



New perspectives on the role of cleaning symbiosis in the possible transmission of fish diseases

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Abstract For the last seven decades, cleaning symbiosis in the marine environment has been a research field of intrigue. There is substantial evidence that, by removing undesired items from their client fishes, cleaner organisms have positive ecosystem effects. These include increased fish recruitment, abundance and enhanced fish growth. However, the intimate association and high frequency of interactions between cleaners and clients potentially facilitates pathogen transmission and disease spread. In this review, we identify knowledge gaps and develop novel hypotheses on the interrelationship between

parasites, hosts and the environment (disease triangle concept), with a particular emphasis on the potential role of cleaner organisms as hosts and/or transmitters of parasites. Despite evidence supporting the positive effects of cleaner organisms, we propose the *cleaners as transmitters hypothesis*; that some parasites may benefit from facilitated transmission to cleaners during cleaning interactions, or may use cleaner organisms as transmitters to infect a wider diversity and number of hosts. This cost of cleaning interactions has not been previously accounted for in cleaning theory. We also propose the *parasite hotspot hypothesis*; that parasite infection pressure may be higher around cleaning stations, thus presenting a conundrum for the infected client with respect to cleaning frequency and duration. The impact of a changing environment, particularly

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climate stressors on cleaners' performance and clients' cleaning demand are only beginning to be explored. It can be expected that cleaners, hosts/clients, and parasites will be impacted in different ways by anthropogenic changes which may disrupt the long-term stability of cleaning symbiosis.

Keywords Cleaners · Clients · Hosts · Parasite transmission · Anthropogenic changes · Ecosystem function

Introduction

The concept of the relationship between environment, parasite and host has been extensively studied (e.g., Wolinska and King 2009; Tseng and Myers 2014; Cai et al. 2018). In the presence of a virulent pathogen, a favourable environment, and a susceptible host, it is very likely that infectious disease will occur (Francel 2001; Scholthof 2007). This theory was initially investigated by Duggar (1909) who suggested that the rise of a disease is linked to environmental factors that can potentially affect hosts and pathogens independently, as well as the interrelations between them (Francel 2001). Later, the concept of a disease triangle was explicitly defined (McNew 1960; Stevens 1960). Currently, the disease triangle is a well-established and commonly used concept, with a series of modified versions that often include other elements such as 'time', 'vector' or 'humans' (Francel 2001; Scholthof 2007). The addition of other elements is case-specific and is used to illustrate how the original interactions among host, pathogens and environment will respond when facing changes. Cleaner organisms may be included as a fourth element in the disease triangle because they present an important and complex influence on the way disease interactions may occur. Cleaner organisms, most often fishes or shrimp, typically establish a cleaning station, recognised by 'client' fishes as a location to directly seek service for the removal of external pathogens, epibionts and dead tissues (Feder 1966). There is an extensive body of work on the ecological, behavioural and physiological aspects of cleaning symbiosis presented under the premise that cleaning limits disease in fish clients and brings extended community benefits (see Côté 2000; Vaughan et al. 2017). However, cleaner fishes and

shrimp exhibit close physical contact with client fishes during cleaning interactions (e.g., entering the gills and mouth; Grutter 2004), suggesting that cleaner organisms potentially risk acquiring pathogens from their clients. However, little is known about the cleaners' potential susceptibility to their clients' pathogens, or the potential for pathogen transmission from cleaners to their fish clients (e.g. Treasurer 1997, 2012; Matejusova et al. 2016).

For this review, we examined cleaning symbiosis in the context of the disease triangle to develop hypotheses on the interrelationships between cleaners, parasites, fish hosts/clients and the environment (Fig. 1). Four elements were used in different contexts and are defined accordingly. For example, in the context of parasitism, we use the word "host" to characterise fishes infected with parasites which may be a cleaner fish or a client fish. In the context of cleaning symbiosis, the cleaner fish seeks to remove external parasites from the client, representing a short-term relationship between fishes. In this review, most of the examples given are focused on host/parasite relationships. However, we acknowledge, through the text, that other organisms such as viruses or bacteria may also be relevant in the context of cleaning symbiosis. We define parasites as organisms that have a specific part of their life cycle dedicated to parasitism whereas pathogens are disease-causing agents, triggering negative changes in the host tissue, causing pathology. Pathogens encompass many organisms such as viruses, bacteria, and parasites.

While shrimp are important as cleaners in marine ecosystems, most of our examples focus on cleaner fishes given that the majority of studies about cleaner organisms investigate cleaner fishes (e.g., ecology, behaviour, physiology) and thus reflect the most evidence.

We reviewed research published on cleaning symbiosis in marine environments with a specific focus on four pathways, with the following aims:

- (1) *Cleaners and parasites* to determine whether cleaner fishes are susceptible to parasite infections from their fish clients;
- (2) *Cleaners and clients* to explore the potential role of cleaner fishes as parasite transmitters in the wild;
- (3) *Parasites and cleaners* to evaluate mechanisms that parasites may use to evade cleaner organisms and maximise their chance of transmission;

