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

Alternative title 1. A critical evaluation of cleaning symbiosis and current global diversity of cleaner fishes and shrimp

Alternative title 2. The global diversity of cleaner fishes and shrimp and a critical evaluation of cleaning symbiosis

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Running title: Cleaning symbiosis

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 6 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 interventions for ectoparasite control. 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.

Key words Cleaner fishes, cleaner shrimp, cleaning symbiosis, *Lysmata*, *Stenopus*

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Introduction

Symbiosis is the living together of two or more different taxa, and includes mutualism, parasitism and commensalism (Martin and Schwab 2013; Fig 1). However, many symbiotic relationships are subtle, and the variables that influence them can often be overlooked (Feder 1966; Egerton 2015), 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 and Schwab 2013). Peacock (2011) labelled the notion of "intimate contact" as imprecise and too restrictive because it is highly scale-dependent. He 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 emphasise 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 semi-permanent or full-time cleaner organism. Yet, both clients and cleaners can live independently, 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.

Cleaning symbiosis

The first possible recorded observation of a cleaning symbiosis between two different species was made by the Greek historian Herodotos in the fifth century BC. Herodotos observed the cleaning interaction between a bird he called “the trochilus” (not to be confused with the hummingbird genus *Throchilus* Linnaeus, 1758) and a Nile crocodile (*Crocodylus niloticus* Laurenti, 1768, 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 and Mooring 1990; Mooring and Mundy 1996; Sazima *et al*. 2012), they appear to be more common and diverse in aquatic environments, particularly in tropical marine environments (Limbaugh 1961; Poulin and Grutter 1996; Grutter 2002). The greater number of observations in tropical aquatic versus 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 (online Table S1). 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 (Becker and 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, 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* Bleeker, 1851 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 *et al.* 1994; Sazima, Grossman and Sazima

2004; 2010), much like wounds and parasites on fishes are also a proximate cause of cleaning (Foster 1985; Arnal and Morand 2001; Grutter 2001; Sikkel, Cheney and Côté 2004; Bertocini *et al.* 2009). 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 and McCutcheon 1964; Feder 1966; Youngbluth 1968; Abel 1971, 1976; Ayling and Grace 1971; Hobson 1971, 1976; Losey 1972, 1974, 1979; Wyman and Ward 1972; Sargent and Wagenbach 1975; Sulak 1975; Brockmann and Hailman 1976; Corredor 1978; Minshull 1985; Sikkel 1986; Stauffer 1991; Soto, Zhang and Shi 1994; Van Tassell, Brito and Bortone 1994; Galeote and Otero 1998; Wicksten 1995, 1998; Poulin and Grutter 1996; Sazima, Moura and Gasparini 1998*b*, Sazima *et al.* 2005; Côté 2000; Shigeta, Usuki and Gushima 2001; Sazima and Moura 2000; Sazima and Sazima 2000; Becker, Curtis and Grutter 2005; Shepherd, Teale and Muirhead 2005; Craig 2007; Bertoncini *et al.* 2009; Horton 2011; Abe *et al.* 2012; Huebner and Chadwick 2012*a*; 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, or may change colour 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* (Linnaeus, 1758), Molidae) and Laysan albatrosses (*Phoebastria immutabilis* (Rothschild, 1893), Diomedeidae) (Abe *et al.* 2012). However, cleaning symbiosis is not restricted to interspecific interactions, and has also been reported between members of the same species (Gooding 1964; Abel 1971, 1976; Hobson 1971, 1976; Sulak 1975; McCourt and Thomson 1984; Sikkel 1986; Soto *et al.* 1994; Shepherd *et al*. 2005; Krajewski 2007; Bertoncini *et al*. 2009; *cf*. Poulin and 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, 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 the positive, temporary contribution to the survival of different animals, the client and cleaner, which results from their communicated cooperation and involves the removal and consumption of materials negatively impacting the client, by the cleaner.

Cleaning symbiosis is the removal and consumption of materials harmful to an animal (client) by a cleaner following their communication, with consequent benefits to both.

