalensis* (Hughes, 1978); *Dendropoma corallinaceum* (Hughes, 1978); *Eualetes tulipa* (Hughes, 1985).

Hughes (1978) compared the feeding behavior of *D. corallinaceum* on exposed shores and *T. natalensis* under stones in sheltered shores in South Africa. They showed that *S. natalensis* have a slower feeding rhythm due to their larger body size, and that neighboring *S. natalensis* individuals have synchronized feeding rhythms to reduce net robbing. *Ceraesignum maximum* also shorten their feeding time when living at high densities, in order to prevent other individuals from depriving their mucus net (Gagern et al., 2008).

Except for Ishida (2003), however, there are no studies on the feeding habits or mucus net use of vermetid gastropods in Japan. Furthermore, only a few studies what food items vermetid gastropods trap with their mucus nets. In this paper, we examined how *Thylacodes adamsii* cast their mucus net in the field, and observed what food resources they trapped in their nets. Since it was difficult to identify the species from the stomach contents of *T. adamsii*, we collected mucus nets cast in the sea and analyzed their contents.

2. Materials and Methods

2.1. Observation of feeding behavior of **T. adamisii in situ**

The survey was conducted in the intertidal zone at the south side of Bansho-zaki, Shirahama on 21 November 2018. Five *T. adamsii* individuals were marked and 10 mm × 10 mm cutting boards were placed at the front of the specimen shell apertures. Specimens were photographed four times: at 5, 10, 15, and 20 minutes after submersion. The size of mucus nets was estimated from the photo images. In addition, one individual was observed in detail for five minutes after submersion. The length and extension of the mucus thread was estimated every minute after submergence using a video recording captured by a waterproof camera. The change of mucus thread length in those five minutes was analyzed.

2.2. Organisms trapped on mucus net

Mucus nets spewed out from *T. adamsii* were collected from three localities: at the north side of Bansho-zaki in Shirahama on 18 November, 2018; at the south side of Bansho-zaki in Shirahama on 20 November, 2018; and at the beach in front of Fisheries Research Station in Maizuru on 30 November, 2018 (see Fig. 1; Kusama et al., 2021).

Samples were obtained from 10 individuals per survey site. Using tweezers, each individual's mucus net was collected from the seawater. In the laboratory, all samples were observed in detail, and the organisms trapped in the mucus nets were identified. The number of each type of trapped organism was categorized by the following indexes, and included five stages: for animal and diatoms, zero individuals (blank), one individual (-), two-five individuals (+), six-20 individuals (++), 21 individuals or more (+++); for algae, zero fragments (blank), one fragment (-), two-five fragments (+), six-20 fragments (++), 21 fragments or more (+++). The size of one alga within the 2 mm × 2 mm frame was defined as "one fragment."

3. Results

3.1. Mucus net spewed out in field

Figs. 1–4 show the change in the area of the mucus nets at 5, 10, 15, and 20 minutes after submersion. The average spreading area of the mucus net in five individuals was 2.1 cm^2 at 5 minutes after submersion, 2.9 cm^2

at 10 minutes, 4.6 cm^2 at 15 minutes, and 6.8 cm^2 at 20 minutes. The size increase of the mucus net was different for each individual.

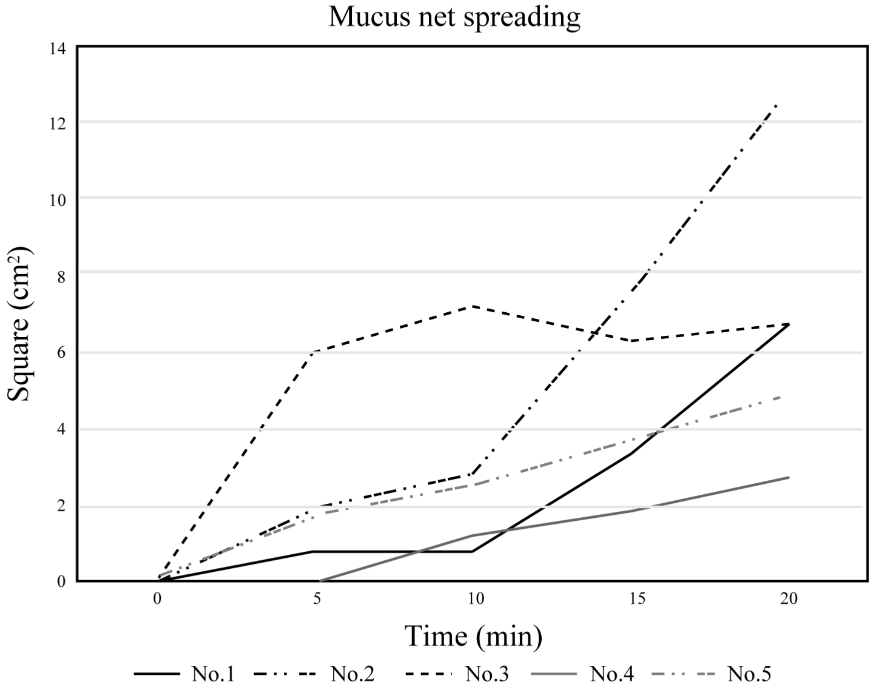

Figure 1. The increase of mucus net spread by *Thylacodes adamsii* in the intertidal rocky shore in Shirahama. The numbers 1–5 indicate each individual.

