



# Mussel biology: from the byssus to ecology and physiology, including microplastic ingestion and deep-sea adaptations

Koji Inoue<sup>1</sup> · Yuri Onitsuka<sup>2,1</sup> · Tomoko Koito<sup>3</sup>

Received: 12 May 2021 / Accepted: 25 August 2021 / Published online: 16 September 2021  
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## Abstract

Mussels are a group of bivalves that includes the dominant species of shallow-sea, freshwater, and deep-sea chemosynthetic ecosystems. Mussels cling to various solid underwater surfaces using a proteinaceous thread, called the byssus, which is central to their ecology, physiology, and evolution. Mussels cluster using their byssi to form “mussel beds,” thereby increasing their biomass per unit of habitat area, and also creating habitats for other organisms. Clustered mussels actively filter feed to obtain nutrients, but also ingest pollutants and suspended particles; thus, mussels are good subjects for pollution analyses, especially for microplastic pollution. The byssus also facilitates invasiveness, allowing mussels to hitchhike on ships, and to utilize other man-made structures, including quay walls and power plant inlets, which are less attractive to native species. Physiologically, mussels have adapted to environmental stressors associated with a sessile lifestyle. Osmotic adaptation is especially important for life in intertidal zones, and taurine is a major component of that adaptation. Taurine accumulation systems have also been modified to adapt to sulfide-rich environments near deep-sea hydrothermal vents. The byssus may have also enabled access to vent environments, allowing mussels to attach to “evolutionary stepping stones” and also to vent chimneys.

**Keywords** *Bathymodiolus* · Foot proteins · Genome · Hypotaurine · Microplastic ingestion · *Mytilus* · *Perna* · Underwater adhesion

## Introduction

Mussels are bivalves, most of which belong to the family Mytilidae (Gosling 1992), although some non-mytilid species, such as quagga and zebra mussels, belong to the family Dreissenidae (Higgins and Vander Zanden 2010). Some

mussel species are familiar to people world-wide because they are abundant in coastal areas, even around human habitations (Veiga et al. 2020). Mussels of the genera *Mytilus* and *Perna* (Fig. 1), distributed from temperate to polar and subtropical to tropical marine zones, respectively, are popular as food and are actively cultured (Gosling 1992; Maquirang et al. 2020; Cabre et al. 2021). In addition, mussels are distributed in freshwater and even in deep seas (Fig. 1), where they often dominate their communities (de Paula et al. 2020; Laming et al. 2018; Lee et al. 2019). However, many mussel species are notoriously invasive, expanding their distributions to non-native areas (Pickett and David 2018; Rajagopal et al. 2006). Some species are major biofoulers, clustering on the hulls of vessels, and invade man-made underwater structures (Amini et al. 2017; de Paula et al. 2020). These unique capacities of mussels derive largely from their ability to attach to underwater surfaces using the proteinous hold-fast called the byssus, which is tough, durable, and resistant to chemical and enzymatic degradation (Waite 2017). In this article, we discuss mussel biology in terms of the byssus,

✉ Koji Inoue  
inouek@aori.u-tokyo.ac.jp

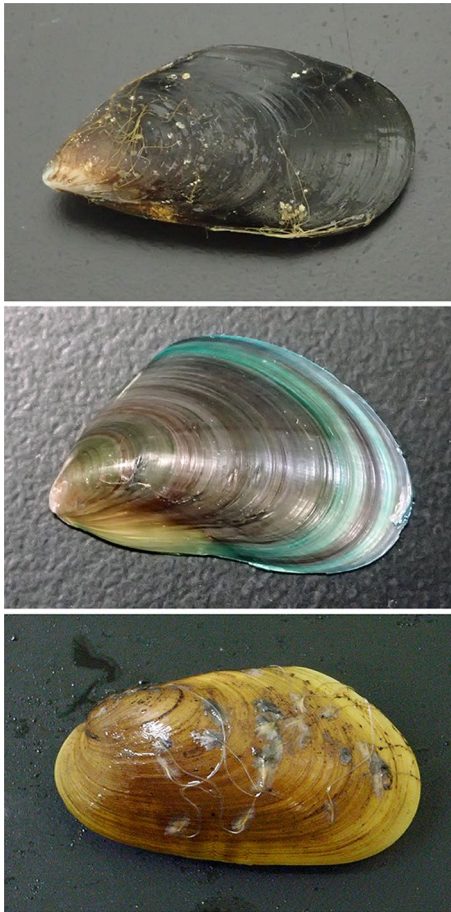
Yuri Onitsuka  
7127933519@edu.k.u-tokyo.ac.jp