Tactile stimulation in cleaning by fishes is considered an important influence on the initiation of cleaning (Losey and Margules 1974; Losey 1979), 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. Wiskin (2009) questioned whether the association between examples of gregarious cleaner shrimp (*Lysmata* spp.) and morays reflected a cleaning symbiosis. However, subtle tactile stimulation with antennae and legs is offered by these shrimp prior to cleaning interactions (Chapuis and Bshary 2009). Furthermore, morays cooperate by opening their mouths in submission to these shrimp, communicating their acceptance to be cleaned (Limbaugh, Pederson and Chase 1961). Morays have poor eyesight and are nocturnal (Riordan, Hussain and 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 co-habit their caves (Quimbayo *et al*. 2012). Morays are also not the only clients that are known to be cleaned by these shrimp (Jonasson 1987; McCourt and Thomson 1984; Côté 2000; Wiksten 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 (Limbaugh *et al*. 1961; Brockmann and Hailman 1976; Kulbicki and Arnal 1999). 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 and Grutter 1996; Wicksten 1998; Wicksten 2009).

Familiar examples of marine cleaning symbioses are the most conspicuous, and usually involve dedicated cleaners, e.g. the bluestreak cleaner wrasse (*Labroides dimidiatus* (Valenciennes, 1839), Labridae) (Bshary 2003), *L. phthirophagus* (Youngbluth 1968), the skunk cleaner shrimp (*Lysmata amboinensis* (de Man, 1888), Hippolytidae) (Chen and 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; online tables S1 and S2). 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 and Lachner 1970) and Alpheidae (Karplus *et al.* 1972; Hou, Liew and Jaafar 2013) 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 and Chadwick 2012*b*).

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 (Randall 1958; Limbaugh *et al*. 1961; Feder 1966; Hobson 1971; Gorlick 1980;

Grutter 1997; Francini-Filho, Moura and Sazima 2000; Arnal, Côté and Morand 2001; Grutter and Bshary 2003; Cheney and Côté 2005; Soares *et al.* 2008; Oates, Manica and Bshary 2010). Cheating is a temporary disturbance in the symbiotic relationship (Bshary and 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 *et al.* 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 (Gorlick 1980; Youngbluth 1968; Grutter 1997; Arnal *et al*. 2001). 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 *et al.* 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 and Grutter 2002; 2005). Client fishes without the option of moving away (e.g. in captivity) generally react more aggressively to cheating (Bshary and 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 and 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 no comparisons have been made of the frequency of cheating by dedicated versus 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. Facultative cleaners such as juvenile fishes rely less on client ectoparasites as a food sources, and may therefore be more inclined to cheat than dedicated cleaners.

Cleaner shrimp have been shown to adjust their cleaning strategy to the clients they serve and the risk of predation (Chapuis and Bshary 2009; Huebner and Chadwick 2012*a*). Cheating by the long-arm cleaner shrimp (*Ancylomenes longicarpus* (Bruce and Svoboda, 1983), Palaemonidae) produced similar client responses as cheating cleaner wrasse (*L. dimidiatus*), and less reaction from predatory species than from non-predatory species (Chapuis and 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* (Chace, 1958), Palaemonidae) may be controlled, to some extent, by some client fishes that interfere with access to the shrimp by other clients (Huebner and Chadwick 2012*a*). However, these shrimp may also influence each other's cheating during cooperative cleaning interactions as cleaner wrasse do (Huebner and Chadwick 2012*a*). It thus appears that both cleaner fishes and shrimp can discern different types of clients and therefore the risk they take if they cheat.

Historically, cheating was thought to inhibit mutualism, resulting in "reciprocal extinction" (Roberts and Sherratt 1998; Doebeli and Knowlton 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.

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 (Fig. 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* Bloch, 1790, Chaetodontidae) observed and photographed (online Fig. S1) by one of us (DBV) for the first time cleaning the brownburnie (*Chaetodon blackburnii* Desjardins, 1836, Chaetodontidae) with a confirmed infection of the parasitic dinoflagellate *Amyloodinium* *ocellatum* (E.Brown) E.Brown and Hovasse, 1946 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 6 families, recorded to exhibit cleaning behaviour (online Tables S1 and S2 respectively; Fig. S2). Although *Urocaridella* sp. a, b and c are discussed in this review as examples of cleaner shrimp in the literature, these shrimp are not listed in online Table S2 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 (online Tables S1 and S2 notes) 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 (Figs. 3, 4). They include freshwater and marine environments for fishes. However, they have only been reported for less than half of likely countries for fish (Fig. 3) and less again for shrimp (Fig. 4). Thus cleaning behaviour is geographically widespread and likely to be more ecologically significant than the present limited observations indicate.

