



Size and stripes: how fish clients recognize cleaners

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Little is known of how individuals find each other in interspecific mutualisms involving free-living partners. We tested the importance of two factors, namely body size and the presence of a lateral body stripe, in the recognition of cleanerfish by their fish clients. Clients on an Indonesian reef flat readily approached wooden models of the bluestreak cleaner wrasse, *Labroides dimidiatus*, which varied in size and stripe characteristics. The composition of the clientele of models was not significantly different from that of natural cleaning stations, suggesting that fish visiting the models were seeking to be cleaned. Normal-sized models of cleaner wrasses attracted significantly more clients, which showed more intense interest and stayed with the models for significantly longer, than super-sized models. For normal-sized models, the number of clients increased as the length of the cleaner's lateral stripe increased (from 0, to 44, 67 and 100% of body length). However, there was no effect of stripe length on client numbers for super-sized models. Client interest also did not vary with stripe length for models of either size. Small body size and the presence of a lateral stripe therefore appear to be long-distance signals that their bearer may be a cleaner, but after initial attraction, client interest is maintained by other cues. Alternative short-distance signals may include colour, other visual signals such as cleanerfish dances, or physical contact between cleaner and client.

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The key ecological roles of interspecific mutualisms in the function of biological communities have often been highlighted (e.g. May 1982; Boucher 1985; Smith & Douglas 1987). However, little is known of how protagonists find each other in mutualisms involving free-living partners, even though such an understanding could yield clues about the origin and evolution of these important interactions (Boucher et al. 1982). The mechanisms by which plants attract their insect pollinators or protectors are probably the best-studied cases of communication in interspecific mutualisms. There is ample evidence that insect–plant interactions are mediated by plant secondary chemistry (e.g. Dodson et al. 1969; Agrawal 1998), often leading to high specificity between mutualists (Janzen

1979). In mutualisms among vertebrates, however, chemical communication may be less important than vocal or visual communication.

Cleaning symbioses among marine fish offer an ideal model system to test the cues that are important in interspecific visual communication. Cleaning interactions involve small fish (the cleaners) which remove ectoparasites and other items from the body of larger, cooperating fish clients (Feder 1966). Such interactions usually occur at traditional sites (Youngbluth 1968), thus facilitating the repeated location of cleaners by clients. Cleaners are also thought to share common colour patterns, which may help clients to recognize them.

Several workers have noted the similarity in colouration of selected groups of cleaning species from different parts of the world, and there may be worldwide guild colorations for cleaners (Eibl-Eibesfeldt 1955; Wickler 1963; Potts 1973). Many cleaners have stripes, as in the Indo-Pacific genus *Labroides* and in the Caribbean gobies *Elacatinus* spp., which may serve to indicate that their bearer is a cleaner (Eibl-Eibesfeldt 1955). A similar convergence of colour pattern has been suggested between the California wrasse señorita, *Oxyjulis californica*, and the Mediterranean wrasse, *Symphodus melanocercus*, both of

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which have a black tail (Potts 1968). In general, the brilliant colour patterns of cleaners contrast greatly with their background. This 'poster' colouration is thought to be particularly marked in tropical cleaners (Feder 1966), although Hobson (1969) pointed out that similar brilliant colours are also common among noncleaning tropical fish.

A recent comparative study of Caribbean cleaning gobies suggested that lateral stripes indeed appear to be associated with cleaning as a foraging mode (Côté 2000). Cleaning gobies are more likely to have complete lateral stripes than noncleaning congeners, and, as a result, have a significantly longer lateral stripe relative to body length. However, among facultative cleaners, which clean only as juveniles and adopt more conventional foraging modes as adults, no universal colour pattern is apparent. Facultative cleaners are neither more striped nor more brightly coloured than their noncleaning relatives.

Small body size may also be an important signal of cleaning propensity. Feder (1966) noted that all cleaners were small. The fact that many species clean only as juveniles seems to support this assertion (Côté 2000). Obligate cleaning gobies and their noncleaning counterparts do not differ in body size, but facultative cleaning species are significantly smaller than their noncleaning relatives (Côté 2000). Although small body size per se may confer an advantage as a cleaner, it could also simply be associated with foraging modes, and hence mouth morphologies, that predispose species to clean (Hobson 1971, 1976; McCourt & Thomson 1984).

