Human impact on symbioses between aquatic organisms and microbes

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REVIEW

Human impact on symbioses between aquatic organisms and microbes

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ABSTRACT: Aquatic organisms rely on microbial symbionts for coping with various challenges they encounter during stress and for defending themselves against predators, pathogens and parasites. Microbial symbionts are also often indispensable for the host's development or life cycle completion. Many aquatic ecosystems are currently under pressure due to diverse human activities that have a profound impact on ecosystem functioning. These human activities are also expected to alter interactions between aquatic hosts and their associated microbes. This can directly impact the host's health and — given the importance and widespread occurrence of microbial symbiosis in aquatic systems — the ecosystem at large. In this review, we provide an overview of the importance of microbial symbionts for aquatic organisms, and we consider how the beneficial services provided by microbial symbionts can be affected by human activities. The scarcity of available studies that assess the functional consequences of human impacts on aquatic microbial symbioses shows that our knowledge on this topic is currently limited, making it difficult to draw general conclusions and predict future changes in microbial symbiont–host relationships in a changing world. To address this important knowledge gap, we provide an overview of approaches that can be used to assess the impact of human disturbances on the functioning of aquatic microbial symbioses.

KEY WORDS: Host–symbiont interactions · Aquatic microbial symbioses · Mutualism · Anthropogenic disturbances

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1. INTRODUCTION

A large fraction of ecological interactions within an ecosystem are symbiotic, which can be defined as a phenomenon in which dissimilar organisms live together (De Bary 1879). Although the term symbiosis is mostly used in the context of mutualistic or commensalistic interactions between 2 species that live in close contact for a substantial amount of time, it encompasses a whole spectrum of outcomes, including parasitism. Furthermore, the outcome of a symbiosis between 2 species is not fixed, and both the strength and direction (positive, neutral or negative) of the interaction can change over time and/or shift depending on the context (Daskin & Alford 2012). Symbiosis can either be obligate, where one or both partners cannot survive without the other, or it can be facultative, with both partners able to survive independently outside of the symbiosis.

Microbial symbiosis refers to the phenomenon where, in general, a larger organism (host) is colonized by smaller unicellular microorganisms (symbionts). In aquatic environments, a wide diversity of eukaryote, bacterial and archaeal phyla engage in microbial symbiosis, either as host or symbiont (Grossart et al. 2013). Microbial symbionts can live as endosymbionts within the cells or as specialized organs of the host. However, many microbial symbionts colonize the surface of epithelial tissues such as the gut mucosa or are externally associated with the host, such as those growing in the phycosphere of microalgae (Zoccarato & Grossart 2019). The assembly of microorganisms found on a host is referred to as the host-associated microbiota, and they form — in combination with their specific habitat and biological activity — the microbiome (sensu Berg et al. 2020;

Fig. 1). This commonly used microbiome definition, however, is not fixed and often varies depending on the referenced source. There has been increased research interest in the host-associated microbiota, facilitated through new DNA sequencing technologies, which has revealed that many host organisms support highly diverse communities of microbial symbionts (Ley et al. 2008, White et al. 2016). In this review, we discuss both specialized endosymbionts and the broader host-associated microbiota, as we expect some parallels in how they interact with the host and how they are affected by environmental change. We only focus on microbial symbionts that provide — at least under some circumstances — a benefit to the host.

Most aquatic organisms start interacting with microbial symbionts from their birth, and sometimes even before (Bates et al. 2006, Nyholm 2020). Furthermore, aquatic organisms acquire bacteria from the environment throughout their life cycle, making the microbiota develop concomitantly with the host's chronological development. For several host organisms, it has also been shown that they exert control over the presence or abundance of specific symbionts, often favouring beneficial symbiont strains (Rawls et al. 2006, McFall-Ngai 2014, Tasiemski et al. 2015, Stock et al. 2019a). These processes often ensure that the microbial community provides the necessary functions throughout the host's life cycle (Sampson & Mazmanian 2015, Dominguez-Bello et al. 2019). Microbiota can be acquired from conspecifics through maternal transmission or other forms of interactions, or they can be acquired through colonization from the available pool of environmental microorganisms (Funkhouser & Bordenstein 2013). The mode of transmission is a key element in eco-evolutionary host–symbiont dynamics and is correlated with symbiont function and degree of specialization (Macke et al. 2017b). Many (especially aquatic) organisms obtain their microbiota through horizontal transmission, and the degree of exposure to environmental sources of microorganisms often plays a major role in determining microbiota assemblies (Adair & Douglas 2017). Intermediate modes, whereby symbionts from the parents are horizontally transmitted to their offspring, have also been observed (Ebert 2013, Björk et al. 2019). Vertically transmitted symbionts, which are transferred with high fidelity from the mother to the offspring
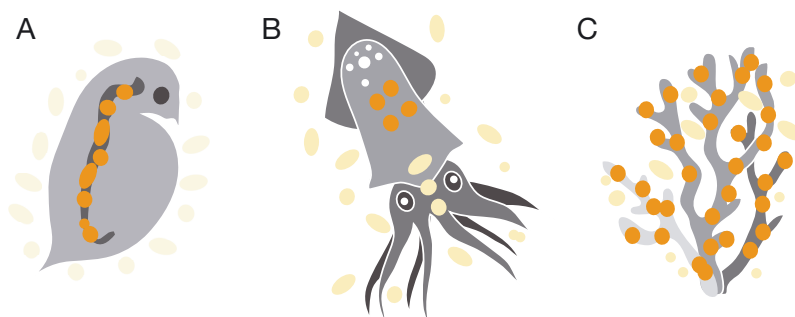

Fig. 1. Examples of aquatic host–symbiont associations. The host (largest organism, grey) with its symbionts (unicellular eukaryotes, *Archaea* and *Bacteria*, coloured). We define the symbionts as the microorganisms living in the host or externally associated with it. Well-studied examples of host–symbiont associations (orange) include (A) *Daphnia magna* and its gut microbiota, (B) *Euprymna scolopes* and the bioluminescent bacterium *Vibrio fischeri* and (C) *Acropora* spp. and the eukaryotic algae *Symbiodinium* spp.

before birth, tend to resemble organelles, and their presence often has higher relevance for the host's fitness (Bright & Bulgheresi 2010, Fisher et al. 2017). Interestingly, aquatic host organisms seem to depend less on vertical transmission than terrestrial hosts (Russell 2019).

It has become clear that, for many organisms, the composition of their symbiont community has a major influence on various physiological processes and, ultimately, overall health. Variation in the gut microbiota composition is known to be caused by complex interactions between a range of factors such as environment, diet, age and medication (Falony et al. 2016, Callens et al. 2020). Alterations in microbiota community composition can have negative effects on the host and can lead to a so-called 'dysbiosis' linked to a variety of diseases, but the causality of this variation on host health is often poorly understood (Flandroy et al. 2018). In contrast, hosts can also be equally healthy when harbouring quite different microbiota, indicating that there is often a certain degree of functional redundancy between symbiont species or communities (Moya & Ferrer 2016, Callens et al. 2018).

Many aquatic ecosystems are currently under pressure due to diverse human activities such as land-use change, hydrological alterations to water bodies, pollution, deep-sea mining and commercial fishing. In addition, the effects of greenhouse gas emissions are expected to increasingly impact aquatic systems through climate change and ocean acidification (Doney et al. 2020). Although many research efforts are currently being undertaken to understand the potential impact of human activity on aquatic ecosystems and find ways to mitigate them, knowledge on the impact of human activity on microbial symbioses is scarce (Evariste et al. 2019, Timmis et al. 2019). This impact is, however, expected to have profound effects on aquatic ecosystems given the exceptional importance of microbial symbiosis for the health of many aquatic organisms (Cavicchioli et al. 2019). Effects of aquatic symbiotic interactions often extend far beyond the involved partners and can provide functions that are fundamental to whole aquatic ecosystems, such as energy provision to coral reefs (Muscatine 1990) and deep-sea hydrothermal vent communities (Jannasch & Mottl 1985), detoxification of seagrass bed sediments (van der Heide et al. 2012) or nutrient cycling in the water column, which can greatly affect primary production (Seymour et al. 2017).

The aim of this review is to assess the potential impact of human disturbances on interactions between aquatic organisms and their microbial symbionts, with a special focus on the consequences for the hosts'

health. In Section 2 ('Importance of the microbiome for aquatic organisms', summarized in Fig. 2A) we provide an overview of the importance of microbial symbionts for coping with various challenges encountered by aquatic organisms. We focus on resource acquisition, physiological stress, predation, pathogens, parasites and host development. In Section 3 ('Effects of anthropogenic disturbance on host–symbiont interactions', summarized in Fig. 2B and Table 1), we consider how the beneficial services provided by microbial symbionts can be affected by various types of human impacts on aquatic ecosystems: eutrophication, global warming, salinity changes, pollution and antibiotics. In Section 4 ('Perspectives'), we highlight the importance of including host–symbiont interactions when assessing the impact of human disturbances on aquatic ecosystems. We also identify some important knowledge gaps concerning the effect of human disturbances on the functioning of aquatic microbial symbioses and indicate how these knowledge gaps might be addressed in future studies.