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 (McCammon, Sikkel and Nemeth 2010; Hou *et al.* 2013). 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 online Table S2 for cleaner shrimp examples). 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 *A. 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 and 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 semi-natural 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 cleaner shrimp species tested removed and consumed juveniles of the parasitic cymothoid isopod *Anilocra haemuli* Williams and Williams, 1981 (Cymothoidae).

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* (Bruce, 1969) (Palaemonidae) and *Urocaridella* sp. c. (Becker and Grutter 2004), *A. pedersoni* (Bunkley-Williams and Williams 1998; McCammon *et al.* 2010), *L. amboinensis* (Militz and Hutson 2015), and *Palaemon adspersus* Rathke, 1837 (Palaemonidae) and *Palaemon elegans* Rathke, 1837 (Palaemonidae) (Östlund-Nilsson, Becker and Nilsson 2005). The view of Spotte (1998) is probably premature. The mechanisms involving costs and benefits of cleaning symbiosis are not yet fully understood (Cushman and Beattie 1991; Poulin and Vickery 1995; Cheney and Côté 2003; Orr 2009), and recent evidence suggests these costs and benefits extend beyond the traditionally defined symbiotic interaction to secondary benefits, including the reduction of ectoparasites in the environment (Bshary 2003; Grutter, Murphy and Choat 2003; Waldie *et al.* 2011; Militz and Hutson 2015).

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 (Bruce and Baba 1973, Bruce 2004, and Baeza 2010, 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* Goy, 1992 (Stenopodidae) and redescription of *Stenopus cyanoscelis* Goy, 1984 (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 he cited dealt with the genus *Stenopus* in its entirety; they only referred to *S. hispidus* and/or *S. scutellatus* (Limbaugh *et al*. 1961; Criales and Corredor 1977; Jonasson 1987; Wicksten 1995, 1998; Côté 2000), or *S. hispidus* and *Stenopus tenuirostris* de Man, 1888 (Stenopodidae) (Yaldwyn 1968) specifically, or included Stenopodidae with six other families from which cleaner shrimp have previously been recorded (Becker and 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; Wicksten 1995;

Debelius 1999). This ambiguity has spilled over into scientific literature. Although Wicksten (1995) probably meant to refer to "cleaner shrimp" as representatives of families Stenopodidae, Palaemonidae, and Hippolytidae, the same error is not applicable for Martinelli-Filho *et al*. (2008), who presented the species *Periclimenes paivai* Chace, 1969 (Palaemonidae), a commensal palaemonid of scyphozoan jellyfish, as "cleaner shrimp". Martinelli-Filho *et al*. (2008, page 134) further justified the use of this term by stating 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* by Okuno and Bruce (2010). Currently, only one species of cleaner shrimp is representative of *Periclimenes*, *P. yucatanicus* (Ives, 1891) (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.

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 (online Table S3), client skin and mucus. Members of the marine isopod family Gnathiidae feature as prey items of 22 cleaner species, representing 15 genera (online Table S3), and may be the most common parasitic prey item available to cleaners (Rohde 2005). These isopods feed on their hosts as immature 'praniza' stages and take a blood meal before vacating the host to complete their life-cycle as non-feeding adults (Rohde 2005). Engorged praniza 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 (online Table S3), 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 (Grutter 1997; Arnal and Côté 2000; Arnal and Morand 2001; Cheney and Côté 2001, 2005; Whiteman and Côté 2002). However, in laboratory experiments the cleaner wrasse *L. dimidiatus* consumed more monogeneans than gnathiids when presented with a choice (Grutter and 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 to the often larger and more visible crustacean ectoparasites. For example, most *Gyrodactylus* von Nordmann, 1832 spp. (Monogenea: Gyrodactylidae) measure 0.4mm – 0.8mm (Kearn 1999) *versus* 1.1mm – 6.1mm for seven representative *Gnathia* Leach, 1814 spp. (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 sclerotised attachment anchors, hooks, clamps or other modified structures that are very small but resist the digestion by proteolytic enzymes (Vaughan and Chisholm 2010). It may be possible to discern these structures in the gut samples of cleaners under high magnification (e.g. Grutter 1997; Becker and Grutter 2004). Various universal primers have been designed for use in metagenomic profiling (Folmer *et al*. 1994; Blankenship and Yayanos 2005; King *et al.* 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 *et al*. 2012; 2014).