We investigated the relative roles of body size and stripe length in cleanerfish recognition by fish clients. We presented wooden models of the commonest Indo-Pacific cleanerfish, the bluestreak cleaner wrasse, *Labroides dimidiatus*, with varying size and stripe characteristics to clients in the wild and recorded their levels of interest. Less realistic models will elicit reactions by conspecifics and posing behaviour by clients, that is, stationary postures used to solicit cleaning (Côté et al. 1998), both in captivity (Fricke 1966; Losey 1979) and in the wild (Potts 1973). By recording the rate of client visits as well as client interest in models of different sizes and stripe length, we made an initial assessment of the visual cues involved in communication between free-living vertebrate partners in an interspecific mutualism.

METHODS

We carried out the study on the shallow reef flat off Hoga Island, in the Wakatobi National Marine Park in southeast Sulawesi, Indonesia, from 1 July to 22 August 2002. Three active cleaning stations, each operated by an adult bluestreak cleaner wrasse, were identified in the back reef area. Each station was located on an isolated coral head surrounded by sand and rubble, approximately 250 m from shore. The cleaning stations were 19–55 m apart and were exposed to maximum water depths of 2 m at high tide and 0.5 m at low tide. By using existing stations for model presentations, we ensured that the sites would be visited by clients seeking to be cleaned (Potts 1973). These

clients could then choose to approach or avoid the model cleaners presented.

We tested eight models, representing a fully factorial design comprising two body lengths (8 and 14 cm) and four lateral stripe lengths relative to body length (0, 44, 67 and 100% of body length). The average length of an adult *L. dimidiatus* at this site is 8 cm (I. M. Côté, unpublished data). Thus, the smaller model represented a normal-sized adult. Both juvenile and adult *L. dimidiatus* exhibit a stripe that flares laterodorsally from the tip of the snout to the end of the tail. The models with full-length (100%) stripes therefore presented the usual pattern found on *L. dimidiatus*. Stripe width on the models was constant at approximately 20% of the body depth (1.5 cm for the small models, 2.0 cm for the larger models), which is an equivalent proportion to that seen mid-body on *L. dimidiatus*.

The models were carved out of wood in the fusiform shape of *L. dimidiatus*, and black lateral stripes were painted on either side with a white background. The models were then sealed with varnish. We made them buoyant by attaching them to a float with a length of nylon string, and small lead weights attached under the model ensured that it remained approximately 30 cm above the reef. A second string attached to the float was pulled rhythmically by one researcher standing 3–5 m away, and hence unaware of fish activity underwater, at an approximate rate of 90 times/min to simulate the jerky dancing behaviour of cleaner wrasses, which is thought to attract clients (Potts 1973).

Each model was tested for 60 min at each of the three stations and we randomized the order in which the eight models were presented at each station. Two models, on average, were tested each day (one per station) between 0800 and 1600 hours, which coincides with the period of diurnal activity of *L. dimidiatus* and their clients. To minimize disturbance, we recorded each 60-min session with a digital video camera in an underwater housing anchored near the cleaning station under observation. Videotaping began 5 min after we set up the equipment, to allow fish to become accustomed to the presence of the camera. The resident cleaners were not removed from the experimental cleaning stations; however, they interfered little with the model presentations, leaving the immediate area of the cleaning stations during the experiments. We could not determine how far they went or whether they cleaned at another temporary location but they were resighted at the original stations between presentations.

From the videotapes, we recorded species identity, number and total length of fish clients approaching the models. Client total length was estimated relative to model size. We also noted the duration of each visit and the level of interest expressed by each client on a scale from 1 to 3: 1 represented a fish client investigating the model (within 10 cm, as estimated on the videotape relative to model length) but departing quickly; 2, a fish client investigating the model (within 10 cm) and showing some aspects of posing behaviour (e.g. stationary swimming) without adopting a full posing posture; and 3, a fish client adopting a full solicitation pose, i.e. remaining stationary in the

water column, usually with the head or tail up, with opercula and fins flared out.

Natural Cleaning Stations

To determine whether the clientele was typical of that visiting bluestreak cleaner wrasses, we observed seven natural cleaning stations on the Hoga reef flat, at 1.3–2.5 m depth (low tide), for three 15-min periods each in August 2002. Each station was observed once between 0700 and 0900 hours, once between 1100 and 1300 hours, and once between 1500 and 1700 hours. During each observation period, we recorded the species and number of clients being inspected by cleaner wrasses.

Statistical Analysis

We first tested for evidence of fish habituation to the models by correlating the number of clients recorded and the duration of interest with the day of testing at each of the three cleaning stations, and for all stations combined.

