

Cleaner fishes and shrimp diversity and a re-evaluation of cleaning symbioses

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Abstract

Cleaning symbiosis has been documented extensively in the marine environment over the past 50 years. We estimate global cleaner diversity comprises 208 fish species from 106 genera representing 36 families and 51 shrimp species from 11 genera representing six families. Cleaning symbiosis as originally defined is amended to highlight communication between client and cleaner as the catalyst for cooperation and to separate cleaning symbiosis from incidental cleaning, which is a separate mutualism preceded by no communication. Moreover, we propose the term 'dedicated' to replace 'obligate' to describe a committed cleaning lifestyle. Marine cleaner fishes have dominated the cleaning symbiosis literature, with comparatively little focus given to shrimp. The engagement of shrimp in cleaning activities has been considered contentious because there is little empirical evidence. Plasticity exists in the use of 'cleaner shrimp' in the current literature, with the potential to cause significant confusion. Indeed, this term has been used incorrectly for the shrimp Infraorder Stenopodidea, involving three families, Stenopodidae, Palaemonidae and Hippolytidae, and to represent all members of *Lysmata* and *Stenopus*. Caution is expressed in the use of grey literature and anecdotal observations to generate data on cleaning interactions, due to the presence of species complexes. Interest in cleaning organisms as biological controls in aquaculture is increasing due to their value as an alternative to various chemical ectoparasite controls. Reports of the importance of cleaner organisms in maintaining a healthy reef ecosystem has also been increasing and we review the current biological knowledge on cleaner organisms, highlighting areas that are understudied.

KEYWORDS

cleaner fishes, cleaner shrimp, cleaning symbiosis, *Lysmata*, *Stenopus*

1 | INTRODUCTION

Symbiosis is the living together of two or more different taxa and includes mutualism, parasitism and commensalism (Martin & Schwab, 2013; Figure 1). However, many symbiotic relationships are subtle, and the variables that influence them can often be overlooked (Egerton, 2015; Feder, 1966), or have been incorrectly interpreted. The term symbiosis is considered by some authors to include only

those interactions in which both symbionts live together in prolonged intimate contact, or where these symbionts are physiologically integrated (Bauer, 2004; Bronstein, 2015). As such, the temporary mutualism representing cleaning symbiosis is considered by these authors as non-symbiotic. However, De Bary (1879) discussed less permanent symbiotic interactions (Peacock 2011; review by Martin & Schwab, 2013). Peacock (2011) labelled the notion of 'intimate contact' as imprecise and too restrictive because it is highly scale dependent. He

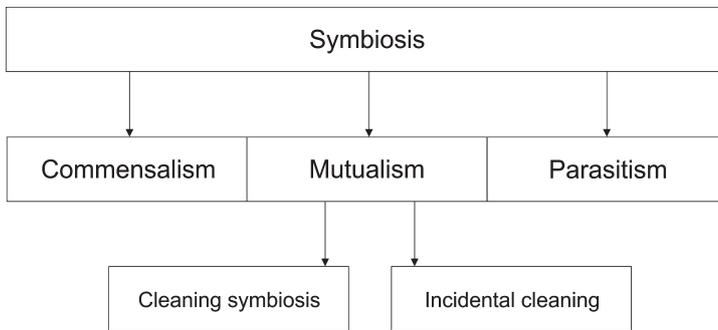


FIGURE 1 Symbiosis is the collective term for commensal, mutual and parasitic associations between organisms. Cleaning symbiosis and incidental cleaning are considered mutualistic associations under symbiosis

added that there are casual interactions between symbionts. The term 'cleaning symbiosis' has thus become widely used in the literature with over 1,000 hits in Google Scholar. We agree that cleaning symbiosis reflects a legitimate symbiosis and follow the view of Peacock (2011).

Cleaning symbiosis was defined by Feder (1966) as the removal of ectoparasites, bacteria, diseased and injured tissue, and unwanted food particles by cleaner organisms from cooperative host organisms. Feder (1966) added that the mutually beneficial behaviour also provides a source of food for the cleaner. Losey (1972) added 'and subsequent ingestion' to emphasize this nutritional benefit for the cleaner. However, the original definition is in need of amendment because it excludes communication as the catalyst for cooperation in these interactions and does not clearly highlight the shared reason for this cooperation; it presents a positive effect on the survival of both client and cleaner.

The use of imprecise terminology in the biological sciences is common (Wilkins, 2005). The frequent misuse or misinterpretation of terms such as 'cleaning symbiosis' or 'cleaner shrimp' over the last 20 years has created significant ambiguity in the literature. The construction of terms of intimacy to attempt to further qualify the degree of the cleaning relationship has created further ambiguity. For example, the term 'obligate' denotes a strict necessity in its mode, outside of which survival is compromised. In the cleaning symbiosis literature, the term 'obligate' is used for a lack of a term to describe a semipermanent or full-time cleaner organism. Yet, cleaners can live independently, and thus, no cleaners are obligate.

This review provides the first taxonomically updated global estimate of cleaner fishes and shrimp diversity. Furthermore, we address inconsistencies and ambiguity in the relevant literature, to refine the definition of a cleaning symbiosis and to explore the attributes that define cleaner organisms. This is the first review to separate incidental cleaning from cleaning symbiosis. We expand on the review of Côté (2000) to include freshwater species and those fishes and shrimp newly identified as cleaners.

2 | CLEANING SYMBIOSIS

The first possible recorded observation of a cleaning symbiosis between two different species was made by the Greek historian Herodotus in the fifth century BC. Herodotus observed the cleaning interaction between a bird he called 'the trochilus' (not to be confused

with the hummingbird genus *Throchilus*, Trochilidae) and a Nile crocodile (*Crocodylus niloticus*, Crocodylidae) which allowed the bird access to its mouth to remove leeches (Herodotos). Although cleaning symbioses are reported from terrestrial ecosystems (e.g., Hart, Hart, & Mooring, 1990; Mooring & Mundy, 1996; Sazima, Jordano, Guimarães, Dos Reis, & Sazima, 2012), they appear to be more common and diverse in aquatic environments, particularly in tropical marine environments (Grutter, 2002; Limbaugh, 1961; Poulin & Grutter, 1996). The greater number of observations in tropical aquatic vs. temperate aquatic environments may reflect greater visibility underwater, higher species richness, as well as biogeographic and habitat distributions of client and cleaner species. The majority of published reports on cleaning symbioses from aquatic environments deal with fishes as cleaners (see supplementary information). Marine crustaceans as cleaning organisms have received far less attention historically, partly due to their often cryptic crevice-living nature. There are currently no reports of cleaning interactions involving freshwater crustaceans. However, cleaner shrimp may have equally important ecological roles to cleaner fishes (Becker & Grutter, 2004).

Cleaner organisms are considered in the majority of the literature as either obligate or facultative. Youngbluth (1968) distinguished between obligate cleaners, those which rely almost exclusively on cleaning, and facultative cleaners which do not. This was based on Limbaugh's (1961) use of 'full-time' cleaners and reflected their diet and habits. Nevertheless, there is no empirical evidence that any cleaner is truly obligate in the strict sense, as this would imply that these cleaning organisms would be compelled to derive all of their nutrition from their clients during such symbiotic interactions, without which they would perish. The definition of 'obligate' in a cleaning symbiosis is equivocal and this term should only be reserved for certain modes of parasitic or other symbioses where it holds true. We propose here the use of the term 'dedicated' to replace 'obligate' when describing those cleaners that exhibit a committed mode of cleaning lifestyle throughout their non-larval ontogeny, and differentiate these from the other varying levels of facultative cleaners, those which are opportunistic, temporary cleaners or interact as cleaners only in part of their ontogeny. The consideration of Limbaugh (1961), that dedicated cleaners are more highly evolved than those that exhibit an opportunistic mode of cleaning, is difficult to evaluate, and may not necessarily be correct. Limbaugh (1961) considered that dedicated cleaners evolved from forms that were more free-living and exhibited opportunistic cleaning, while Gorlick, Atkins, and Losey (1978)

considered that at least members of one genus of dedicated cleaner fishes, *Labroides* (Labridae), may have evolved from an ectoparasitic form. However, Baeza (2009) concluded that, at least for some shrimp, the ancestral lifestyle was likely to have been equally symbiotic or free-living. A simpler explanation may be that animals that evolved to browse on epifauna would also browse on the skin of larger animals, be they mammals, turtles or large fishes. Cleaner fishes and shrimp obtain their food from cleaning and from the wider environment. The relative importance of each source is likely to vary in space and time, depending on client availability and parasite burden, cleaner appetite and perhaps other factors.