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*. Turnbull 1981; Bunkley-Williams and Williams 1998). 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; online Table S2).

Juvenile ectoparasites may be an important food items for cleaner organisms. Apart from the controlled study by Bunkley-Williams and Williams (1998), unspecified stages of juvenile ectoparasitic crustaceans were observed in the gut contents of wild cleaner shrimp by Becker and Grutter (2004). This 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 and Grutter 2004). Laboratory trials using *A. holthuisi* and *Urocaridella* sp. c (Becker and 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, Militz 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* Yamaguti, 1963 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 (online Table S3), 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.

Morphology, colour and behaviour

Côté (2000) analysed body size and signalling colouration 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 and Mehta 2015). Ontogenetic prey use change is known in a large diversity of marine reef fishes (McCormick 1998; Wainwright and Bellwood 2002), and it is unsurprising, given the ubiquity of fish ectoparasites, that so many fishes utilise 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 (Yaldwyn 1968; Östlund-Nilsson *et al*. 2005; Karplus 2014), 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 and Anderson 1979). Conversely, the paragnaths in carnivorous crustaceans are less intricate than those of non-carnivores (Hunt, Winsor and 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 *et al*. 2003), all considerations of cleaner colouration 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*. 2015), and ultraviolet reflective body patterns have been demonstrated as a means of communication in fishes that can visualise ultraviolet (Siebeck *et al*. 2010). Therefore, we hypothesise 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* for the first time (Caves, Frank and 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 and 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.

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 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, Atkins and Losey (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 (Metsterton-Gibbons and 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) was 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 juvenile fishes onto the reef (Waldie *et al*. 2011). 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 (1996*a*) for the lemon damselfish (*Pomacentrus moluccensis* Bleeker, 1853, 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* Jordan and Seale, 1906, 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. 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* Quoy and Gaimard, 1825, 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.

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 1993*a*; 1996), namely Rook cook (*Centrolabrus exoletus* (Linnaeus, 1758), Labridae), goldsinny (*Ctenolabrus rupestris* (Linnaeus, 1758), Labridae), Corkwing (*Symphodus melops* (Linnaeus, 1758), Labridae), cuckoo wrasse (*Labrus mixtus* Linnaeus, 1758, Labridae) and juvenile ballan wrasse (*Labrus bergylta* Ascanius, 1767, Labridae). Now several million of these cleaner fishes are routinely used in Norway, mostly wild captured (Bjordal 1991; Darwall *et al*. 1993; Skiftesvik *et al*. 2014). Initially it was believed that only juvenile *L. bergylta* showed cleaning behaviour (Costello 1993*b*), but it has since been shown that adults will clean larger salmon (Skiftesvik *et al.* 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* Linnaeus, 1758, Cyclopteridae) are being developed for use as cleaner fish on farms (Imsland *et al*. 2014*a*). 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 (Costello *et al.* 2001; Costello 2006; Aaen *et al.* 2015). 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* (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*. 2014*a*, *b*). However, the wrasse species do hover above the seabed in the wild and clean fishes that remain stationary in their territory (Costello 1993*b*, 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* have been investigated for their potential as biological controls against ectoparasites, particularly against monogeneans. *Elacatinus genie* (Böhlke and Robins, 1968) (Gobiidae) and *Elacatinus oceanops* Jordan, 1904 (Gobiidae) have shown promise against the problematic monogenean *Neobenedenia melleni* (MacCallum, 1927) Yamaguti, 1963 (Capsalidae) on cultured euryhaline tilapias (Cowell *et al*. 1993), and *Elacatinus figaro* Sazima, Moura and Rosa, 1997 (Gobiidae) was recently tested successfully for its efficacy against *N. melleni* on the aquaculture candidate species *Epinephelus marginatus* (Lowe, 1834) (Serranidae) in Brazil (de Souza *et al*. 2014). *Elacatinus oceanops* has also been used successfully with cultured mutton snapper (*Lutjanus analis* (Cuvier, 1828), Lutjanidae) and greater amberjack (*Seriola dumerili* (Risso, 1810), Carangidae) (Benetti *et al.* 2007; de Souza *et al.* 2014), and cobia (*Rachycentron canadum* (Linnaeus, 1766), 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 *et al.* (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 and 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 and 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 visualisation. Indeed, communication by other sensory mechanisms also require 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.