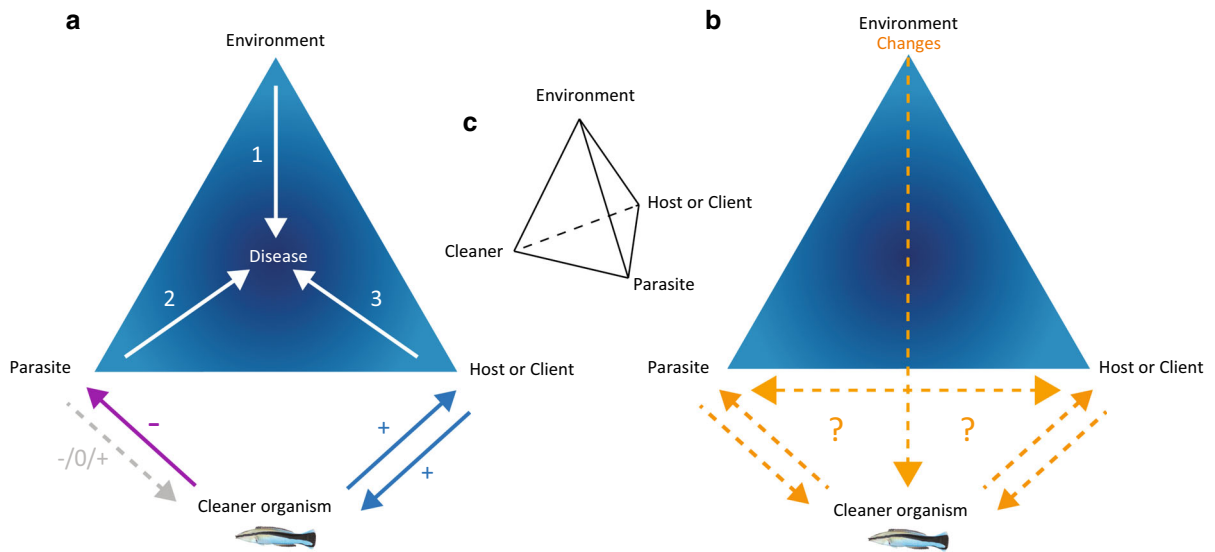


Fig. 1 Cleaner organisms as the fourth element of the disease triangle and effects on environment, parasite, and host. **a** For disease to occur, a favourable environment (1), parasite virulence (2) and a susceptible host (3) are needed. With cleaners added, arrows represent potential interactions between the cleaner organism, the parasite and the host. Blue arrows represent positive interactions between hosts, which also act as clients, and cleaners through cleaning symbiosis. The purple arrow represents negative effects of cleaners on parasites through parasite removal and consumption. We propose these pathways could include parasites using cleaner fishes as new

hosts (– negative effect on the cleaner), and/or cleaners as transmitters to infect other fishes (0 no effect on the cleaner) or parasites being eaten by cleaner fish (+ positive effect on the cleaner) (grey dotted arrow). **b** When interactions between cleaners and the environment were considered, we identified knowledge gaps in the literature on the potential effect of these disturbances on cleaner-host or client and cleaner-parasite relationships. The resulting tetrahedron **c** encompasses the extra corner created when cleaner organisms are added as a fourth element to this system. Cleaner organisms are represented by the cleaner wrasse *Labroides dimidiatus*

- (4) *Cleaners and environment* to examine the impact of global and local scale human impacts on cleaning symbiosis.

Role of cleaner organisms in marine environments

Marine cleaner organisms remove external parasites and diseased or damaged tissue from clients (Feder 1966). These items compose an important food source for the cleaners (Feder 1966). Cleaners can be defined as dedicated or facultative, depending on their degree of dependence on cleaning interactions for accessing food (Vaughan et al. 2017). While dedicated cleaners rely almost exclusively on cleaning interactions as a source of food, facultative cleaners are more opportunistic cleaners. Clients of dedicated cleaners (see Bshary 2003; Côté and Soares 2011) and some facultative cleaners (see Arnal and Morand 2001; Narvaez et al. 2015) visit cleaner territories called ‘cleaning stations’ and often adopt specific poses by

opening their fins and inclining their body to signal willingness to be cleaned (Randall 1958; Losey 1972; Poulin 1993; Côté et al. 1998). The main cleaner organisms in aquatic systems are teleost fishes and decapod shrimp, with a total of 208 fishes (with 16 dedicated and 192 facultative fishes) and 56 shrimp species so far reported as cleaners (Vaughan et al. 2017; Wirtz and Muller 2020). Among dedicated cleaner fishes, cleaner wrasses from the genus *Labroides* and cleaner gobies from the genus *Elacatinus* are the best studied (Côté and Soares 2011; Vaughan et al. 2017). While the genus *Labroides* includes five species, all of which are considered dedicated cleaners restricted to the Indo-Pacific region (Vaughan et al. 2017), the bluestreak cleaner wrasse, *Labroides dimidiatus* (Valenciennes, 1839) is the most common and geographically widespread. This species can consume around 1,200 ectoparasitic gnathiid isopods per day and may spend an average of 4.5 h inspecting an average 2,300 clients each day (Grutter 1996). Facultative cleaner fishes include a

wide assortment of families, including other members of Labridae (e.g., species in *Bodianus*, *Coris*, *Haliichoeres* and *Thalassoma*), butterflyfishes (Chaetodontidae), damselfishes (Pomacentridae) and 23 other families, reviewed in Vaughan et al. (2017). Their impact on client health and the degree of effectiveness with which they engage in cleaning is variable and, in general, is much less well-known than their dedicated counterparts (Vaughan et al. 2017). Still, in parts of the globe where no dedicated cleaner fishes occur, these facultative cleaner fishes and shrimps comprise one of few sources of cleaning interaction for fishes (e.g., Moosleitner 1980; Sazima et al. 1999; Arnal and Morand 2001; Östlund-Nilsson 2005; Narvaez et al. 2015; Morais et al. 2017).

Cleaner shrimp have also been shown to effectively remove and eat parasites in laboratory conditions and in the wild from fish clients (e.g., Bunkley-Williams and Williams 1998; Becker and Grutter 2004; Vaughan et al. 2018a, b). This includes breaking infection cycles by feeding on parasite eggs, cysts, and cocoons present in the environment (non-infective stage) in the laboratory (Vaughan 2018a, b; Barton et al. 2020), a function so far only known to be performed by cleaner shrimp. The degree of reliance on cleaning interactions is largely unknown for most shrimp species, mainly due to their secretive and often nocturnal habits (Bonaldo et al. 2015; Bos and Franssen 2018; Vaughan et al. 2018a). Besides removing

parasites, at least one species of tropical cleaner shrimp, *Lysmata amboinensis* (de Man, 1888), is also capable of attending to injured clients by feeding on diseased tissue in laboratory conditions (Vaughan et al. 2018c). In doing so, *L. amboinensis* helps their clients' wounds to heal, with direct health benefits that transcend parasite removal or stress relief.