2. IMPORTANCE OF THE MICROBIOME FOR AQUATIC ORGANISMS

2.1. Role of the microbiome in host development

Microbial symbionts have often been found to be essential for the development of multicellular aquatic hosts. Many hosts receive growth factors and vitamins required for their development from their microbiota (Sokolovskaya et al. 2020). Sea lettuce *Ulva mutabilis*, for example, requires multiple regulatory factors produced by its associated bacteria to develop into a 'blade' with rhizoids (Provasoli 1958, Wichard et al. 2015). In the absence of bacteria, sea lettuce develops into callus-like colonies consisting of undifferentiated cells. Several aquatic metazoan larvae (Porifera, Cnidaria, Acoelomorpha and Mollusca) require bacteria for their settlement (Tran & Hadfield 2011, Sneed et al. 2014, Fieth et al. 2016) whilst the presence of dinoflagellates belonging to the Symbiodinaceae seems to be required for successful metamorphosis in multiple marine organisms (Mies et al. 2017). In the sponge *Amphimedon queenslandica*, a bacterial symbiont belonging to the order *Chromatiales* supplies the amino acid L-arginine, which is essential for the sponge larvae to successfully settle and metamorphose (Fieth et al. 2016). Zebrafish *Danio rerio* display incomplete development and impaired function of their gastrointestinal tract in the absence of gut microbiota. This can, how-
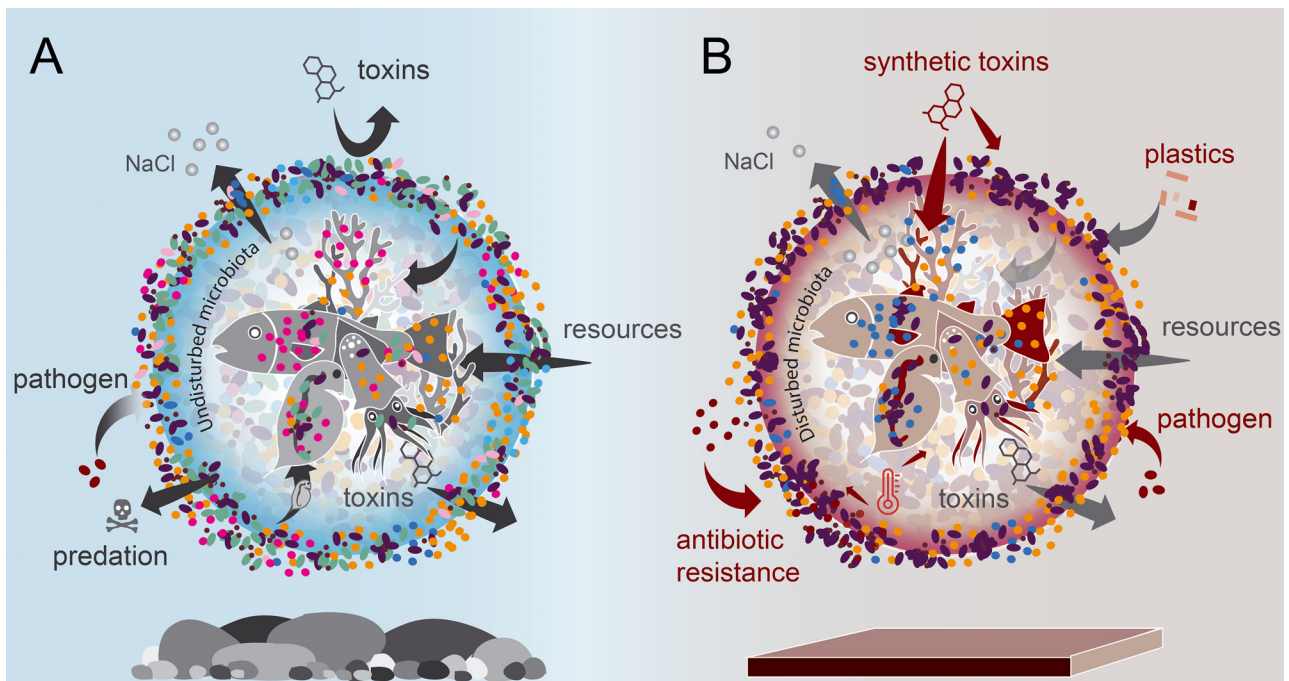
Fig. 2. Schematic depiction of beneficial services provided by microbial symbionts and the potential impact of human activities on the interaction between aquatic hosts and their microbiota. (A) Important functions of the microbiota in pristine systems, including (from top, clockwise) defence against external toxins, provision of secondary metabolites, acquisition of resources, production of toxins, host development, predation defence, pathogen defence and osmoregulation. (B) Anthropogenic disturbances that can affect the host's microbiome, including (red arrows from top, clockwise) synthetic toxins, micro- and nanoplastic pollution, altered habitat structure (i.e. channelling of water bodies), increased abundance of antibiotic resistant and pathogenic microorganisms and increased temperature. The potential impacts of disturbing the microbiome on the host's health are indicated by grey arrows (from top, clockwise): reduced resource acquisition, increased pathogenic infections, lower toxin expulsion or degradation and reduced osmoregulation

ever, be reversed by inoculating them with their conventional microbiota, providing direct evidence for the role of the gut microbiota in gastrointestinal tract development (Bates et al. 2006). Furthermore, experimental evidence suggests that the microbiota is also required for a normal early life neurobehavioral development in zebrafish (Phelps et al. 2017).

Although less studied, associated microbiota can also play a role in the life cycle completion of unicellular aquatic hosts. This has been shown for the diatom *Seminavis robusta*, where its associated bacteria are known to affect sexual reproduction. They do this through modulation of the host's production of the sexual attraction pheromone diproline, which influences physical pairing of compatible cells and subsequent gametogenesis (Cirri et al. 2019).

2.2. Role of the microbiome in obtaining resources

Obtaining sufficient resources for growth, reproduction and meeting daily energy demands poses an important challenge for all aquatic organisms. To cope with this challenge, many aquatic organisms rely on microbial symbionts that can either provide their host with organic carbon derived from primary production or with essential nutrients, enhance food digestion or help attract prey.

Autotrophic microbial symbionts often directly provide their aquatic host with energy derived from solar radiation (photosynthetic symbionts; Smith et al. 1969) or oxidation of electron donors (chemoautotrophic symbionts; Jannasch 1985). This relationship can result in a reduced dependency on external food resources for the host and may even result in an *in se* heterotrophic host obtaining all its required carbon from symbiotic primary producers (e.g. Hinzke et al. 2019). Symbiotic associations with photosynthetic microorganisms are widespread in the photic zone of aquatic environments. The endosymbiosis of the unicellular dinoflagellate *Symbiodinium* with cnidarian corals is a well-studied example of such an association (Freudenthal 1962). *Symbiodinium* provides oxygen and organic compounds to the coral and, in

Table 1. Potential functional impacts of anthropogenic disturbances on host–symbiont interactions

Anthropogenic disturbance	Functional impact of disturbance	Host	References
Changes in nutrient availability/eutrophication	Reduced calcification rates	Coral	van Oppen & Blackall (2019)
	Increased invasion of opportunistic pathogens	Coral	Voss & Richardson (2006), Gochfeld et al. (2012), Bourne et al. (2016)
	Dysbiosis of skin microbiota	Fish	Krotman et al. (2020)
	Increase in beneficial bacteria	Fish	Xie et al. (2011), Dong et al. (2013)
Global warming	Changes in the microbiome metabolism	Frog	Fontaine & Kohl (2020)
	Changes in digestive performance of the host	Salamander	Fontaine et al. (2018)
	Reduced exchange of symbiont-derived photosynthates	Coral	Baker et al. (2018)
	Adaptation of symbionts to higher temperature and increased bioluminescence	Squid	Cohen et al. (2019)
	Increased susceptibility to disease	Bivalve	Li et al. (2019)
Anthropogenic structures	Increase in epifauna and potential pathogens	Kelp	Marzinelli et al. (2009, 2018)
Salinity changes	Increased osmolyte production, sulphur oxidation and nitrogen fixation	Coral	Röthig et al. (2016)
	Reduced digestion of algal diet	Brine shrimp	Nougué et al. (2015)
	Changes in digestive and osmoregulatory capacity	Snail	Kivistik et al. (2020)
Chemical pollution	Increase in xenobiotic biodegradation capacity	Bivalve	Milan et al. (2018)
	Reduced body weight	Fish	Kan et al. (2015)
Antibiotics	Changes in ecological interactions within microbiota which affect host growth rates	Water flea	Callens et al. (2018)
	Reduced fitness under poor dietary conditions	Water flea	Akbar et al. (2020)
	Increased body weight and altered liver function	Fish	Keerthisinghe et al. (2020)
	Increased mortality when challenged with a pathogen	Fish	Zhou et al. (2018)
	Changes in host development	Fish	Yu et al. (2020)
	Impaired intestinal morphology, permeability and dysbiosis	Fish	Limbu et al. (2018)

turn, receives inorganic nutrients and protection from the host (Gordon & Leggat 2010). Other well-studied associations include the freshwater cnidarian *Hydra* with the green algae *Chlorella* (Ye et al. 2020), an association known since the 1920s (Goetsch 1924), and the sacoglossan sea slug *Elysia chlorotica* with the stramenopile algae *Vaucheria litorea* (West 1981, Chan et al. 2018). The latter association differs from the former since the host does not retain viable symbionts but merely the algal plastids. Many protists also harbour eukaryotic or prokaryotic microalgal symbionts that provide their host with photosynthates (Stoecker et al. 2009, Decelle et al. 2015, Leles et al. 2017). Furthermore, these photosynthetic symbionts often provide their host with additional biochemical functions (Nowack & Melkonian 2010). For instance, some foraminiferans host diatoms or dino-

flagellates, from which they obtain photosynthates, and simultaneously host cyanobacteria, which provide photosynthesis-dependent nitrogen (N) fixation (Lee 2006, Prazeres & Renema 2019).