Conflict of interest

The authors declare no conflicts of interest.

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Supporting information

Additional supporting information can be found in the online version of this article.

Fig. S1. *Chaetodon kleinii* juvenile cleaning a *Chaetodon blackburnii* infected with the parasitic dinoflagellate *Amyloodinium ocellatum* in captivity at the Two Oceans Aquarium, Cape Town, South Africa.

Fig. S2. Cleaner fishes and shrimp family-level diversity.

Table S1. List of fishes currently considered as cleaners.

Table S2. List of crustaceans currently considered as cleaners.

Table S3. Ectoparasite or epibiont categories and their nutritional source, from the gut contents of wild cleaners, or removed and consumed by captive cleaners.

Figure legends:

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.

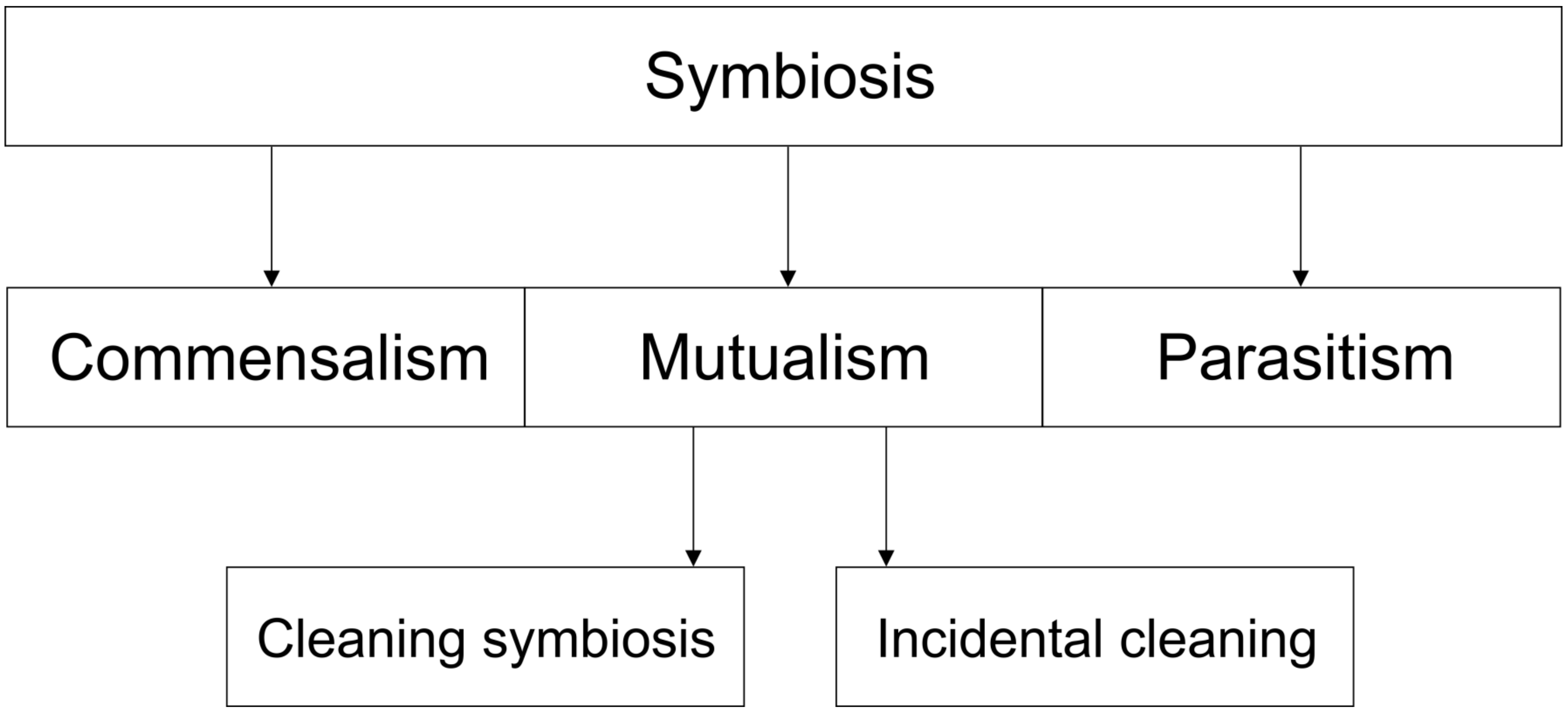
Figure 2. Cumulative records of different cleaner fishes and shrimp.