In the past decade, there has been a large body of work on the effects of cleaner fish on reef communities using large spatial scale and long-term experimental removals of cleaners. For example, in the absence of the cleaner wrasse *Labroides dimidiatus*, many fishes grow to smaller sizes and become less abundant, suggesting that *L. dimidiatus* affects growth rates, survivorship, recruitment success, and movement patterns of fishes (Bshary 2003; Grutter et al. 2003; Clague et al. 2011; Waldie et al. 2011; Sun et al. 2015). The processes involved appear to include increases in ectoparasite abundances which occur over the short-term (1–12 days; Grutter 1999; Grutter and Lester 2002) and long-term absence of cleaners (1.5–18 years, Clague et al. 2011; Grutter 2012; Grutter et al. 2018, 2019; Sikkell et al. 2019). The negative effects fishes incur may involve direct or indirect effects of cleaner presence (Grutter et al. 2018) with complex consequences to clients, such as changes in predator aggression, cognition, and various blood parameters in clients (Cheney et al. 2008;

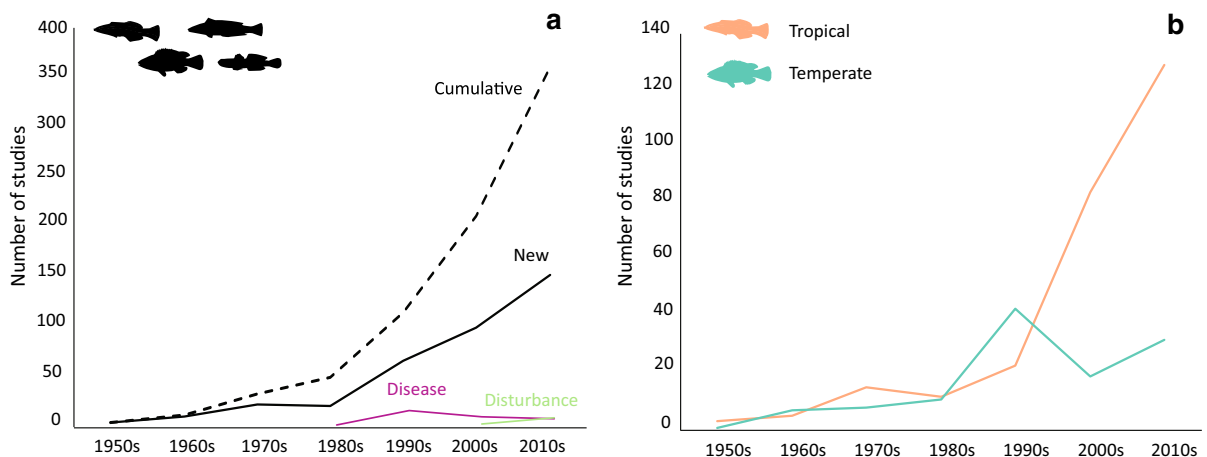


Fig. 2 Compilation of research investigations ($n = 359$) on marine cleaner fishes from 1950 to 2020. **a** the overall cumulative number of studies (dashed line) and new studies on marine cleaner fishes each decade (solid black line). Studies investigating disease of cleaner fishes (purple line) and

disturbance in cleaning interactions (green line) were added to emphasise the limited literature available regarding these two topics. **b** New studies separated by tropical vs temperate cleaner fish studies each decade

Soares et al. 2011; Binning et al. 2018; Demairé et al 2020).

Cleaning symbiosis by marine fishes: collective body of knowledge, limitations and developing fields

Overall, research interest on cleaner fishes has grown in the last three decades (Fig. 2a), with considerable disparity in the fields investigated. Between 1950 and 2020, studies on tropical species comprised 68% of the entire literature on cleaner fishes, while temperate species studies comprised 32% (Fig. 2b). Almost half of all temperate work (47%) has been related to the use of temperate cleaner fishes as biocontrols in aquaculture (see Online Resource 1 for methods and references). From the 1950s to 1980s, most research described observations of symbiotic behaviour on coral reefs, aiming to understand ecological implications (e.g., Eibl-Eibesfeldt 1955; Youngbluth 1968; Losey 1972, 1979). In the 1960s, investigations were expanded to other environments, such as temperate ones (Von Wahlert and Von Wahlert 1961; McCutcheon and McCutcheon 1964; Gotshall 1967). Studies in aquaculture began in the 1980s and were the most common field of research in cleaning symbiosis in the 1990s, mainly due to investigations on the use of facultative temperate cleaner fishes as potential biological controls of ectoparasites in aquaculture in

Northern Europe (Costello 1993). This body of research also triggered interest in parasite communities and diseases of cleaner wrasses used to clean farmed fish from the 1990s (Fig. 2a). More recently, in the 2010s, research on the effects of climate change on cleaner organisms started to gain traction (Fig. 2a; Online Resource 1 for methods and references). Ongoing global climate changes, such as global warming and ocean acidification, are known to affect physiological processes (e.g. Paula et al. 2019a). Since many behaviours involved in cleaning symbiosis are directly associated with physiological processes (Soares et al. 2012, 2019a; Cardoso et al. 2015; Messias et al. 2016; Triki et al. 2017, 2019), climate change is likely to interfere directly and indirectly with cleaning interactions. Globally, the proportion of studies investigating (i) effects of environmental changes on cleaning symbiosis and (ii) the diseases or parasites involved in cleaning symbiosis are negligible (Fig. 2). However, these fields of research will be critical to understanding the future of marine cleaning symbiosis in the next decade as they comprise intrinsic elements of the disease triangle. Below, we deduce expected trends from unlinked, yet comparable, systems for four major pathways involving cleaners and the disease triangle.



Fig. 3 Cleaning symbiosis involves close physical contact which could enable the transmission of infectious taxa from the client to the cleaner and vice versa. Here, two adult bluestreak cleaner wrasse *Labroides dimidiatus* (represented by the white

arrows) inspect and clean the mouth and the gills of the parrotfish *Scarus frenatus* Lacepède, 1802 at Lizard Island, in the northern Great Barrier Reef, Australia. This type of interaction may last for a few minutes. Photos by PN

Pathway 1—Cleaners and parasites: determining whether cleaner fishes are susceptible to parasite infections from their fish clients

During cleaning, cleaner organisms inspect the body and may enter the gills and the buccal cavity of some of their clients (Fig. 3). For example, the cleaner wrasse *Labroides dimidiatus* spends between 48 and 78% of the total time in cleaner interactions inside the gills of its client fish, *Hemigymnus melapterus* (Bloch, 1791) (Grutter et al. 2002). This same cleaner species also uses its fins for tactile stimulus (i.e., massage) of clients, resulting in high rates of physical contact between cleaner and client (Soares et al. 2011). Direct contact such as skin to skin contact, bites and touching are characterised as common routes of pathogens transmission (e.g., Antonovics et al. 2017) and in the context of cleaning symbiosis, prolonged and direct physical contact could enable direct transfer of parasites between cleaners and clients. This hypothesis is indirectly supported by findings reported by Hobson (1971) who demonstrated that 70% of the temperate facultative cleaner wrasse *Oxyjulius californica* (Günther, 1861) individuals previously observed to clean other fishes, were infected with the same copepod parasite species found to infect their clients (i.e., *Lepeophtheirus* sp. Nordmann, 1832; *Caligus hobsoni* Cressy 1969; and *C. serratus* Shinno 1965). In contrast, only 10% of *O. californica* individuals that were not observed cleaning other fishes were infected with caligid parasites (*Lepeophtheirus* sp.; *C. hobsoni*; see Hobson 1971). It is plausible that cleaner wrasse became infected with the copepods when cleaning their clients, given that members of the Caligidae are mobile and can easily move around the surface of their host or swim short distances from one host to another (Ritchie 1997).