Tomoko Koito  
koito.tomoko@nihon-u.ac.jp

<sup>1</sup> Atmosphere and Ocean Research Institute, The University of Tokyo, Kashiwa, Japan

<sup>2</sup> Graduate School of Frontier Sciences, The University of Tokyo, Kashiwa, Japan

<sup>3</sup> Department of Marine Science and Resources, College of Bioresource Sciences, Nihon University, Fujisawa, Japan

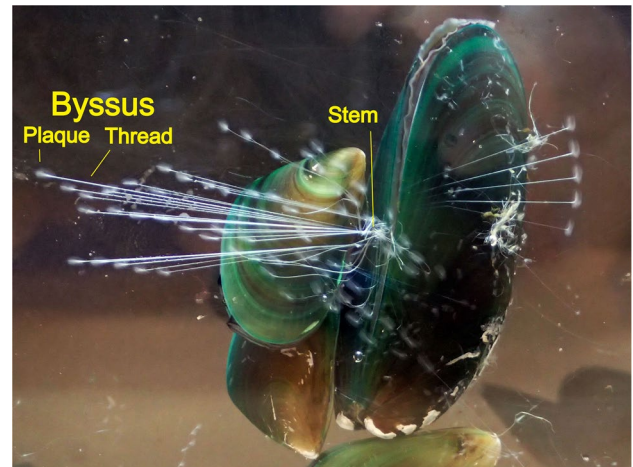


**Fig. 1** Mytilid mussels. Upper panel, *Mytilus galloprovincialis*; middle panel, *Perna viridis*; lower panel, *Bathymodiolus septemdiarum*. Adapted from Sassa et al. (2019)

and we discuss the significance of their sessile lifestyle in regard to mussel ecology, physiology, and evolution.

## Byssus

The byssus is used by the mussel to attach to underwater surfaces. It is composed of a thread and an adhesive plaque (Fig. 2) (Waite 2017). These plaques can attach to various surfaces such as concrete, metal, and plastic, in addition to rock, and not surprisingly, the adhesion mechanisms function underwater (Lin et al. 2007). Several byssi are bundled at a stem (Fig. 2) and connect to byssus retractor muscles in the shell (Waite 1992). Therefore, the strength of mussel attachment depends both on the strength of the byssus (Waite et al. 2002) and on the mussel's muscular endurance, known as the “catch phenomenon” (Funabara et al. 2003). Components of the byssus have been studied since the 1980s (Waite and Tanzer 1981), and many protein components have been discovered and characterized (Waite 1992;



**Fig. 2** Green mussels *Perna viridis*, attached to a transparent acrylic board, using the byssus. Adapted from Inoue et al. (2021)

2017; Bandara et al. 2013; Priemel et al. 2017 for review). Such studies are motivated by basic science, to understand the phenomenon of tough, durable underwater adhesion, but also by practical applications to develop underwater or surgical adhesives and useful polymers (Forooshani and Lee 2017; Zhang et al. 2017a, b; Guo et al. 2020; Basak 2021), and to develop antifouling paints or materials by understanding plaque chemistry (Damodaran and Murthy 2016; Amini et al. 2017). The main structure of the thread comprises a gradient of stiff and elastic collagens (Col-D and Col-P, respectively) connected by a third type (Col-NG) (Qin and Waite 1998; Waite et al. 2002). In the plaque and in the cuticle surrounding the byssus, proteins known as foot proteins (Fps) have been identified. Since the discovery of Fp-1 in *Mytilus edulis* (Waite and Tanzer 1981), Fps-2 through -6 have been discovered (Bandara et al. 2013; Waite 2017), and corresponding proteins and genes have also been identified in *Perna viridis* (Guerette et al. 2013; Zhang et al. 2019). Fps-3, -5, and -6 are thought to function at the plaque–substrate interface (Hwang et al. 2010). In addition, many other Fps have been suggested from transcriptomic analyses of *Mytilus californianus* (DeMartini et al. 2017). Most Fps contain 3,4-dihydroxyphenylalanine (Dopa) residues, which are thought to contribute to polymerization of Fps (Bandara et al. 2013; Waite 2017). These Dopa residues are encoded as tyrosine in corresponding genes (Inoue and Odo 1994; Inoue et al. 1995a; 1996), and are hydroxylated posttranslationally (Waite 2017). Tyrosinases, which convert tyrosine to Dopa, have been discovered by molecular cloning, transcriptomic, genomic, and proteomic analyses (Guerette et al. 2013; Qin et al. 2016; Zhang et al. 2017a, b; Wang et al. 2019; Zhang et al. 2019; Inoue et al. 2021). Other enzymes involved in collagen and Fp processing have also been suggested by transcriptomic and genomic analyses (Inoue et al.