Cleaning symbiosis was previously separated into two distinct categories; those examples which reflected traits that may have evolved to support cleaning and those which reflected incidental cleaning. Côté (2000) considered incidental cleaning between organisms, under cleaning symbiosis, to include the removal and consumption of epibionts and debris lodged on the body surface of one organism, by others as they might from any other suitable substrate. This category of cleaning symbiosis was not considered for further discussion in the review of Côté (2000) because neither 'cleaner' nor 'client' reflected any particular adaptation towards their respective roles (Côté, 2000). The 'clients' and 'cleaners' from incidental cleaning interactions may both benefit from these interactions. However, incidental cleaning cannot be considered as cleaning symbiosis. Cleaning symbiosis is defined by the communication to clean or to be cleaned, either through assertion, or submission, resulting in cleaning through mutual cooperation. Assertion is the act of seeking out the cleaning interaction, either by the client or the cleaner, and is followed by the submission of the cleaner to clean, or the client to be cleaned. There is no apparent communication in incidental cleaning, which represents opportunistic mutualism. It may also be possible that all forms of communication that precede cleaning symbiosis have not yet been identified.

Recent publications on marine turtles suggest that their epibiont burdens are a proximate cause of cleaning interactions with both fishes and shrimp (Losey, Balazs, & Privitera, 1994; Sazima, Grossman, & Sazima, 2004, 2010), much like wounds and parasites on fishes are also a proximate cause of cleaning (Arnal & Morand, 2001; Bertoncini, Machado, Barreiros, Hostim-Silva, & Verani, 2009; Foster, 1985; Grutter, 2001; Sikkell, Cheney, & Côté, 2004). Such turtles actively seek out cleaners and submit to them, to have their epibiont burdens removed, illustrating the importance of communication between client and cleaner to cooperate in a cleaning symbiosis. All true cleaning symbiosis interactions are preceded by some level of communication through assertion or submission, either by client or cleaner or both (examples discussed by Limbaugh, 1961; Tyler, 1963; McCutcheon & McCutcheon, 1964; Feder, 1966; Youngbluth, 1968; Abel, 1971; Able 1976; Ayling & Grace, 1971; Hobson, 1971, 1976; Losey, 1972, 1974, 1979; Wyman & Ward, 1972; Sargent & Wagenbach, 1975; Sulak, 1975; Brockmann & Hailman, 1976; Corredor, 1978; Minshull, 1985; Sikkell, 1986; Stauffer, 1991; Soto, Zhang, & Shi, 1994; Van Tassell, Brito, & Bortone, 1994; Galeote & Otero, 1998; Wicksten, 1995, 1998; Poulin & Grutter, 1996; Sazima, Moura, & Gasparini, 1998; Sazima, Krajewski, Bonaldo, & Sazima, 2005; Côté, 2000; Shigeta, Usuki,

& Gushima, 2001; Sazima & Moura, 2000; Sazima & Sazima, 2000; Becker, Curtis, & Grutter, 2005; Shepherd, Teale, & Muirhead, 2005; Craig, 2007; Bertoncini *et al.*, 2009; Horton, 2011; Abe, Sekiguchi, Onishi, Muramatsu, & Kamito, 2012; Huebner & Chadwick, 2012a; Karplus, 2014). Dedicated cleaners and facultative cleaners actively assert their intentions to clean often by using conspicuous dances, or through tactile stimulation. Clients often pose submissively to signal a desire to be cleaned. Communication to cooperate is clearly the catalyst for cleaning interactions that not only transcends species boundaries in the same environment, but has also recently been shown to occur between the ocean sunfish (*Mola mola*, Molidae) and Laysan albatrosses (*Phoebastria immutabilis*, Diomedidae) (Abe *et al.*, 2012). However, cleaning behaviour is not restricted to interspecific interactions and has also been reported between members of the same species (Gooding, 1964; Abel 1971; Able 1976; Hobson, 1971, 1976; Sulak, 1975; McCourt & Thomson, 1984; Sikkell, 1986; Soto *et al.*, 1994; Shepherd *et al.*, 2005; Krajewski, 2007; Bertoncini *et al.*, 2009; cf. Poulin & Vickery, 1995).

Survival is difficult to quantify, but has an important effect on symbioses (Dickman, 1992). However, where some symbioses may positively influence the survival of one symbiont, for example parasitism, mutualisms, such as cleaning symbiosis, influence the survival of both symbionts positively. To highlight the importance of communication that results in cooperation between client and cleaner, an amended definition of cleaning symbiosis is proposed:

Cleaning symbiosis is a cooperative interspecific behaviour where a cleaner removes and consumes materials that negatively impact a client and is preceded by their communication.

Tactile stimulation in cleaning by fishes is considered an important influence on the initiation of cleaning (Losey, 1979; Losey & Margules, 1974), but may also be used to manage potential aggression shown by the client towards the cleaner (Grutter, 2004), and may be a simple way of confirming that the cleaner is not a prey item because prey items are not likely to engage in direct contact with their predators. Wicksten (2009) questioned whether the association between examples of gregarious cleaner shrimp (*Lysmata* spp., Hippolytidae) and morays reflected a cleaning symbiosis. However, subtle tactile stimulation with antennae and legs is offered by these shrimp prior to cleaning interactions (Chapuis & Bshary, 2009). Furthermore, morays cooperate by opening their mouths in submission to these shrimp, communicating their acceptance to be cleaned (Limbaugh, Pederson, & Chase, 1961). Morays have poor eyesight and are nocturnal (Riordan, Hussain, & McCann, 2004). Therefore, visually based communication by cleaners probably has less significance to morays than tactile stimuli. Indeed, tactile stimuli are considered significantly important for initiating cleaning interactions in fishes by cleaner shrimp and do elicit submissive client posture (Karplus, 2014). Client fishes have been observed responding to these tactile stimuli at night, while relying more on sight during the day (Corredor, 1978). In addition, morays are not known to actively seek out cleaning stations and may therefore rely more specifically on these facultative cleaners

which cohabit their caves (Quimbayo *et al.*, 2012). Morays are also not the only clients that are known to be cleaned by these shrimp (Côté, 2000; Jonasson, 1987; McCourt & Thomson, 1984; Wicksten, 2009).

Additional anecdotal observations by SCUBA divers further add support that communication is the catalyst for cooperation in a cleaning symbiosis. Several images of diver-solicited cleaning responses of both fishes and shrimp to hands, feet and even teeth have been documented in the popular and social media (DBV personal observations) and in some of the scientific literature (Brockmann & Hailman, 1976; Kulbicki & Arnal, 1999; Limbaugh *et al.*, 1961). Communication also appears to be important when ending a cleaning interaction, where clients twitch to indicate their desire to break the interaction, or they may also simply depart by swimming away (Feder, 1966; Losey, 1979; Poulin & Grutter, 1996; Wicksten, 1998, 2009).

