

Gobies as Cleaners

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INTRODUCTION

In 1928, the renowned American ocean explorer and naturalist Charles William Beebe published his 12th book, *Beneath Tropic Seas: A Record of Diving among the Coral Reefs of Haiti*. The best-selling book relates in eclectic detail the first American expedition to explore the underwater world of the Caribbean Sea. Equipped with helmet, hose and pump, Beebe observed a wide variety of brilliantly coloured fish, corals and sponges. His observations, made in passing, of small fish picking at the mouth of parrotfish provide the earliest written record of cleaning behaviour. Cleaning interactions, in which a small fish or shrimp removes ectoparasites and other materials from the body surface of larger-bodied clients, have since proved to be widespread in the marine realm and have been the focus of intense study by behavioural and evolutionary ecologists over the past two decades (Côté, 2000). A number of cleanerfish species are found in the

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Caribbean, and the object of William Beebe's attention were young wrasses. This is surprising because gobies, and not wrasses, are the most ubiquitous and only group of obligate cleanerfish in the region.

In this chapter, we focus on gobies as cleanerfish. The chapter is divided into three parts. First, we begin by examining the distribution of cleaning behaviour in the family Gobiidae, make inferences about the number of independent evolutionary occurrences of this behaviour, and describe the evolutionary correlates of cleaning in gobies. Second, we review current knowledge of the costs and benefits of cleaning by gobies and how the use of market and game theory has increased our understanding of how cleaning gobies interact with their fish clients. Finally, we examine the role cleaning gobies play in the fish communities in which they exist. Throughout, we draw parallels with cleaner wrasses—especially *Labroides dimidiatus*, the most ubiquitous cleaners in the Indo-Pacific and a model for the development of many ideas about the evolution of cleaning behaviour.

EVOLUTION OF CLEANING IN GOBIES

Who Cleans in The Goby Family?

Fourteen species of gobies are currently known to clean (Table 4.3.1). All cleaning gobies are restricted to the genus *Elacatinus* Jordan (formerly *Gobiosoma*), one of the largest neotropical genera of gobies. Within this genus, the number of cleaning species is distributed unevenly between the two recognized subgenera *Elacatinus* (*sensu stricto*) and *Trigrigobius* Fowler (Eschmeyer, 1998). The subgenus *Elacatinus* comprises 18 species, of which 10 clean. All but one (*E. puncticulatus*) are found in the western Atlantic. The subgenus *Tigrigobius* is composed of 13 species, of which only four clean. All are found in the eastern Pacific.

Evolutionary Correlates of Cleaning in Gobies

Taylor and Hellberg (2005) recently constructed a molecular phylogeny of 31 taxa in the *Elacatinus* group which provides a framework for exploring the evolutionary history and correlates of cleaning in this group. The overall phylogeny suggests the existence of three major clades: *Elacatinus* (*sensu stricto*) (13 Atlantic and 1 Pacific species), *Tigrigobius* (3 Atlantic species, none of which cleans) and *Risor* (5 Atlantic and 5 Pacific species) (Fig. 4.3.1). In the two clades with cleaning species, there is evidence of associations between cleaning, habitat, morphology and colour.

Table 4.3.1 Cleaning gobies *Elacatinus* spp. reported as cleaners in the wild (partially adapted from Côté, 2000). Common names, distribution and maximum length obtained from Fishbase (www.fishbase.org). TL = Total length, SL = Standard length. References pertain to information on reliance of species on cleaning as foraging mode. ? indicates uncertainty in assessing information on reliance on cleaning.

Subgenus	Species	Authority	Common name	Distribution	Maximum	Reliance size (cm)	Mouth position on cleaning	Reference
<i>Elacatinus</i>	<i>E. evelynae</i>	(Böhlke and Robins, 1968)	Sharknose goby	Atlantic	4	Obligate	Subterminal	(Losey, 1974) (Colin, 1975)
	<i>E. figaro</i>	Sazima, Moura and Rosa, 1997	Barber goby	Atlantic	4.5	Facultative?	Terminal	(Sazima, 1997) (Rocha <i>et al.</i> , 2000)
	<i>E. genie</i>	(Böhlke and Robins, 1968)	Cleaner goby	Atlantic	4.5	Obligate	Subterminal	(Colin, 1975)
	<i>E. illecebrosus</i>	(Böhlke and Robins, 1968)	Barsnout goby	Atlantic	4	Obligate	Subterminal	(Colin, 1975)
	<i>E. oceanops</i>	Jordan, 1904	Neon goby	Atlantic	5	Obligate	Subterminal	(Eibl-Eibesfeldt, 1955) (Colin, 1975)
	<i>E. phthirophagus</i>	Sazima, Carvalho-Filho and Sazima, 2008		Atlantic	3.2	Obligate?	Subterminal	(Sazima <i>et al.</i> , 2008)
	<i>E. pridisi</i>	Guimarães, Gasparini and Rocha, 2004	Trindade cleaner goby	Atlantic	2.8	Obligate	Subterminal	(Guimarães <i>et al.</i> , 2004)
	<i>E. prochilos</i>	(Böhlke and Robins, 1968)	Broadstripe goby	Atlantic	4	Obligate	Terminal	(Darcy <i>et al.</i> , 1974) (Colin, 1975) (Arnal and Côté, 2000)

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<i>E. randalli</i>	(Böhlike and Robbins, 1968)	Yellownose goby	Atlantic	4.6 TL	Obligate?	Terminal	(Colin, 1975)
<i>E. puncticulatus</i>	(Ginsburg, 1938)		Pacific	4.4 SL	Facultative?	Terminal	(Michael, 1993), in (Sazima and Moura, 2000)
<i>Triggobius E. digueti</i>	(Pellegrin, 1901)	Banded cleaner goby	Pacific	3.2 SL	Facultative	Terminal	(Hobson, 1968) (Colin, 1975; Allen and Robertson, 1994)
<i>E. inornatus</i>	Bussing, 1990	Inornate goby	Pacific	3.3 SL	Facultative	Terminal	(Allen and Robertson, 1994)
<i>E. limbaughi</i>	Hoese and Reader, 1991	Widebanded cleaning goby	Pacific	-	Facultative	Terminal	(Allen and Robertson, 1994)
<i>E. nesiotis</i>	Bussing, 1990	-	Pacific	2.3 SL	Facultative?	Terminal	(Grove and Lavenberg, 1997)

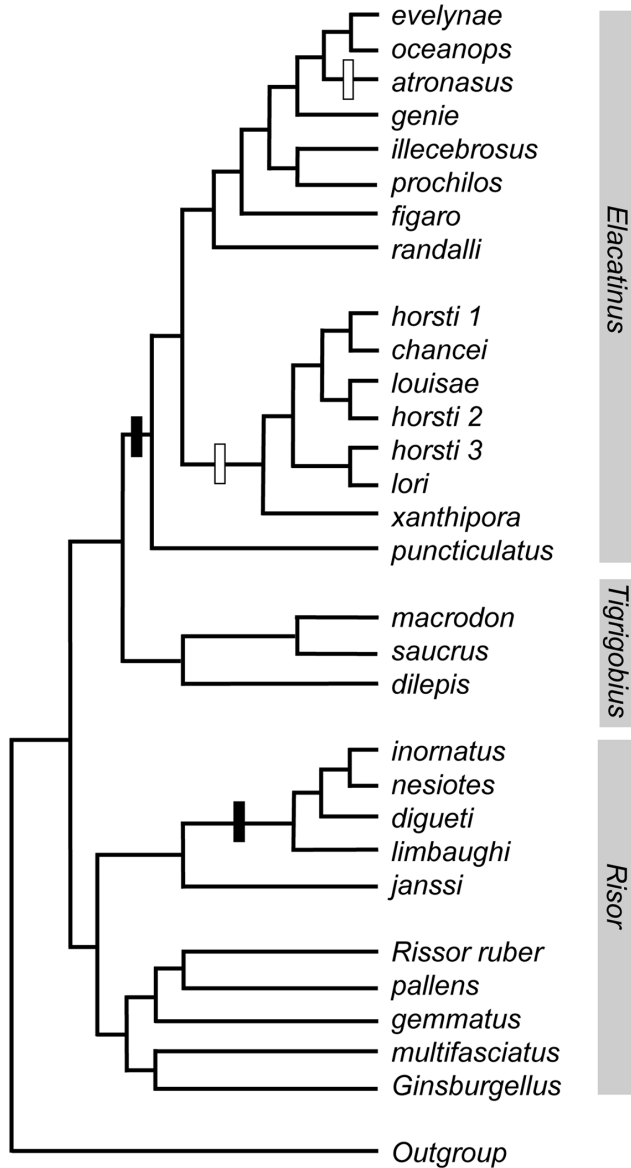


Fig. 4.3.1 Maximum likelihood phylogeny of *Elacatinus* gobies based on three independent molecular markers. Black bars represent possible evolutionary origins of cleaning behaviour. White bars represent possible losses of cleaning behaviour. Redrawn and modified from Taylor and Hellberg (2005).