In the tropics, gnathiid isopods, the most frequent item (95%) in the diet of cleaner wrasse *Labroides dimidiatus* (see Grutter 1997, 2000) are among the most common ectoparasites on tropical reefs. Gnathiid isopods live in the substrate, and temporarily attach to their host for a blood meal before releasing and returning to the substrate to moult to the next developmental stage (Grutter 1994; Grutter and Poulin 1998). While gnathiid isopods show a strong preference for infecting fishes of the family Labridae (Nagel and Grutter 2007), a previous study did not find them on wild *L. dimidiatus* (Smit et al. 2006). However,

anecdotal reports by Grutter (2002) indicated that *L. dimidiatus* could become infected with gnathiid isopods under laboratory conditions and they were also recently found to infect wild *L. dimidiatus* off Lizard Island, GBR, Australia (PN, unpublished data). Given the high susceptibility of other wrasses to gnathiid infection, it is not surprising that cleaner wrasse can also be infected with gnathiid isopods directly from the reef or also plausibly through horizontal transmission from infected client fishes. Indeed, gnathiids can easily drop off from their hosts if disturbed (Grutter 1995a) and cleaning interactions likely represent a threat for them that could trigger detachment.

To our knowledge, the endoparasitic bucephalid trematode (Platyhelminthes), *Rhipidocotyle labroidei* Jones, Grutter and Cribb, 2003 is the only parasite reported in *L. dimidiatus* and is likely acquired from clients through cleaning interactions (Jones et al. 2004; Gibson et al. 2005). The typical life cycle of bucephalid trematodes is complex. They are found as sporocysts in the internal organs of bivalves, the first intermediate host. Then, they develop as metacercariae in the organs of fishes as their second intermediate host (Muñoz et al. 2015). Finally, adult bucephalids are found in the digestive tract of their definitive hosts, piscivorous fishes (Jones et al. 2003). Piscivorous fishes become infected following the consumption of prey with encysted metacercariae (Jones et al. 2004). Yet, *L. dimidiatus* feeds mostly on ectoparasites of fishes (Grutter 2000). It is possible that *L. dimidiatus* becomes infected by removing encysted bucephalid metacercariae from the exterior skin surface of client fishes (Jones et al. 2004). In this scenario, the metacercariae subsequently develop, mature and produce eggs in the gastrointestinal tract (rectum) of *L. dimidiatus* (see Jones et al. 2003). This represents atypical transmission by a bucephalid trematode, and we hypothesise that this parasite species exploits cleaning behaviour as a mechanism to infect cleaner organisms. Future research into the life cycle of *R. labroidei* will enable identification of susceptible intermediate host fish and microhabitat specificity. Nevertheless, this example of infection of a dedicated cleaner fish by a bucephalid worm indicates a clear potential for cleaning interactions to select for novel parasite transmission pathways from clients to cleaners. Despite the intense research interest in cleaner organisms, there is a remarkable

paucity of information on the parasite communities of wild cleaner organisms, their susceptibility to infection, and how this may influence parasite transmission dynamics in cleaner-client interactions. As suggested by Soares et al. (2019b), investigating the skin microbiome community of both cleaner fishes and clients is also crucial to understand if other organisms such as bacteria can be transmitted and/or shared between cleaner and client via cleaning symbiosis.

Pathway 2—Cleaners and clients: exploring the potential role of cleaner fishes as parasite transmitters in the wild

In Northern Europe salmonid aquaculture, cleaner wrasses are commonly used as biological controls to remove copepod parasites in intensive fish production. However, many species of wrasse that act as cleaners naturally carry parasites and some are susceptible to salmonid pathogens. For example, five cleaner fish species tested in aquaculture, *Ctenolabrus rupestris* (Linnaeus, 1758), *Centrolabrus exoletus* (Linnaeus, 1758), *Crenilabrus melops* (Linnaeus, 1758), *Labrus bergylta* Ascanius, 1767 and *Labrus mixtus* Linnaeus, 1758 were found to be infected with between 22 to 35 parasite species each in the wild (Costello 1996; Treasurer 1997). Moreover, some of these cleaners used as biocontrols in salmon farming are susceptible to salmon pathogens. For example, *C. rupestris* and *C. exoletus* are infected with the bacterium *Aeromonas salmonicida* Griffin, Snieszko and Friddle, 1953, and *S. melops* and *C. rupestris* are infected with *Vibrio* spp. Müller, 1773 (Laidler et al. 1999; Bergh and Samuelson 2007). Moreover, parasitic infections such as *Paramoeba perurans* (Young, Crosbie, Adams, Nowak & Morrison, 2007), that cause amoebic gill disease, have been found to infect *L. bergylta* (see Karlsbakk et al. 2013). This situation demonstrates that in captive environments, cleaner fishes can act as heterospecific transmitters of harmful disease agents (i.e., transmitters being organisms not susceptible to disease but that can transport viable parasites; Evans et al. 2020). To the best of our knowledge, the implications of cleaner organisms as diseases transmitters in the wild has not been previously explored.

While there is an extensive body of work suggesting that cleaner fishes have negative impact on parasites by selectively removing them (Grutter

1995b, 1996, 1997), some parasites with low host-specificity may, in some situations, take advantage of cleaning symbiosis. If wild cleaner fishes are susceptible to generalist parasites (Fig. 4a) they may act as a temporary host or transmitter (Fig. 4b) of the wide range of infectious taxa to the large number of clients they encounter daily (Fig. 4 c, d).