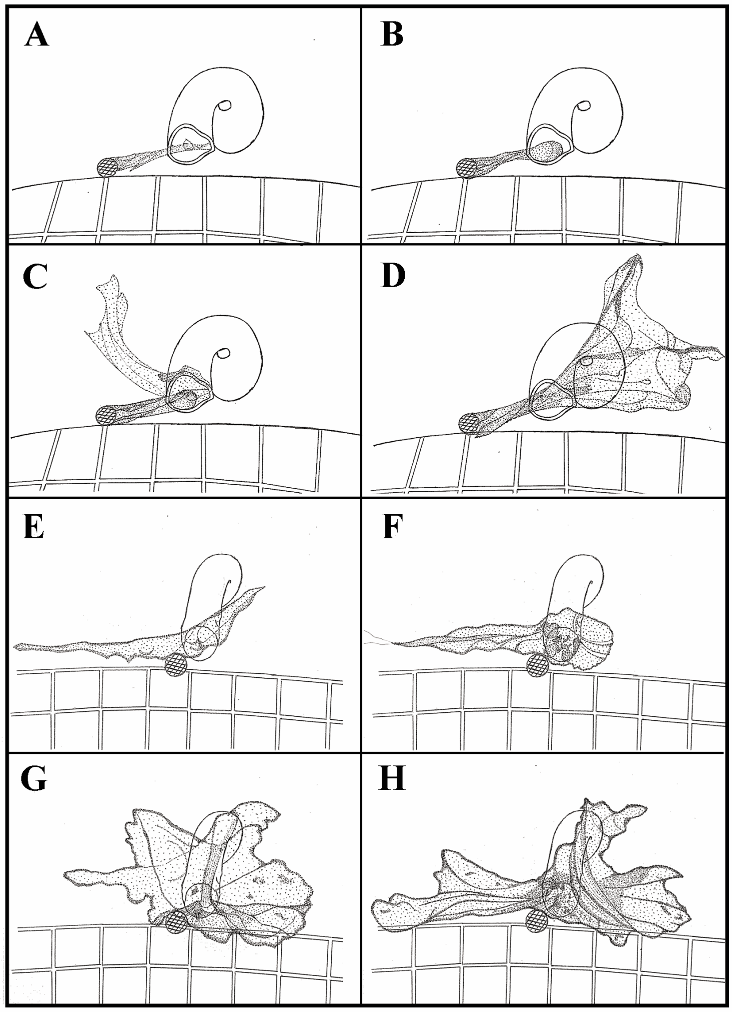

Figure 2. (A)–(D) Mucus spreading of No. 1 individual at 5, 10, 15 and 20 minutes after submergence respectively. (E)–(H) Mucus spreading of No. 2 individual at 5, 10, 15 and 20 minutes after submergence respectively.

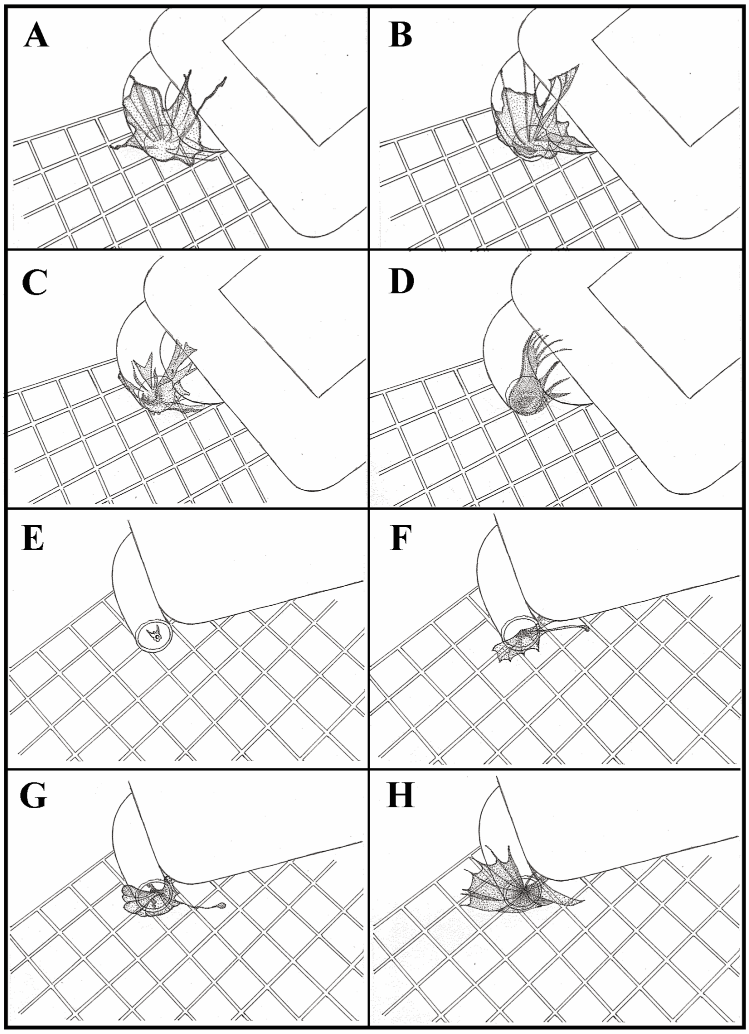

Figure 3. (A)–(D) Mucus spreading of No. 3 individual at 5, 10, 15 and 20 minutes after submergence respectively. (E)–(H) Mucus spreading of No. 4 individual at 5, 10, 15 and 20 minutes after submergence respectively.