Familiar examples of marine cleaning symbioses are the most conspicuous and usually involve dedicated cleaners, for example the bluestreak cleaner wrasse (*Labroides dimidiatus*, Labridae) (Bshary, 2003), Hawaiian cleaner wrasse (*Labroides phthiophagus*, Labridae) (Youngbluth, 1968), the skunk cleaner shrimp (*Lysmata amboinensis*, Hippolytidae) (Chen & Huang, 2012) and *Urocaridella* sp. c, Palaemonidae (Becker *et al.*, 2005). These cleaners are often synonymous with cleaning stations located at strategic points on the reef and have been relatively well studied. Facultative cleaner fishes have been comparatively underinvestigated, but may forage more widely than dedicated cleaners. There appears to be a greater diversity of facultative cleaner species than dedicated cleaners (Côté, 2000; see supplemental information). However, comparatively little work has been done to evaluate differences in client diversity between dedicated and facultative cleaners. Some cleaners are adapted to live closely with their clients. These include some members of the Echeneidae (Cressey & Lachner, 1970) and Alpheidae (Hou, Liew, & Jaafar, 2013; Karplus, Szlep, & Rsumamal, 1972) which interact with their clients as true commensals (Strasburg, 1959) as well as cleaners. Some dedicated cleaner shrimp are also known to associate with anemones, which they use for shelter and protection but also to signal the locations of their cleaning stations to client fishes (Huebner & Chadwick, 2012b).

3 | CHEATING

Cleaners have been reported to remove and ingest client fish mucus and scales in addition to their ectoparasites; clients have been reported to eat their cleaners. Both are classic examples of cheating in a cleaning symbiosis (Arnal, Côté, & Morand, 2001; Cheney & Côté, 2005; Feder, 1966; Francini-Filho, Moura, & Sazima, 2000; Gorlick, 1980; Grutter, 1997; Grutter & Bshary, 2003; Hobson, 1971; Limbaugh *et al.*, 1961; Oates, Manica, & Bshary, 2010; Randall, 1958; Soares, Bshary, Cardoso, & Côté, 2008). Cheating is a temporary disturbance in the symbiotic relationship (Bshary & Würth, 2001), not isolated to cleaning symbiosis, but is common in many mutualisms, and results when one partner provides less commodity for their benefit received (Ferreire, Bronstein, Rinaldi, Law, & Gauduchon, 2001). Several studies conducted on cleaner fishes have indicated that fish

mucus is a potentially valuable and more reliable source of food for the cleaner than ectoparasites whose abundance may vary seasonally, between localities and client species (Arnal *et al.*, 2001; Gorlick, 1980; Grutter, 1997; Youngbluth, 1968). This may tempt the cleaner to cheat by taking mucus and scales instead of ectoparasites when afforded the opportunity. In the cleaner wrasse *L. dimidiatus*, individuals of a male and female pair cleaning together reduce each other's cheating when working together (Bshary, Grutter, Willener, & Laimar, 2008). However, when they operate individually, they show a higher rate of cheating in both males and females (Bshary *et al.*, 2008). Client fishes often respond to cheating by terminating the interaction by swimming away, or by chasing the cleaner in what has been considered as cleaner punishment (Bshary & Grutter, 2002, 2005). Client fishes without the option of moving away (e.g. in captivity) generally react more aggressively to cheating (Bshary & Grutter, 2002). Client fishes that may not have been directly involved in a cheating event may also show reluctance to be cleaned by a cheating cleaner. Client fishes may exhibit an image-scoring strategy which involves bystander clients observing the quality of cleaning offered by the cleaner to other clients (Bshary, 2002; Bshary & Grutter, 2006). Through observation of cleaning behaviour, client fishes may then show a preference to interact with cleaners that show a lower tendency to cheat (Bshary, 2002).

The majority of reports on cheating in marine cleaning symbioses deal with cleaners as the cheater, and few comparisons have been made of the frequency of cheating by dedicated vs. facultative cleaners. Cheating is generally considered supportive of the biological market hypothesis, where cheating by cleaners is proportional to the number of clients available to cleaners (Akçay, 2015). However, facultative cleaners probably have less to lose from dishonest interactions than dedicated cleaners, but recent evidence suggests that some facultative cleaner fishes (wrasses) cheat less than dedicated cleaner fishes. This is thought to result from them not feeding against their food preference of client ectoparasites (Barbu, Guinard, Bergmüller, Alvarez, & Bshary, 2011, unlike the dedicated *L. dimidiatus* which is known to prefer host mucus under certain conditions (Bshary & Grutter, 2005, 2006).

Cleaner shrimp have been shown to adjust their cleaning strategy to the clients they serve and the risk of predation (Chapuis & Bshary, 2009; Huebner & Chadwick, 2012a). Cheating by the long-arm cleaner shrimp (*Ancylomenes longicarpus*, Palaemonidae) produced similar client responses as cheating cleaner wrasse (*L. dimidiatus*), and less reaction from predatory species than from non-predatory species (Chapuis & Bshary, 2009). This suggested that the shrimp can distinguish between these types of clients. The observed variability in cleaning behaviour in Perderson's shrimp (*Ancylomenes pedersoni*, Palaemonidae) may be controlled, to some extent, by some client fishes that interfere with access to the shrimp by other clients (Huebner & Chadwick, 2012a). However, these shrimp may also influence each other's cheating during cooperative cleaning interactions as cleaner wrasse do (Huebner & Chadwick, 2012a). It thus appears that both cleaner fishes and shrimp can discern different types of clients and therefore the risk they take if they cheat.

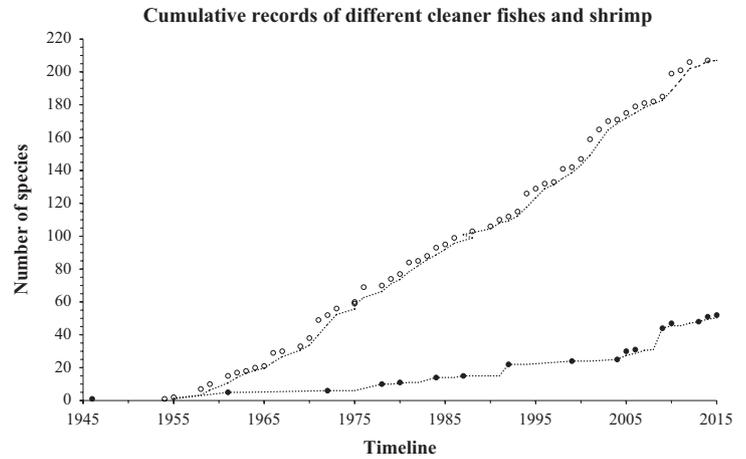


FIGURE 2 Cumulative records of different cleaner fishes and shrimp

Historically, cheating was thought to inhibit mutualism, resulting in ‘reciprocal extinction’ (Doebeli & Knowlton, 1998; Roberts & Sherratt, 1998). However, Ferreire *et al.* (2001) proposed that cheating can establish a foundation to support competitively superior mutualists which may result in the evolution of different related and unrelated cheater and mutualist phenotypes and their coexistence.

4 | HOW MANY CLEANERS ARE THERE?