2021). Moreover, a recent genomic and foot-specific transcriptome analysis in *P. viridis* revealed that many proteinase inhibitors and defense proteins are expressed in the foot and are thought to protect the byssus from degradation (Inoue et al. 2021). Interestingly, despite the tough and durable nature of the byssus, attachment of mussels is not permanent; mussels can gradually change their positions by making new byssi and discarding old ones (Imai S, Takabayashi Y, unpublished observations in *M. galloprovincialis*).

## Byssus and mussel beds

Using their byssi, mussels can also attach to another. By so doing, mussels can form large aggregations called “mussel beds.” From an ecological viewpoint, mussel beds are very important (Gosling 1992; Engel et al. 2017). These multi-layered structures enable mussels to achieve extremely high biomass. Mussels actively capture plankton and small particles in the water by filter feeding, which influences entire ecosystems, and occupy important positions in the food web. In addition, mussels are known as ecosystem engineers as mussel beds offer habitat or shelter for other organisms (Koivisto and Westerborn 2012; Engel et al. 2017; de Fouw et al. 2020; Ricklefs et al. 2020). Spaces between individual mussels are especially suitable habitat for small organisms. Thus, the byssus is central to mussel ecology.

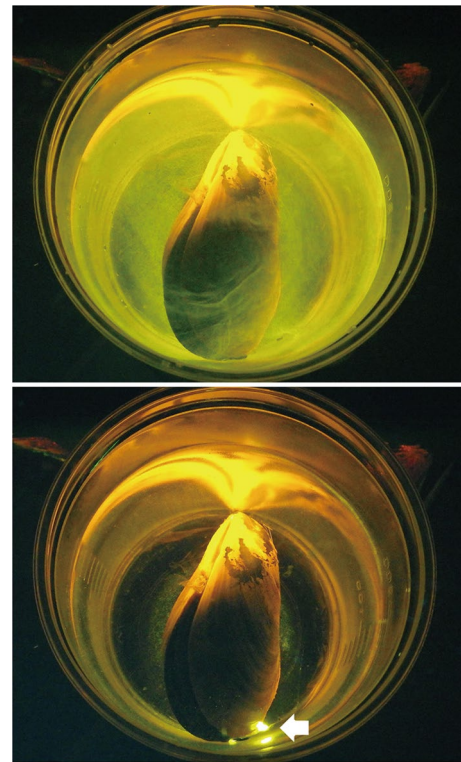
## Filter feeding and pollution studies

Filter feeding (Jorgensen 1996; Hawkins et al. 1998) is an efficient way for sessile animals to collect food. Mussels in beds hardly move as they are interconnected by multiple byssi. Mussels filter water through the gills, trapping plankton, detritus, and biotic and abiotic particles, which are passed by cilia to the digestive tract.

As mussel body composition reflects the condition of the environment, mussels have been objects of environmental pollution studies (Viarengo and Canesi 1991; Beyer et al. 2017). Some *Mytilus* species are particularly accessible. For that reason, Goldberg (1975) proposed the “mussel watch” concept to monitor global aquatic pollution (see also Farrington et al. 2016), and this concept has been expanded to include *Perna* species for monitoring warmer waters (Monirith et al. 2003; Ramu et al. 2007).