Figure 3. Cleaner fishes reported per region from the research cited in Table S1, 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 4. Cleaner shrimp reported per region from the research cited in Table S2, 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 S1. Juvenile *Chaetodon kleinii* Bloch, 1790 cleaning *Chaetodon blackburnii* Desjardins, 1836 infested with *Amyloodinium ocellatum* (E.Brown) E.Brown and Hovasse, 1946.

Figure S2. Cleaner fishes and shrimp family-level diversity.



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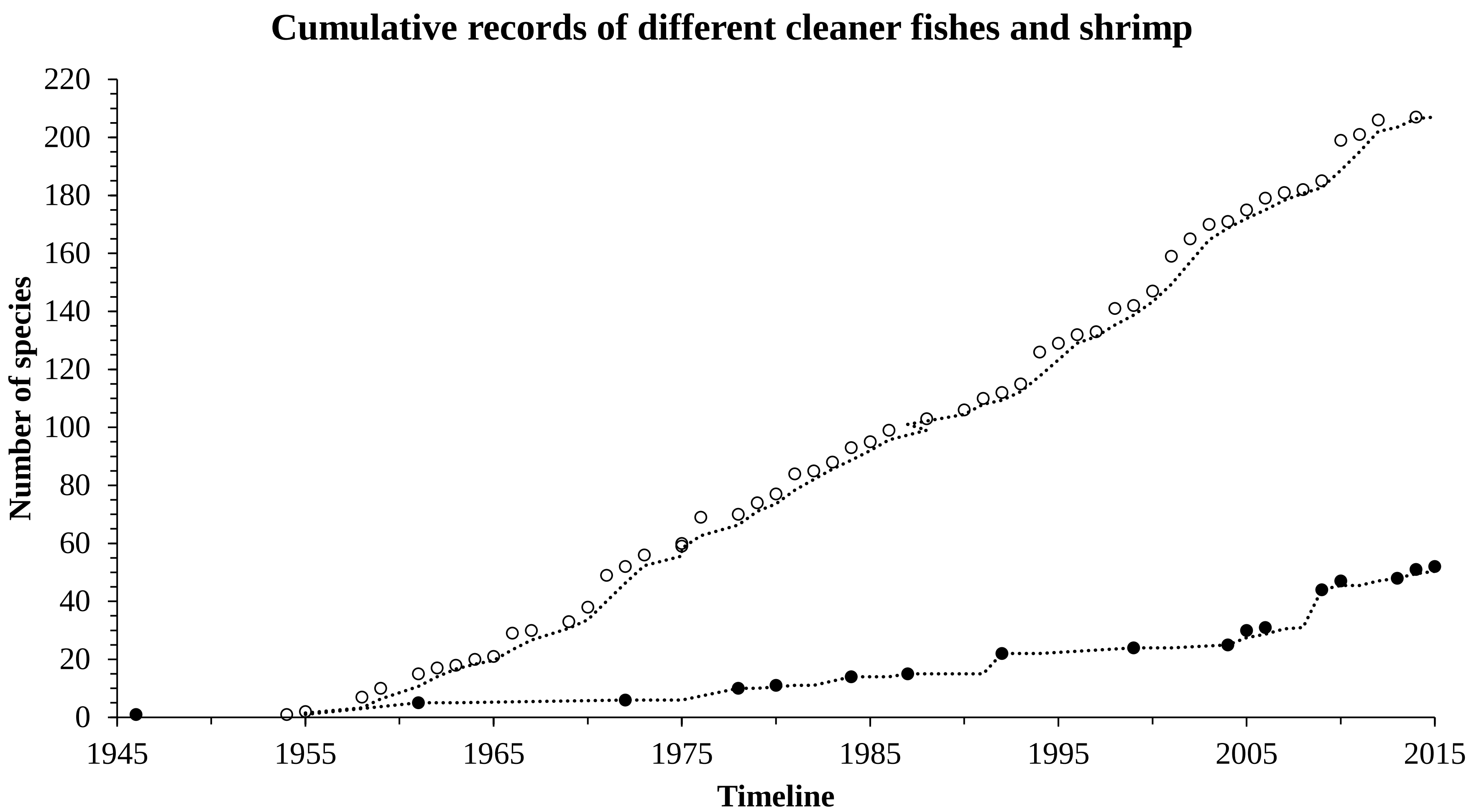

Fig. 2. Comparison of cumulative records of cleaner fish (cirlces) and shrimp (solid dots) species over the past ˜50 years.