Aquatic organisms that acquire energy from associated chemoautotrophic microorganisms are mostly found around deep-sea vents (Dubilier et al. 2008). Several tube-dwelling annelids nutritionally associate with aerobic methane-oxidizing bacteria (Gofredi et al. 2020), and the giant hydrothermal vent tubeworm *Riftia pachyptila* relies entirely on sulfide-oxidizing chemoautotrophic microorganisms for nutrition (Hinzke et al. 2019). Symbiont-hosting vesicomyid clams can take up hydrogen sulfide from the sediment through their foot, and thioautotrophic bacteria that live in the gills of the clams can utilize this hydrogen sulfide as the main energy source (Lan et

al. 2019). Cold seep sponges from the genus *Suberites* receive energy from their archaeal symbionts, which carry out ammonia oxidation and carbon fixation within the sponge (Tian et al. 2017).

Gut microbiota play a vital role in food digestion for heterotrophic organisms. This holds true for many aquatic organisms, ranging from invertebrates such as crustaceans (Harris 1993, Callens et al. 2016, Holt et al. in press) to fishes (Egerton et al. 2018) and whales (Miller et al. 2020). For some organisms, bacteria provide essential enzymes to digest complex food sources. This is, for instance, the case in terendinid wood-boring bivalves — known as ship-worms — who depend on their associated bacteria to successfully digest wood (Sabbadin et al. 2018). Heterotrophic organisms also often rely on their gut microbiota to supply them with essential vitamins (Putnam & Goodman 2020).

Many aquatic phototrophs rely on their associated microorganisms to enhance the uptake of limited nutrients or to get access to nutrient resources that are otherwise unavailable to them. Through remineralisation and respiration, heterotrophic bacteria regenerate carbon dioxide out of leaked photosynthates, thereby facilitating nutrient circulation and increasing carbon availability for the host (Christie-Oleza et al. 2017). Algae-associated bacteria increase bioavailability of iron through siderophore production (Amin et al. 2009, Kurth et al. 2019), whilst N_2-fixing cyanobacteria, often as endosymbionts in microalgae, provide N in return for photosynthetically fixed carbon from the host (Villareal 1992, Foster & Zehr 2019). In addition to specific growth factors such as the auxin phytohormone indole-3-acetic acid (Seyedsayamdost et al. 2011, Amin et al. 2015), heterotrophic bacteria supplement various algae with vitamins (Croft et al. 2005, Sokolovskaya et al. 2020), complementing the host's nutritional needs.

An additional mechanism through which microbial symbionts can provide their heterotrophic host with food is by enhancing their capability to catch prey. This is the case in anglerfish, who host bioluminescent bacteria belonging to the genus *Photobacterium* in a light organ at the tip of their 'fishing rod' where they produce the necessary light to detect or attract prey (Hellinger et al. 2017, Michiels et al. 2018).

2.3. Role of the microbiome in dealing with physiological stress

Harsh environmental conditions can induce pronounced physiological stress in aquatic organisms.

Although the underlying mechanisms are not always evident, case studies suggest that associated microbiota can play a relevant role in reducing physiological stress in their host (White & Torres 2009).

Several unicellular aquatic hosts are known to gain protection against harmful solar radiation through their microbial symbionts. In the ciliate *Paramecium bursaria*, the presence of algal symbionts can reduce photo-oxidative stress caused by high UV radiation, most likely through the activity of antioxidants produced by the symbiotic algae countering reactive oxygen species production (Hörtnagl & Sommaruga 2007). In the marine benthic ciliate *Maristentor dinoferus*, mycosporine-like amino acids produced by a symbiotic *Symbiodinium* are also known to minimize damage from exposure to solar UV radiation (Sommaruga et al. 2006). Furthermore, endosymbiotic *Symbiodinium* in corals are known to gain protection not only against light but also thermal stress from their associated bacteria that produce the carotenoid zeaxanthin, which potentially mitigates the effect of environmental stress due to its antioxidant activity (Motone et al. 2020).

Many heavy metals are essential micronutrients for aquatic organisms but can become highly toxic at higher concentrations (Morel & Price 2003). A plethora of host-associated bacteria have been found to carry heavy metal resistance factors on mobile genetic elements and could indirectly confer heavy metal resistance to the host (Selvin et al. 2009, Chaturvedi et al. 2015). Bacteria associated with the green alga *Enteromorpha compressa* demonstrated a high copper tolerance and were suggested to play a role in reducing the negative impact of copper on the algae (Riquelme et al. 1997). Similarly, increased copper tolerance was observed in the cnidarian *Hydra* when it was associated with microalgal symbionts (Karntanut & Pascoe 2005). However, the exact mechanisms by which the symbionts increase copper tolerance in their host were not evident. The mussel *Bathymodiolus* sp., living in metal-rich hydrothermal vent environments, harbours symbiotic bacteria that can absorb metal ions and subsequently excrete the metals in particulate forms, thereby detoxifying heavy metals for their host (Hardivillier et al. 2004). Kayath et al. (2019) showed that intestinal bacteria isolated from guppy fish living in hydrocarbon- and trace metal-contaminated wastewater could tolerate trace metals such as Hg, Co, Zn and Pb to a higher degree. Additionally, many of these bacteria were able to degrade gasoline or diesel fuel hydrocarbons. These studies indicate that the associated microbiota potentially have an important role in mitigating the

effects of various forms of environmental stresses such as pollution in many aquatic organisms.

The associated microbiota can also protect the host against physiological stress induced by secondary compounds present in the food. For example, in the water flea *Daphnia magna*, tolerance to the toxic cyanobacterium *Microcystis aeruginosa* is mediated by its gut microbiota (Macke et al. 2017a). Moreover, cyanobacterial tolerance was shown to be dependent on multiple microbial interactions within the *D. magna* host (Boudry et al. 2020). Given that toxin production is commonly found in various freshwater and marine microalgae that cause harmful algae blooms, symbiont-mediated protection against these toxins might be important for many aquatic hosts.

Microbial symbionts have also been shown to provide protection against osmotic stress in several hosts. In response to high salinity levels, the algal symbiont *Symbiodinium* produces high levels of the osmolyte 2-O-glycerol-α-d-galactopyranoside (floridoside), thereby increasing the capacity of the coral to cope with the effects of osmotic stress (Ochsenkühn et al. 2017). For the seaweed *Ectocarpus*, bacteria are essential to make the switch from marine to freshwater conditions. Without its bacteria, the algal host does not survive the transition to freshwater, indicating that bacteria can provide essential functions to mitigate the negative effects of salinity changes (Dittami et al. 2016).

2.4. Role of the microbiome in the host defence against natural enemies

Aquatic organisms have to cope with various natural enemies in their environment, including predators, grazers and parasites. As a consequence, many aquatic organisms have symbiotic interactions with microorganisms that protect them against these enemies. Defensive symbioses exhibit a variety of mechanisms through which the host gains protection against its natural enemies (Clay 2014).

Defensive symbioses against predators and grazers can be mediated through symbiont-derived secondary metabolites that render the host unpalatable or toxic. This mechanism is well known from sponges and tunicates, which rely heavily on chemical defences (Flórez et al. 2015). For example, the dictyoceratid sponge *Dysidea herbacea* is host to the intracellular symbiotic cyanobacterium *Oscillatoria spongeliae* that produces various halogenated compounds such as dysideathiazole, which are fish-feeding deterrents, protecting the sponge against predation (Ridley et al.

2005). Recently, it was shown that *Haliclona* sp. sponges have intracellular renieramycin-producing bacteria with a strongly reduced genome in specialized chemobacteriocytes, indicating that both partners evolved a highly specialized symbiosis (Tianero et al. 2019). These renieramycins are known to be highly cytotoxic and are hypothesized to protect the sponge against predators and pathogens. Tetrodotoxin (TTX) is a neurotoxin that is frequently used by many aquatic organisms to protect themselves against predation. Organisms containing TTX span a wide range of taxonomic groups such as red algae, pufferfish, blue-ringed octopuses, crabs, starfish, flatworms and amphibians (Jal & Khora 2015) and have evolved resistance through modification of their sodium channels (Venkatesh et al. 2005, Vaelli et al. 2020). Although this toxin can be accumulated by feeding on TTX-containing prey, several studies have shown the importance of symbiotic TTX-producing bacteria for host defence (e.g. Noguchi et al. 1986, Vaelli et al. 2020). Interestingly, this toxin is produced by a wide array of bacterial phyla (*Actinobacteria*, *Bacteroides*, *Firmicutes*, *Proteobacteria*) associated with various host organisms (Jal & Khora 2015), which could explain its widespread occurrence as a defensive mechanism. In addition to relying directly on microbial symbionts for protection, some animals depend on symbioses between their prey and its symbionts for chemical defence. This relationship was recently shown by Zan et al. (2019) for the sacoglossan sea slug *Elysia rufescens* and the algae *Bryopsis* sp., which both rely on the toxic lipopeptide kahalalide F for chemical defence. *Bryopsis* sp. obtains this toxin by housing symbiotic kahalalide-producing intracellular bacteria. *E. rufescens*, in turn, relies on this symbiosis to extract and sequester kahalalide F through feeding on *Bryopsis* sp. that contain kahalalide-producing symbionts. This example nicely shows that host–symbiont interactions can have consequences that extend beyond the involved partners in their influence on aquatic food webs and ecosystems.