The most parsimonious scenario to explain the distribution of cleaning in gobies is that this behaviour has evolved independently twice in this group (see also (Rüber *et al.*, 2003). One evolutionary transition probably occurred following the divergence of the *Elacatinus* and *Tigrigobius* clades (Fig. 4.3.1), explaining the occurrence of cleaning in the Pacific species *E. puncticulatus* and the Atlantic species *E. evelynae*, *E. oceanops*, *E. genie*, *E. illecebrosus*, *E. prochilos*, *E. figaro* and *E. randalli*. Cleaning behaviour was then lost in *E. atronasus*, perhaps with the adoption of a schooling, non-benthic habit (Taylor and Akins, 2007), and in the *horsti* group (Rüber *et al.*, 2003). It is likely that cleaning in the two newly described Brazilian species *E. phthirophagus* (Sazima *et al.*, 2008) and *E. pridisii* (Guimaraes *et al.*, 2004) also arose in the same event. A second origin of cleaning must have occurred some time after the separation of the Atlantic and Pacific species of the *Risor* clade (Fig. 4.3.1), which explains the presence of cleaning in four of the five species in this group. The fifth, *Elacatinus janssi*, does not appear to clean (although little is known about this species).

In the *Elacatinus* clade, the absence of cleaning appears to be associated with a sponge-dwelling habit or, conversely, the presence of cleaning is associated with living on substrata other than sponge (Rüber *et al.*, 2003; Taylor and Hellberg, 2005). This alternative substratum is often, but not always, live coral (e.g. Sazima *et al.*, 2000; Whiteman and Côté, 2002; Sazima *et al.*, 2008). Interestingly, this habitat-feeding mode link also occurs intra-specifically. For example, in Barbados, the broadstripe cleaning goby *E. prochilos* occurs on both sponge and live coral (Whiteman and Côté, 2004a), and its foraging mode and social systems differ between the two substrata. Coral-dwelling *E. prochilos* are active cleaners (Arnal and Côté, 2000; Whiteman and Côté, 2002) that live in singly or in small groups (Whiteman and Côté, 2002) while sponge-dwelling *E. prochilos* occur in large, dominance-structured groups and feed predominantly on polychaete worms that burrow within sponge tissues (Whiteman and Côté 2004b). Variable habitat use has been noted in other species, such as *E. evelynae* (White *et al.*, 2007) and *E. figaro* (Rocha *et al.*, 2000), and in both cases, sponge-dwelling individuals did not clean. Note that there appears to be geographic variation in habitat associations: *E. evelynae* in Barbados occur virtually exclusively on live coral (Whiteman and Côté, 2002) while in the US Virgin Islands, they are found on coral as well as in basket sponges (White *et al.*, 2007).

Habitat associations are also apparent in the *Risor* clade (Fig. 4.3.1). Groups of non-cleaning species in this clade are specifically associated with chiton burrows, sea urchin spines, live coral or sponges (Taylor and

Hellberg, 2005). However, the group in which cleaning has arisen lacks strong habitat specialization. In both the *Elacatinus* and the *Risor* clades, it therefore appears that specialization in feeding mode (i.e., cleaning) has emancipated gobies from habitat specialization, although both types of specialization effectively lead to ecological separation that may have promoted the early stages of diversification in this group (Streelman and Danley, 2003).

Foraging specialization is often accompanied by morphological adaptations. It has been long thought that a 'picker-type', terminally located mouth may pre-adapt fish for cleaning (Hobson, 1971, 1976; McCourt and Thomson, 1984). Most *Elacatinus* (*sensu lato*) gobies do indeed have a terminal mouth; however, this ancestral morphology has been replaced in four species in the *Elacatinus* clade—*E. evelynae*, *E. oceanops*, *E. genie* and *E. illecebrosus*—by a subterminal, inferior mouth. Molecular evidence suggests a polyphyletic origin for this new mouth position (Taylor and Hellberg, 2005). In hindsight, the initial notion that terminal mouths would be well-suited to removing ectoparasites was a sensible one, but only for species that clean in mid-water, such as the damselfishes and wrasses observed by Hobson (1971, 1976) and McCourt and Thomson (1984). For species with a benthic habit, such as gobies which lie on their clients as they would on the substratum, a ventrally located mouth would facilitate cleaning. If so, the question becomes why has an inferior mouth evolved in some but not all cleaning gobies? The retention of a terminal mouth could be linked to flexibility in foraging mode. This could explain mouth morphology in cleaning gobies of the *Risor* clade, which have been described as facultative cleaners (Humann, 1993; Allen and Robertson, 1994), and in *E. prochilos* and *E. figaro*, which are both known to exhibit different foraging modes when occupying different substrata (Rocha *et al.*, 2000; Whiteman and Côté, 2002). However, *E. evelynae* also shows habitat-dependent foraging modes (White *et al.*, 2007) and yet has a subterminal mouth. Some insight into the evolutionary link between feeding morphology and cleaning behaviour could be gained by examining other cleaning taxa (e.g. the family Labridae).

The final potential correlate of cleaning behaviour is colour pattern. The presence of a cleaner signaling coloration was posited long ago by researchers who were struck by the similarity in colour patterns of cleaning species from various parts of the world (Eibl-Eibesfeldt, 1955; Wickler, 1963; Potts, 1973a). Côté (2000) provided the first test of this hypothesis and showed that cleaning gobies have a longer lateral stripe, relative to body length, than their non-cleaning relatives. By contrast, among more

varied taxa of Caribbean facultative cleanerfish, there was no evidence that cleaners were more likely to be striped but they tended to be more brightly coloured than non-cleaning congeners. Although this analysis was based on taxonomy, the conclusions were later supported by Arnal *et al.* (2006) who, using a well-resolved molecular phylogeny, found that cleaning behaviour in wrasses is associated with the presence of a dark lateral stripe. In addition, in field experiments using wooden models of cleaner wrasses with and without stripes, the former attracted many more fish clients (Stummer *et al.*, 2004). In the *Elacatinus* clade, there appears to be an association between a subterminal mouth position and blue lateral stripe (Taylor and Hellberg, 2005). Incidentally, the spectral reflectance of the blue stripe in gobies appears to be similar to that of the ubiquitous Indo-Pacific cleaner wrasse *Labroides dimidiatus* (Taylor and Hellberg, 2005), which is distinct from the blue hue of virtually all other coral reef fishes (except for the cleanerfish mimic *Plagiotremus rhynorhynchos*, Cheney *et al.*, 2008). In the *Risor* clade, however, the four cleaning species, as well as their non-cleaning clade-mates are variously banded or spotted rather than striped. Taken together, these studies suggest that a cleaner 'guild coloration' exists but it may not be universal. Much work remains to understand the exceptions to the stripe rule.

CLEANING BEHAVIOUR OF CLEANING GOBIES

Generic Cleaning Sequence

The behavioural patterns of cleaning gobies and their clients have been described in detail (Limbaugh, 1961; Losey, 1972; Colin, 1975), and these patterns bear similarities with those exhibited by cleaner wrasses (*Labroides* spp.), the well-studied counterparts of cleaning gobies on Indo-Pacific reefs (e.g. Potts, 1973b). Interactions between cleaning gobies and their fish clients, like those of cleaner wrasses, usually occur at cleaning stations—relatively fixed sites on reefs which are often, although not always, located on top or near the base of large coral heads or other prominent features (IMC and MCS, personal observations). Clients approach cleaning stations and adopt a species-specific posture which may entail an immobile head-stand or tail-stand position with all fins spread and the opercula flared (Losey, 1971; Côté *et al.*, 1998). These poses may be accompanied by dramatic colour changes (Feder, 1966) and have been shown to increase the likelihood of being cleaned (Côté *et al.*, 1998). Cleaning gobies may then swim onto and 'inspect' the client, before starting to feed on the client's body, in its mouth

or gills, or returning to the station without feeding. Cleaning interactions may also be terminated by clients by twitching to signal their intention to depart and allow the cleaner to return to the station (Feder, 1966).