Furthermore, there is emerging evidence from the study of skin microbiomes that pathogens may be shared between cleaners and their clients in the wild. Recently, Xavier et al. (2019) investigated the bacterial community from the skin of the Caribbean goby *Elacatinus prochilos* (Böhlke & Robins, 1968), which has two ecotypes: cleaners (coral-dwellers) and non-cleaners (sponge-dwellers). The authors found that the skin microbiome of the cleaner ecotype had higher alpha diversity (i.e. intra-sample diversity) compared to the non-cleaner ecotype. Of particular interest, significantly more Vibrionaceae bacteria, such as *Vibrio* O.F. Müller, 1773 and *Photobacterium* Beijerinck 1889, were found on the cleaner ecotype than on the non-cleaner ecotype (Xavier et al. 2019). Because these two bacterial genera are potential pathogens found in fishes, the authors hypothesised that there is a chance of pathogen transmission from diseased clients to cleaners and vice-versa. In the absence of research on the parasite community of cleaner organisms, it is challenging to identify the diversity of pathogen species that may use cleaner organisms as transmitters in the wild and how frequently it may occur. Yet given that pathogens are known for complex evolutionary adaptations that maximise their chance of transmission (e.g. Reece et al. 2009; Binning et al. 2017), we hypothesise that some pathogens species likely exploit cleaning behaviour as a mechanism to infect a wider diversity of clients.

Pathway 3—Parasites and cleaners: evaluating mechanisms that parasites may use to evade cleaner organisms and maximise their chance of transmission

Some cleaner fishes and shrimp establish fixed cleaning stations within their territories, with high attendance by parasitised clients (Vaughan et al. 2017). These cleaning stations are analogous to a doctor's waiting room, where patients (= clients) converge and wait to be treated (Potts 1973; Bshary and Schäffer

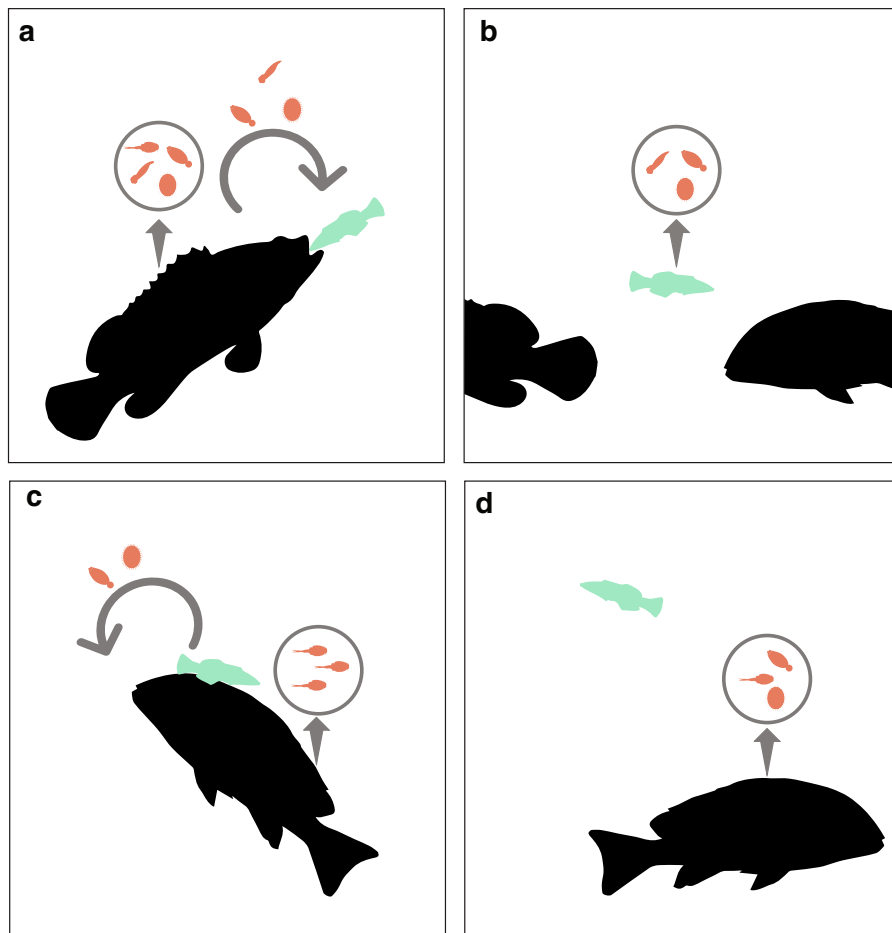


Fig. 4 Cleaners as transmitters hypothesis. **a** Client fish (black) soliciting a cleaning interaction by posing and opening its mouth. The cleaner wrasse (green) becomes exposed to potential pathogen infection (orange) from the client through direct physical contact. **b** Cleaner fish may act as a transmitter, moving these pathogens to new clients. **c** When a new client visits the cleaning station, new physical contacts such as tactile

stimulation (i.e., massage to the client using the pectoral and pelvic fins) may promote pathogen transmission from the cleaner to the client. **d** At the end of the cleaning interaction, the second client may leave the cleaning station with pathogens that were transmitted indirectly from the first client. In this scenario the cleaning interaction facilitates pathogen transmission from one client to another via the cleaner fish transmitter

2002; Shepherd et al. 2005; Fig. 5). Studies in human health have shown that people are more likely to get sick after visiting the doctor by being exposed to multiple routes of transmission. These routes include horizontal transmission via direct contact with health-care workers and via indirect contact in the waiting rooms by airborne pathogens (Simmering et al. 2014; Laskowski et al. 2011; Hope et al. 2012). Nevertheless, waiting rooms are often overlooked as a potential source of disease and transmission (Botelho-Nevers et al. 2012). When considering the analogy between doctors' waiting rooms and cleaning stations, we propose that cleaning stations could act as disease

'hotspots', where clients could be exposed, as human patients, to a potential high infection pressure of infectious species while waiting at the cleaning station to interact with the cleaners. Besides the direct contact between cleaner fishes and clients, environmental transmission from water containing infection life stages and fomite transmission through contaminated objects (Antonovics et al. 2017) could affect clients waiting at the cleaning stations. To the best of our knowledge, no studies have investigated client waiting times at cleaning stations. Quantifying mean client waiting times is therefore critical to understand the potential cost–benefit for clients waiting to be cleaned.