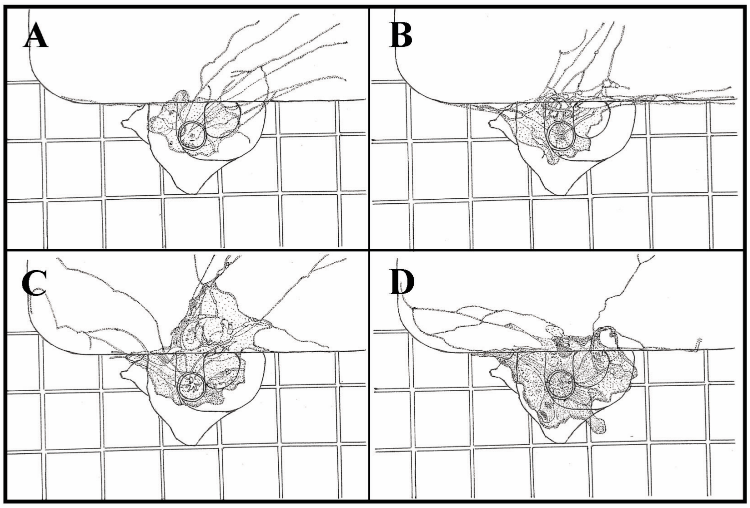

Figure 4. (A)–(D) Mucus spreading of No.5 individual at 5, 10, 15 and 20 minutes after submergence respectively.

Figs. 5 and 6 show the change in the longest distance of the mucus net within 5 minutes after submersion. Just after submersion, there was a very short mucus thread, 1.1 cm long. Five minutes after submergence, the thread had increased in length by 0.84 cm per minute.

From our video recording, we observed the following feeding habit: The immediate elongation of mucus thread was mainly observed at the moment when seawater flowed from behind the shell aperture. This elongation occurred many times, and several mucus threads were elongated. The tip of each mucus thread was attached to the substrate. The motion of the water caused the mucus threads to entangle with each other, eventually forming a net shape.

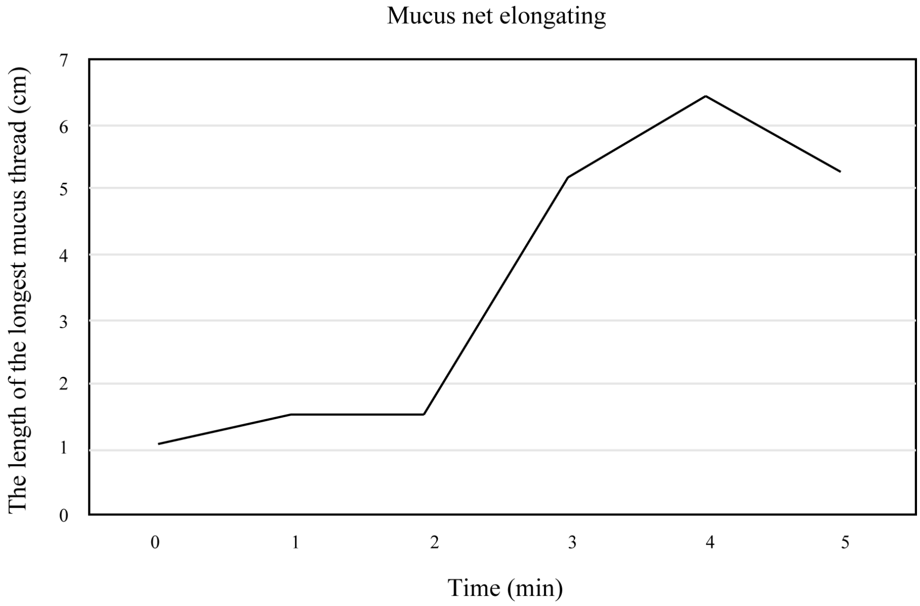

Figure 5. The increase of mucus thread elongated by *Thylacodes adamsii* in the intertidal zone in Shirahama.

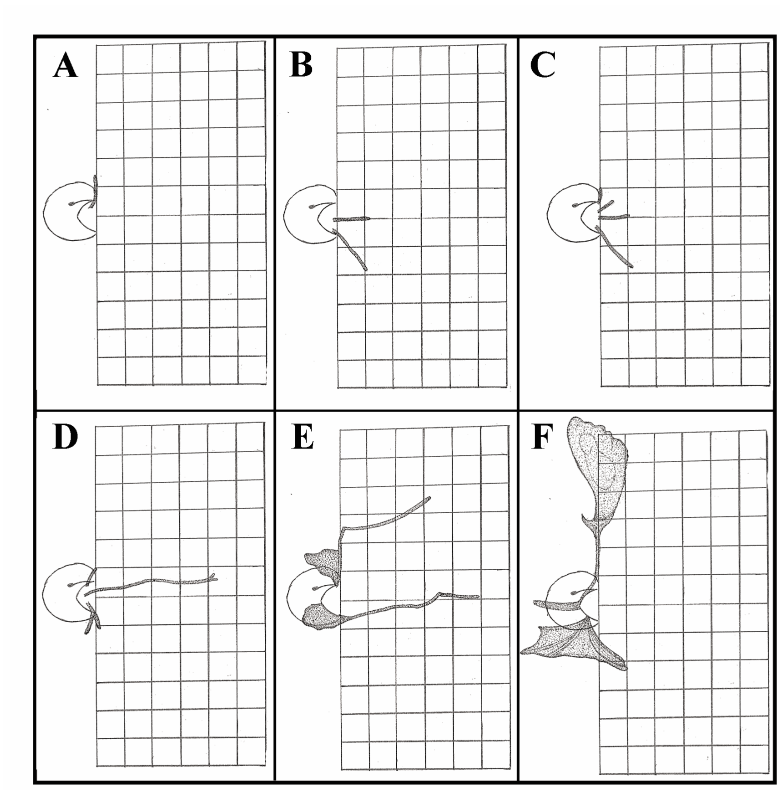

Figure 6. (A)–(F) Mucus spreading of *Thylacodes adamisii* in 0, 1, 2, 3, 4, and 5 minutes after submergence respectively.