## Ingestion of microplastics

As active filter feeders, mussels ingest microplastic particles (Fig. 3 and Online Resource 1 for time-lapse movie), which have become a world-wide concern. Since early reports



**Fig. 3** Ingestion of microplastic particles by the Mediterranean mussel *Mytilus galloprovincialis*. A mussel was placed in a 200 mL beaker filled with filtered seawater. Then, 200  $\mu$ L of water containing 2.5% (w/v) fluorescent-labeled polystyrene (PS) particles (Fluoresbrite YG, Polysciences, 90  $\mu$ m in diameter, Warrington, PA, USA) was added to the seawater. Photographs were taken under an LED illuminator (Oriental Instruments, Sagami-hara, Japan). The upper photo was taken just after addition of PS particles, and the lower photo was taken 72 min later. PS particles appear as a yellow mist just after addition. The mussel ingested most of the PS particles, and the seawater became clear within 30 min. Some PS particles were excreted as pseudofeces (arrow in lower panel) without proceeding to the alimentary canal. A time-lapse movie is also available in Online Resource 1

about microplastic contamination in mussels (Browne et al 2008; von Moos et al. 2012; Wegner et al. 2012), an increasing number of papers have been published, mainly on species of *Mytilus* and *Perna* (Chae and An 2020; Gedik and Eryasar 2020; Kazour and Amara 2020; Piarulli and Airoidi 2020; Christoforou et al. 2020; Cole et al. 2020; Li et al. 2020a; Stamataki et al. 2020; Wakkaf et al. 2020; Webb et al. 2020; Alnajjar et al. 2021; Cappello et al. 2021; Cho et al. 2021; Klasios et al. 2021; Kumar et al. 2021; Liu et al. 2021; Perez et al. 2021; Seuront et al. 2021; Wang et al. 2021a,b). Considering their distributions around cities and other human habitations, mussels are ideal organisms for monitoring microplastic pollution. They are also useful in laboratory experiments to understand effects of microplastics, because laboratory rearing and experimental administration of microplastic particles are quite easy. For

example, we have reported size-dependent elimination patterns of ingested particles (Kinjo et al. 2019a). Such studies are important because *Mytilus* and *Perna* are popular seafoods that are consumed whole; thus, they vector microplastics to humans. In addition to ingestion by filter feeding, direct interaction of microplastics with the byssus has also been reported (Li et al. 2019).

## The byssus and metals

Byssi have also been the object of metal pollution analyses because the metal content of byssi is higher than that of soft tissues (Yap et al. 2003; Szefer et al. 2006). However, as metals are important for crosslinking of byssal proteins (Sever et al. 2004; Harrington et al. 2010; Waite 2017), mussels may incorporate metals selectively for that purpose. Therefore, more studies are needed to understand the metal content of the byssus. For example, proteins involved in metal intake, transportation, binding, and exclusion should be identified and characterized. Omics-based studies may offer clues to understand such mechanisms (Zhang et al. 2017a, b; 2019). Also, known and novel metal-regulatory genes or proteins can be searched from omics data (Sassa et al. 2021). Since byssal proteins contain many reactive side chains and have affinities for various metals, Montroni et al. (2020) proposed the use of mussel byssi, collected from aquaculture waste, for bioremediation of metal-polluted water.

## The byssus and biological invasion

Another ecological issue is invasiveness. Major mussel species are expanding their geographic distributions owing to human activities, and they are disturbing local ecosystems at invasion sites. For example, *Mytilus galloprovincialis* and *Dreissena polymorpha* are included among 100 of the World's Worst Invasive Alien Species (Lowe et al. 2000). Also, *M. galloprovincialis*, *Perna viridis*, *Xenostrobus securis*, and *Limnoperna fortunei* are included in the List of Invasive Species of Japan ([https://www.nies.go.jp/biodiversity/invasive/resources/listen\\_molluscs.html](https://www.nies.go.jp/biodiversity/invasive/resources/listen_molluscs.html); accessed on 12 May 2021). The invasion of Japan by *M. galloprovincialis* has been described by Kuwahara (1993) and Inoue et al. (1997). Kimura et al. (1999) and Iwasaki (2013) detailed the arrival of *Xenostrobus securis*, Ueda (2001) and Yoshiyasu et al. (2004) discussed *Perna viridis*, and Kimura et al. (2011) have written about *Limnoperna fortunei*. Expansion of invasive species has been accelerated by increased over-sea traffic, and ballast water of vessels is a major carrier of plankton and planktonic larvae around the globe (Lim et al. 2020). However, among the many marine organisms that