Over the last half century, the number of fishes and crustaceans considered as cleaners has increased significantly, demonstrating the development of our understanding of cleaning symbiosis (Figure 2). Here, the extensive primary literature to date was reviewed and cross-referenced, and a current list of marine and freshwater fishes and marine crustaceans populated which includes a number of species either missed by previous workers, or species for which evidence

of cleaning has been published since the last reviews of Côté (2000) and Karplus (2014). In addition, the list also includes the juvenile sunburst butterflyfish (*Chaetodon kleinii*, Chaetodontidae) observed and photographed by one of us (DBV) for the first time cleaning the brownburnie (*Chaetodon blackburnii*, Chaetodontidae) with a confirmed infection of the parasitic dinoflagellate *Amyloodinium ocellatum* (Oodiniaceae) in captivity. Observations of cleaning symbiosis in captivity were excluded by Côté (2000), but these are included here because it cannot be assumed that captivity produces only artificial behaviour, and well-known cleaner organisms of various species observed cleaning in the wild are also observed to exhibit the same cleaning behaviour in captivity and are exploited in home and public aquaria, and in aquaculture for this reason. There are currently approximately 208 species of cleaner fishes from 106 genera representing 36 families and 51 species of cleaner shrimp from 11 genera representing six families, recorded to exhibit cleaning behaviour (see supplemental information; Figure 3). Although *Urocaridella* sp. a, b and

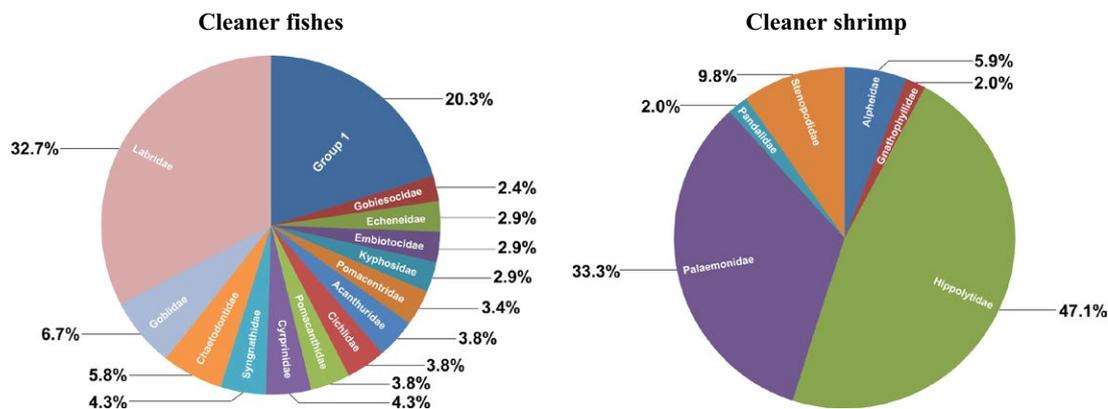


FIGURE 3 Representation of all known cleaners, at family level, from the supplementary tables, expressed as a percentage. Note. This is not a depiction of the percentage of species in a family that are cleaners. A. Group 1 (1–4 species per family): Apogonidae, Balistidae, Cyprinodontidae, Doradidae, Enoplosidae, Gasterosteidae, Monodactylidae, Odacidae, Ostraciidae, Percidae, Poeciliidae, Serrasalmidae and Terapontidae – one species each; Bleriidae, Callichthyidae, Grammatidae and Haemulidae – two species each; Carangidae, Centrarchidae and Tetraodontidae – three species each; Fundulidae, Sparidae and Tripterygiidae – four species each; Gobiococidae – five species; Echeneidae, Embiotocidae and Kyphosidae – six species each; Pomacentridae – seven species; Acanthuridae, Cichlidae and Pomacanthidae – eight species each; Cyprinidae and Syngnathidae – nine species each; Chaetodontidae – 12 species; Gobiidae – 14 species; Labridae – 68 species. B. Alpheidae – three species; Gnathophyllidae and Pandalidae – one species each; Hippolytidae – 24 species; Palaemonidae – 17 species; Stenopodidae – five species

c (Palaemonidae) are discussed in this review as examples of cleaner shrimp in the literature, these shrimp are not listed in the supplemental information because they remain currently undescribed. Both tables consider only valid described taxa and are updated to the current relevant taxonomy. Synonyms are included in the footnotes of both tables. Reports of other putative cleaners (see supplemental information) are excluded for a lack of supporting evidence or verifiable source, or because their taxonomic identity could not be confirmed, or due to their original listing in error by other authors. Observations of cleaning interactions by fishes and shrimp span the Americas, Europe, Africa, Asia and Oceania (Figures 4,5). They include freshwater and marine environments for fishes. However, they have only been reported for less than half of likely countries for fish (Figure 4) and less again for shrimp (Figure 5). Thus, cleaning behaviour is geographically widespread and likely to be more ecologically significant than the present limited observations indicate.

5 | CONSIDER THE GREY LITERATURE WITH CAUTION

The grey literature and the correspondence of divers are both difficult to assess for accuracy. Becker and Grutter (2004) reviewed the scientific, marine, SCUBA and aquarium hobbyist guides to produce more than 40 species records of cleaner shrimp and this estimate has been generally accepted in the field (Hou *et al.*, 2013; McCammon, Sikkil, & Nemeth, 2010). Although observations should not be discounted as empirical evidence, they do require verification. The identification of many cleaner fishes and shrimp is not simple and many cleaners have

been confused, misidentified and/or form part of a species complex (see supplemental information). This suggests that misidentification of species, resulting from the lack of proper taxonomic verification, may significantly influence the bias of data from grey literature or observer accounts of cleaning interactions. Therefore, these accounts should be carefully evaluated before being incorporated into scientific literature.

Spotte (1998) had a more cautionary view and dismissed the contributions of all observations on cleaner shrimp in the historic literature as anecdotal, with the exception of Turnbull's (1981) unpublished PhD thesis which Spotte (1998) considered the only work to properly assess a shrimp cleaning symbiosis at that time. Turnbull (1981) found no remnants of ectoparasites in the foregut of *Ancylomenes pedersoni*, nor did he observe the removal of conspicuous crustacean ectoparasites from client skin surfaces by *A. pedersoni*. In conclusion, Turnbull (1981) stated that *A. pedersoni* did not possess the functional morphology to confirm this shrimp was a cleaner (Limbaugh, 1961). However, his observations by SCUBA were undoubtedly of larger adult stages of parasitic crustaceans, as these were visible, and the midgut section of the shrimp may have revealed remnants of ectoparasites (Tziouveli, Bastos Gomes, & Bellwood, 2011). Although Spotte (1998) considered this evidence enough to suggest that cleaner shrimp as cleaners of fishes be dismissed, Bunkley-Williams and Williams (1998) and McCammon *et al.* (2010) provided empirical evidence to the contrary for the same species in a laboratory trial and seminatural exhibit system, respectively. The study of Bunkley-Williams and Williams (1998) was the first laboratory study to provide such evidence in support of cleaning by a shrimp species. Their results also suggested that cleaner shrimp may be specialists rather than generalists because only one of the four

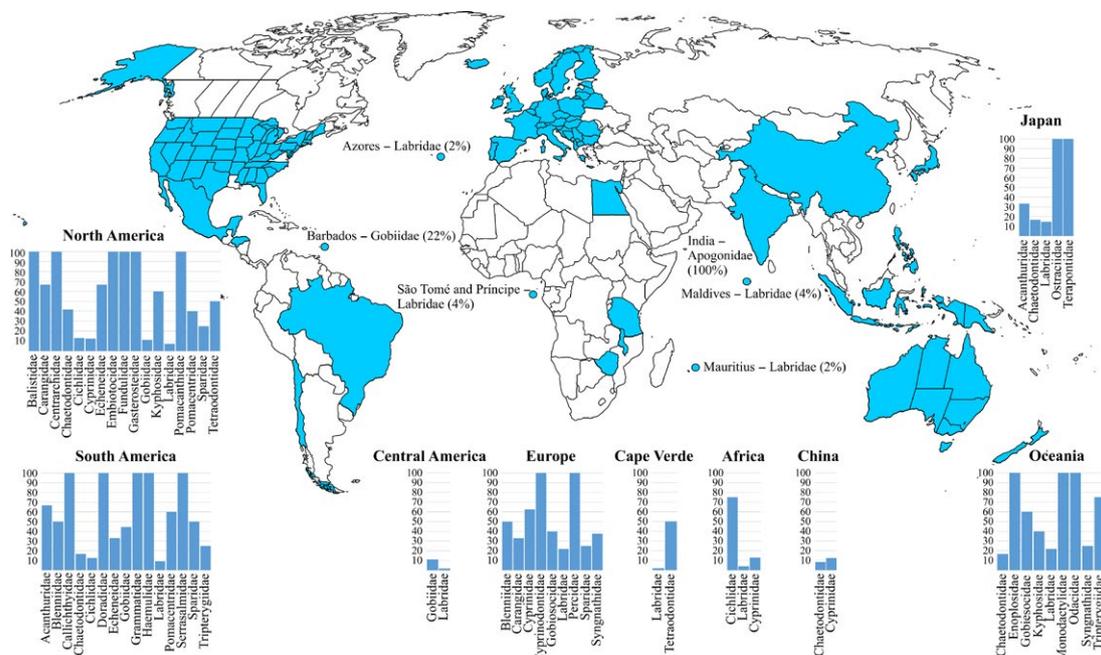


FIGURE 4 Cleaner fishes reported per region from the research cited in the supplementary tables, expressed as a percentage of the total per family.