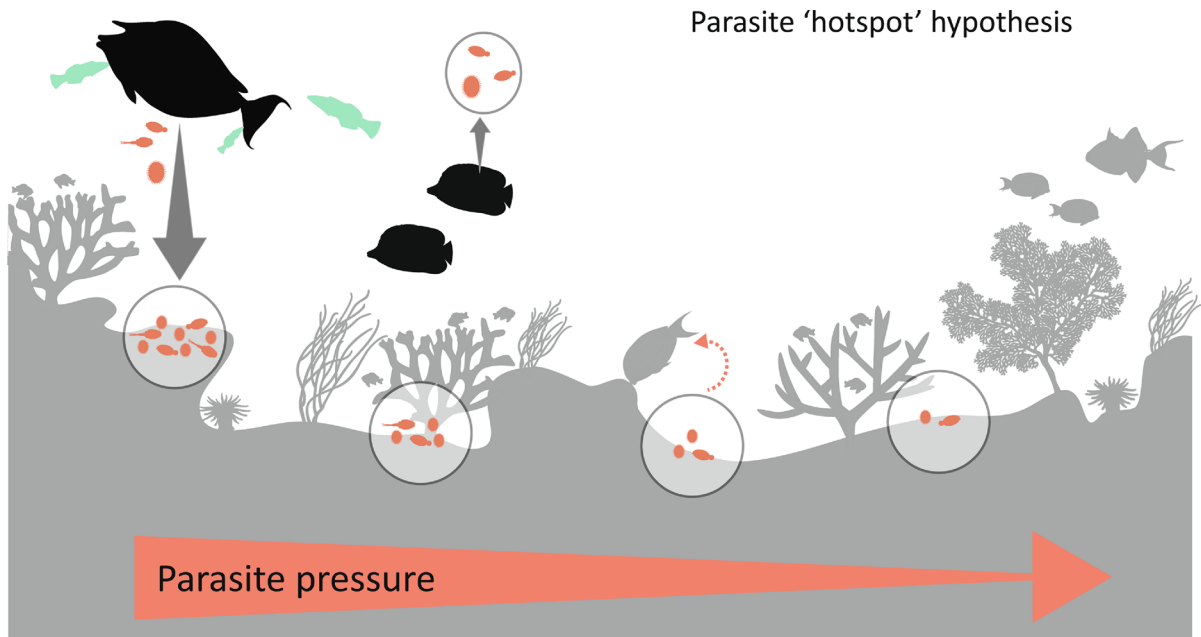


Fig. 5 Parasite hotspot hypothesis: parasite infection pressure is higher around cleaning stations in marine environments. Here, cleaner wrasse *Labroides dimidiatus* (green) cleaning a client fish (black) disturbs ectoparasites attached to the client. Ectoparasites detach and parasite eggs are released into the water column during cleaning interactions (grey arrow).

Longer waiting times at cleaning stations may present clients with a higher risk of parasitic infection from other infected clients in close proximity. It has been shown that the abundance and the diversity of client fishes near cleaning stations is high, with an average (\pm SE) of 94 (\pm 11) individual fish within 1 m radius of a cleaning station of juvenile *Labroides dimidiatus* ($n = 79$ cleaning stations, D. Sun pers. comm.), with more than 100 species recorded within this same area (Sun et al. 2016). In a study comparing the abundance of fishes on patch reefs with and without cleaner fish, there were four times more fish on patch reefs with cleaner wrasses compared to patch reefs without (Grutter et al. 2003). We propose that the diversity and density of parasites around cleaning stations is likely to be high, despite the fact that client fishes purportedly leave cleaning stations with fewer parasites than before being cleaned. In addition to factors such as temporal and spatial scales (Buck et al. 2018), large aggregations of several organisms (both terrestrial and marine) can lead to increased parasite prevalence (e.g., Mikheev et al. 2015; Krkošek 2017; van Schaik and Kerth 2017) suggesting transmission

of parasites in the water column find new hosts or eggs entangled on the substrate hatch and infect new hosts in the vicinity (orange dashed arrow). A gradient of parasite infection pressure is expected with the increasing distance from the cleaning station in the direction of prevailing currents (orange solid arrow)

of parasites can be correlated with host aggregation. When considered in the context of cleaning stations, where there is a high frequency of parasitised client fishes visiting the area resulting in a high concentration aggregated around the station, we suggest cleaning stations could constitute hotspots of parasitic infection.

Cleaner organisms are predators of ectoparasites, and consequently, ectoparasites on clients that seek cleaning are exposed to the risk of predation. However, ectoparasites may deal with these risks in sophisticated ways (e.g., Whittington 1996). For example, ectoparasites that are not permanently attached to their host may drop-off or release eggs when disturbed by cleaner organisms. Many copepod parasites have egg strings, which readily detach when disturbed (Svensson 1996), and some monogenean also release eggs when disturbed (Whittington and Kearn 1988). Some crustaceans and monogenean species can swim short distances (Ritchie 1997; Höglund and Thulin 1988; Cable et al. 2002) or even drift in the water column and re-infect fishes (Soleng et al. 1999) when disturbed. Gnathiid isopods have the

capacity to detach quickly when their host is subjected to stress (Grutter 1995a). Therefore, cleaning stations could serve as disease hotspots if cleaning interactions trigger the release of parasites and/or eggs that then remain in the vicinity of the cleaning station (Fig. 5).

It is clear that parasitised fishes spend significantly more time seeking cleaner fishes. In a laboratory study, parasitised *Hemigymnus melapterus* with gnathiid isopods spent significantly more time around *Labroides dimidiatus* than unparasitised *H. melapterus* (see Grutter 2001). In situ, various client fishes sought *L. dimidiatus* more frequently when their species' ectoparasite load was high (Grutter 1995b). For example, wild individual rabbitfish *Siganus doliatus* Guérin-Méneville 1829–38, usually highly parasitised (i.e., 110 ectoparasites per individual on average), interacts with *L. dimidiatus* an average 114 times per day (Grutter 1995b). However, clients may interact differently, and spend more or less time in the interaction depending on the cleaner species/individual and vice versa (Soares et al. 2007; 2008; 2013). Moreover, the availability of ectoparasites may also vary geographically and may also result in differing cleaning needs in client fishes (Sikkel et al. 2004; Soares et al. 2013). An understanding of the role of the cleaning stations as a potential source of parasitic infection is critical to clarify more subtle links in the complex interconnection between cleaners, clients (as hosts) and parasites in the wild.

Pathway 4—Cleaners and environment: examining the impact of global and local scale human impacts on cleaning symbiosis

In this section, we examine how changes in the environment may influence other elements of the disease tetrahedron. We review the potential impacts of environmental changes on fish interactions (i.e., between cleaners and clients) and on ectoparasites.