There are, however, marked differences in behaviour between cleaning gobies and cleaner wrasses. Cleaner wrasses often begin cleaning interactions by performing a 'dance'—a conspicuous, vertical zig-zag swimming pattern which appears to attract clients (Potts, 1973b; Gorlick *et al.*, 1978; Grutter, 2004). Cleaning gobies do not perform such advertising dances (IMC, MCS, personal observations). In addition, during inspections, cleaner wrasses often deliberately stroke the body surface of their clients with their pectoral fins—a behaviour termed 'tactile stimulation' (Bshary and Würth, 2001). The delivery of tactile stimulation appears to influence the decision of clients to remain at cleaning stations, both before cleaning and after cleaners deliver bites that appear painful to clients (Bshary and Würth, 2001). Its preferential use with potentially dangerous clients (e.g. hungry piscivores) suggests that it is also a pre-conflict management strategy (Grutter, 2004). This conspicuous behaviour is absent in cleaning gobies (Soares *et al.*, 2008a). We return to the significance of these behavioural differences later (see section on Insights from Biological Market Theory).

Clients of Cleaning Gobies

Cleaning gobies interact with a large variety of client species (Table 4.3.2). For example, Soares *et al.* (2007) noted a total of 46 different client species serviced by *E. evelynae* and *E. prochilos* on two Barbadian reefs (Table 4.3.2). In this instance, comparisons with cleaner wrasses are not useful, given the much greater diversity of potential client species in the Indo-Pacific. However, gobies do not hold a cleaning monopoly in the Caribbean. Other species of fish clean facultatively, particularly as juveniles, and several species of obligate cleaner shrimp also provide services. Few studies have compared the cleaning activity and client diversity between cleaning gobies and other cleaners within the same location but those that have repeatedly found that gobies attend a higher diversity and greater number of clients (Darcy *et al.*, 1974; Losey, 1974; Wicksten, 1998; Francini-Filho and Sazima, 2008; Table 4.3.2).

It is perhaps the interactions between cleaning gobies and piscivorous species that hold the greatest interest for biologists and lay people alike (Fig. 4.3.2A). The ability of cleaning gobies (and cleaner wrasses in the Indo-Pacific) to enter the mouth of piscivorous clients during inspections, and to re-emerge unscathed, was interpreted early on as an example of altruism

Table 4.3.2 Summary of client diversity of cleaning gobies (*Elacatinus* spp.) and other Caribbean cleaners.

Location	Cleaning species	Number of clients species	Number of client families	Total observation time	Source
Cleaning gobies					
Barbados	<i>E. evelynae</i> and <i>E. prochilos</i>	46	21	52 h	(Soares <i>et al.</i> , 2007)
Barbados	<i>E. evelynae</i> and <i>E. prochilos</i>	38	17	83 h	(Soares <i>et al.</i> , 2008c)
Barbados	<i>E. evelynae</i> and <i>E. prochilos</i>	25	14	25 h	(Arnal <i>et al.</i> , 2000)
St Croix (US Virgin Islands)	<i>E. evelynae</i> and <i>E. prochilos</i>	?	6	?	(Darcy <i>et al.</i> , 1974)
Barbados	<i>E. evelynae</i>	34	16	114 h	(Whiteman and Côté, 2002)
St Croix (US Virgin Islands)	<i>E. evelynae</i>	?	4	6.8 h	(White <i>et al.</i> , 2007)
St Croix (US Virgin Islands)	<i>E. evelynae</i>	25	14	?	(Johnson and Ruben, 1988)
Barbados	<i>E. prochilos</i>	28	14	78 h	(Whiteman and Côté, 2002)
Brazil	<i>E. figaro</i>	34	16	53 h	(Sazima <i>et al.</i> , 2000)
Brazil	<i>E. randalli</i>	22	13	~14 h	(Francini-Filho and Sazima, 2008)
Panama	<i>E. illecebrosus</i>	9	3	?	(Bohlke and McCosker, 1973)
Bonaire	<i>Elacatinus</i> spp.	43	19	?	(Wicksten, 1998)
Other cleanerfish					
Bonaire	<i>Thalassoma bifasciatum</i>	16	10	?	(Wicksten, 1998)
St Croix (US Virgin Islands)	<i>Thalassoma bifasciatum</i>	10	4	?	(Johnson and Ruben, 1988)
St Croix (US Virgin Islands)	<i>Thalassoma bifasciatum</i>	?	4	?	(Darcy <i>et al.</i> , 1974)

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<i>Conid.</i>						
Brazil	<i>Thalassoma noronhanum</i>	19	11	~ 14 h	(Francini-Filho and Sazima, 2008)	
Brazil	<i>Thalassoma noronhanum</i>	19	9	38 h	(Francini-Filho <i>et al.</i> , 2000)	
Bonaire	<i>Bodianus rufus</i>	12	9	?	(Wicksten, 1998)	
St Croix (US Virgin Islands)	<i>Bodianus rufus</i>	15	9	?	(Johnson and Ruben, 1988)	
Bonaire	<i>Pomacanthus paru</i>	2	2	?	(Wicksten, 1998)	
Brazil	<i>Pomacanthus paru</i>	31	19	19 h	(Sazima <i>et al.</i> , 1999)	
Cleaner shrimp						
Bonaire	<i>Periclimenes pedersoni</i>	28	12	?	(Wicksten, 1998)	
St Croix (US Virgin Islands)	<i>Periclimenes pedersoni</i>	10	5	?	(Johnson and Ruben, 1988)	
Bermuda	<i>Periclimenes anthophilus</i>	10	7	30 h	(Sargent and Wagenbach, 1975)	
Bonaire	<i>Stenopus hispidus</i>	?	4 (3)	?	(Wicksten, 1998)	

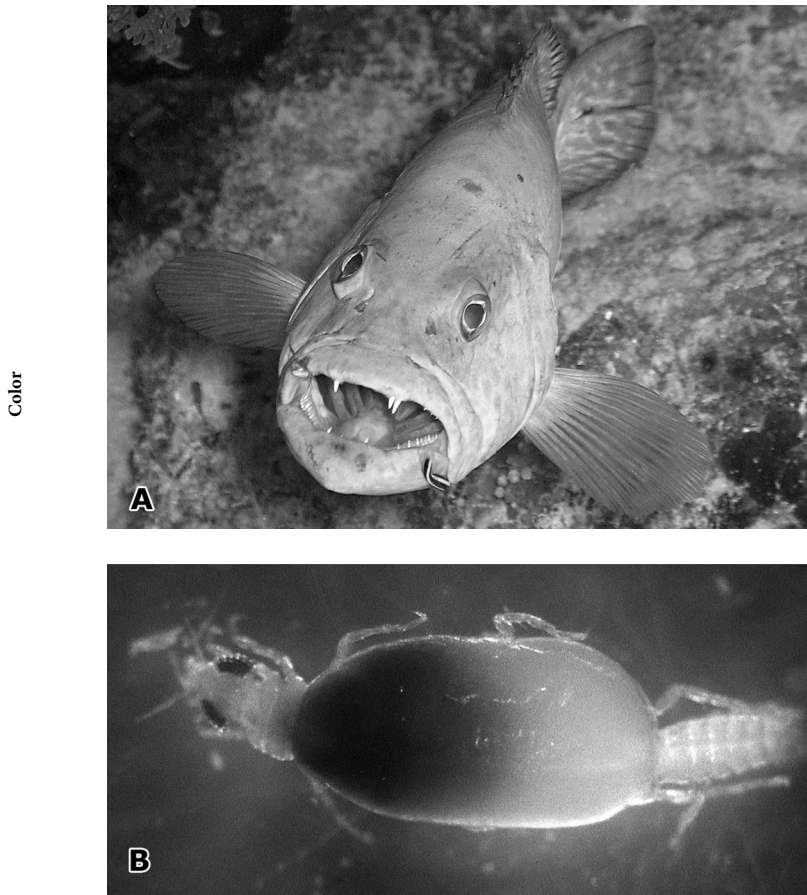


Fig. 4.3.2 A Cleaning goby *Elacatinus* sp. inspecting the buccal area of a tiger grouper *Mycteroperca tigris* on a Little Cayman reef. Photo: Isabelle Côté. B Gnathiid isopod larva—the most ubiquitous ectoparasite found in stomach contents of cleaning gobies. Photo courtesy of Paul Sikkel.