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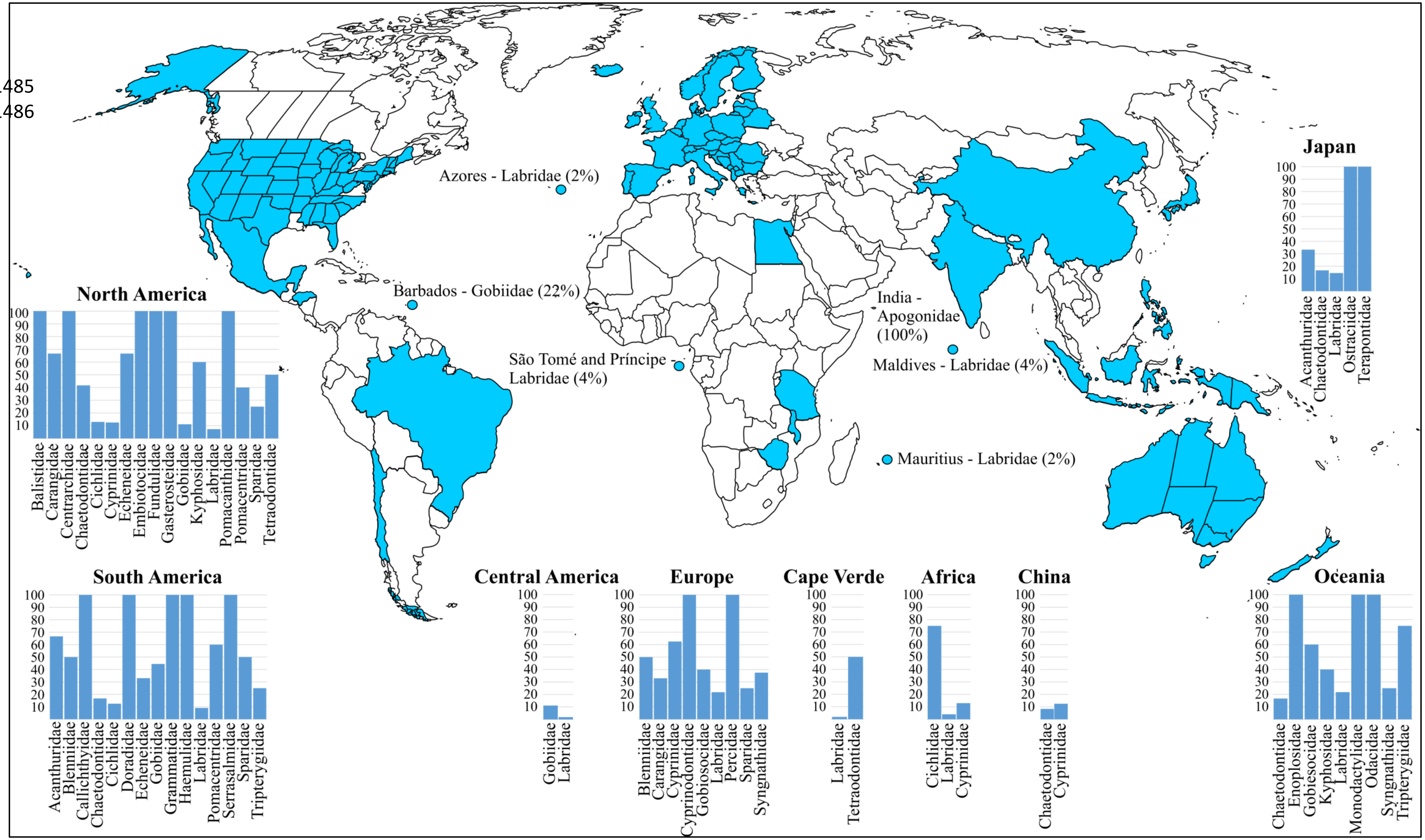