(1) Impacts on cleaner organisms and client fishes

To the best of our knowledge, only seven studies have directly investigated the impact of human disturbances on cleaning symbiosis. These studies have been focused on (1) the effect of increasing temperature and ocean acidification on the behaviour and physiology of cleaner organisms (Rosa et al. 2014; Di Santo and Lobel 2016; Paula et al. 2019a, b); (2) the

impacts of fishing on cleaning interactions (Silvano et al. 2012), (3) the impacts of severe disturbances, such as cyclones and bleaching, on cleaner fish abundance and behaviour (Triki et al. 2018; Sikkel et al. 2019) and (4) the impacts of boat noise on cleaning symbiosis (Nedelec et al. 2017). These studies suggest that human disturbances will likely have negative effects on cleaner organisms. For example, physiological responses of the cleaner shrimp *Lysmata amboinensis*, such as lactate and the activity of antioxidant enzymes, as well as heat shock responses are negatively affected by ocean warming (Rosa et al. 2014). Moreover, under laboratory conditions simulating future ocean warming and ocean acidification, the number of interactions between *Labroides dimidiatus* and clients declined and was physiologically translated by alterations of the dopaminergic (quality of the cleaning interaction) and serotonergic (motivation of cleaners to interact) systems (Paula et al. 2019a). In the wild, after environmental perturbations on the Great Barrier Reef (i.e., two cyclones and one coral bleaching event) *L. dimidiatus* densities have been reported to decrease locally by up to 80% (Triki et al. 2017). In experimental tests, this decrease in abundance was reflected by a decrease in sophisticated strategies employed by *L. dimidiatus* such as feeding against their preference to maintain a good reputation in the presence of a waiting client and prioritising certain clients over others (i.e., residents vs visitors; Triki et al. 2017). Finally, boat activity near cleaning stations has been shown to disrupt cleaning interactions (Nedelec et al. 2017). While the noise emitted by motorboats did not change the clientele composition or number, client fishes reacted negatively to cleaners more frequently and *L. dimidiatus* spent significantly more time inspecting their clients (Nedelec et al. 2017). These results suggest that acoustic disturbances can distract, confuse, and lead to a decrease in cooperation by the cleaners, affecting cleaning symbiosis (Nedelec et al. 2017). Our knowledge on parasite transmission during cleaning interactions between fishes is very limited as highlighted in Pathways 1, 2 and 3. However, parasites presumably exploit cleaning symbiosis in many ways and we propose that the transmission of potential parasites during cleaning interaction may also be affected by future global change scenarios.

In cleaning symbiosis, visual communication between cleaners and clients is one of the most crucial

features resulting in mutual cooperation (Vaughan et al. 2017). This communication can be initiated by: 1) clients seeking cleaning attention by posing to signal their willingness to be cleaned, and 2) cleaners, which frequently have characteristic colouration (e.g. lateral yellow/blue body stripes, Stummer et al. 2004; Cheney et al. 2009) and sometimes display ‘dancing behaviours’ (Côté et al. 1998; Stummer et al. 2004) to attract clients. It seems self-evident that visual displays are a key feature of cleaning interactions, particularly true for ones involving fishes. For instance, the wide variety of colour patterns among coral reef fishes is a good indicator of the usefulness of vision to communicate and exchange information about species identity and ontogenetic phase (Rowland 1999; Marshall 2000). However, this is not exclusive to fishes, since the cleaner shrimp *Urocaridella* sp. have also been reported to display a “rocking dance” to attract clients and to advertise cleaning services (Becker et al. 2005). The cleaner shrimp *Periclimenes longicarpus* (Bruce & Svoboda, 1983) also use clapping behaviour as a signal to avoid predation (Chapuis and Bshary 2010). Since visual cues are an apparent important means of communication in cleaning interactions, one type of anthropogenic effect on marine ecosystem likely to affect cleaning interactions is the increased prevalence of suspended sediments on reefs (Wenger et al. 2012; Bainbridge et al. 2018). This is associated with increased discharge of sediments from land to the ocean (Brodie et al. 2012), increasing turbidity and generating a series of effects on a range of organisms on coral reefs. High levels of turbidity diminish the ability of some coral reef fishes to use visual cues to detect and migrate to their preferred habitat (Wenger and McCormick 2013), or to feed (Johansen and Jones 2013). These can alter prey-predator interactions (Chivers et al. 2013; Wenger et al. 2013), reduce growth rates and increase mortality in the juvenile life-phase (Wenger et al. 2012). To our knowledge, only one field-based study by Hobson (1971) commented on how cleaning interactions respond to increased turbidity, he briefly reported that cleaning activities declined considerably in turbid conditions compared to clear conditions in temperate waters off California.

On the other hand, it is important to emphasise that cleaner shrimp often engage in cleaning interactions during the night (Vaughan et al. 2018a). Cleaner shrimp species generally have vision characterised by

low spatial resolution, not allowing them to distinguish colour patterns of client fishes or conspecifics (Caves et al. 2016). This poor eyesight suggests that cues other than visible cues might be more relevant to their ability to interact (Vaughan et al. 2017). Chemical cues generated by the parasite’s odour could mediate cleaning interactions by cleaner shrimp. Indeed, reliance on chemical cues to recognise conspecifics, locate mates and find food and suitable habitats is widespread in crustaceans (Breithaupt and Thiel 2013). For example, it has been shown that social behaviours in crustaceans, such as mating and attraction, as well as foraging and defence, can be negatively affected by various pollutants associated with boat use (Olsén 2011). On the other hand, fishes use chemical cues to escape predators and alert conspecifics (Sorensen 2015). Indeed, experiments in situ showed that settlement stage damselfish, living among live coral, are not able to detect alarm odour cues when within up to 2 m distance from colonies of dead corals (McCormick et al. 2017b). This has been attributed to the presence of chemicals emitted by dead-coral colonisers, such as cyanobacteria, diatoms and red algae, which hinder fish perception and their ability to respond to odour alarm cues (McCormick et al. 2017b). These sensory impairments have been directly linked to decreased survivorship of common coral reef prey fishes (McCormick et al. 2017a), but, to our knowledge, interactions other than predator–prey have not been investigated for these chemicals after or during disturbance cues. Furthermore, although very little is known about how other groups of marine organisms (i.e., crustaceans) behave under these same chemically altered circumstances, their reliance on chemical cues suggests cleaner shrimp interactions could be particularly affected by chemical changes in the environment.