Color image of this figure appears in the color plate section at the end of the book.

on the part of clients which could easily eat the cleaner (e.g. Trivers, 1971). An untested alternative explanation is that cleaning gobies are unpalatable (Colin, 1975). Nevertheless, cleaning gobies do inspect potentially dangerous clients regularly (Darcy *et al.*, 1974; Johnson and Ruben, 1988; Wicksten, 1998; Arnal *et al.*, 2000; Sazima and Moura, 2000; Sazima *et al.*, 2000; Soares *et al.*, 2007), and more often than cleaner shrimp or other non-obligate cleanerfish on Caribbean reefs (Losey, 1974; Wicksten, 1998). Wicksten (1998), for example, reported that 63% of groupers (Serranidae)

seen at cleaning stations in Bonaire were cleaned by *Elacatinus* spp. Gobies are also the only Caribbean cleaners to have been observed interacting with elasmobranchs: whitetip reef sharks *Triaenodon obesus* and nurse sharks *Ginglymostoma cirratum* are cleaned by *E. puncticulatus*, Caribbean reef sharks *Carcharhinus perezi* by *E. phthirophagus* (Michael, 1993; Sazima *et al.*, 2008), large-eyed stingrays *Dasyatis macrophthalma* by *E. figaro* and Southern stingrays *D. americana* by *E. puncticulatus* (Sazima and Moura, 2000).

Cleaning gobies show distinct preferences towards some client species over others. They express these biases by cleaning a greater proportion of all visiting individuals of some species (Soares *et al.*, 2007), spending more time inspecting these species (Arnal *et al.*, 2000) and by attending to preferred visitors most quickly (Soares *et al.*, 2007). Ectoparasite load is a relatively good predictor of whether a visitor will be inspected or not (Soares *et al.*, 2007). However, swiftness of service is best explained by client trophic level: piscivorous clients are not made to wait (Soares *et al.*, 2007). This preference appears to be explained by the negative effect of the presence of piscivores on the abundance of other clients at cleaning stations. Hence, the quicker a piscivore is cleaned, the sooner it departs and other clients of cleaning gobies can return.

The Adaptive Significance of Cleaning

A function for cleaning was first suggested by the discovery of parasites in the gut of cleaner wrasses by Randall (1955, 1958). Soon after, a cleaner-removal experiment by Limbaugh (1961) from two Bahamian reefs resulted in dramatic immigration of fish from cleaning goby-free areas as well as a marked increase in disease in those individuals that remained. This apparently crucial role played by cleaning gobies in maintaining the health of their clients, combined with evidence that cleaners actually feed on ectoparasites, implied that cleaning was a co-operative interaction occurring between cleaner and client. Cleaning symbioses were viewed from then on as textbook examples of mutualistic interactions (Trivers, 1971; McFarland, 1985; Begon *et al.*, 1990; Thompson, 1994).

It has taken a surprisingly long time for researchers to verify this long-held perception. However, it is now agreed that the interactions between cleaner wrasses and their clients are largely mutualistic, on the basis of the significant decrease in client parasite loads effected by cleaner wrasses (e.g. Grutter, 1999) and the large effects of on client fish density and community structure resulting from cleaner removal (Bshary, 2003; Grutter *et al.*, 2003).

However, the evidence has not been as strongly forthcoming for cleaning gobies.

Cleaning gobies do remove ectoparasites from the fish they inspect (Fig. 4.3.3). The identifiable diet of coral-dwelling *Elacatinus prochilos*, for example, is composed largely of larval gnathiid isopods (Whiteman and Côté, 2002), the commonest ectoparasites found in the stomach contents of cleanerfish worldwide. Client fish tend to visit cleaning stations more in the morning (Côté and Molloy, 2003; Sikkel *et al.*, 2004), which coincides with periods of peak ectoparasite infestation (Chambers and Sikkel, 2002; Sikkel *et al.*, 2006). There is also evidence that reef fish that have access to cleaning gobies (*E. evelynae* and *E. prochilos*) have lower parasites loads. For example, Barbadian longfin damselfish *Stegastes diencaeus* that visit these cleaning gobies often, by virtue of having a cleaning station within their territories, have significantly fewer ectoparasites than damselfish that live further away from cleaners and hence visit them less frequently (Cheney and Côté, 2001). This difference is not simply due to differences in damselfish quality because a similar effect was observed at the end of a 6-month experiment in which half of the damselfish 'lost' the cleaning gobies that were originally in their territories (Cheney and Côté, 2003a). However, in both cases, the difference in ectoparasite load was small—approximately 1 gnathiid per damselfish—and such a small reduction did not result in a detectable decline in damselfish breeding output in Barbados (Cheney and Côté, 2003a).

The apparently small benefit of being cleaned by gobies may be biased by the fact that these studies have all been conducted in Barbados, where ectoparasite abundance is generally very low. In other parts of the Caribbean (e.g. in Puerto Rico) where there are more ectoparasites, the benefit of being cleaned by gobies can be twice as high (Cheney and Côté, 2005), but this still amounts to only two 1-mm long gnathiids per fish (Fig. 4.3.2B). Nevertheless, if gnathiids are an important source of skin irritation or vectors for blood diseases (e.g. Davies *et al.*, 1994), then the removal of a few parasites may have an appreciable impact on host fitness and health.

Geographic variation in benefit of being cleaned by gobies should be accompanied by variation in willingness of clients to incur costs of seeking cleaners. The costs of being cleaned, for clients, include travelling time to cleaning stations, risk of predation during travel, and resources lost from temporarily abandoned territories. Most of these are linked to travel distance (Cheney and Côté, 2001). Thus, in areas where ectoparasites are abundant and the scope of a benefit of being cleaned is high, clients should be more willing to travel long distances to be cleaned. Conversely, when the

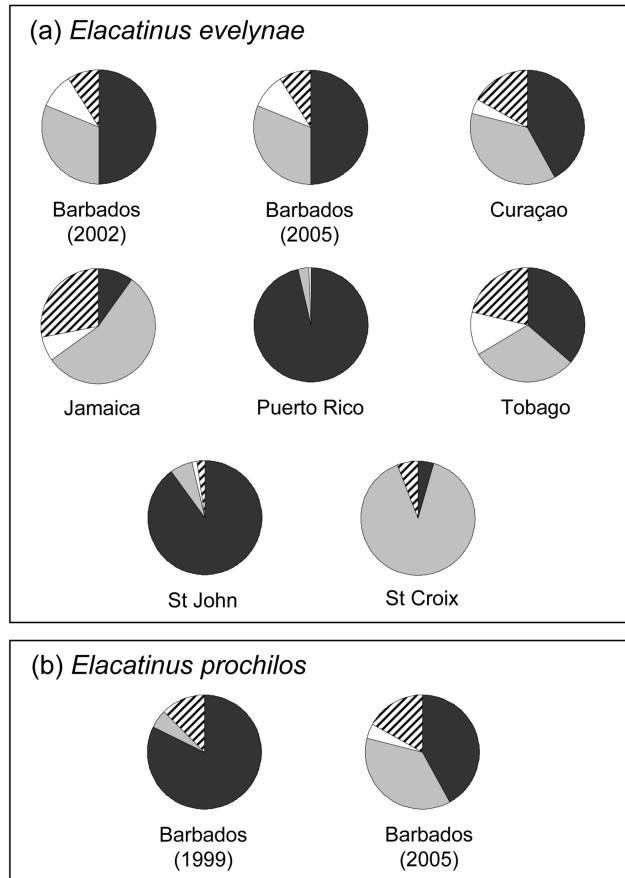


Fig. 4.3.3 Diet of cleaning gobies at various locations across the Caribbean. (a) *Elacatinus evelynae* and (b) *E. prochilos*. Dietary items shown are ectoparasites (black), fish scales (grey), fish mucus (white), and other items (hatched), which include non-parasitic, client-gleaned crustaceans as well as benthic invertebrates. Proportions are expressed as % of identified stomach contents. Sample sizes vary from 12 to 117 fish. Sources: *E. evelynae* and *E. prochilos* for Barbados (2005): M.C. Soares, unpublished data; *E. evelynae* for St Croix: (White *et al.*, 2007); *E. prochilos* for Barbados (1999): (Arnal and Côté, 2000); all others: (Cheney and Côté, 2005).

potential benefit of being cleaned is low, clients should only visit cleaners that are nearby. In this way, clients can attempt to tip the balance sheet, however slightly, in favour of a mutualistic relationship.