have planktonic larval stages, mussels seem to be one of the most widespread groups of organisms. One possible reason for their success is their high environmental adaptability, which will be mentioned later. Another reason is that individual adults can hitchhike on ships by attaching to the hulls (van der Gaag et al. 2016). When adult mussels are transported to new locations, they immediately start reproducing. In addition, exposure to changing environmental conditions during transport may offer them an opportunity to adapt to stresses associated with the new location (Lenz et al. 2018). Moreover, in destination areas after transport, mussels often occupy vacant or less competitive niches, e.g., piers, quay walls, inlets of power plants, and aquaculture nets (Gilg et al. 2010), using their byssi. Thus, not only appropriate management of ballast water but also development of antifouling strategies is important to reduce invasion by mussels.

## Species markers based on byssal protein sequences

For surveys of invasive species, accurate species identification is important. However, morphological identification of mussels is often challenging. In particular, distinguishing three major mussels, *Mytilus edulis*, *M. galloprovincialis*, and *M. trossulus*, which all belong to the *M. edulis* species complex, is quite difficult (McDonald et al. 1991; Kuwahara 2001). For this purpose, a convenient polymerase chain reaction (PCR) marker to distinguish the three species was designed using the sequence of a byssal protein gene (Fp-1) (Inoue et al. 1995b). This marker has been utilized for more than 25 years, but is still robust (Larraín et al. 2019), perhaps because it is based on a 12- or 54-bp insertion/deletion site, which may be less variable than nucleotide substitutions. However, species identification using single markers is not infallible, especially for specimens containing introgressed sequences (Larraín et al. 2019; Vendrami et al. 2020).

## Environmental adaptations of intertidal mussels

Mussels, as well as other sessile organisms, must cope physiologically with various environmental stresses because they have no means to escape from sudden, unfavorable changes of environmental conditions. Species inhabiting intertidal zones must have high tolerance for environmental changes, as they are continuously exposed to fluctuation of ambient conditions, including temperature and salinity (Gosling 2003; Gracey et al. 2008). Various studies have investigated physiological adaptations to temperature changes and their impact on species distributions (Pernet et al. 2007; Tomanek and Zuzow 2010; Somero

2012; Seuront et al. 2019; Moyen et al. 2020; Chao et al. 2020; Popovic and Riginos 2020). Mechanisms of osmotic adaptation have also been studied, through physiological, transcriptomic and proteomic, and behavioral analyses (Gosling 2003; Lockwood and Somero 2011; Tomanek et al. 2012; Wang et al. 2013). Mussels are generally considered osmoconformers, as are other bivalves, which adjust body fluid osmolality to that of the environment, although osmoregulatory ability has been suggested for *Perna perna* (Rola et al. 2017). In *Mytilus* spp., free amino acids are thought to facilitate osmoconforming (Gosling 2003), and glycine and taurine are reported as the major osmolytes (Kube et al. 2006). In addition, the taurine transporter (TAUT) is involved in adaptation (Hosoi et al. 2005; Toyohara et al. 2005). Interestingly, TAUT expression is elevated under hypoosmotic conditions, although the authors suggested that TAUT expression responds to decreased taurine rather than to osmotic changes (Hosoi et al. 2005; Toyohara et al. 2005).

### Mussels inhabiting deep-sea hydrothermal vent areas

Interestingly, more than 25 mytilid species, including those of the genus *Bathymodiolus*, have been reported from hydrothermal vent and seep habitats, according to the World Register of Marine Species (<http://www.marinespecies.org/aphia.php?p=taxdetails&id=138214>, accessed on 12 May 2021) (Lorion et al. 2013). Vent- and seep-adapted species are thought to have evolved from an ancestral species inhabiting shallow seas, and whale carcasses and sunken wood may have mediated the transition to deep-sea habitats (Distel et al. 2000; Smith et al. 2015). Bathymodiolin mussels form dense beds around hydrothermal vents and cold seeps (Fig. 4), and their large biomass is supported by “chemosynthetic bacteria” that synthesize organic matter using chemical substances, such as hydrogen sulfide, hydrogen, and methane, abundant in vent or seep effluents (Dubilier et al. 2008). Bathymodiolin mussels maintain chemosynthetic bacteria as symbionts in their gill tissues (Duperron et al. 2009; Fujinoki et al. 2012a, b; Ikuta et al. 2016); thus, they obtain nutrients without foraging. Accordingly, mussels are obliged to stay near vents or seeps, to absorb chemical substances, and to deliver them to the symbionts. Typical symbionts are sulfur-oxidizing bacteria that use hydrogen sulfide, which is toxic to most organisms (Powell and Somero, 1986). Therefore, mussels harboring sulfur-oxidizing bacteria must cope with hydrogen sulfide toxicity; however, mechanisms to accomplish that are not fully understood.