Note: this is not a depiction of regional diversity or taxa distributions, rather an estimate of regional research to demonstrate understudied areas for future focus

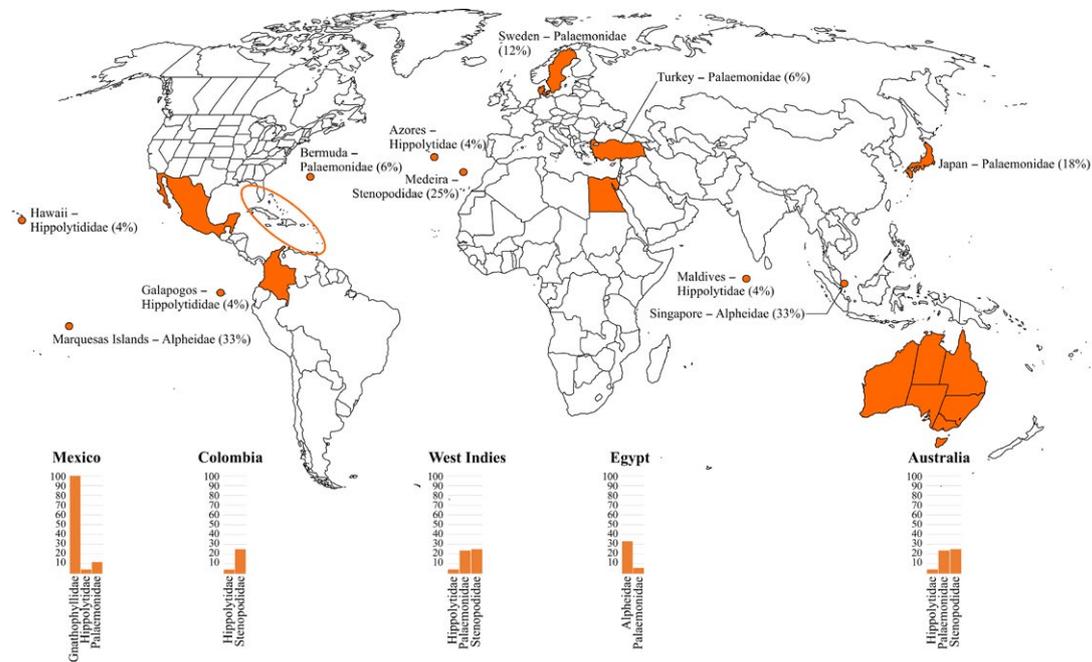


FIGURE 5 Cleaner shrimp reported per region from the research cited in the supplementary tables, expressed as a percentage of the total per family.

Note: this is not a depiction of regional diversity or taxa distributions, rather an estimate of regional research to demonstrate understudied areas for future focus

cleaner shrimp species tested removed and consumed juveniles of the parasitic cymothoid isopod *Anilocra haemuli* (Cymothoidea).

If we were to consider the view of Spotte (1998) to the exclusion of all observations of cleaning interactions in the literature, there would only be six shrimp considered as cleaners, notably *Ancylomenes holthuisi* (Palaemonidae) and *Urocaridella* sp. c. (Becker & Grutter, 2004), *A. pedersoni* (Bunkley-Williams & Williams, 1998; McCammon *et al.*, 2010), *Lysmata amboinensis* (Militz & Hutson, 2015), and *Palaemon adspersus* (Palaemonidae) and *Palaemon elegans* (Palaemonidae) (Östlund-Nilsson, Becker, & Nilsson, 2005). The view of Spotte (1998) is probably premature. The mechanisms involving costs and benefits of cleaning symbiosis are not yet fully understood (Cheney & Côté, 2003; Cushman & Beattie, 1991; Orr, 2009; Poulin & Vickery, 1995), and recent evidence suggests these costs and benefits extend beyond the traditionally defined symbiotic interaction to secondary benefits, including the reduction in ectoparasites in the environment (Bshary, 2003; Grutter, Murphy, & Choat, 2003; Militz & Hutson, 2015; Waldie, Blomberg, Cheney, Goldizen, & Grutter, 2011).

6 | LITERARY AMBIGUITIES AND INCONSISTENCIES

Cleaner shrimp are only known from the marine environment. The colloquial term 'cleaner shrimp' was used broadly by Davie (2002) for all members of the Infraorder Stenopodidea and by Wicksten (1995) to refer to the shrimp families Stenopodidae, Palaemonidae and Hippolytidae. However, not all genera and species representing these families have been observed to form cleaning symbioses (Baeza, 2010;

Bruce, 2004; and Bruce & Baba, 1973; respectively). Debelius (1999) used the same colloquial term for all *Lysmata* species and also mentioned that all species of *Stenopus* were 'probably' cleaners. However, the original description of *Stenopus chrysexanthus* (Stenopodidae) and redescription of *Stenopus cyanoscelis* (Stenopodidae) only assumed that both these species *may* be cleaner shrimp. This assumption was based on their similar morphology with other species known to engage in cleaning symbiosis, but it was not supported by observations or additional data on recorded symbiotic interactions. These species were therefore not included in the comprehensive review on cleaner fishes and crustaceans by Côté (2000) and remain excluded here. Subsequently, Poore (2004) introduced species of *Stenopus* as 'fish cleaners', and in a later publication, Goy (2010) made the explicit statement that all members of *Stenopus* enter into mutualistic cleaning symbiosis with coral reef fishes, citing Limbaugh *et al.* (1961), Yaldwyn (1968), Criales and Corredor (1977), Jonasson (1987), Wicksten (1995, 1998), Côté (2000), and Becker and Grutter (2004). However, none of these authors that Goy cited dealt with the genus *Stenopus* in its entirety; they only referred to *Stenopus hispidus* (Stenopodidae) and/or *Stenopus scutellatus* (Stenopodidae) (Côté, 2000; Criales & Corredor, 1977; Jonasson, 1987; Limbaugh *et al.*, 1961; Wicksten, 1995, 1998), or *S. hispidus* and *Stenopus tenuirostris* (Stenopodidae) (Yaldwyn, 1968) specifically, or included Stenopodidae with six other families from which cleaner shrimp have previously been recorded (Becker & Grutter, 2004).