Given environmental changes in terms of both chemistry and visibility that follow coral mortality and increased sediment inputs (McCormick et al. 2017a; Brodie et al. 2012; Bainbridge et al. 2018), understanding the degree of reliance on visual, olfactory and other chemical cues by cleaner organisms (i.e. both fishes and shrimp) will be more important than ever. We anticipate that chemical disruption might affect mostly cleaning interactions led by shrimp, whereas suspended sediments might affect mostly those led by cleaner fishes. Nevertheless, experiments confirming the reliance (or absence thereof) of cleaner fishes and

shrimp on chemical cues, and how these might be disturbed under changed odour scapes will be essential.

(2) Impacts on ectoparasites

Ectoparasites that have a direct life cycle (i.e., that require only one fish host to complete their development), need to identify, attach to a suitable host, and find a mate (Mordue Luntz 2003; Sharma et al. 2019). Studies investigating which sensory cues are used by ectoparasites in fish farming industries, are gaining more attention (e.g., Devine et al. 2000; Ingvarsdóttir et al. 2002; Genna et al. 2005; Fields et al. 2007; Skilton et al. 2020). For example, the sea louse *Lepeophtheirus salmonis* on Atlantic salmon (*Salmo salar*) respond to light intensity due to a relatively highly developed visual system (Flamarique et al. 2000), can detect swimming hosts using water oscillation as mechanical stimuli (Heuch and Karlsen 1997), and can also react to fish odour when reattaching on new hosts (Devine et al. 2000). Other fish ectoparasites, such as *Argulus* spp., rely on visual cues to search for hosts early in their ontogeny (Mikheev et al. 2004). Gnathiid isopods, common fish ectoparasites on tropical coral reefs (Artim et al. 2017) and the main food of *Labroides dimidiatus* (Grutter 2000), also respond to visual cues to detect and attach to suitable hosts (Nagel et al. 2008; Sikkel et al. 2011). Despite a considerable number of studies investigating which sensory cues ectoparasites use to detect, settle and attach to a specific host, there have been few studies investigating if and how the use of sensory cues by ectoparasites might be altered by global and local scale human impacts.

To our knowledge, only three studies evaluated impacts of climate change on the survivorship or abundance patterns of tropical gnathiid ectoparasites. The first study reported that, in the wild, gnathiid isopods were lower in abundance during a marine heatwave that generated widespread coral bleaching in the Great Barrier Reef compared to cooler months (Sikkel et al. 2019). The authors suggested a mechanism whereby altered developmental rates would mediate an apparent low tolerance of gnathiids to temperature fluctuations (Sikkel et al. 2019; Shodipo et al. 2020). In a different study, gnathiids demonstrated a clear preference for dead coral rubble compared to live corals (Santos and Sikkel 2017), suggesting that physiological impacts from climate change could be offset, to some

extent, by larger availability of desirable microhabitats. So far, the only study to experimentally test the effects of climate change on gnathiids observed no impacts on their survivorship from exposition to elevated CO₂ concentrations (Paula et al. 2020). Altogether, the small available evidence indicates that impacts of climate change on marine ectoparasites could be complex and involve both positive and negative effects at different temporal and biological scales, i.e. organisms vs populations.

Other local impacts from human activities have also been shown to alter the ectoparasite community on coral reefs. Indeed, parasite communities have been increasingly used as biological indicators of water quality, which often reflects ecosystem health (e.g., Williams et al. 1992; Palm and Rückert 2009; Sures et al. 2017). As an example, the crustacean ectoparasite community of cardinal fishes has been shown to vary significantly according to local pollution sources and hydrodynamics in New Caledonia (Sasal et al. 2007). Overall, these ectoparasites were more abundant in locations with less detectable chemical and biological pollution (such as ammonium, nitrate, phosphate, turbidity) present in the water and higher rates of water renewal. This suggested a potential susceptibility of the ectoparasites to eutrophic and polluted conditions. However, other ectoparasites, such as trichodinid ciliates, have been shown to be positively affected by increasing organic pollution (i.e., eutrophication; Ogut and Palm 2005). This has also been found for monogenean parasites, which responded positively to eutrophication, crude oil and industrial effluents (Lafferty 1997). Thus, the differential responses of fish ectoparasites appear to be largely case-specific, with evidence for both vulnerability and facilitation relative to poor water quality.

Emerging diseases in aquaculture are another example of how human activities can impact the dynamics between fish parasite and their hosts. Several factors may affect how new diseases develop such as i) the high density of fishes in a limited area generating stress and increasing the risk of infections, ii) the introduction of disease from exotic fishes, and iii) the movement of contaminated fomites (Murray and Peeler 2005). Nevertheless, investigating the effects of human impacts on ectoparasites communities (be it survivorship, infection and transmission rate or abundance) remains a challenging research field due to the varying nature of different impacts and the

high morphological and functional diversity in parasites.

Conclusion and final remarks

There is a strong body of work showing the positive effects of cleaner organisms on client fishes, ranging from a reduction in parasite infection rates (Grutter 1999, 2008; Clague et al. 2011; Grutter et al. 2018) to affecting overall fish recruitment and abundance (Grutter et al. 2003; Clague et al. 2011; Waldie et al. 2011; Sun et al. 2015). Despite almost seven decades of ecological and behavioural research on cleaning symbiosis, the impact of cleaner organisms on the interrelationships between clients, parasites, and environment, i.e., the disease tetrahedron (Fig. 1) are still poorly understood. Here, we have highlighted examples of when cleaner fishes may be susceptible to parasites while engaging in cleaning interactions. We also hypothesised the role of cleaners as potential transmitters for disease spread in reef communities. Parasites have evolved numerous, often unique pathways to ensure the successful infection of hosts and to maximise their chance of transmission. In the cleaning symbiosis context, there exists compelling evidence that a species of digenean parasite has evolved to exploit cleaning interactions for transmission to the dedicated cleaner fish *Labroides dimidiatus* (see Jones et al. 2003, 2004). We hypothesise that numerous parasites could be spread through cleaning stations to infect a wide diversity of client fishes. In fact, mutualism interaction also involves costs (Bronstein 2001) and if cleaners act as transmitters for parasite transmission, this represents a cost to the cleaning interaction that has not been accounted for in cleaning theory to date. Contrarily, if cleaners are not susceptible to generalist parasites, this suggests that cleaners could have evolved specific behavioural or physiological strategies to avoid parasite infection. In both cases, future research involving the disease tetrahedron will not only reveal insights on the evolution of this key mutualistic symbiosis, but also, be critical to predict their long-term stability in the wake of global changes.

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Data availability All references used to generate Fig. 2 are contained in the Online Resource 1.

Compliance with ethical standards

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