Another mechanism for defensive symbiosis against predators is through counter-illumination with the purpose of host camouflage. Ventrally directed luminescence produced by symbiotic bacteria disrupts the shadow of the host that is cast by light coming from above, providing camouflage to avoid detection from below. This type of symbiosis is found in several species of squid and marine fish that host bacteria from the *Vibrionaceae* family (*Vibrio* sp. or *Photobacterium* sp.) in specialized light organs (Dunlap et al. 2007). These bacteria are acquired from the environment, and their hosts have evolved ways to select only ben-

eficial symbionts to populate the light organ (McFall-Ngai 2014). This interaction was shown to be structured through quorum sensing between the bacterial strains (Verma & Miyashiro 2013). For several species of squid and leiognathid fish, it has been shown that the hosts can regulate the intensity, colour, angular distribution and patterns of ventral light emission in response to environmental light conditions by modifying the tissues surrounding the light organ (McFall-Ngai & Morin 1991).

A peculiar form of a microbial symbiosis that confers protection against predation can be found in ciliates of the genus *Euplotidium* that live in tide pools along rocky shores. A well-defined cortical band on the dorsal surface of the ciliate host is often colonized by bacterial episymbionts, referred to as epixenosomes, that belong to the genus *Verrucomicrobia* (Petroni et al. 2000). After attachment to the host, epixenosome cells differentiate themselves to form a sophisticated extrusive apparatus that can eject a ribbon in response to external signals. It has been experimentally shown that colonization by epixenosomes effectively protects *Euplotidium* from ingestion by the ciliate predator *Litonotus* sp. (Rosati et al. 1999).

The associated microbiota of aquatic organisms often play a crucial role in the host′s resistance or tolerance to pathogen infection (Kimura & Tomaru 2014, Dheilly et al. 2015, Greenspan et al. 2019, Davoodi & Foley 2020, Schellenberg et al. 2020, Portet et al. 2021). For instance, Huot et al. (2020) reported a congruence of vector snails′ phylogeny and their associated microbiome, combined with variable susceptibility between snail species and even populations of the same species, suggesting that the snail′s microbiome might play a role in parasite resistance. Microbiota-induced pathogen resistance or tolerance has 3 underlying mechanisms: competition for resources and space, production of antimicrobial substances and stimulation of the host's immune response (Dheilly et al. 2015, Mallon et al. 2015, Knutie et al. 2017).

An example of colonization resistance through resource competition can be found in the associated microbiota of the coral *Acropora palmata*. In this host species, both the commensal microbiota and the white-pox-causing pathogen *Serratia marcescens* are known to employ glycosidases and N-acetyl-glucosaminidase to utilize components present in the coral mucus. Krediet et al. (2013) showed that several members of the *A. palmata* microbiota have the ability to inhibit the induction of these catabolic enzymes in *S. marcescens.* This inhibition gives the pathogen a competitive disadvantage when growing in coral mucus, which results in reduced virulence.

Antimicrobials produced by the associated microbiota can also play a crucial role in the pathogen resistance of the host. In the marine sponge *Erylus discophorus*, a large and diverse fraction of the associated microbiota is known to produce antimicrobial compounds (Graça et al. 2013). However, sometimes the presence or absence of one specific bacterial strain producing antimicrobial substances can determine pathogen susceptibility or resistance. For example, the presence of the bacterium *Janthinobacterium lividum* in the cutaneous microbiota of the mountain yellow-legged frog *Rana muscosa* leads to a significantly reduced mortality as a consequence of infections by the lethal fungus *Batrachochytrium dendrobatidis*. This bacterial strain is capable of producing the anti-chytrid metabolite violacein, effectively reducing the chytrid pathogen burden on the mountain yellow-legged frog (Harris et al. 2009).

The associated microbiome can also stimulate the host′s immune response (Knutie et al. 2017, Murdoch & Rawls 2019). Knutie et al. (2017) showed that early-life disturbance of the bacterial communities associated with Cuban tree frog *Osteopilus septentrionalis* tadpoles results in a significantly higher infection by the parasitic worm *Aplectana hamatospicula* in adulthood. In contrast, disturbance of the associated bacterial communities of adult frogs did not result in a higher parasitic burden. This study indicates that the microbiota likely plays an important role in priming the immune system of juvenile frogs, protecting the host from parasites later in life. In zebrafish larvae, the immune response is boosted by an increase in microbiota complexity, but can also be affected by specific bacterial strains. By comparing germ-free to conventional zebrafish larvae, it became apparent that many of the immunity-related genes are microbiota-regulated (Murdoch & Rawls 2019).

It is worth noting that the diversity of the microbiota is often found to be positively correlated with colonization resistance, although a specific mechanistic explanation is often lacking. On the one hand, such a pattern could be caused by competition, as communities with high species richness occupy more niches and hence are more resistant to invading pathogens by leaving less space and nutrients available for the pathogen to exploit (Mallon et al. 2015). On the other hand, it could be that key species providing resistance (e.g. through the production of antimicrobial substances) are often missing in less diverse communities. A positive correlation between microbiota diversity and colonization resistance was

observed in the European common frog *R. temporaria*, which showed increased resistance to the emerging *Ranavirus* with a more diverse skin microbiome (Harrison et al. 2019). When the microbiota diversity in zebrafish is reduced through exposure to the antibiotic olaquindox, they also become more susceptible to infection by the pathogen *Aeromonas hydrophila* (He et al. 2017).

3. EFFECTS OF ANTHROPOGENIC DISTURBANCE ON HOST–SYMBIONT INTERACTIONS

3.1. Eutrophication and shifts in oxygen availability and nutrient ratios

Altered nutrient availability is one of the greatest disturbances for aquatic ecosystems globally. Excessive inflow of nutrients, mainly phosphorus (P) and N from different anthropogenic reservoirs, such as wastewater and agriculture, is a key factor in the process of eutrophication in lakes and coastal areas. The enhanced primary production resulting from eutrophication, in turn, encourages microbial activity and the consumption of dissolved oxygen in bottom waters and benthic habitats. The consequent hypoxia of these habitats is extremely destructive for aquatic life (Diaz & Rosenberg 2008, Rousi et al. 2019). Microbial responses to hypoxia are intimately tied to the geochemistry, in both sediments and the water column. Mat-forming microbes are a macroscopic feature of benthic marine ecosystems subjected to severe hypoxia. These mats are formed largely of filamentous sulfide-oxidizing bacteria. Many protozoans and metazoan animals live in association with mats of mega- and macro-bacteria, including some eukaryotes with symbiotic bacteria. A hypothesis is that large mat-forming, sulfide-oxidizing bacteria detoxify sediment by removing sulfide, and thus facilitate metazoan habitation (Levin et al. 2009). Changing temporal micro-environments with respect to oxygen depletion at alternating locations has been shown to exist, e.g. in sponges, and provides suitable conditions for the activity of its anaerobic microbial symbionts, fuelling the holobiont's metabolism (Lavy et al. 2016).

Increasing inputs of anthropogenic N and CO_2 from the atmosphere are also perturbing ocean nutrient levels, generating a progressive shift towards P or N limitation (Bindoff et al. 2019). Imbalanced carbon:nutrient ratios are known to strongly affect animal assimilation efficiencies, nutrient excretion, growth and reproduction, whether nutrients are in deficit or excess (Darchambeau et al. 2003, Laspoumaderes et al. 2015, Zoccarato & Grossart 2019). Although understudied relative to classic ecological systems, it is reasonable to hypothesize that the diversity of an organism's microbiome might, at least partially, be governed by nutrient availability. For example, patchiness in microbial communities in the oligotrophic North Atlantic Ocean relies on microbial associations with copepods as a source of nutrients and shows synchronous changes with variability in copepod nutritional content. As a consequence, bacterial communities associated with copepods in the oligotrophic ocean may not face nutrient limitation to the same extent as the surrounding free-living community (Shoemaker et al. 2020).

Changes in nutrient availability could also alter microbiome composition or functioning. Some organisms, such as sponges, have a highly stable microbiome when changing from oligotrophic to eutrophic conditions (Gochfeld et al. 2012, Simister et al. 2012, Luter et al. 2014). The great functional diversity and physiological plasticity of their microbiomes might contribute to their high ability to survive under variable environmental conditions (Baquiran & Conaco 2018). On the other hand, other aquatic organisms, such as the cyanobacterium *Trichodesmium* sp. (Frischkorn et al. 2017), larvae of the starfish *Acantasther* (Carrier et al. 2018) or the benthic foraminiferan *Amphistegina lobifera* (Prazeres et al. 2017), among others, were reported to have a dynamic microbiome composition in response to changing nutrients. In all these cases, the plasticity of their microbiomes or the capacity to acquire different symbionts may underpin their success in changing systems and could represent an advantage in determining their resilience under changing environmental conditions.

Other groups are less tolerant of nutrient fluctuations. In corals, for example, an increase in N disrupts the finely tuned equilibrium in their microbiome, exacerbating the impact of increasing temperatures, slowing down calcification (van Oppen & Blackall 2019) and promoting the invasion of opportunistic pathogens (Voss & Richardson 2006, Gochfeld et al. 2012, Bourne et al. 2016). Zalewski et al. (2011) suggested that the *Daphnia* microbial gut flora competes with the host for P. Nutrient availability seems to change the host's microbiome communities and, in turn, the microbiota (including pathogens) play a role in how nutrients are used by the *Daphnia* host (Duffy et al. 2012, Aalto et al. 2015, Reyserhove et al. 2017). Krotman et al. (2020) showed how sporadic nutrient pollution events drove fish skin communities to dysbiosis through the alteration of the microbiome

bacterial groups reducing fish health. Macronutrients seem to also influence the composition and activity of intestinal microflora in fish. P and N supplementation increased the bacterial diversity of the gut microbiome, but in this case, with a trend to stimulate beneficial bacteria (Xie et al. 2011, Dong et al. 2013).