3.2. Animals, diatoms, and algae trapped on mucus net

At the north side of Bansho-zaki in Shirahama, trapped organisms in the mucus nets comprised 13 species in six phyla of animals including Dinophyta, Nematoda, Annelida, Arthropoda, Gastropoda, and Chordata, two species of Rodophyta, two species of Chlorophyta, and one species of Diotomea. At the south side of Bansho-zaki in Shirahama, trapped organisms in the mucus nets comprised 11 species in five phyla of animals including Dinophyta, Nematoda, Annelida, Gastropoda, and Arthropoda, two species of Rodophyta, three species of Chlorophyta, and three species of Diotomea. At the beach in front of Fisheries Research Station in Maizuru, trapped organisms in the mucus nets were composed of three species in one phyla of Arthropoda, two species of Diotomea and no algae. The quantity of each organism at each survey site is summarized in Appendix Tables 1–3. Representatives of animal, diatom, and alga trapped on mucus net are shown in Plates 1–6.

4. Discussion

4.1. Expansion of mucus net

In field observations, *T. adamsii* spread its mucus net within 20 minutes after submergence. For individuals distributed in the intertidal zone, as in Shirahama, it may be important create a network of mucus threads immediately after submergence for efficient feeding. Vermetid gastropods that make mucus net in order to trap suspended food items show a series of eating behaviors. Prior studies examined the feeding cycle of other vermetid gastropods. In the Red Sea, the feeding cycle of C. maximum was observed at 13 minutes for discharge and 2 minutes for recovery (Hughes and Lewis, 1974) or 31 minutes for discharge and 3 minutes for recovery (Kappner et al, 2000).

In this survey, it was observed that *T. adamsii* partially ate their mucus net and spewed out new mucus thread after forming a full net. However, they did not collect the mucus net completely and create a new net from scratch. Therefore, the feeding cycle of the individuals in Shirahama may consist of both partial withdrawal and partial emission of the mucus net.

4.2. Trapped organisms on mucus net

Thylacodes adamsii individuals living on rocky shores captured a variety of organisms in their mucus nets, including Dinophyta, Nematoda, Annelida, Arthropoda, Gastropoda, and Chordata, and particles of seaweeds. Similarly, Kappner et al. (2000) found Diatom, Nematoda, Copepoda, and fragments of macroalgae in the mucus net of *C. maximum* in shallow reefs. Irrespective of the type of substrata, vermetid gastropods trap similar organisms using mucus net in intertidal zones. However, whereas a variety of organisms were seen on mucous net of *T. adamsii* in Shirahama, the most frequently trapped organisms in Maizuru were diatoms. The difference of trapped organisms between Shirahama and Maizuru is probably due to the distinct vertical distribution of the *T. adamsii* individuals. The population at Shirahama inhabits the intertidal rocky shores, while, the population at Maizuru live in the subtidal zone on mud flats (Kusama et al., 2021). The population of T. adamsii inhabiting the intertidal zone may be able to trap the organisms efficiently due to the complicated water currents in the intertidal zone, whereas it may be difficult to trap organisms in subtidal zone without sufficient water current.

Hughes & Lewis (1974) reported that *C. maximum* cannot digest shells and seaweed fragments larger than 2 mm. Hughes (1978) also suggested that many particles on mucus net are filtered out and rejected in the pseudofaeces. Vermetid gastropods can remove the debris when indigestible particles increased on their mucus net (Kappner et al., 2000). It was difficult to identify the species from the stomach contents of T. adamsii, we observed the organisms on the mucus net. For T. adamsii in Shirahama, larger algal fragments and micro gastropods may be difficult to digest. Therefore, the larger organisms are likely to be removed as indigestible particles. In Maizuru, on the other hand, small diatoms may be the main feed resource, and there is a possibility that bait resources can be utilized more efficiently than in Shirahama.

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Appendix Table 1. The list of organisms observed in the mucus net of *Thylacodes adamsii* in the north side of Banshozaki, Shirahama.

The amount of each organism was categorized in 5 stages; 0, blank; 1, -; 2–5, +; 6–20, ++; 21–, +++.

		1	2	3	4	5	6	7	8	9	10
Animals	*Noctiluca scintillans*	-	-			-					-
	Nematoda sp.					+			+		
	Polychaeta sp.					-					
	Copepoda sp. 1	+	+	-	+	+	-	+	+		+
	Copepoda sp. 2							-			
	Copepoda sp. 3		+		+	++	-	+			
	Copepoda sp. 4				+						
	Ostracoda sp.	-	-						-	+	-
	Hydrachnellae sp.					-				-	
	The exuvium of Cirripedia sp. 1	-		-		+		-	+	-	+
	Gastropoda sp.				-						
	Creseis sp.						-	+		-	
	Oikopleuridae sp.		-	-				-			
Algae	Rhodophyta sp. 1	+	+	+		-	+				-
	Rhodophyta sp. 2	+	+	++	+	+	+	++	++	+	-
	Chlorophyta sp. 1					-					
	Chlorophyta sp. 2	-	-	+	-	+		-	+	-	+
Diatoms	Bacillariophyceae sp. 1					-					

Appendix Table 2. The list of organisms observed in the mucus net of *Thylacodes adamsii* in the south side of Banshozaki, Shirahama.
The amount of each organism was categorized in 5 stages; 0, blank; 1, -; 2–5, +; 6–20, ++; 21–, +++.