This careful accounting by clients can be thrown into disarray by cheating cleaners. It has long been known that cleanerfish remove not

only parasites but mucus and scales from their clients (e.g. Gorlick, 1980). Cleaning gobies are no exception (Whiteman and Côté, 2002; Cheney and Côté, 2005) (Fig. 4.3.3). Dishonesty by gobies is clearly evidenced by the content of their stomachs, but also by the behaviour of their clients which jolt or shudder in response to cheating bites (Soares *et al.*, 2008b). Cleaning gobies take more scales and mucus at locations where ectoparasites are rare (Bansemer *et al.*, 2002; Cheney and Côté, 2005), which makes it sometimes difficult for cleaning relationships to remain mutualistic from the client's point of view. However, because ectoparasite abundance varies temporally, the outcome of cleaning at any locale will vary periodically from positive to negative, preventing the long-term breakdown of these interactions.

The issue of cheating is worth further examination because how clients deal with dishonest cleaners differs strikingly between cleaning gobies and cleaner wrasses. The clients of cleaner wrasses fall into two broad categories: those that live in small home ranges and have no choice of which cleaning station they visit, and those with larger home ranges which could take their custom to a number of different cleaners. Cleaner wrasses generally give priority of access to the latter class (Bshary and Schaffer, 2002; Bshary and Grutter, 2002a). These different classes of clients also retaliate to cheating by cleaner wrasses in different ways. Resident fish, which lack choice options, aggressively chase cheating cleaners after a bite, whereas transient fish with choice options simply swim away and withhold further visits for a while (Bshary and Grutter, 2002a). These retaliatory tactics result in a greater likelihood of cleaner honesty in subsequent interactions (Bshary and Grutter, 2002a, 2005). By contrast, the clients of cleaning gobies never chase cheating cleaners and do not take longer to return to a cleaner that had previously given a poorer service than to one that was honest (Soares *et al.*, 2008a). Similarities and differences between these two cleanerfish systems, and some of the general intricacies of cleaning mutualisms, become more clearly understood when placed in the framework of biological market theory.

Insights from Biological Market Theory

Ronald Noë and colleagues (Noë, 1990; Noë *et al.*, 1991; Noë and Hammerstein, 1994) first suggested that cooperative interactions among animals resemble various forms of human trading and proposed human market theory as a general framework for cooperation. In biological markets, just like in their human counterparts, two classes of traders exchange commodities to their mutual benefit. Such markets exhibit three defining characteristics: (1) competition within trader classes that is rarely

overtly agonistic, but that occurs instead by outbidding, (2) preference for partners offering the highest value, and (3) conflicts over the exchange value of commodities (Noë and Hammerstein, 1994; Noë, 2001, 2006).

The parallels between biological markets and cleaning interactions were first noted by Bshary (2001). In cleaning, there are two classes of traders, each providing a reciprocal service: one removes parasites (the cleaners) and the other (the clients) offers a meal (in the form of parasites). Both classes advertise their services: the cleaners (at least in wrasses) by dancing and the clients by posing. Both classes prefer partners that give them the highest benefit, hence cleaners prefer clients that offer more food (e.g. larger clients) and clients prefer honest cleaners. However, conflicts may arise if clients only want their parasites removed but cleaners remove other items. Because of interactions between individual cleaners and clients are repeated multiple times, partner choice becomes a powerful weapon, particularly for clients, to enforce honesty in cleaners. Manipulative behaviours may also be expected to arise in dishonest traders to appease wronged parties and promote continued interactions. Bshary and colleagues have over the years produced a remarkable body of work, elucidating the cleaner wrasse market with evidence from both the field and from cleverly designed laboratory experiments (Bshary and Schaffer, 2002; Bshary and Grutter, 2002a, 2002b, 2003, 2005).

While cleaner wrasses and their clients fit perfectly the expectations of biological markets, this is not so much the case for cleaning gobies. As described previously, cleaning gobies do not advertise their services, they do not provide tactile stimulation to their clients, and while gobies do cheat, their clients do not appear to exercise strong control over cleaner dishonesty through partner choice. Why? The answer may lie in the low level of conflict between cleaning gobies and their clients (Soares *et al.*, 2008a). When given a choice between fish ectoparasites and mucus, cleaner wrasses almost invariably prefer mucus (Grutter and Bshary, 2003, 2004), giving rise to a conflict because mucus loss is costly for clients. In cleaning gobies, this conflict of interests appears to be much less important. Circumstantial evidence suggests cleaning gobies may primarily focus on removing client ectoparasites rather than mucus (Arnal *et al.*, 2001). In addition, cleaning gobies show a clear preference for clients with more ectoparasites (Soares *et al.*, 2007). This does not mean that cleaning gobies never cheat but simply that they may less readily do so than cleaner wrasses.

A reduced conflict of interest between cleaners and clients has several repercussions. First, there is little need to advertise cleaning services because variation among cleaners in service quality (i.e., how honestly

they clean) is limited. Second, there is little need for clients to use tactics to control cheating by cleaners. Thus when cleaning gobies do cheat, their clients simply interrupt the interaction and swim away instead of punishing the cleaner by chasing or by withholding further visits (Soares *et al.*, 2008a). Finally, there is also little need for cleaners to attempt to manipulate the behaviour of their clients after cheating. If ectoparasites are the primary target of cleaning gobies, then gobies will usually cheat once client ectoparasite loads have been depleted (Soares *et al.*, 2008b). There is therefore little incentive for cleaning gobies to encourage clients, via tactile stimulation, to remain at their cleaning station.

The application to biological market thinking to cleaning has undoubtedly deepened our understanding of these interactions. The fact that some cleanerfish species fit the model well and others, such as cleaning gobies, do not has nevertheless increased our appreciation of the diversity of cleaning systems.

ECOLOGICAL ROLE OF CLEANING GOBIES

The ecological role of some cleanerfish can go far beyond their function as ectoparasite consumers. This has been clearly shown to be the case for the cleaner wrasse *L. dimidiatus*. On reefs with few or no cleaner wrasses, either because of natural downturns in population size or experimental removals, reef fish species diversity can decrease by up to 50%, and abundance by ~75% over periods of 4 to 18 months (Bshary, 2003; Grutter *et al.*, 2003). Natural and experimental additions of cleaners to reefs have the reverse effect, which is noticeable in only a few weeks instead of a few months (Bshary, 2003). The effects are particularly marked for client species that move among reefs, but less so for resident clients, thus leading to changes in fish community composition. Surprisingly, the presence (or absence) of cleaners can also affect the distribution of non-client resident species (Bshary, 2003). The reasons for this latter effect are not clear, but Bshary (2003) suggested that if the higher species diversity of reefs with cleaners results in higher overall fish densities, this could lead to greater relative safety or lower ectoparasite availability (through dilution effects) for all fish, including those that rarely interact with cleaners.

In light of the relatively smaller apparent benefit for clients of being cleaned by gobies, one might surmise that gobies that clean play a more limited ecological role in Caribbean coral reef communities. In this respect, it is unfortunate that Limbaugh's (1961) early Caribbean cleaner removal experiment—which, admittedly, was carried out on only two reefs, included

removal of all cleaners (not just gobies), and lacked a control—has never been replicated. There are nevertheless a few recent studies that shed some light on the influence of cleaning gobies on client distribution and abundance.