3.2. Global warming

The rise in global CO_2 concentration since 2000 is about 20 ppm decade^{-1} (NOAA 2021). As a result, the Earth is heating up rapidly, yet is at a significant distance from thermal equilibrium due to the large flux of thermal energy currently entering the world's water bodies (Huntingford et al. 2020). The increasing water temperatures are decreasing oxygen solubility and increasing respiration rates and therefore amplifying the hypoxic conditions resulting from eutrophication.

Changes in environmental temperatures can influence the host's microbiome through direct effects of temperature on the associated microbiota community, or indirectly through temperature effects on the host phenotype, which in turn influences the microbiota (Kohl & Yahn 2016, Li et al. 2018, Fontaine & Kohl 2020). Shifts in the microbiota community composition can arise through changes in the external microbial pool to which hosts are exposed, and through host-mediated differences (Fan et al. 2013, Seedorf et al. 2014, Sullam et al. 2018). Indeed, differences in the effects of temperature on microbial community composition have been described under similar conditions between genotypes of the same species (Sullam et al. 2018, Frankel-Bricker et al. 2020) and between closely related species (Fontaine & Kohl 2020). Indirect changes of the associated microbiota can occur through modifications in active and passive selectivity for particular microbes in the host and are expected for several reasons (Nishiguchi 2000, Webster et al. 2008). Warming alters many aspects of ectotherm physiology, such as immune function (Maniero & Carey 1997) and gut transit time (van Marken Lichtenbelt 1992), which can influence microbial community structure (Hooper et al. 2012, Kashyap et al. 2013). Increased temperatures may also accelerate host metabolic rates (Kirk et al. 2018), leading to an increased host demand for carbon (carbohydrates) compared to N (amino acids) (Bestion et al. 2019). This was, for example, supported by enrichment in 2 of the 3 microbial carbohydrate metabolism pathways and a general decrease in microbial amino acid metabolism pathways under increased temperatures in frogs (Fontaine & Kohl 2020). The changes in host metabolism and physiology can destabilize associations between hosts and microbial symbionts. For instance, in corals *Orbicella faveolata*, warming made the associated *Symbiodinium* parasitic, resulting in higher retention of its photosynthates (Baker et al. 2018).

In general, increasing water temperatures do not seem to affect microbial alpha diversity in a wide range of aquatic organisms (e.g. the water flea *Daphnia magna*: Sullam et al. 2018, Frankel-Bricker et al. 2020; *Lithobates* frogs: Kohl & Yahn 2016, Fontaine & Kohl 2020). Yet several exceptions have been documented where increased water temperatures reduced (e.g. Huyben et al. 2018, Li et al. 2018) or increased (e.g. Li et al. 2019) the alpha diversity, both of which may be associated with negative effects for the host. A reduction of gut-associated bacterial taxa may decrease the stability of the gut microbial communities (Fan et al. 2013) and reduce the host's resilience under stressful conditions (Lozupone et al. 2012). For example, increasing water temperatures caused the genus *Reyranella*, which plays a role in immune function (Peng et al. 2019), to be largely absent from the gut of the bullfrog *L. catesbeianus* (Fontaine & Kohl 2020). Furthermore, in the salamander *Plethodon cinereus*, the abundance of the genus *Janthinobacterium*, which protects amphibians against the fungal disease *Chytridiomycosis*, decreased under rising temperatures (Fontaine et al. 2018). An increased alpha diversity may also negatively impact the host when it reflects proliferation of opportunistic pathogens. For example, Li et al. (2019) indicated that the increase in *Vibrio* and *Arcobacter* under heat stress in the mussel *Mytilus galloprovincialis* increased its susceptibility to diseases, thereby contributing to increased mortality.

Elevated water temperatures typically alter the associated microbial community composition, as has been documented for many organisms including algae (e.g. Webster et al. 2011, Stratil et al. 2013), aquatic invertebrates (e.g. mussels: Li et al. 2018, Li et al. 2019; rotifers: Eckert et al. 2021; water fleas: Sullam et al. 2018, Frankel-Bricker et al. 2020) and vertebrates (e.g. fish: Huyben et al. 2018; frogs: Kohl & Yahn 2016, Fontaine & Kohl 2020). For example, the gut microbial communities of tadpoles of the invasive bullfrog *L. catesbeianus* change more rapidly and have more temperature-dependent bacterial functional pathways in response to higher temperatures than those of the non-invasive green frog *L. clamitans* (Fontaine & Kohl 2020). Such microbially mediated mechanisms may contribute to invasive

species being often more phenotypically plastic than native species (Davidson et al. 2011, Houwenhuyse et al. 2018).

Rapid evolutionary changes of the associated microbiota in response to increased temperatures might mitigate the negative effects of global warming experienced by the host. *Vibrio fischeri* evolved an increased ability to colonize the *Euprymna scolopes* squid host in response to higher temperatures resulting in an increase in bioluminescence (Cohen et al. 2019). Studies on *D. magna* showed that host clones from thermally different geographic regions harboured microbial communities that differed in structure, despite being reared under similar lab conditions for many years. However, the response in the gut microbiome to an increased temperature was similar for clones from different geographic regions, and the water flea population was still an important factor in explaining microbiome variation, indicating the potential for rapid evolution (Frankel-Bricker et al. 2020).

Next to the heating effect, the absorbance of enhanced CO_2 concentrations causes acidification of surface waters, which is particularly problematic for calcifying organisms such as foraminifera, corals and mussels (Orr et al. 2005). Corals growing close to a natural CO_2 seep hosted less symbiotic bacteria than the same corals growing further from the seep (Morrow et al. 2015). In addition, bacteria linked with diseases and stress seem to be more dominant in corals growing at a reduced pH (Meron et al. 2011). Negative feedback as a result of changes in the associated microbial community caused by acidification seems to worsen the effects of increased CO_2 concentrations on corals. Other species might benefit from the increased CO_2 levels. The same study (Morrow et al. 2015) that compared corals growing close to seeps to those growing at control sites also reported more photosynthetic microbes in sponges growing near the seeps, potentially providing the sponges with increased nutritional benefits.

3.3. Anthropogenic structures

Human interventions have changed residence time in lotic systems and created entirely new lentic systems, including reservoirs and canals. Additionally, many artificial structures such as windmill farms, oil rigs and aquaculture farms provide hard substrates for organisms to adhere to and shelter where previously there was none. Microorganisms can have a potential role in their host's adaptation to anthropo-

genically created habitats. They could do so by conferring resistance in the host to heavy metals from antifouling agents used to coat the structures (see Section 2.3) and extending the host's niche to better fit artificial local conditions. Overall, the impact of anthropogenic structures on the host-associated microbiota has hardly been explored.

Man-made structures, such as riverbank reinforcements and pier pilings, differ markedly from natural substrates by having different physico-chemical properties, orientation, shading etc. and generally strongly impact biological communities (Ferrario et al. 2016, Phillips & Prestie 2017, Reyne et al. 2021). Due to their effects on environmental conditions and biota, these structures can be expected to influence the host-associated microbiota and their interactions with the host (e.g. Jani & Briggs 2018). Marzinelli et al. (2009, 2018) showed that the kelp *Ecklonia radiata* growing on artificial pier-pilings was covered by more epifauna, and more of its epiphytic bacteria were associated with macroalgal diseases compared to kelp growing on neighbouring natural rocky reefs. Lower levels of light on the pier due to the shading of the pilings were put forward as one of the probable causes of the observed differences. Although the kelp populations did not differ in photosynthetic capacity, these results suggest a negative impact of the artificial structures on the host. Artificial substrates tend to provide suitable opportunities for novel, often invasive, organisms to settle (Mayer-Pinto et al. 2015, Ros et al. 2016). The same goes for newly introduced bacteria, which can potentially establish more easily on anthropogenic substrates where there may be a lower biological diversity (Amalfitano et al. 2015). Artificial substrates might therefore provide opportunities for novel associations between hosts and microorganisms.

3.4. Salinity changes

Salinization of freshwater environments is expected due to the global rate of mean sea-level rise at an average rate of 3.2 ± 0.4 mm yr^{-1} since 1993 (Nicholls & Cazenave 2010). In combination with reduced rainfall, sea-level rise causes saltwater intrusion into coastal freshwater environments, converting them to brackish environments (Neubauer 2013). In addition, salt application for de-icing of roadways has been recognized as a major source of chloride ions to groundwater, streams, rivers and lakes (Dugan et al. 2017).

Changes in salinity are likely to result in differences in the abundance of key microorganisms (Herlemann

et al. 2011), shifts in microbial metabolism (Neubauer 2013) and nutrient cycling (Marton et al. 2012). The host's internal environment can shift as a consequence of salinity changes, which in turn may affect the microbiome structure. Taxonomy-based functional profiling of the host-associated microbiota in the osmoconforming coral *Fungia granulosa* after long-term increased salinity exposure resulted in a shift in the bacterial community towards increased osmolyte production, sulphur oxidation and N fixation (Röthig et al. 2016). Also in osmoregulators, changes can be expected, e.g. when salmon move from freshwater to saltwater, they drink continuously to counteract water loss to the hyperosmotic environment, thereby increasing the luminal alkalinity to that of the surrounding medium. Additionally, novel pathogens, microbes and dietary items are encountered in the saltwater environment, which suggests major changes and unique profiles in the intestinal microbiota following movement to saltwater (Dehler et al. 2017).