**Fig. 4** A colony of deep-sea mussels *Bathymodiolus septemdierum*, in a hydrothermal vent area at a depth of approximately 1303 m at Myojin Knoll Caldera. New active chimneys (1, 2) are growing between old “dead” chimneys (3, 4). Chimney 1 is actively spouting, and chimney 2 is slowly emitting hot seawater containing hydrogen sulfide. Mussels are attached where they are not exposed directly to vent effluent, but can access effluent diluted with ambient seawater. The surface of chimney 2, exposed directly to effluent from chimneys 1 and 2, is occupied by polychaete worms, *Paralvinella hessleri* and Polynoidae gen. sp. (Koito et al. 2018). The crab *Gandalfus yunohana* is a common species around beds of *B. septemdierum*. Osmolalities of vent effluent, just above the mussel and polychaete colonies and of surrounding seawater, are presented in Table 1. The photograph was taken by remotely operated vehicle Hyper-Dolphin during research cruise NT11-09 of the research vessel, Natsushima, in 2011. Copyright, The Japan Agency for Marine-Earth Science and Technology (JAMSTEC)

### Hypotaaurine of deep-sea mussels

Hypotaaurine, a substance similar to taurine, and hydrogen sulfide ion can be converted to thiotaurine, a nontoxic substance that can be passed to symbionts (Pruski and Fiala-Médioni 2003; Yancey 2005; Koito et al. 2010; Nagasaki et al. 2018; Kuroda et al. 2021). As mussels are always exposed to sulfides in hydrothermal-vent water, gill cells must maintain high hypotaaurine levels. To accumulate hypotaaurine in the gill, involvement of the taurine transporter (TAUT) has been reported (Inoue et al. 2008). In addition, GAT-1, a transporter for gamma-aminobutyric acid (GABA), may participate in this process (Kinjo et al. 2019b). Moreover, cysteine dioxygenase (CDO) and cysteine sulfinate decarboxylase (CSAD) may synthesize hypotaaurine from cysteine (Nagasaki et al. 2015, 2018).

As mentioned above, TAUT is reportedly involved in osmotic adaptation by shallow-sea mussels (Hosoi et al. 2005; Toyohara et al. 2005). As TAUT involvement in osmotic adaptation is also reported in oysters (Hosoi et al. 2007), it is likely a common mechanism among shallow-sea bivalves. Phylogenetic analysis of TAUT and related

transporters indicated that bathymodiolin TAUT is quite similar to that of shallow-sea *Mytilus* (Koito et al. 2010; Kinjo et al. 2013). Although CDO and CSAD have not been characterized in shallow-sea mussels, like TAUT, they are found in the oyster taurine synthesis pathway, and their roles in osmotic adaptation have been suggested (Meng et al. 2013; Zhao et al. 2017). Therefore, these transporters and enzymes have not evolved specifically for adaptation to hydrothermal vents. Rather, they may have been co-opted for osmotic adaptation in an ancestor that inhabited shallow seas, although functions of individual components may have been modified to augment hypotaaurine accumulation (Koito et al. 2016; Nagasaki et al. 2018). Interestingly, seawater ejected from hydrothermal vents at Myojin Knoll and Suiyo Seamount is slightly hypoosmotic relative to surrounding seawater (Fig. 4, Table 1, and Nakamura-Kusakabe et al. 2016), and this may influence TAUT mRNA expression (Nakamura-Kusakabe et al. 2016).