On a very small scale, if being cleaned is important, then proximity to cleaning stations should be an asset to fish that are limited in movement, such as territorial species. However, there is no indication of aggregations of territorial adult damselfish around cleaning stations operated by cleaning gobies (Whiteman *et al.*, 2002). An effect of cleaning gobies could be masked if young damselfish settling on a reef do indeed preferentially take up residence near cleaning stations, but damselfish longevity exceeds the tenure of gobies at a given site. Many adult damselfish are therefore near where cleaning stations used to be, but the cost of relocating closer to a current cleaning station may be too high given the limited benefit. However, this does not seem to be a plausible scenario because even when the cost of relocating is experimentally reduced (i.e. by creating a vacancy next to a cleaning station), damselfish still do not seek territories near cleaners (Cheney and Côté, 2003b).

At a larger, inter-reef scale, cleaning gobies appear, at first glance, to be more influential. As the density of coral-dwelling cleaning gobies increases, so does the total density of clients (Cheney and Côté, 2003c). This relationship does not seem to reflect a general habitat quality effect since there is no association between the abundances of sponge-dwelling gobies—which do not clean but feed instead on sponge-dwelling invertebrates ((Whiteman and Côté, 2002; White *et al.*, 2007)—and of fish clients (Cheney and Côté, 2003c). But does cleaning goby abundance drive client abundance, or vice-versa? The small-scale observations suggest that client abundance is probably the driver, i.e. cleaning gobies recruit to client-rich areas rather than the other way around. However, only replicated experiments in which either gobies or their clients are removed will provide a definite answer to this question.

Taken together, the evidence to date suggests that cleaning gobies do not affect client distribution or abundance greatly, certainly not to the extent demonstrated for cleaner wrasses. Immigration of clients away from cleaner-free reefs probably largely depends on client ectoparasite load: the greater the benefit of being cleaned, the more likely immigration becomes, and the greater the effect of cleaners on the distribution of their clients.

CONCLUSIONS AND FUTURE DIRECTIONS

Cleaning in gobies is definitely a more muted affair than it is in Indo-Pacific cleaner wrasses. The service is less conspicuous, by virtue of the smaller size of gobies and the lack of advertisement dancing, the transaction more straightforward, owing to the absence of tactics to counter cheating, and the outcome in terms of parasite removal only marginally beneficial, at least from the client's point of view. There has even been a suggestion that adopting a cleaning lifestyle is making the best of a bad situation, based on the observation that the growth rates of juvenile and survival rates of adult *E. evelynae* that live on sponges (where they do not clean) are higher than those of *E. evelynae* that live on coral (where they do clean) (White *et al.*, 2007). This is clearly not the case everywhere or for every cleaning goby species with dichotomous habits (e.g. Whiteman and Côté, 2004a), but such observations highlight the fact that cleaning behaviour, particularly in gobies, is far from well understood, either evolutionarily or ecologically.

Key questions remain to be answered. One concerns the outcome of cleaning. How substantial is the benefit of being cleaned by cleaning gobies? The studies that have focused on ectoparasite numbers suggest a very small effect, but other metrics might be important. The issue of ectoparasites as vectors for diseases was raised earlier. In addition, there is evidence that cortisol levels—a marker of physiological stress—are lower in clients interacting with cleanerfish (Bshary *et al.*, 2007). Thus, as a result of being cleaned, the general health of clients may therefore be improved in ways that are poorly reflected by simple parasite counts.

Another important question relates to the ultimate cause of the discrepancies observed between cleaner wrasses and cleaning gobies. We outlined earlier how a preference by cleaning gobies for ectoparasites over mucus or other client-gleaned items could potentially explain these large interspecific differences, but the evidence to date is only circumstantial. Experiments of the type carried out with cleaner wrasses, in which cleaners are simultaneously offered different food items (e.g. Grutter and Bshary, 2003, 2004) or allowed to forage on an anaesthetised client that cannot retaliate to cheating (Bshary and Grutter, 2002a), need to be performed with cleaning gobies to measure their foraging preferences. Alternative causes **also should to be** considered. For example, if cleaning gobies inflict very small costs on their clients when cheating, the cleaner control tactics displayed by clients of cleaner wrasses would be largely unnecessary, as might be the advertisement of (honest) cleaning service. In addition, punishing a cleaner that misbehaves is useful to a client only if the cleaner changes

its behaviour in subsequent interactions with the punisher. The cognitive ability required is considerable, as the cleaner needs to recall the act that led to punishment as well as the identity of the individual that retaliated. Cleaner wrasses, which have been described as having a 'Machiavellian intelligence' (Bshary and Würth, 2001), are able to do this (Tebbich *et al.*, 2002; Bshary and Grutter, 2002a), but we do not know whether cleaning gobies can.

Finally, the apparently limited role played by cleaning gobies in determining client abundance or community structure needs to be confirmed (or refuted). Interested researchers should note in this context that the earliest cleaner wrasse removal experiments invariably concluded that cleaner wrasses had little or no effect on client populations (Youngbluth, 1968; Gorlick *et al.*, 1987; Grutter, 1996, 1997). Yet, later efforts with longer-running and better-replicated field experiments concluded the opposite (Bshary, 2003; Grutter *et al.*, 2003).

Given that so much of our recent understanding of cleaning behaviour has been influenced by research on cleaner wrasses, should we study cleaning gobies at all? Our answer is an emphatic yes! Work on cleaning gobies has revealed that cleaner wrasses are not a universal model to which all cleanerfish conform. This comparison has given, and will continue to provide, deep insights into the evolution of cleaning interactions. We have only begun to unravel the mysteries of cleaning gobies.

References

- Allen, G.R. and D.R. Robertson. 1994. *Fishes of the Tropical Eastern Pacific*. University of Hawaii Press, Honolulu.
- Arnal, C. and I.M. Côté. 2000. Diet of broadstripe cleaning gobies on a Barbadian reef. *Journal of Fish Biology* 57: 1075-1082.
- Arnal, C., I.M. Côté and S. Morand. 2001. Why clean and be cleaned? The importance of client ectoparasites and mucus in a marine cleaning symbiosis. *Behavioral Ecology and Sociobiology* 51: 1-7.
- Arnal, C., O. Verneau and Y. Desdevises. 2006. Phylogenetic relationships and evolution of cleaning behaviour in the family Labridae: importance of body colour pattern. *Journal of Evolutionary Biology* 19: 755-763.
- Arnal, C., I.M. Côté, P. Sasal and S. Morand. 2000. Cleaner-client interactions on a Caribbean reef: influence of correlates of parasitism. *Behavioral Ecology and Sociobiology* 47: 353-358.
- Bansemer, C., A.S. Grutter and R. Poulin. 2002. Geographic variation in the behaviour of the cleaner fish *Labroides dimidiatus* (Labridae). *Ethology* 108: 353-366.