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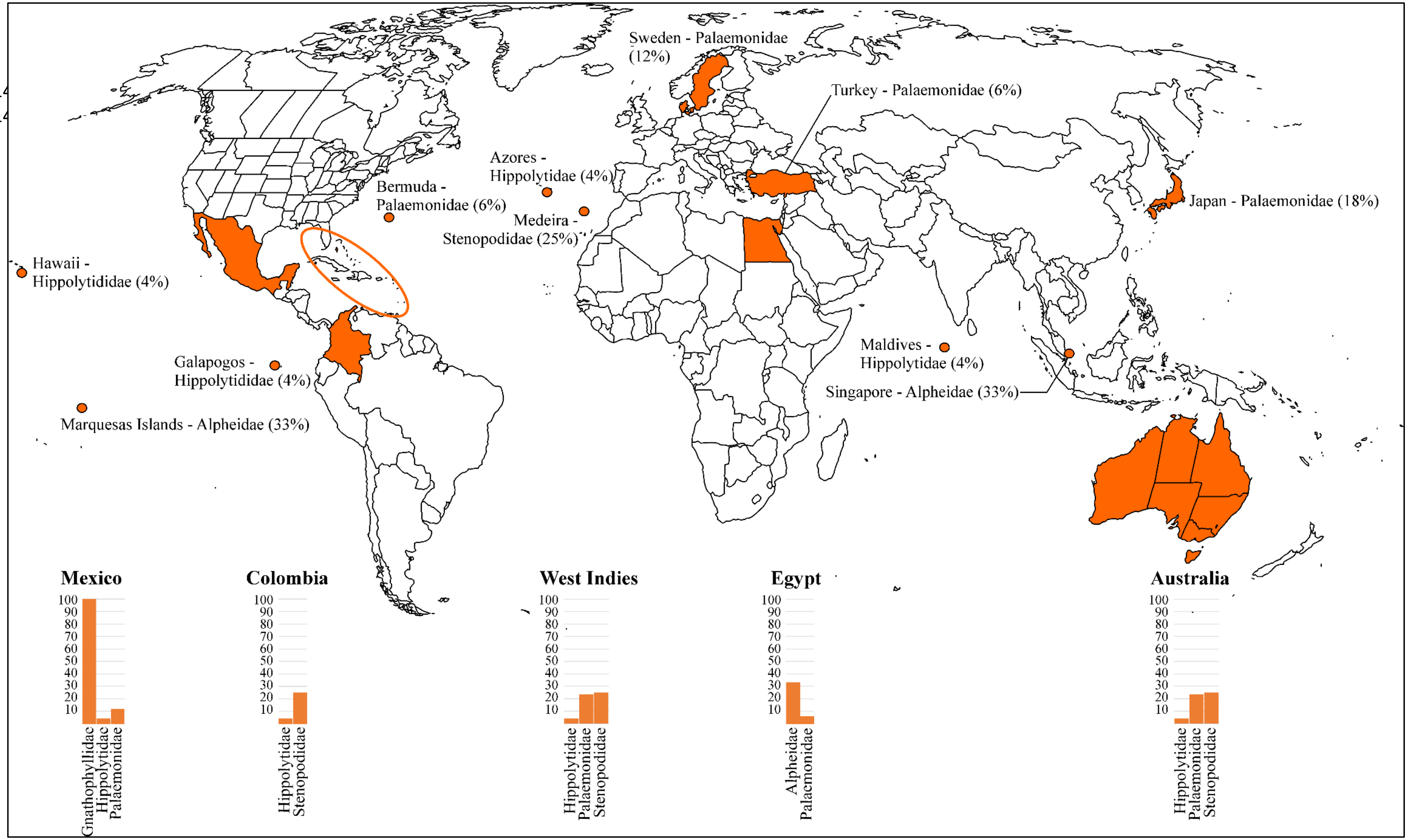

Fig. 4. Cleaner shrimp reported per region from the research cited in Table S2, expressed as a percentage of the total per family. Note: this is not a depiction of regional diversity or taxa distributions, rather an estimate of regional research to demonstrate understudied areas for future focus.