Three problems emerge from defining shrimp genera or families as 'cleaner shrimp'. Firstly, the colloquial term 'cleaner shrimp' is used ambiguously for taxa that are known to engage in cleaning symbioses and for related taxa that currently are not known to (e.g. Davie,

2002; Debelius, 1999; Wicksten, 1995). This ambiguity has spilled over into scientific literature. Martinelli-Filho, Stampar, Morandini, and Mossolin (2008) recently presented the species *Periclimenes paivai* (Palaemonidae), a commensal palaemonid of scyphozoan jellyfish, as 'cleaner shrimp'. Martinelli-Filho *et al.* (2008, page 134) stated that 'the genus *Periclimenes* contains more than 175 species of small carideans, commonly known as cleaner shrimps'. The genus *Periclimenes* Costa, 1844, was represented by 10 cleaner shrimp species prior to the transfer of most of these to the new genus *Ancylomenes* (Palaemonidae) by Okuno and Bruce (2010). Currently, only one species of cleaner shrimp is representative of *Periclimenes*, *P. yucatanicus* (Palaemonidae). Second, shrimp species unconfirmed as cleaners are conferred 'cleaner' status by association with their close relatives for which there is empirical cleaning evidence. Examples of this include the introduction of *Stenopus* by Poore (2004) as 'fish cleaners', and the 'cleaner symbionts' of Davie (2002) for *S. chrysexanthus* and *S. cyanoscelis*, citing Goy (1992). Third, the cited historic literature by several authors does not support the claim that all *Stenopus* species enter into cleaning symbioses. The likely explanation for this is that the statements of Debelius (1999), Poore (2004) and Goy (2010) must reflect other legitimate field or laboratory observations, but which have remained unpublished. Indeed, correspondence with one of these authors confirmed that this information originated from the combination of laboratory studies and correspondence from numerous SCUBA divers. The possible argument that the above claim is common knowledge is unfounded because there is no original verifiable source. We therefore encourage the use of the term 'cleaner shrimp' only for representing shrimp that have documented observations of cleaning behaviour.

7 | DIET

There is no evidence to suggest that cleaner organisms will eat all perceivably diverse ectoparasites as might be inferred by the original definition of a cleaning symbiosis. Cleaners feed mainly on crustacean ectoparasites (see supplemental information), client skin and mucus. Members of the marine isopod family Gnathiidae feature as prey items of 22 cleaner species, representing 15 genera (see supplemental information), and may be the most common parasitic prey item available to cleaners (Rohde, 2005). These isopods feed on their hosts as three juvenile unfed zuphea stages and take a blood meal before vacating the host to moult into the next juvenile stage or complete their life cycle as non-feeding adults (Rohde, 2005). The engorged 'praniza' stages may present a particularly rich source of food for the cleaner, much like engorged ticks do for several birds observed in terrestrial cleaning interactions (Rohde, 2005; Sazima *et al.*, 2012). Although crustacean ectoparasites may appear from the literature to be superior prey items for cleaners, this may reflect sampling bias because only crustacean exoskeletons provide a reliable means of identification in morphological gut analyses (Kearn, 1978). Additionally, several publications have excluded other parasite taxa from their analyses and focussed almost exclusively on crustaceans (Arnal & Côté, 2000; Arnal & Morand, 2001; Cheney & Côté, 2001, 2005; Grutter, 1997; Whiteman &

Côté, 2002). However, in laboratory experiments the cleaner wrasse *L. dimidiatus* consumed more monogeneans than gnathiids when presented with a choice (Grutter & Bshary, 2003).

Monogenean ectoparasites, leeches, and protists, unlike the crustaceans, are soft-bodied which presents a problem for their identification in gut analyses. Many of these ectoparasites that infest fishes are very small in comparison with the often larger and more visible crustacean ectoparasites. For example, most *Gyrodactylus* spp. (Gyrodactylidae) measure 0.4 mm–0.8 mm (Kearn, 1999) vs. 1.1 mm–6.1 mm for seven representative *Gnathia* spp. (Gnathiidae) (Diniz *et al.*, 2008). Although many of the soft-bodied ectoparasites of fishes present no structures that remain intact after digestion that can be used for potential taxon identification, the majority of monogeneans do. Monogeneans attach to their host fishes using the posterior attachment organ, the haptor, which often contains sclerotized attachment anchors, hooks, clamps or other modified structures that are very small but resist the digestion by proteolytic enzymes (Vaughan & Chisholm, 2010). It may be possible to discern these structures in the gut samples of cleaners under high magnification (e.g. Becker & Grutter, 2004; Grutter, 1997). Various universal primers have been designed for use in metagenomic profiling (Blankenship & Yayanos, 2005; Folmer, Black, Hoeh, Lutz, & Vrijenhoek, 1994; King, Read, Traugott, & Symondson, 2008) and a highly sensitive molecular approach may be successful in providing some resolution on what different organisms are consumed by different cleaners in the wild. This has been achieved for free-living marine decapod larvae (O'Rorke, Laverty, Wang, Nodder, & Jeffs, 2014; O'Rorke *et al.*, 2012).

Adult parasitic stages of some parasites may simply be too large for some cleaners to remove from the client, which might explain the differences in observations between studies on the same cleaner species (*cf.* Bunkley-Williams & Williams, 1998; Turnbull, 1981). Differences in cleaning performance or feeding preferences are known in cleaner fishes (Costello, 1996), and this may be true for cleaner shrimp. The differences in morphology between cleaner shrimp species may limit them to feeding on specific types or life stages of certain parasites or may even limit them as wound cleaners. Indeed, Bunkley-Williams and Williams (1998) were unsure of the mechanism of juvenile *Anilocra haemuli* removal employed by *Ancylomenes perdersoni* in their experiments, and no studies have been conducted to evaluate whether there is a relationship between the functional morphology and the types of parasites removed and cleaning performed. Some shrimp are well documented as dedicated fish cleaners and exhibit strong symbiotic associations with fishes, whereas others are opportunistic facultative cleaners that are also scavengers, or the cleaning association remains insufficiently known (Davie, 2002; see supplemental information).

Juvenile ectoparasites may be an important food items for cleaner organisms. The study of Becker and Grutter (2004) was the first study to provide evidence of parasitic removal and consumption in wild cleaner shrimp. These cleaner shrimp, *A. holthuisi* and *Urocaridella* sp. c, consumed juvenile parasitic gnathiids and copepods that were identified to family and class, respectively. No other work since Becker and Grutter (2004) has examined the gut contents of wild cleaner shrimp. However, both these shrimp species appeared to have different diet preferences and/or consumption rates of ectoparasites (Becker &

Grutter, 2004). Laboratory trials using *A. holthuisi* and *Urocaridella* sp. c (Becker & Grutter, 2004), and *Palaemon adspersus* and *P. elegans* (Östlund-Nilsson *et al.*, 2005) revealed that cleaner shrimp can also consume monogenean ectoparasites. Monogeneans have never been found in the gut contents of wild shrimp. However, Miltz and Hutson (2015) indicated for the first time that the cleaner shrimp *Lysmata amboinensis*, a dedicated cleaner, was highly efficient in consuming the monogenean eggs and free-swimming larvae of the monogenean *Neobenedenia* sp. (Capsalidae) in the captive environment, and thus reduced reinfection success.

Approximately 111 fish ectoparasite records exist from dietary constituents of 49 different cleaner fishes (see supplementary information) and have been confirmed through wild fishes' gut content analyses, or observed being removed by cleaner fishes in captivity. However, the potential diversity of dietary components of cleaner shrimp remains uninvestigated. It is unknown whether cleaner shrimp consume other pathogenic agents, including other parasitic groups such as leeches and protists, bacteria and water moulds. Foster (1985) documented wound healing of injured reef fishes by three different cleaner fishes and suggested that cleaner shrimp removal of necrotic or diseased tissue may also promote wound healing. Although some anecdotal information claims that cleaner shrimp remove or consume dead skin from wounds (Corredor, 1978; Crump, 2009) or tend bacterial infections (Limbaugh, 1961), the effects of cleaner shrimp on wound healing also remains uninvestigated and controlled experiments are needed to accurately address these questions.