		1	2	3	4	5	6	7	8	9	10
Animals	*Noctiluca scintillans*			+		-					
	Nematoda sp.	-	+	+	+		+	+	+	+	-
	Polychaeta sp.	-		+	-			-			
	Copepoda sp. 1	+		+	-	+		+		+	-
	Copepoda sp. 2		-								-
	Copepoda sp. 3								-		
	Ostracoda sp.										
	Hydrachnellae sp.							-			-
	The exuvium of Cirripedia sp. 1	+						+			
	The exuvium of Decapoda sp.									-	
	Gastropoda sp.									+	-
Algae	Rhodophyta sp. 1	++	++	+	+	++	-	+	+	++	+
	Rhodophyta sp. 2	++	+++	++	++	+	+	++	+++	+++	+++
	Chlorophyta sp. 1	-						+	+	+	
	Chlorophyta sp. 2	+++	+++	+++	++	++	++	+++	+++	+++	+++
	Chlorophyta sp. 3										
Diatoms	Bacillariophyceae sp. 1			+					-		+
	Bacillariophyceae sp. 2	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++
	Bacillariophyceae sp. 3						+				

Appendix Table 3. The list of organisms observed in the mucus net of *Thylacodes adamsii* in Maizuru.
The amount of each organism was categorized in 5 stages; 0, blank; 1, -; 2–5, +; 6–20, ++; 21–, +++.

		1	2	3	4	5	6	7	8	9	10
Animals	Copepoda sp. 5							-			
	The exuvium of Cirrpedia sp. 2										-
	The exuvium of Decapoda sp.									-	
Diatoms	Bacillariophyceae sp. 4	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++
	Bacillariophyceae sp. 5	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++

Plate 1. Animals observed in the mucus net of *Thylacodes adamsii* in Shirahama. (A) *Noctiluca scintillans*, (B) Nematoda sp., (C) Polychaeta sp., (D) Copepoda sp. 1, (E) Copepoda sp. 2, (F) Copepoda sp. 3. Scale bars = 0.1 mm.