- Begon, M., J.L. Harper and C.R. Townsend. 1990. *Ecology: Individuals, Populations, and Communities*. Blackwell Scientific, Cambridge, MA. 2nd Edition.
- Bohlke, J.E. and J.E. McCosker. 1973. Two additional West Atlantic gobies (genus *Gobiosoma*) that remove ectoparasites from other fishes. *Copeia* 6: 609-610.
- Bshary, R. 2001. The cleaner fish market. In: *Economics in Nature*, R. Noé, J.A.R.A.M. van Hooff and P. Hammerstein (eds.), Cambridge University Press, Cambridge, pp. 146-172.
- Bshary, R. 2003. The cleaner wrasse, *Labroides dimidiatus*, is a key organism for reef fish diversity at Ras Mohammed National Park, Egypt. *Journal of Animal Ecology* 72: 169-176.
- Bshary, R. and M. Würth. 2001. Cleaner fish *Labroides dimidiatus* manipulate client reef fish by providing tactile stimulation. *Proceedings of the Royal Society of London Series B-Biological Sciences* 268: 1495-1501.
- Bshary, R. and D. Schaffer. 2002. Choosy reef fish select cleaner fish that provide high-quality service. *Animal Behaviour* 63: 557-564.
- Bshary, R. and A.S. Grutter. 2002a. Asymmetric cheating opportunities and partner control in a cleaner fish mutualism. *Animal Behaviour* 63: 547-555.
- Bshary, R. and A.S. Grutter. 2002b. Experimental evidence that partner choice is a driving force in the payoff distribution among cooperators or mutualists: the cleaner fish case. *Ecology Letters* 5: 130-136.
- Bshary, R. and A.S. Grutter. 2005. Punishment and partner switching cause cooperative behaviour in a cleaning mutualism. *Biology Letters* 1: 396-399.
- Bshary, R., R.F. Oliveira, T.S.F. Oliveira and A.V.M. Canario. 2007. Do cleaning organisms reduce the stress response of client reef fish? *Frontiers in Zoology* 4: 21-29.
- Chambers, S.D. and P.C. Sikkel. 2002. Diel emergence patterns of ecologically important, fish-parasitic, gnathiid isopod larvae on Caribbean coral reefs. *Caribbean Journal of Science* 38: 37-43.
- Cheney, K.L. and I.M. Côté. 2001. Are Caribbean cleaning symbioses mutualistic? Costs and benefits of visiting cleaning stations to longfin damselfish. *Animal Behaviour* 62: 927-933.
- Cheney, K.L. and I.M. Côté. 2003a. The ultimate effect of being cleaned: does ectoparasite removal have reproductive consequences for damselfish clients? *Behavioral Ecology* 14: 892-896.
- Cheney, K.L. and I.M. Côté. 2003b. Habitat choice in adult longfin damselfish: territory characteristics and relocation times. *Journal of Experimental Marine Biology and Ecology* 287: 1-12.
- Cheney, K.L. and I.M. Côté. 2003c. Do ectoparasites determine cleaner fish abundance? Evidence on two spatial scales. *Marine Ecology-Progress Series* 263: 189-196.
- Cheney, K.L. and I.M. Côté. 2005. Mutualism or parasitism? The variable outcome of cleaning symbioses. *Biology Letters* 1: 162-165.

- Cheney, K.L., A.S. Grutter and N.J. Marshall. 2008. Facultative mimicry: cues for colour change and colour accuracy in a coral reef fish. *Proceedings of the Royal Society B-Biological Sciences* 275: 117-122.
- Colin, P. 1975. *The Neon Gobies: The Comparative Biology of the Gobies of the Genus Gobiosoma, Subgenus Elacatinus (Pisces: Gobiidae) in the Tropical Western North Atlantic Ocean*. T.H.F. Publications, Neptune City.
- Côté, I.M. 2000. Evolution and ecology of cleaning symbioses in the sea. *Oceanography and Marine Biology* 38: 311-355.
- Côté, I.M. and P.P. Molloy. 2003. Temporal variation in cleanerfish and client behaviour: Does it reflect ectoparasite availability? *Ethology* 109: 487-499.
- Côté, I.M., C. Arnal and J.D. Reynolds. 1998. Variation in posing behaviour among fish species visiting cleaning stations. *Journal of Fish Biology* 53 (Supplement A): 256-266.
- Darcy, G.H., E. Maisel and J.C. Ogden. 1974. Cleaning preferences of gobies *Gobiosoma evelynae* and *Gobiosoma prochilos* and juvenile wrasse *Thalassoma bifasciatum*. *Copeia* 1975: 375-378.
- Davies, A.J., J.C. Eiras and R.T.E. Austin. 1994. Investigations into the transmission of *Haemogregarina bigemina* Laveran and Mesnil, 1901 (Apicomplexa, Adeleorina) between intertidal fishes in Portugal. *Journal of Fish Diseases* 17: 283-289.
- Eibl-Eibesfeldt, I. 1955. Über Symbiosen, Parasitismus und andere besondere zwischenartliche Beziehungen tropischer Meeresfische. *Zeitschrift für Tierpsychologie* 12: 203-219.
- Eschmeyer, W.N. 1998. *Catalog of Fishes*. California Academy of Sciences, San Francisco.
- Feder, H.M. 1966. Cleaning symbiosis in the marine environment. In: *Symbioses*, S.M. Henry (ed.), Academic Press, New York, pp. 327-380.
- Francini-Filho, R.B. and I. Sazima. 2008. A comparative study of cleaning activity of two reef fishes at Fernando de Noronha Archipelago, tropical West Atlantic. *Environmental Biology of Fishes* 83: 213-220.
- Francihi-Filho, R.B., R.L. Moura and I. Sazima. 2000. Cleaning by the wrasse *Thalassoma noronhanum*, with two records of predation by its grouper client *Cephalopholis fulva*. *Journal of Fish Biology* 56: 802-809.
- Gorlick, D.L. 1980. Ingestion of host fish surface mucus by the Hawaiian cleaning wrasse, *Labroides phthirophagus* (Labridae), and its effect on host species preference. *Copeia* 1981: 863-868.
- Gorlick, D.L., P.D. Atkins and G.S. Losey. 1978. Cleaning stations as water holes, garbage dumps, and sites for evolution of reciprocal altruism. *American Naturalist* 112: 341-353.
- Gorlick, D.L., P.D. Atkins and G.S. Losey. 1987. Effect of cleaning by *Labroides dimidiatus* (Labridae) on an ectoparasite population infecting *Pomacentrus vaiuli* (Pomacentridae) at Enewetak Atoll. *Copeia* 1988: 41-45.

- Grove, J.S. and R.J. Lavenberg. 1997. *The Fishes of the Galapagos Islands*. Stanford University Press, Stanford.
- Grutter, A.S. 1996. Experimental demonstration of no effect by the cleaner fish *Labroides dimidiatus* (Cuvier and Valenciennes) on the host fish *Pomacentrus moluccensis* (Bleeker). *Journal of Experimental Marine Biology and Ecology* 196: 285-298.
- Grutter, A.S. 1997. Effect of the removal of cleaner fish on the abundance and species composition of reef fish. *Oecologia* 111: 137-143.
- Grutter, A.S. 1999. Cleaner fish really do clean. *Nature* 398: 672-673.
- Grutter, A.S. 2004. Cleaner fish use tactile dancing behavior as a preconflict management strategy. *Current Biology* 14: 1080-1083.
- Grutter, A.S. and R. Bshary. 2003. Cleaner wrasse prefer client mucus: support for partner control mechanisms in cleaning interactions. *Proceedings of the Royal Society of London Series B-Biological Sciences* 270: S242-S244.
- Grutter, A.S. and R. Bshary. 2004. Cleaner fish, *Labroides dimidiatus*, diet preferences for different types of mucus and parasitic gnathiid isopods. *Animal Behaviour* 68: 583-588.
- Grutter, A.S., J.M. Murphy and J.H. Choat. 2003. Cleaner fish drives local fish diversity on coral reefs. *Current Biology* 13: 64-67.
- Guimaraes, R.Z.P., J.L. Gasparini and L.A. Rocha. 2004. A new cleaner goby of the genus *Elacatinus* (Teleostei : Gobiidae), from Trindade Island, off Brazil. *Zootaxa*: 1-8.
- Hobson, E.S. 1968. Predatory behaviour of some shore fishes in the Gulf of California. *U.S. Fish and Wildlife Service Research Report* 73: 1-92.
- Hobson, E.S. 1971. Cleaning symbiosis among California inshore fishes. *Fishery Bulletin* 69: 491-524.
- Hobson, E.S. 1976. Rock wrasse, *Halichoeres semicinctus*, as a cleaner fish. *California Fish and Game* 62: 73-78.
- Humann, P. 1993. *Reef Fish Identification: Galapagos*. New World Publications, Jacksonville, FL.
- Johnson, W.S. and P. Ruben. 1988. Cleaning behavior of *Bodianus rufus*, *Thalassoma bifasciatum*, *Gobiosoma evelynae*, and *Periclimenes pedersoni* along a depth gradient at Salt River submarine canyon, St Croix. *Environmental Biology of Fishes* 23: 225-232.
- Limbaugh, C. 1961. Cleaning symbiosis. *Scientific American* 205: 42-49.
- Losey, G.S. 1971. Communication between fishes in cleaning symbiosis. In: *Aspects of the Biology of Symbioses*, T.C. Cheng (ed.), University Park Press, Baltimore, pp. 45-76.
- Losey, G.S. 1972. Ecological importance of cleaning symbiosis. *Copeia* 820-833.
- Losey, G.S. 1974. Cleaning symbiosis in Puerto Rico with comparison to tropical Pacific. *Copeia* 960-970.
- McCourt, R.M. and D.A. Thomson. 1984. Cleaning behavior of the juvenile Panamic sergeant major, *Abudefduf troschelii* (Gill), with a resume of cleaning