8 | MORPHOLOGY, COLOUR AND BEHAVIOUR

Côté (2000) analysed body size and signalling coloration of cleaner fishes. Her analyses were limited due to a lack of phylogenetic information on fishes at that time, and the correlation between body size and adult feeding type. Subsequently, Baliga and Mehta (2015) determined the kinematic basis of cleaning in three cleaner fishes of the family Labridae, suggesting that a small mouth gape and the ability to perform rapid gape cycles (opening and closing of the mouth) on individual prey items may be a cleaner prerequisite. Certainly, many juvenile fishes that are facultative cleaners have a small gape, which may support a rapid and dextrous ability to remove ectoparasites on clients (Baliga & Mehta, 2015). Ontogenetic prey-use change is known in a large diversity of marine reef fishes (McCormick, 1998; Wainwright & Bellwood, 2002), and it is unsurprising, given the ubiquity of fish ectoparasites, that so many fishes utilize this resource during their ontogenetic development.

Cleaner shrimp vary considerably in size between species and genera. Their size may influence the ability to remove and consume certain ectoparasites, for which they use their chelae (Karplus, 2014; Östlund-Nilsson *et al.*, 2005; Yaldwyn, 1968), but small size also facilitates access into areas of the mouth and gill chamber of client fishes (Karplus, 2014). An increase in the robustness of the mandibles, as well as the morphological intricacy of the gastric mill reflects a carnivorous feeding habit in crustaceans (Kunze & Anderson, 1979). Conversely, the

paragnaths in carnivorous crustaceans are less intricate than those of non-carnivores (Hunt, Winsor, & Alexander, 1992). The investigation of the comparative morphology of these structures between different cleaning shrimp may help determine what these shrimp consume in the wild (Tziouveli *et al.*, 2011).

The concept of a universal colour guild for cleaners was not conclusively supported by the analyses of Côté (2000), and whether cleaners use colour to signal cleaning services remains untested. Although longitudinal striping is a common feature of dedicated cleaner fishes (Côté, 2000) and is now demonstrated for a facultative cleaner (see Carvalho, Arruda, & Zuanon, 2003), all considerations of cleaner coloration or patterning made to date have been limited to the visible light spectrum. Ultraviolet light has a fundamental function in the mutualism between angiosperms and their pollinators (Papiorek *et al.*, 2016), and ultraviolet reflective body patterns have been demonstrated as a means of communication in fishes that can visualize ultraviolet (Siebeck, Parker, Sprenger, Mäthger, & Wallis, 2010). Therefore, we hypothesize that ultraviolet patterning may be important for cleaner recognition and suggest that future investigations should include ultraviolet patterning of cleaner organisms.

Cleaner shrimp vision is likely monochromatic. Recent work investigated the visual ability of *Ancylomenes pedersoni*, *Lysmata amboinensis* and *Urocaridella antonbruunii* (Palaemonidae) for the first time (Caves, Frank, & Johnsen, 2016). The spatial resolution of these shrimp, and possibly others, is less than for sea snails and scallops and decreases with a decrease in light (Caves *et al.*, 2016). This research suggests that cleaner shrimp cannot assess client fish for ectoparasites visually, as suggested in part by Becker and Grutter (2005), and that tactile and chemical stimuli are used to detect ectoparasites on client fishes. The colour limitation of cleaner shrimp vision also suggests that the change in client pigmentation often seen during cleaning may be a visual signal to other client fishes, rather than the cleaner (Caves *et al.*, 2016).

Becker and Grutter (2005) provided evidence that ectoparasite load and cleaner shrimp hunger levels influence cleaning interactions. Apart from these factors, very little information is available on what drives the processes behind the cleaner shrimp–client interactions (Titus, Daly, & Exton, 2015). However, recent evidence suggested that temporal patterns of cleaning between *A. pedersoni* and cleaner gobies differed, but the client species and localities were the same. Titus *et al.* (2015) considered that the ectoparasites targeted by the shrimp may be different to those targeted by the cleaner gobies, which would explain the apparent lack of competition for the same clients. In addition, there are no data to compare the difference in cleaning quality between cleaner shrimp species.

9 | THE ECOLOGICAL IMPORTANCE OF CLEANING SYMBIOSES ON CORAL REEFS

Cleaner organisms maintain an ecological balance that is not yet fully understood, although it is clear that the removal of ectoparasites is beneficial for the health of reef fishes. Several authors have attempted to quantify the effects of cleaner fishes on reef fish diversity by

testing the hypothesis that the removal of cleaners presents a perturbation of the ecosystem, resulting in reef fishes' emigration, or mitigation by remaining and/or unfamiliar cleaners (Losey, 1972). Limbaugh (1961) was the first to present observations on the possible effects of cleaner removal from a reef. He removed all known cleaner organisms from two isolated parts of Bahamian reef containing a high diversity of fishes. This resulted in a considerable reduction in the number of fishes observed, as well as the observed increase in visible lesions on remaining territorial fishes (Limbaugh, 1961). Presumably, these lesions resulted from the absence of cleaners.

In a similar *Labroides phthirophagus* depopulation experiment off Hawaii, Youngbluth (1968) did not observe a significant decrease in the number of fishes after the removal of cleaners. In comparison, Youngbluth (1968) considered the possibility that differences in the physical properties of the reefs in both studies may have influenced the movement of fishes to different areas. Gorlick *et al.* (1978) were highly critical of Limbaugh (1961), and in a subsequent cleaner wrasse (*L. dimidiatus*) depopulation study off the Marshall Islands (see Gorlick, Atkins, & Losey, 1987), these authors found no significant change in the density of fishes before and after cleaner removal. However, Losey (1972) removed all *L. phthirophagus* from patches of reef in Hawaii and found that there was a change in the behaviour in some client species that relocated to patches of reef with a remaining *L. phthirophagus*, and some facultative cleaners that increased their cleaning activity to some degree. Losey (1972) did not find a significant reduction in ectoparasites after the removal of *L. phthirophagus*, which was in contrast with the suggestion of Limbaugh (1961) that 'cleaners maintain the health of the marine population' and that of Gorlick *et al.* (1987) who determined that *L. dimidiatus* reduced ectoparasite biomass. Variation in the importance of cleaner fishes and shrimp is to be expected. Host abundance, parasite burdens and pathogenicity, and cleaner abundance and appetite will vary in space and time. Further research is required to clarify the importance of cleaners in food webs and ecosystems through their effects on client health.

The role of time in symbiotic relationships is important in determining functional outcomes and avoiding their misinterpretations. The balance between costs and benefits may change with time, which in turn may influence these functional outcomes (Mesterton-Gibbons & Dugatkin, 1992, 1997). Limbaugh's (1961) observations were for a period of two weeks, while the studies of Youngbluth (1968) and Gorlick *et al.* (1987) were concluded after one and six months, respectively. Losey's (1972) cleaner removal experiment was for eight months. Bshary (2003) considered the removal of *L. dimidiatus* for less than four months to be short term, with subsequently few observed effects on fish diversity. However, a significant decline in reef fish diversity was evident over a longer period of up to twenty months (Bshary, 2003). Conversely, the introduction of an additional cleaner wrasse, or the relocation of one to a patch of reef previously without one, influenced a rapid increase in fish diversity (Bshary, 2003). This suggested that the studies of Limbaugh (1961) and Losey (1972) reflected a rare effect or that the studies of Youngbluth (1968) and Gorlick *et al.* (1987) were too short to identify a significant ultimate outcome.