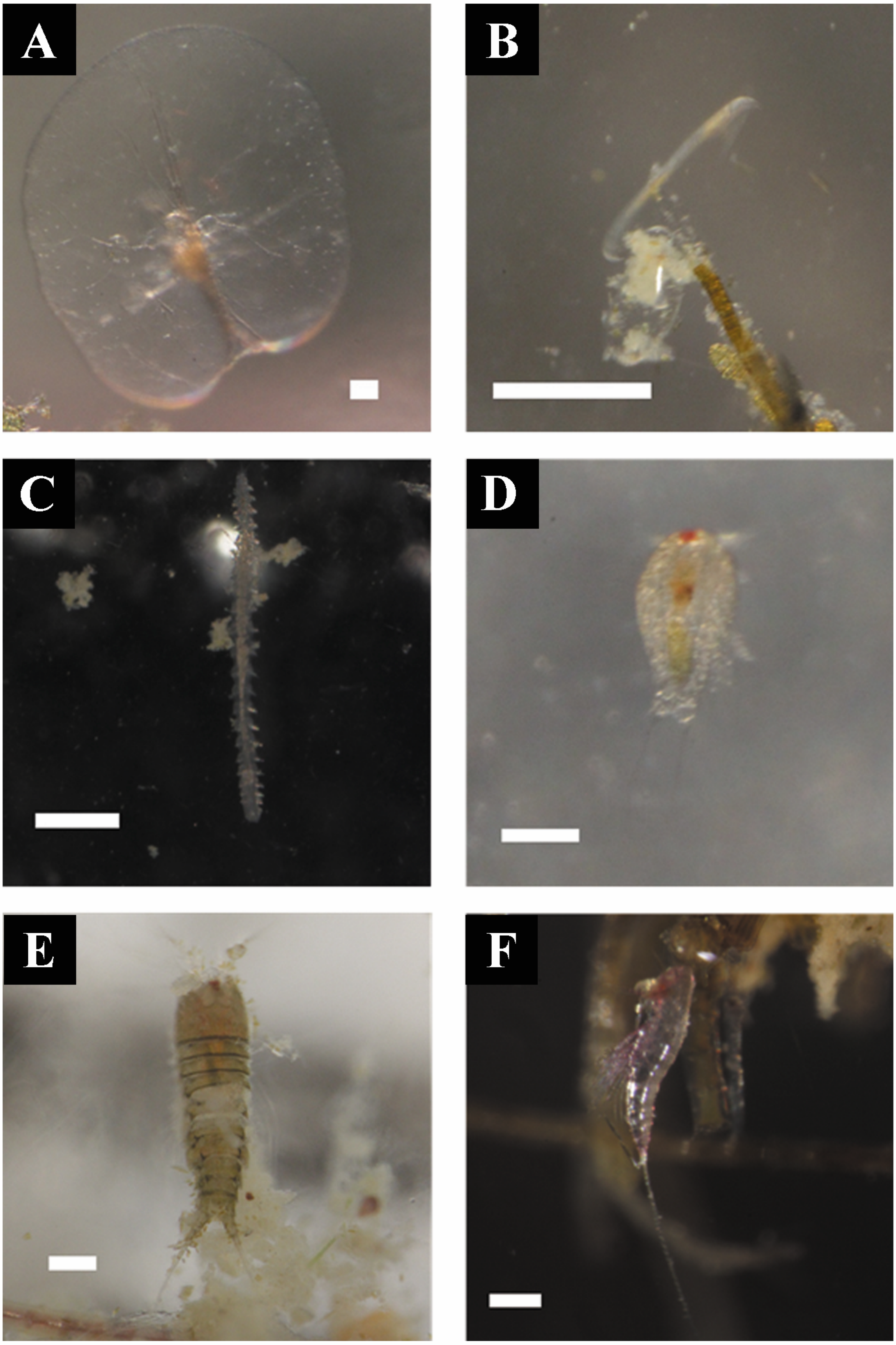

Plate 2. Animals observed on the mucus net of *Thylacodes adamsii* in Shirahama. (A) Copepoda sp. 4., (B) Ostracoda sp., (C) Hydrachnellae sp., (D) the exuvium of Cirripedia sp. 1, (E) Gastropoda sp., (F) the exuvium of Decapoda sp. Scale bars = 0.1 mm.

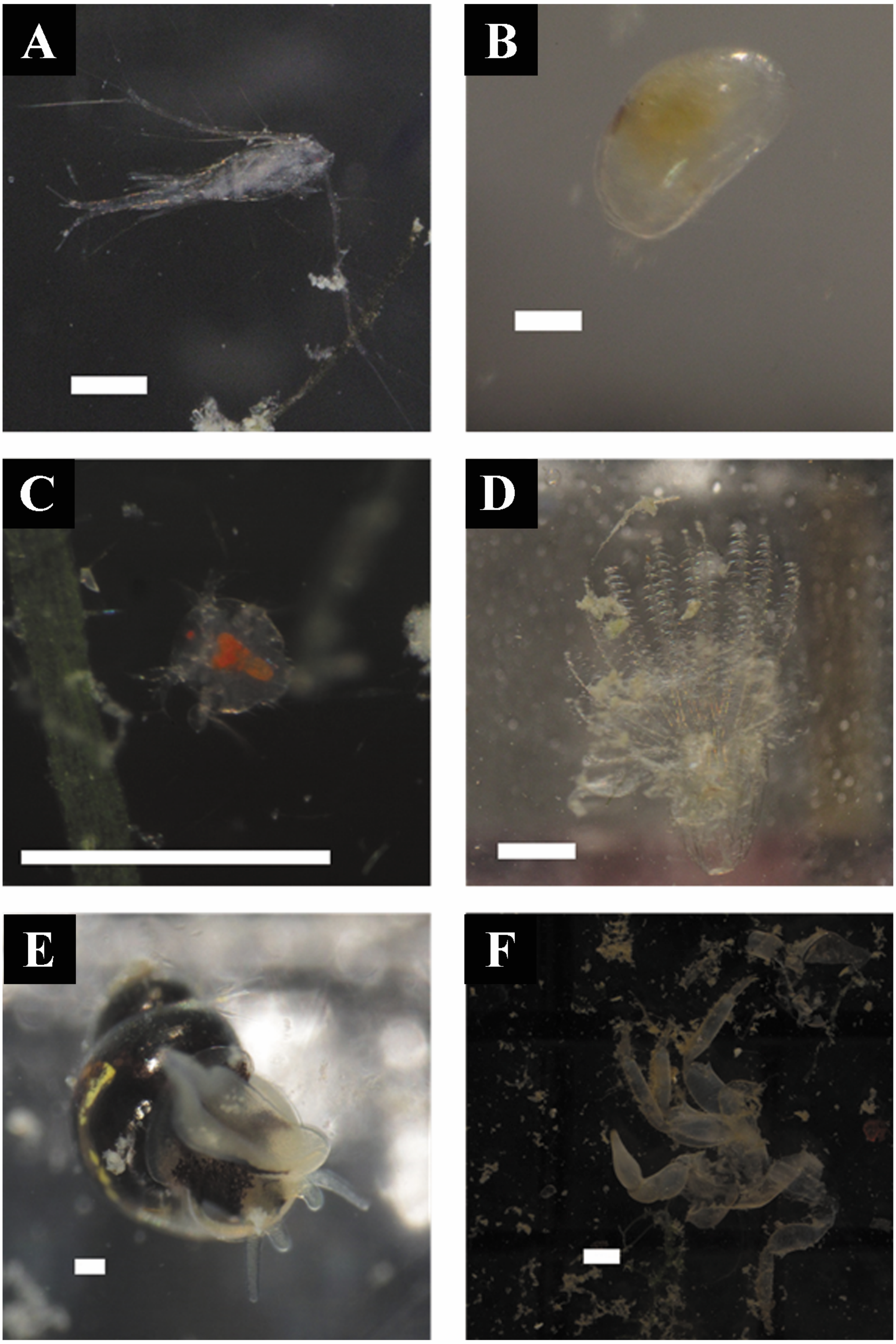

Plate 3. Animals observed in the mucus net of *Thylacodes adamsii* in Shirahama. (A) *Creseis* sp., (B) Oikopleuridae sp. Scale bars = 0.1 mm.