- associations in the Gulf of California and adjacent waters. *California Fish and Game* 70: 234-239.
- McFarland, D. 1985. *Animal Behaviour: Psychobiology, Ethology and Evolution*. Pitman, London.
- Michael, S.W. 1993. *Reef Sharks and Rays of the World*. Sea Challengers, Monterey, CA.
- Noë, R. 1990. A veto game played by baboons: a challenge to the use of the Prisoner's Dilemma as a paradigm for reciprocity and cooperation. *Animal Behaviour* 39:78-90.
- Noë, R. 2001. Biological markets: partner choice as a driving force behind the evolution of mutualism. In: *Economics in Nature*, R. Noë, J.A.R.A.M van Hooff and P. Hammerstein (eds.), Cambridge University Press, Cambridge, pp. 146-172.
- Noë, R. 2006. Digging for the roots of trading. In: *Cooperation in Primates and Humans: Mechanisms and Evolution*, P.M. Kappeler and C.P. van Schaik (eds.), Springer-Verlag, Berlin, pp. 233-261.
- Noë, R. and R. Hammerstein. 1994. Biological markets — Supply and demand determine the effect of partner choice in cooperation, mutualism and mating. *Behavioral Ecology and Sociobiology* 35: 1-11.
- Noë, R., C.P. Vanschaik and J. Vanhooff. 1991. The market effect — an explanation for pay-off asymmetries among collaborating animals. *Ethology* 87: 97-118.
- Potts, G.W. 1973a. Cleaning symbiosis among British fish with special reference to *Crenilabrus melops* (Labridae). *Journal of the Marine Biological Association of the United Kingdom* 53: 1-10.
- Potts, G.W. 1973b. Ethology of *Labroides dimidiatus* (Cuv and Val) (Labridae, Pisces) on Aldabra. *Animal Behaviour* 21: 250-291.
- Randall, J.E. 1955. Fishes of the Gilbert Islands. *Atoll Research Bulletin* 47: 143-144.
- Randall, J.E. 1958. A review of the genus *Labroides*, with description of two new species and notes on ecology. *Pacific Science* 12: 327-347.
- Rocha, L.A., I.L. Rosa and B.M. Feitoza. 2000. Sponge-dwelling fishes of northeastern Brazil. *Environmental Biology of Fishes* 59: 453-458.
- Rüber, L., J.L. Van Tassell and R. Zardoya. 2003. Rapid speciation and ecological divergence in the American seven-spined gobies (Gobiidae, Gobiosomatini) inferred from a molecular phylogeny. *Evolution* 57: 1584-1598.
- Sargent, R.C. and G.E. Wagenbach. 1975. Cleaning behavior of shrimp, *Periclimenes anthophilus* Holthuis and Eibl-Eibesfeldt (Crustacea, Decapoda, Natantia). *Bulletin of Marine Science* 25: 466-472.
- Sazima, I. and R.L. Moura. 2000. Shark (*Carcharhinus perezi*), cleaned by the goby (*Elacatinus randalli*), at Fernando de Noronha Archipelago, Western South Atlantic. *Copeia* 297-299.
- Sazima, I., R.L. Moura and R.S. Rosa. 1997. *Elacatinus figaro* sp. n. (Perciformes: Gobiidae), a new cleaning goby from the western South Atlantic. *Aqua Journal of Ichthyology and Aquatic Biology* 2: 33-38.

- Sazima, I., R.L. Moura and C. Sazima. 1999. Cleaning activity of juvenile angelfish, *Pomacanthus paru*, on the reefs of the Abrolhos Archipelago, western South Atlantic. *Environmental Biology of Fishes* 56: 399-407.
- Sazima, I., A. Carvalho and C. Sazima. 2008. A new cleaner species of *Elacatinus* (Actinopterygii: Gobiidae) from the Southwestern Atlantic. *Zootaxa* 177: 27-32.
- Sazima, I., C. Sazima, R.B Francini and R.L. Moura. 2000. Daily cleaning activity and diversity of clients of the barber goby, *Elacatinus figaro*, on rocky reefs in southeastern Brazil. *Environmental Biology of Fishes* 59: 69-77.
- Sikkel, P.C., K.L. Cheney and I.M. Côté. 2004. In situ evidence for ectoparasites as a proximate cause of cleaning interactions in reef fish. *Animal Behaviour* 68: 241-247.
- Sikkel, P.C., C.S. Schaumburg and J.K. Mathenia. 2006. Diel infestation dynamics of gnathiid isopod larvae parasitic on Caribbean reef fish. *Coral Reefs* 25: 683-689.
- Soares, M.C., S.C. Cardoso and I.M. Côté. 2007. Client preferences by Caribbean cleaning gobies: food, safety or something else? *Behavioral Ecology and Sociobiology* 61: 1015-1022.
- Soares, M.C., I.M. Côté, S.C. Cardoso and R. Bshary. 2008a. The cleaning goby mutualism: a system without punishment, partner switching or tactile stimulation. *Journal of Zoology* 276: 306-312.
- Soares, M.C., R. Bshary, S.C. Cardoso and I.M. Côté. 2008b. The meaning of jolts by fish clients of cleaning gobies. *Ethology* 114: 209-214.
- Soares, M.C., R. Bshary, S.C. Cardoso and I.M. Côté. 2008c. Does competition for clients increase service quality in cleaning gobies? *Ethology* 114: 625-632.
- Streelman, J.T. and P.D. Danley. 2003. The stages of vertebrate evolutionary radiation. *Trends in Ecology and Evolution* 18: 126-131.
- Stummer, L.E., J.A. Weller, M.L. Johnson and I.M. Côté. 2004. Size and stripes: how fish clients recognize cleaners. *Animal Behaviour* 68:145-150.
- Taylor, M.S. and L. Akins. 2007. Two new species of *Elacatinus* (Teleostei: Gobiidae) from the Mexican coast of the Gulf of Mexico. *Zootaxa* 177: 45-51.
- Taylor, M.S. and M.E. Hellberg. 2005. Marine radiations at small geographic scales: speciation in neotropical reef gobies (*Elacatinus*). *Evolution* 59: 374-385.
- Tebbich, S., R. Bshary and A.S. Grutter. 2002. Cleaner fish *Labroides dimidiatus* recognise familiar clients. *Animal Cognition* 5: 139-145.
- Thompson, J.N. 1994. *The Coevolutionary Process*. University of Chicago Press, Chicago, IL.
- Trivers, R.L. 1971. Evolution of reciprocal altruism. *Quarterly Review of Biology* 46: 35-57.
- White, J.W., C.J. Grigsby and R.R. Warner. 2007. Cleaning behavior is riskier and less profitable than an alternative strategy for a facultative cleaner fish. *Coral Reefs* 26: 87-94.

- Whiteman, E.A. and I.M. Côté. 2002. Cleaning activity of two Caribbean cleaning gobies: intra- and interspecific comparisons. *Journal of Fish Biology* 60: 1443-1458.
- Whiteman, E.A. and I.M. Côté. 2004a. Individual differences in microhabitat use in a Caribbean cleaning goby: a buffer effect in a marine species? *Journal of Animal Ecology* 73: 831-840.
- Whiteman, E.A. and I.M. Côté. 2004b. Dominance hierarchies in group-living cleaning gobies: causes and foraging consequences. *Animal Behaviour* 67: 239-247.
- Whiteman, E.A., I.M. Côté and J.D. Reynolds. 2002. Do cleaning stations affect the distribution of territorial reef fishes? *Coral Reefs* 21: 245-251.
- Wickler, W. 1963. Zum Problem der Signalbildung, am Beispiel der Verhaltens-Mimikry zwischen *Aspidontus* und *Labroides*. *Zeitschrift für Tierpsychologie* 20: 657-679.
- Wicksten, M.K. 1998. Behaviour of cleaners and their client fishes at Bonaire, Netherlands Antilles. *Journal of Natural History* 32: 13-30.
- Youngbluth, M.J. 1968. Aspects of the ecology and ethology of the cleaning fish, *Labroides phthirophagus* Randall. *Zeitschrift für Tierpsychologie* 25: 915-932.