Longer-term studies on the ecological influence of cleaners have revealed limitations in short-term studies. Grutter *et al.* (2003) and

Waldie *et al.* (2011) found evidence of a decrease in general fish diversity and abundance after the experimental removal of *L. dimidiatus* from patches of reef off Lizard Island, Australia. Grutter *et al.* (2003) noted a reduction in transient fishes after 18 months, and Waldie *et al.* (2011) noted the reduction for both transient and territorial fishes over an eight-and-a-half-year period with the removal of *L. dimidiatus*. The reduction in territorial species including pomacentrids and the shift towards smaller individuals in two pomacentrids in the study by Waldie *et al.* (2011) were considered the result of lower growth rates and/or the reduced survivorship of these species in the absence of cleaner wrasse. The length of the study also demonstrated the influence of cleaner wrasse on the recruitment of the juveniles of transient fishes onto the reef (Waldie *et al.*, 2011) as did an even longer 12-year study involving juveniles of territorial fish (Sun *et al.*, 2015). The consideration of transient and territorial fishes in these studies plays a subtle yet important role. Grutter *et al.* (2003) were the first authors to suggest the importance of distinguishing between these types of fishes in these types of studies. Pomacentrids, for example, and particularly the monodomous species (Fishelson, 1998), can confound such results of reef species movement because of their strict territorial habits (Bardach, 1958). Pomacentrids are more likely to remain in their territories after cleaner organism removal, as shown by Grutter (1996a) for the lemon damselfish (*Pomacentrus moluccensis*, Pomacentridae) observed in a previous depopulation study on cleaner wrasse (*L. dimidiatus*). Similarly, Bshary (2003) showed that the presence or absence of cleaner wrasse (*L. dimidiatus*) had the weakest effect on territorial species. However, neither Youngbluth (1968) nor Gorlick *et al.* (1987) made the distinction between transient and territorial fishes in their studies. Gorlick *et al.* (1987) specifically included the territorial ocellate damselfish (*Pomacentrus vaiuli*, Pomacentridae) in their study, but did not list the other client species involved in the depopulation study, and it is unclear what influence this and possibly other territorial species could have had on their results.

No comparative depopulation studies have been conducted for cleaner shrimp, although this would also prove to be extremely difficult because cleaner shrimp are cryptic and physically delicate. In addition, many species of shrimp may currently be unknown cleaners, similar to the growing list of fish cleaners that has developed over the past 50 years (see Figure 2). However, this does pose the question of the involvement of cleaner shrimp in the above-mentioned cleaner fish depopulation studies. One unidentified shrimp was observed by Losey (1972) cleaning the millet butterflyfish (*Chaetodon miliaris*, Chaetodontidae), but Gorlick *et al.* (1987) did not observe any cleaner shrimp. Whether this reflects sampling and observation bias, or an extended observation of 'cleaning structure discordance' between fishes and shrimp as mentioned by Titus *et al.* (2015), remains to be elucidated.

10 | EXPLOITATION OF CLEANING IN CAPTIVITY

The published observations of Potts (1973) may have inspired the first investigations using cleaner fishes as alternative methods of

ectoparasite control in aquaculture. Caligid copepod sea lice are the most persistent and economically significant parasite in marine salmonid farming worldwide (Costello, 2006, 2009). Following reports from fish farmers using cleaner fishes (Labridae) to control lice on salmon in farm cages in Norway, experiments in Ireland and Scotland showed that five common labrids in northern Europe could reduce lice abundance on farmed salmon to non-pathogenic levels within weeks (Costello, 1993a, 1996), namely Rook cook (*Centrolabrus exoletus*, Labridae), goldsinny (*Ctenolabrus rupestris*, Labridae), Corkwing (*Symphodus melops*, Labridae), cuckoo wrasse (*Labrus mixtus*, Labridae) and juvenile ballan wrasse (*Labrus bergylta*, Labridae). Now several million of these cleaner fishes are routinely used in Norway, mostly wild captured (Bjordal, 1991; Darwall, Costello, Donnelly, & Lysaght, 1992; Skiftesvik *et al.*, 2014). Initially it was believed that only juvenile *L. bergylta* showed cleaning behaviour (Costello, 1993b), but it has since been shown that adults will clean larger salmon (Skiftesvik, Bjelland, Durif, Johansen, & Browman, 2013). Research into culturing certified disease-free labrids to supply the farms is also underway (e.g. Skiftesvik *et al.*, 2013). In addition, lumpsucker (*Cyclopterus lumpus*, Cyclopteridae) are being developed for use as cleaner fish on farms (Imsland *et al.*, 2014a). The use of cleaner fishes reduces or avoids the need to use parasiticides to control lice, thereby improving fish health, saving costs, and the farmed fish can be harvested without drug residues. Options for lice control are constrained because lice have developed resistance to all the parasiticides used on the farms to date (Aaen, Helgesen, Bakke, Kaur, & Horsberg, 2015; Costello, 2006; Costello *et al.*, 2001). The main limitations to using cleaner fishes have been adequate supply, their ability to escape and the influence of environmental conditions on cleaning activity and ectoparasite growth rates (Costello, 2006). Recent concerns suggest that wrasse species used as cleaners in Europe may also be the reservoirs of diseases in Atlantic salmon culture, for example viral haemorrhagic septicaemia (Munro *et al.*, 2015; Wallace *et al.*, 2015), amoebic gill disease (Karlsbakk *et al.*, 2013) and *Aeromonas salmonicida* (Aeromonadaceae) (Treasurer, 2012), further supporting certification of disease-free cultured cleaners.

There have been no observations of either client (salmonid) or cleaner (labrid or lumpfish) communication to cooperate prior to cleaning interactions in the farms or laboratory (e.g. Imsland *et al.*, 2014a, 2014b). However, the wrasse species do hover above the seabed in the wild and clean fishes that remain stationary in their territory (Costello, 1993b, MJC personal observations). It is possible that this communication has been overlooked in captivity or that the cleaning interactions in intensive cage culture simply reflect incidental cleaning (opportunistic mutualism) and not true cleaning symbiosis.

In tropical aquaculture, the cleaner gobies of the genus *Elacatinus* (Gobiidae) have been investigated for their potential as biological controls against ectoparasites, particularly against monogeneans. *Elacatinus genie* (Gobiidae) and *Elacatinus oceanops* (Gobiidae) have shown promise against the problematic monogenean *Neobenedenia melleni* (Capsalidae) on cultured euryhaline tilapias (Cowell, Watanabe, Head, Grover, & Shenker, 1993), and *Elacatinus figaro* (Gobiidae) was recently tested successfully for its efficacy against *N. melleni* on the

aquaculture candidate species *Epinephelus marginatus* (Serranidae) in Brazil (De Souza *et al.*, 2014). *Elacatinus oceanops* has also been used successfully with cultured mutton snapper (*Lutjanus analis*, Lutjanidae) and greater amberjack (*Seriola dumerili*, Carangidae) (Benetti *et al.*, 2007; De Souza *et al.*, 2014) and cobia (*Rachycentron canadum*, Rachycentridae) broodstock (Benetti *et al.*, 2007). Tropical cleaner wrasse species have not yet been considered for aquaculture. *Labroides dimidiatus* is, however, used as a biological control against ectoparasites in public aquaria (Paul Lötter pers. comm.), and cleaner fish were suggested as a biological control for the ectoparasites of captive rays by Chisholm, Whittington, and Fischer (2004).

Cleaner shrimp have not been used as biological controls in aquaculture. However, Becker and Grutter (2004) and Militz and Hutson (2015) suggested their potential benefits for ectoparasite control in aquaculture. One of the advantages of cleaner shrimp over cleaner fishes in aquaculture is their unlikely function as disease reservoirs or vectors compared with cleaner fishes (Militz & Hutson, 2015), given the paucity of reports of diseases affecting shrimp being transmitted to fishes. Cleaner shrimp also actively consume environmental parasite stages such as monogenean eggs and larvae (Militz & Hutson, 2015) which implies their usefulness as direct and indirect cleaners. They could be integrated into sections of the aquaculture system itself, away from client fishes, particularly in recirculating systems. There may also be value in the integration of both cleaner wrasse and shrimp in combination in aquaculture.

It has been documented that some client fishes change colour during posturing; its reason is unclear. Future research priorities should include the investigation of possible cleaner and client recognition by ultraviolet reflective patterning, and whether client posturing may enhance their visibility and/or that of their ectoparasites. Indeed, communication by other sensory mechanisms also requires study. Additionally, understanding the ecological role of cleaner shrimp can be advanced using a combined morphological and molecular investigation of gut contents to elucidate the diversity of prey items consumed.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

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