Depending on their salinity tolerance, strict freshwater bacteria may be extinguished while saline-tolerant bacteria may survive and marine bacteria could immigrate. Salinity shifts therefore also favour habitat generalists with a broad salinity tolerance (Székely & Langenheder 2014). *Artemia* survive at very high salinity levels but have a strongly reduced fitness at reduced salinity. Nougué et al. (2015) showed that this reduction in fitness is caused by the impact of salinity changes on the host's gut microbiota. The gut microbiota, necessary for algal digestion, was shown to grow better at high than at low salinity, and its functionality might thus be compromised at low salinity. Further evidence for the microbiota-mediated effect of salinity on host fitness was provided by the observation that axenic *Artemia* do not have reduced fitness at low salinity when feeding on easily digestible food. Kivistik et al. (2020) artificially increased or decreased the salinity level in water containing *Theodoxus fluviatilis* snails that originated from freshwater or mesohaline environments. They found that an increase in salinity in the water containing freshwater snails resulted in a strong change in the associated bacterial community, and typical marine bacteria became more pronounced in the digestive tract. However, the composition of the digestive tract microbiome of mesohaline snails did not alter after either an increase or decrease in salinity. Analysis of the functional profile of the digestive tract microbiomes showed that mesohaline snails have the ability to maintain the original bacterial community with high cellulolytic potential and the ability to produce osmolytes, while freshwater snails

were not able to compensate for the loss of functions by a shift in the bacterial community (Kivistik et al. 2020). This finding suggests that changes in salinity can result in compositional changes in the gut bacterial community, which in turn changes its functional profile and can have an effect on the host's fitness.

3.5. Chemical pollution

Anthropogenic activities such as food production and industrial activity cause the release of various chemicals into the environment that can have a considerable impact on the biotic properties of natural aquatic ecosystems. There is clear evidence that anthropogenic chemical pollutants adversely affect aquatic ecosystems through ecosystem destruction, habitat modification, water chemistry alteration and direct addition or removal of species (Malmqvist & Rundle 2002, Schallenberg & Armstrong 2004, Englert et al. 2013).

Chemical pollution with microplastics, silver nanoparticles, pesticides and heavy metals in aquatic environments can also disturb the associated microbiota of aquatic hosts living in those environments. For example, Milan et al. (2018) found that the hepatopancreas microbiota composition of the Manilla clam *Ruditapes philippinarum* was influenced by the variation in overall chemical pollutant concentrations in its environment. In addition, they observed an over-representation of several pathways involved in xenobiotic biodegradation in the microbiota, suggesting a potential detoxifying action of the microbiome that can have consequences for the host's susceptibility to environmental chemicals. Alterations in the host-associated microbiota induced by chemical pollution can, in turn, have further effects on host physiology, growth and survival (Evariste et al. 2019).

Microplastics, defined as plastic debris smaller than 5 mm (Moore 2008), are a widespread environmental pollutant in both freshwater and marine environments (Welden & Cowie 2016). These microplastics can be ingested by many aquatic animals and have been found to negatively affect both phytoplankton and fauna in aquatic ecosystems (Wang et al. 2019). Two recent studies showed that exposure of zebrafish *Danio rerio* to polystyrene microplastics has significant effects on the phylum-level composition and diversity of its gut microbiota community (Qiao et al. 2019, Wan et al. 2019). Qiao et al. (2019) observed a decrease in *Proteobacteria*, while *Fusobacteria* increased as a result of polystyrene exposure. Wan et al. (2019) observed a decrease in *Gammaproteo-*

bacteria and *Bacteroidetes*, while *Firmicutes* significantly increased. Both studies indicated that these polystyrene-induced shifts in gut microbiota could be associated with the observed dysbiosis causing gut inflammation, metabolic disorders, oxidative stress or neurotoxicity. Silver nanoparticles decreased *Betaproteobacteriales* (mainly *Curvibacter* and *Undibacterium*) in the microbiomes of the freshwater planarian *Schmidtea mediterranea* (Bijnens et al. 2021). These studies show that the presence of synthetic micro- and nanoparticles can have pronounced effects on host–microbiota interactions.

Pesticides commonly used in agriculture are found to be widely present in aquatic ecosystems due to runoff (Sánchez-Bayo et al. 2016). Kan et al. (2015) found that exposure of goldfish *Carassius auratus* to the pesticide pentachlorophenol (PCP) was associated with an increased abundance of *Bacteroidetes*, especially members from the *Bacteroides* genus, and a decreasing *Firmicutes*/*Bacteroidetes* ratio. The abundance of 4 other gut microbial taxa was furthermore negatively correlated with this increase in *Bacteroidetes*. These PCP-induced changes in gut microbiota community structure were thought to play a crucial role in the reduced body- and liver weight of these fishes when exposed to PCP. In contrast, exposure to pesticides does not necessarily always affect microbiota communities or symbiotic interactions. For example, Knutie et al. (2017) showed that exposure of the Cuban tree frog *Osteopilus septentrionalis* to environmental concentrations of the herbicide atrazine only had minimal effects on its associated microbiota, and no effects on the host's susceptibility to infection with the chytrid fungus *Batrachochytrium dendrobatidis*.

Elevated concentrations of heavy metals are often found in aquatic ecosystems due to runoff from mining, agriculture or industrial waste. Dahan et al. (2018) exposed larval zebrafish to environmental concentrations of arsenic (between 10 and 100 ppb). They found that even at the lowest concentration of arsenic there were significant changes in the gut microbiota community structure. Although the authors suggested that arsenic exposure induced a dysbiosis in the zebrafish microbiota, health consequences of this shift in microbiota for the host were not measured. Similarly, changes in gut microbiota community composition were found when zebrafish were exposed to lead (Xia et al. 2018). Here, the authors also suggested that the observed changes in gut microbiota composition might impact the host's metabolism, although direct effects of lead exposure on the host could not be excluded.

3.6. Antibiotics

Antibiotics are commonly used to treat or prevent bacterial infections in humans and animals, and traces can be found in aquatic systems as a result of the absence of (or incomplete) removal from wastewater (Giger et al. 2003). Concentrations of these antibiotics are in the range of ng or a few µg l^{-1}, and it is considered even lower for coastal sea waters (Gothwal & Shashidhar 2015). However, some studies report concentrations in the mg l^{-1} range for sulphonamides (Bilal et al. 2020, Bojarski et al. 2020). At higher concentrations, antibiotics often have toxic or growth-inhibiting effects, e.g. on *Daphnia* (Wollenberger et al. 2000, Gorokhova et al. 2015) and fish (Bojarski et al. 2020). Even at very low doses, antibiotics can show effects on microbiota composition and diversity in aquatic animals (Callens et al. 2018) as they have been shown to act as signal molecules (Sengupta et al. 2013). Such effects of individual antibiotics might be more pronounced considering that the exposure to such compounds is likely continuous and composed of a highly variable cocktail of various antibiotics (Evariste et al. 2019). The actual impact of this contamination on the microbiota of animals in nature is unknown since few studies have tackled the effect of this low-dose exposure, and many of them used concentrations that are in the upper range or above environmentally relevant ones. Here, we only discuss studies using <50 µg l^{-1} of antibiotics and their related effects on microbiota. Yet all of the currently available literature used only 2 model systems — *Daphnia* or fish — which renders a generalization of these results difficult.

The few available data suggest that the impact of low-dose antibiotics on diversity and community composition as well as the resilience of the host-associated microbiota depend on both the antibiotic itself and on the host: a long-term exposure of juvenile zebrafish to relatively low concentrations of tetracycline (1 µg l^{-1}) showed a shift of the microbial community and indicated an increase in microbiota diversity. Bacterial taxa benefiting from the presence of the antibiotic included *Fusobacter*, *Firmicutes* and *Bacteroidetes* (Keerthisinghe et al. 2020). Consequently, an increase in fish body weight which altered the liver function was observed (Keerthisinghe et al. 2020). Exposure to a slightly higher concentration of Rifampicin (25 µg l^{-1}) for about 6 d resulted in a strong shift in the composition of both skin and gut microbiota of the western mosquitofish *Gambusia affinis* and a strong decrease of microbial diversity and culturability. Culturability of bacteria quickly increased during

antibiotic exposure, indicating higher growth of the selected resistant strains. However, neither skin nor gut microbiota composition or diversity were resilient to antibiotic disturbance and still showed highly altered microbiota composition after 1 wk without antibiotics. On the other hand, in a study where larval fathead minnows *Pimephales promelas* were exposed to low levels of Triclosan (100 ng l^{-1}), the antibiotic had an immediate effect on community composition and diversity, but the gut community recovered from this disturbance after 2 wk of antibiotic absence. The different studies used different antibiotics, animals and recovery times, thus more standardized experiments would be needed to draw generalized conclusions on the resilience of the animal-associated microbiota after antibiotic-induced disturbances.

Sometimes the effect of low-dose antibiotics is not visible at the level of the microbiota composition. When zebrafish were exposed for 2 mo to oxytetracycline at 10 µg l^{-1}, the microbiota diversity was not impacted and the community composition was rather similar to the one of the no-antibiotic treatment. However, the microbiota composition of the surrounding water community shifted strongly in the presence of the antibiotic (Almeida et al. 2019). This suggests that compared to free-living communities host-associated communities might in some cases be more resistant to antibiotic exposure. In a different study on zebrafish, the same antibiotic at even lower concentration (420 ng l^{-1}) did shift the microbial community, but no shift was observed with sulfamethoxazole (260 ng l^{-1}) (Zhou et al. 2018).