## The byssus and deep-sea mussels

Given that hypotaaurine can be accumulated by modifying taurine biosynthesis and its transport mechanisms, many other mollusks also have the potential to adapt to the hydrothermal vent environment, because mollusks generally contain high levels of taurine (Allen 1961; Welborn and Manahan 1995). Then, what is the basis of the success of mussels there? It may also be related to attachment using the byssus. Deep-sea hydrothermal vents generally form tall, steep structures called “chimneys” (Fig. 4), composed of minerals contained in vent fluid. After ejection, the hot mineral-rich water cools in contact with surrounding seawater, and minerals are deposited around the vent, forming chimneys. Environments with such topographic relief are advantageous for sessile organisms, which may be a reason that mussels have flourished in these habitats.

Attachment using the byssus may be more advantageous than other forms of attachment. Chimneys are not stable structures. They become taller with time because minerals

are deposited continuously, and they sometimes decay (Nozaki et al. 2016). Chimneys may go dormant when vent fluid is rerouted to new locations, forming new chimneys. Bathymodiolin mussels seem to have the capacity to adjust their positions to the vicinities of new vents (Fig. 4). If they are too far from a vent, they cannot obtain the raw materials needed for chemosynthesis, such as hydrogen sulfide. In contrast, if they are too close to the vent, high temperatures and hydrogen sulfide concentrations become prohibitive. Therefore, vent mussels likely adjust their positions to keep adequate distance to the vent, by means of the byssus. We have observed that the hydrothermal vent mussel, *Bathymodiolus septemdierum*, reared in the laboratory, can move by making new byssi and cutting old ones (Nemoto S. and Sugimura M., unpublished observations).

Furthermore, as mentioned above, deep-sea vent and seep mussels are thought to have evolved from shallow-sea mussels in stages by utilizing whale falls or sunken wood as “evolutionary stepping stones” (Distel et al. 2000; Smith et al. 2015). Byssi are ideal for this, and attachment to and clustering on whale bones using byssi has been reported in several mussel species (Okutani et al. 2003; Okutani and Miyazaki 2007). Mussels on sunken wood are also likely to “hang on” using byssi (Pailleret et al. 2007). While the foregoing materials provide substrates for attachment, they are also thought to have offered sulfide-rich environments suitable for chemosynthesis (Smith et al. 2015). Therefore, the byssus has contributed to evolution of symbiotic relationships with chemosynthetic bacteria, allowing mussels to exploit deep-sea environments.

## Conclusion

As described above, the byssus is central to the ecology, physiology, and evolution of mussels, and the ecosystems in which they reside. Enormous numbers of studies have been conducted on the components, structure, and polymerization processes of the byssus, employing chemical, biochemical, histological, molecular biological, and behavioral approaches, although this review cannot possibly cover all of them. However, detailed mechanisms of byssus formation, adhesion, and many other related phenomena are still little understood. Fortunately, “omics” data about mussels have begun rapidly accumulating in recent years. Genomic information regarding mussels has accumulated much more rapidly than for many other marine invertebrates (Murgarella et al. 2016; Sun et al. 2017; Uliano-Silva et al. 2018; Gerdol et al. 2020; Li et al. 2020b; Inoue et al. 2021 for mytilids; Calcino et al. 2019 for a dreissenid). Such comprehensive information is expected to unify knowledge from molecular biological and chemical studies.

**Table 1** Osmolality of seawater and vent effluent around a hydrothermal vent at Myojin Knoll Caldera, shown in Fig. 4

Water sampling points	Osmolality (mOsm/kg)
Vent effluent of active chimney 1	982
Seawater just above a polychaete colony on chimney 2	995
Seawater just above a mussel colony on chimney 3	999
Seawater 3.5 m above chimneys	1007
Seawater 635 m above chimneys	1014
Surface seawater	1012

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s12562-021-01550-5>.

**Acknowledgements** The authors thank the crew of research vessels, Natsushima, Kaiyo, and Shinsei-maru, the operation team of the remotely operated vehicle, Hyper-Dolphin, and the scientists who have joined these cruises. The authors also thank Suguru Nemoto, Makoto Sugimura, and other members of Enoshima Aquarium for their support in deep-sea mussel experiments. A series of studies by the authors introduced in this article have been supported by JSPS KAKENHI (grant numbers 19380110, 22880037, 22380107, 24658187, 15K14801, 15K18616, 16K12604, 18H02261, and 19K06844), JSPS Core-to-core CREPSUM JPJSCCB20200009, and The University of Tokyo FSI-Nippon Foundation Research Project on Marine Plastics.

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