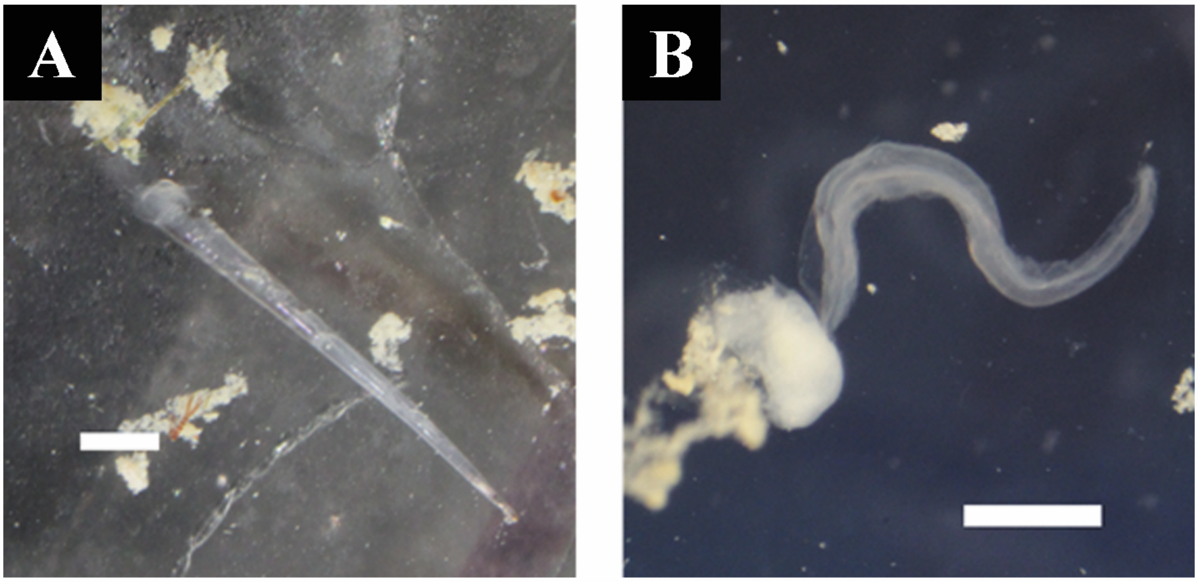

Plate 4. Algae observed in the mucus net of *Thylacodes adamsii* in Shirahama. (A) Rhodophyta sp. 1, (B) Rhodophyta sp. 2, (C) Chlorophyta sp. 1, (D) Chlorophyta sp. 2, (E) Chlorophyta sp. 3.
Scale bars = 1 mm.