Despite these small shifts in microbiota community composition, the presence of antibiotics can also affect the host's physiology or susceptibility, either through the direct action of the antibiotic on the host or indirectly through impacts on the microbiome. In the above-mentioned study, for example, the presence of both antibiotics was associated with higher mortality of the fish when challenged with a pathogen (Zhou et al. 2018). The same oxytetracycline, also in low dose, had a very strong effect on the development of the animals in other experiments (Yu et al. 2020), indicating a high potential of the antibiotic to affect the fish's physiology via changes in its microbiota. Exposure of Nile tilapia *Oreochromis niloticus* to low doses of sulfamethoxazole and oxytetracycline only slightly changed microbial community and diversity, but chronic exposure to antibiotics impaired intestinal morphology, permeability and induced microbiota dysbiosis with a very strong negative impact on the fish's physiology, nutritional metabolism and immune system (Limbu et al. 2018).

Moreover, combined effects might play an important role: in an experiment with the *D. magna* model system and low concentrations of ciprofloxacin, an effect on the microbiome composition (with increased abundances of *Pseudomonas*-related taxa) and on animal fitness was only observed when the diet was poor. No effect, however, was detected when animals were grown on a healthy diet (Akbar et al. 2020). Effects of antibiotics on the animal microbiota at very low concentrations (<10 ng l^{-1}), found in many central European freshwater systems (Szymańska et al. 2019), are so far unstudied. Furthermore, sub-inhibitory concentrations of antibiotics often modulate bacterial gene expression, and many antibiotics are assumed to act as signalling molecules in microbial communities (Yim et al. 2007, Sengupta et al. 2013). As such, even in the absence of bacteriocidal or bacteriostatic effects, antibiotics might affect the physiology of microbial symbionts and ecological interactions between them. This, in turn, can affect the benefit they provide to their host. Thus, longterm exposure experiments with low antibiotic concentrations and additional model systems should be a focus of future research.

4. PERSPECTIVES

4.1. Significance of human-driven symbiotic shifts

The ever-increasing list of examples of beneficial effects of microbial symbionts on aquatic organisms indicates that our current knowledge on this topic is mainly limited by research efforts and that much remains to be discovered. Despite the overwhelming evidence for the importance of microbial symbiosis for aquatic organisms, we know very little about how human activities affect these symbioses, and what the consequences are for the hosts. Furthermore, studies investigating human impacts on microbial symbioses are often descriptive, reporting only changes in the presence or abundance of microbial symbionts without inferring fitness consequences for the host. The fact, however, that many descriptive studies often do report large shifts in the microbiota community suggests that disturbances in mutualistic interactions can be expected. This is supported by a number of studies — albeit limited — that found a significant impact of human activities on the symbiotic interaction itself (Table 1).

Obtaining a better insight into the role of the microbiome is crucial, given that it affects human and, more generally, ecosystem health as indicated

in the 'One Health' framework, where human and environmental health are considered to be interconnected and interdependent (Flandroy et al. 2018, Berg et al. 2020). Ecosystem health depends to a large degree on intact relationships between hosts and their microbiomes or symbionts. Major issues to be resolved in order to evaluate the importance of such symbioses for ecosystem health include evaluating how taxonomically/functionally redundant microbiota are with respect to their impact on host fitness (Koedooder et al. 2019) and what the ecosystem-level effects are, e.g. if keystone species (such as *Daphnia*) are impacted (Macke et al. 2020). In line with this 'One Health' framework, it has become apparent that integrating the interaction between multiple symbionts, their host and the environment is crucial for understanding disease aetiology and ecosystem health (Bass et al. 2019). Many infections have zoonotic reservoirs from which they can (re-)emerge (J. P. Webster et al. 2016, Leger & Webster 2017), while others may even pose conservation threats for wildlife populations (Thompson et al. 2010, Heard et al. 2013). Although the link between host health and its microbiota has mainly been considered in a medical context, its importance in other areas such as conservation biology is becoming increasingly clear (Trevelline et al. 2019). One way that humans have triggered wildlife declines is by transporting disease-causing agents to remote areas of the world (Byrne et al. 2019). Considering the importance of a host's microbiome in disease resistance and host health, one would expect the microbiome of aquatic hosts to play an important role in their resistance to and spread of infections (Toledo & Fried 2011). This role has been shown for the resistance of amphibians to the fungal pathogen *Batrachochytrium dendrobatidis* (Flandroy et al. 2018, Greenspan et al. 2019). The realization that mass drug treatments alone do not suffice to control diseases renewed the focus on the control of their vectors. Similar to malaria control, manipulating the microbiome of aquatic vectors could be a sustainable way of controlling these diseases without negatively affecting local ecosystems. As a first step, resistance-inducing strains could be identified, such as the *Enterobacter* bacterium in the mosquito *Anopheles gambiae* which

makes its host almost completely resistant to *Plasmodium* infections (Cirimotich et al. 2011). Such research is especially relevant in the Anthropocene as human activities alter ecosystems, reduce the microbial diversity in the environment and spread disease-transmitting species across the world (Houwenhuyse et al. 2018, Lachnit et al. 2019, Vanhove et al. 2020).

4.2. Future challenges

In this last section, we postulate 5 major challenges to be addressed in future microbiome–host studies in relation to anthropic pollution stresses (summarised in Fig. 3):

4.2.1. How can we distinguish direct effects of human activities on the host from indirect effects through their impact on symbiotic interactions?

One of the main challenges when assessing the effects of anthropogenic disturbances on symbiotic interactions is the difficulty in separating this impact from direct effects on the host (Fig. 3A). Indeed, direct effects on aquatic hosts have been recorded for all of the above-mentioned disturbances (e.g. Silvestre et
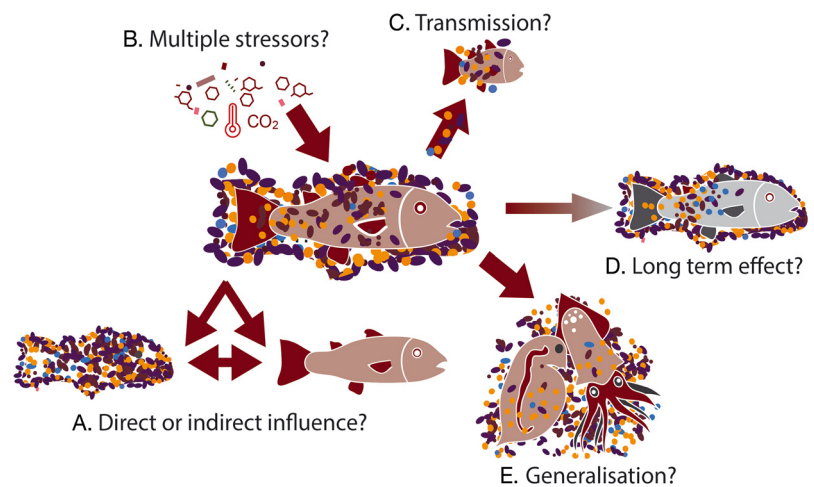

Fig. 3. Challenges to tackle in aquatic microbial research to improve our understanding of anthropogenic effects on symbioses between aquatic organisms and microbes. Over time, increasing anthropogenic pressures on an aquatic host (from left to right) inflict stress on the host and change its associated microbiota. The identified knowledge gaps are: (A) Do stressors directly impact the host or indirectly through the microbiota? (B) How do multiple stressors simultaneously impact the symbiotic interactions? (C) How do human activities impact microbial symbiont transmission? (D) What are the long-term effects of anthropogenic pressure on the symbioses and host persistence? (E) Can findings be generalised to other species?

al. 2012). Two methodological approaches can be used to separate such direct from indirect effects.

In a first approach, negative impacts on symbiotic interactions are indirectly inferred based on a profound knowledge of the functioning of the symbiosis, and on observations of changes in parameters that are known to be important for the symbiosis. This can be relatively straightforward if the benefit provided by a specific symbiont is well-described and the anthropogenic disturbance shows a clear effect on the presence, abundance or functioning of this symbiont (e.g. coral bleaching under temperature stress; Glynn 1991). Data on the effect size of symbionts on the host's phenotype through experiments manipulating their presence or abundance (e.g. Rosati et al. 1999, Becker et al. 2009) can furthermore be used to examine if the effect sizes of the human impact on the host are in the same range. However, indirect inference of negative effects on host–symbiont interactions is often not as straightforward because a benefit provided by symbionts can depend on complex interactions, and anthropogenic disturbances can impact microbiota communities in complex ways through changes in composition and metabolic functioning. The use of multi-omics approaches could provide insight into the magnitude of the impact of a disturbance on symbiotic interactions. For example, if the gut microbiota community benefits the host through the production of a specific metabolite; (meta)genomics, (meta)transcriptomics, (meta)proteomics and (meta)metabolomics could be used to investigate the impact of a disturbance on, respectively, the presence of genes needed for the production of this metabolite, the expression of these genes and the concentration of gene products or the metabolite itself (Douglas 2018, He et al. 2020).