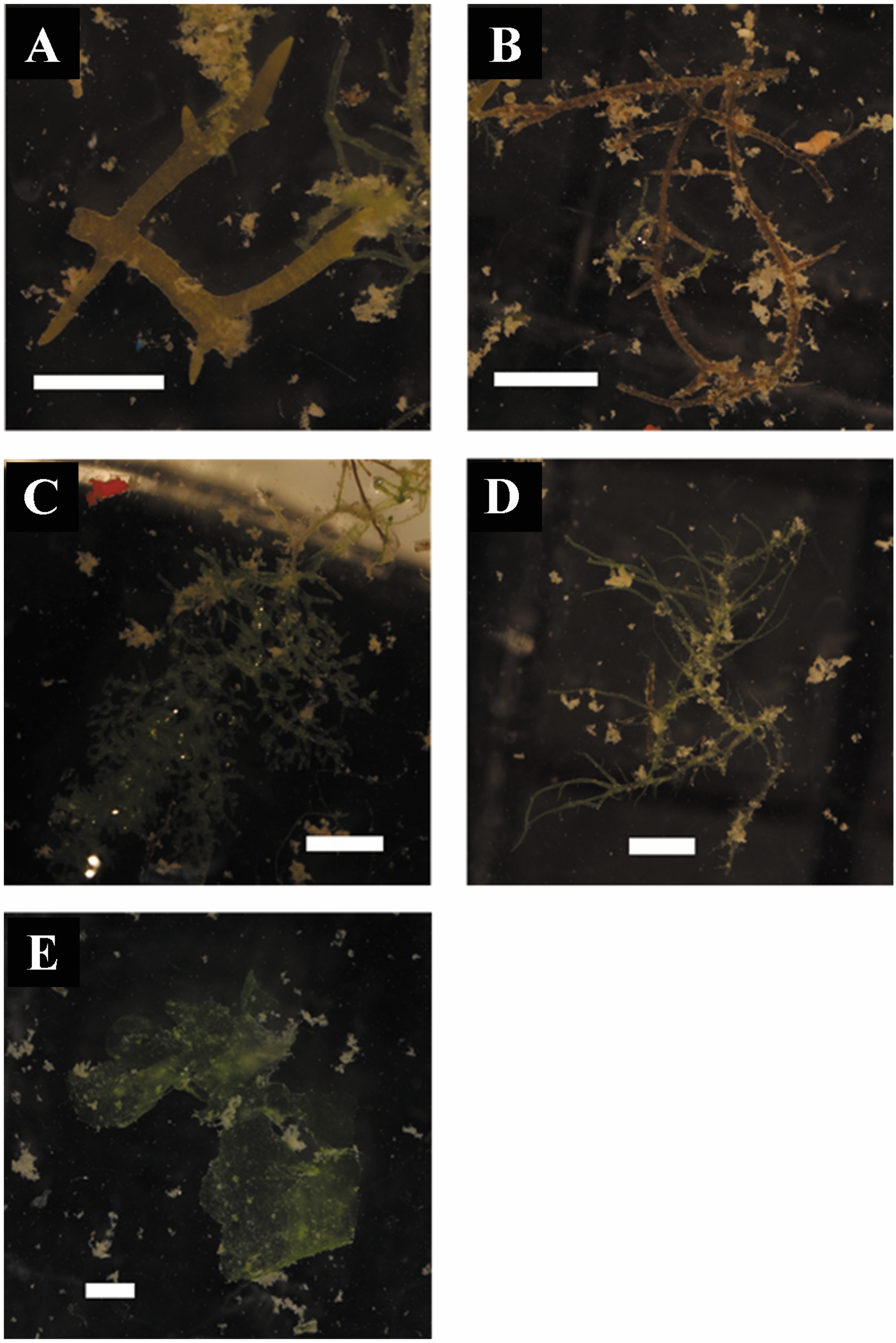

Plate 5. Diatoms observed in the mucus net of *Thylacodes adamsii* in Shirahama. (A) Bacillariophyceae sp. 1, (B) Bacillariophyceae sp. 2, (C) Bacillariophyceae sp. 3. Scale bars = 0.1 mm.

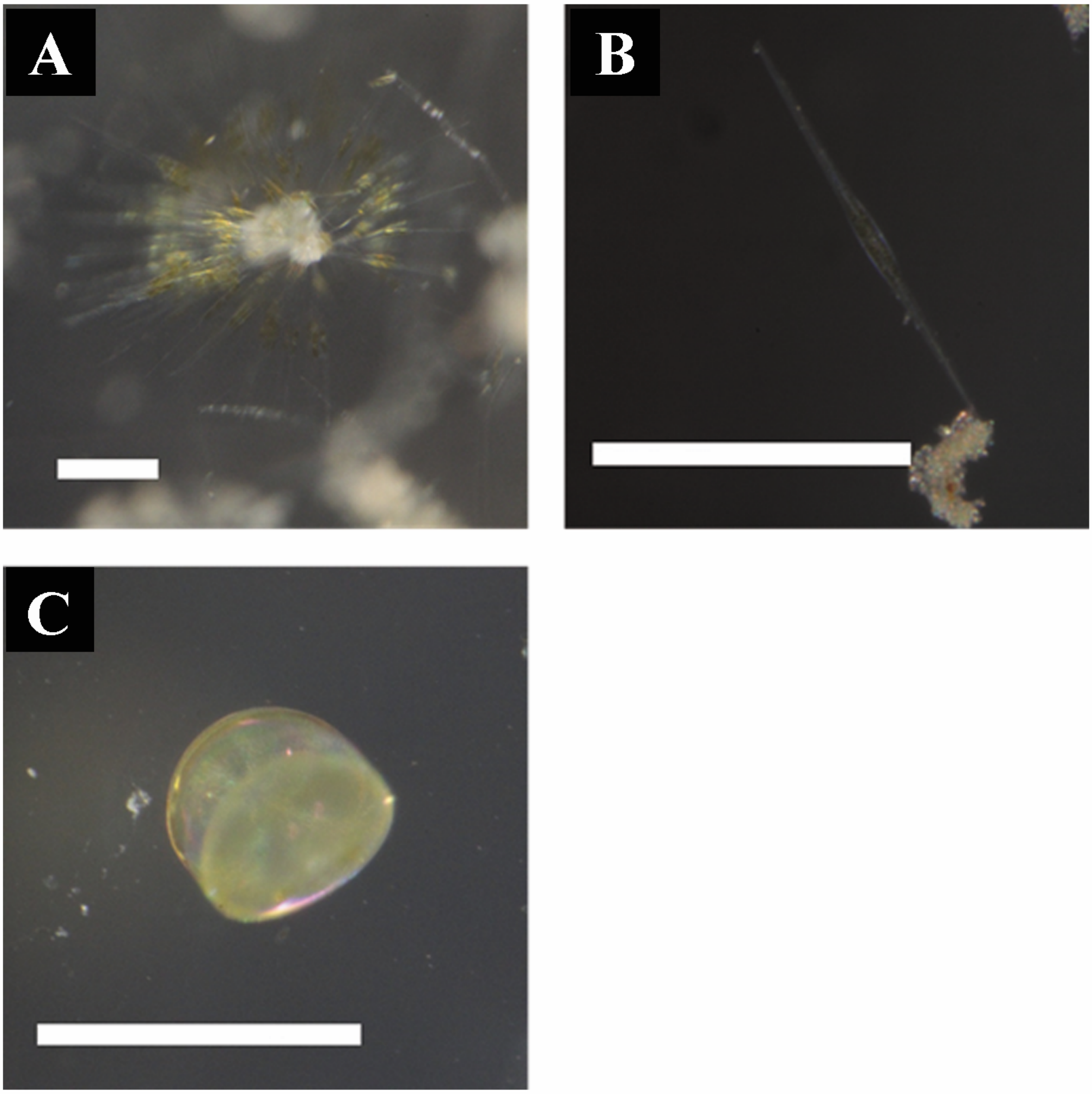

Plate 6. Organisms observed in the mucus net of *Thylacodes adamsii* in Maizuru. (A) Copepoda sp. 5, (B) the exuvium of Cirripedia sp. 2, (C) the exuvium of Crustacea sp., (D) Bacillariophyceae sp. 4, (E) Bacillariophyceae sp. 5. Scale bars = 0.1 mm.