The second approach involves directly measuring the effect of a disturbance in the associated microbiota on the host's phenotype. When an environmental factor causes a change in the presence or abundance of symbionts, this change can be mimicked in the host without exposing this host to the factor responsible for this change. This process allows the effect of changes in the microbiota community on the host phenotype to be measured by removing the direct effect of the environmental factor on the host. Two methods can be used to achieve this, both of them starting with an initially germ-free host, followed by the inoculation of microbial symbionts. In transplant experiments, hosts and their associated microbiota are exposed for some time to a stressor (or a combination of stressors) of interest (e.g. high temperature, toxic cyanobacteria, pesticides), allowing the microbiota to respond to this change. Microbiota communities are subsequently extracted from the exposed hosts and transplanted into germ-free recipient hosts. This approach has been successfully used to directly measure the effect of environmentally induced changes in the microbiota on phenotypic traits of various animals such as mice, desert woodrats and *Daphnia* water fleas (Ridaura et al. 2013, Kohl et al. 2014, Macke et al. 2017a). Synthetic communities can also mimic the effect of a disturbance on the associated microbiota through precise inoculation of cultivated microbiota members. Although this method is still in its infancy due to a lack of representative collections of microbiota isolates, this approach is becoming feasible for some model organisms like *Caenorhabditis elegans* (Rafaluk-Mohr et al. 2018, Dirksen et al. 2020) and *Drosophila melanogaster* (Douglas 2018). Both methods hold great promise for directly measuring the effect on changes in the microbiota composition on the host phenotype, but it must be noted that accurately mimicking environmentally induced changes in the absence of the environmental factor can be challenging (Callens et al. 2018). Furthermore, metabolic changes in the microbiota as a result of removing the environmental factor of interest are also not taken into account.

4.2.2. Can we expect that the measured impact of single stressors will be additive in multi-stress environments?

The impact of humans on aquatic systems is clearly multifaceted, and aquatic organisms are therefore likely to face different challenges simultaneously (Fig. 3B). Examples have shown that stressors can amplify one another (e.g. acidification and temperature increase; N. Webster et al. 2016), but more complex effects are equally possible. For instance, a high salinity tolerance in a coral–*Symbiodinium* system also confers increased thermotolerance (Gegner et al. 2017), and the presence of cyanobacteria affects white fat cell disease in *Daphnia*, potentially mediated through changes in the microbiome (Coopman et al. 2014, Macke et al. 2017a). The complexity of multi-stressor interference on host–microbiome interactions calls for more realistic experiments evaluating the effects of multiple stressors on aquatic organisms simultaneously. Such a multi-stressor experimental approach will provide a more accurate insight into the performance of aquatic organisms in an anthropogenically disturbed environment.

4.2.3. What is the impact of human disturbances on microbiota transmission?

Very little is known about the consequences of an acute disturbance on symbiont transmission (Fig. 3C). Many of the examples discussed above have shown that anthropogenic disturbances can severely affect the presence or abundance of beneficial symbionts. These changes can subsequently disturb the symbiont transmission chain, affecting the transmission probability of beneficial symbionts to the next generation (Koskella & Bergelson 2020). This, in turn, can strongly affect subsequent assembly of host-associated microbiota communities and the host's phenotype (Callens et al. 2018). In laboratory populations of mice, a 'legacy effect' is often observed, where differences in microbiota composition are maintained between groups of co-housed individuals who transmit microbiota among each other but not with members of other groups (Robertson et al. 2019). This observation indicates that changes in the microbiota of an interacting population of hosts can be maintained over time, even if the stressor is no longer present.

Ecological frameworks such as metapopulation theory (e.g. used to understand the transmission of microbial infections; Gandon et al. 1996, Haag & Ebert 2004, Laine & Hanski 2006) and metacommunity theory (Leibold et al. 2004, Mihaljevic 2012) can be used to estimate the consequences of an anthropogenic impact on symbiont transmission between hosts, and the consequences of changes in transmission on host-associated symbiont communities. Microbiota studies can be perfectly treated as a metacommunity ecology problem, i.e. to adapt methods from metacommunity ecology to understand dispersal, diversity patterns and community assembly of symbionts (Macke et al. 2017b).

4.2.4. What is the potential for long-term mitigation of human impacts on symbiotic interactions?

Most environmental disturbances have marked and reasonably well-studied short-term effects on the interactions which are generally reflected by shifts in the host-associated microbial community as well as changes in the host's metabolism and physiology. The resulting changes in the symbiotic interactions can lead to dysbiosis (e.g. Krotman et al. 2020), worsening the impact of anthropogenic changes on the host, or shift the interaction towards a novel equilibrium between host, microbiota and the environment (e.g. Röthig et al. 2016). The long-term stability of this newly attained equilibrium has hardly been explored, yet is likely to determine how the hosts will endure the unremitting human pressure on aquatic ecosystems (Fig. 3D).

Understanding the ecological dynamics, whereby the symbiotic community changes as a result of anthropogenic impacts, and the evolutionary dynamic, a product of the adaptations of the host and its associated symbionts to anthropogenic impacts, is key to predicting long-term stability of the host–microbiota interactions and host persistence. Some host–microbiota systems might inherently be more robust to changes, either due to higher plasticity of the host, as is the case for some invasive species (e.g. Fontaine & Kohl 2020), or due to a more diverse associated microbial community with a high degree of functional redundancy (Callens et al. 2018). Anthropogenically induced environmental changes could, in these robust systems, result in a microbial community with a very similar functional make-up, providing similar health benefits for the host.

Host–microbiota systems with a less diverse microbial community or highly coevolved partners, on the other hand, are likely to be more sensitive to perturbations as replacement or complementation of the symbionts might not be possible. Rapid adaptations of the host, the microbiota or both might still aid these systems to persist under anthropogenic pressure.

If evolutionary rescue occurs, enabling the host and its associated microbiota to recover from anthropogenic pressure, it is likely driven by the evolutionary potential of the microbial community, which is generally much higher than that of the host (Koskella et al. 2017, De Meester et al. 2019). It is worth noting that adaptation of the microbial symbionts does not need to happen in association with the host but can even occur independently and still have implications for the health of the host. For instance, the adaptation of the bacterium *Vibrio fischeri* to temperature and pH stress affected its bioluminescence levels when present in its squid host (Cohen et al. 2019, 2020).

Long-term persistence of the organisms does not only depend on how changes in host–microbiota interactions will affect the health of the host, but also on how they will impact the fitness of the host compared to the other organisms present. Studies comparing how changes in the microbial symbiont community affect multiple competing species are rare for aquatic systems (Koedooder et al. 2019). Such studies can help explore how microbiome-driven changes in relative fitness can, in the long-term, result in alternate communities (terHorst & Zee 2016).

4.2.5. Can we generalize the anthropogenic impact on symbioses between aquatic organisms and symbionts?

Most studies are limited to a restricted set of organisms that either show drastic effects when microbial symbionts are disturbed (e.g. coral bleaching in the coral–zooxanthellae symbiosis; Muller-Parker et al. 2015) or freshwater organisms that are easily amenable to experimentation (e.g. *Hydra*, Deines & Bosch 2016 and *Daphnia*, Sison-Mangus et al. 2015, Callens et al. 2016, Macke et al. 2017b). Considering the large aquatic diversity which is, particularly at broad taxonomic scales, much higher than in terrestrial systems (Grosberg et al. 2012, Tadesse 2018), the limited set of focal organisms does not allow us to draw general conclusions upon how the disturbance of microbial symbioses might influence aquatic ecosystem functioning (Fig. 3E). This urges us to diversify the experimental systems in which these interactions are investigated. Broadening the scope of suitable host–microbiota systems poses important challenges, including developing the appropriate genetic tools and establishing axenization protocols, but major efforts are currently being made at overcoming these hurdles for a wide array of aquatic organisms (Dittami et al. 2021).

Generalization is further hampered by limited insight into how genetic diversity within species impacts the host–microbiota interactions. It is clear that different genotypes of the same species can have markedly different microbiomes (e.g. Callens et al. 2020, Frankel-Bricker et al. 2020), respond differently to environmental changes (Stock et al. 2019b) and affect the environmental microbial communities differently (Macke et al. 2020, Massol et al. 2021). Studies using a single genotype might thus not be representative of the response of genetically diverse species, hampering generalization of human impacts even on the level of a single species. A relevant discussion in this respect is whether there are consistent patterns to be detected between field and lab microbiomes. For some aquatic (especially vertebrate) species, there seems to be a certain consistency in the microbiome, e.g. the presence of *Proteobacteria*, *Fusobacteria* and *Firmicutes* in gut microbiomes of zebrafish *Danio rerio* and many other fishes (Roeselers et al. 2011, Ghanbari et al. 2015). For many other aquatic organisms, however, no consistent patterns have thus far been recorded. For *Daphnia*, some bacterial strains (e.g. *Limnohabitans* sp.) have been persistently found in lab cultures (Peerakietkhajorn et al. 2015), but *Daphnia* also associates with oppor-

tunistic species from the natural environment depending on particular conditions (Eckert & Pernthaler 2014, Callens et al. 2020). Nevertheless, that does not exclude the possibility that adaptive patterns cannot be found across field and lab microbiomes given the strong genotype × microbiome interactions detected (Macke et al. 2017a, Houwenhuyse et al. 2021). It is likely that there are multiple 'healthy' microbial profiles depending on the context. Although the diversity of microbes may be different between field and lab conditions, the functional profile of these communities may be similar (Burke et al. 2011, Adamovsky et al. 2018).

In conclusion, well-designed experiments covering the vast aquatic diversity will greatly improve our mechanistic understanding of which microbial symbionts improve the health of hosts. These insights will allow for the design of powerful models to project the multitude of anthropogenic impacts on aquatic organisms and ecosystems. Validation of such models will require more *in situ*, observational data. Long-term data series that span periods of changing anthropogenic influences on environmental and organism-associated microbiomes will be essential to substantiate and fine-tune model projections, in order to enable the development of adequate measures to counteract the potential negative consequences for organismic and environmental health.

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