To compare clientele composition between natural and experimental cleaning stations, we performed an analysis of similarity (ANOSIM) based on species presence/absence using the software PRIMER (Plymouth Routines in Multivariate Ecological Research v. 5.2.4; PRIMER-E Ltd, Plymouth Marine Laboratory, Plymouth, U.K.). For this analysis, each cleaning station was considered a sample, and all observations pertaining to a sample were pooled. Counts of clients at each station were converted to species presence/absence, a necessary transformation owing to the differences in abundance of potential clients at 0.5–1.5 m (experimental stations) and 1.5–2.5 m depth (natural stations; I. M. Côté, unpublished data), and Bray–Curtis similarity coefficients between pairs of samples (stations) were computed (Clarke & Warwick 1994). The nonparametric permutation procedure ANOSIM was then carried out on the similarity matrix to compare natural and experimental cleaning stations. ANOSIM generates an *R* statistic, which usually varies between 0 (similarities within and between samples are the same) and 1 (all stations within groups are more similar to each other than to any stations across groups) and which is tested for difference from zero with a permutation test (N_{\max} in this study = 120 permutations, thus minimum possible $P = 0.01$). ANOSIM is recommended in preference to multivariate analysis of variance for analyses of community structure because multispecies abundance or presence data rarely meet the assumptions of parametric testing (Clarke & Warwick 1994).

To compare the rates of visits to natural and experimental cleaning stations, we pooled observations from the three time periods for each station. Preliminary analysis revealed no diel variation in cleaning rates or duration at natural cleaning stations (I. M. Côté, unpublished data).

We examined the effects of model body size and stripe length on client numbers, level of interest, duration of visits and client size with two-way analyses of variance (ANOVA), using the three experimental cleaning stations as replicates. For each model, we obtained means for each

variable at each experimental cleaning station. Interest intensity scores were normally distributed (Kolmogorov–Smirnov test: $Z = 0.43$, $N = 24$, $P = 0.99$) and were therefore treated as a continuous variable.

RESULTS

We recorded 503 fish clients of 61 species as expressing interest towards the cleaner models, with 201 clients (40%) adopting partial or full incitation poses. We found no evidence of habituation to the models by clients. Neither the number of clients nor the duration of interest was correlated with the day of testing, either for each cleaning station separately or for all stations combined (Pearson correlations: NS for all tests). The clientele visiting the models was not significantly different in composition from the clientele recorded at natural cleaning stations at similar depths on the same reef (ANOSIM: $R = 0.25$, $P = 0.14$). The rates of client visits, however, were significantly higher at natural cleaning stations ($\bar{X} \pm \text{SD} = 11.4 \pm 3.3$ clients/15 min) than at the experimental stations when visits to all models were combined (4.4 ± 0.1 clients/15 min; t test: $t_8 = 5.69$, $P = 0.007$). This difference disappeared when only visits to the small models with full-length stripes were considered (natural stations: 11.4 ± 3.3 clients/15 min; experimental stations: 9.9 ± 3.0 clients/15 min; t test: $t_8 = 0.67$, $P = 0.52$).

Both model size and stripe length influenced significantly the number of clients approaching the models. Significantly more clients were recorded near the 8-cm models than near the larger models (two-way ANOVA: $F_{1,16} = 23.76$, $P < 0.001$; Fig. 1a). Stripe length had a significant effect on client numbers ($F_{3,16} = 4.69$, $P = 0.016$; Fig. 1a) and there was a significant interaction between model size and stripe length ($F_{3,16} = 5.12$, $P = 0.011$). Hence, the number of clients increased with increasing stripe length for the normal-sized models (Pearson correlation: $r_2 = 0.99$, $P = 0.01$), whereas stripe length had no effect on client numbers with the super-sized models ($r_2 = -0.04$, $P = 0.96$).

Clients showed significantly more intense interest in the normal-sized than in the super-sized models (two-way ANOVA: $F_{1,16} = 7.10$, $P = 0.017$) and they remained near the normal-sized models for significantly longer ($F_{1,16} = 9.19$, $P = 0.008$; Fig. 1b). By contrast, stripe length had no effect on either the intensity of interest ($F_{3,16} = 0.27$, $P = 0.84$) or the duration of visits ($F_{3,16} = 0.22$, $P = 0.88$; Fig. 1b). There was no interaction between model size and stripe length for intensity of interest ($F_{3,16} = 0.68$, $P = 0.58$) or the duration of visits ($F_{3,16} = 0.17$, $P = 0.91$).

Clients of similar lengths visited normal- and super-sized models (two-way ANOVA: $F_{1,16} = 0.52$, $P = 0.48$) and client sizes did not vary with model stripe length ($F_{3,16} = 0.17$, $P = 0.91$).

DISCUSSION

A small body size and the presence of a lateral stripe appear to be cues involved in cleanerfish recognition by client fish. Normal-sized models with a full-length lateral stripe received significantly more visitors than

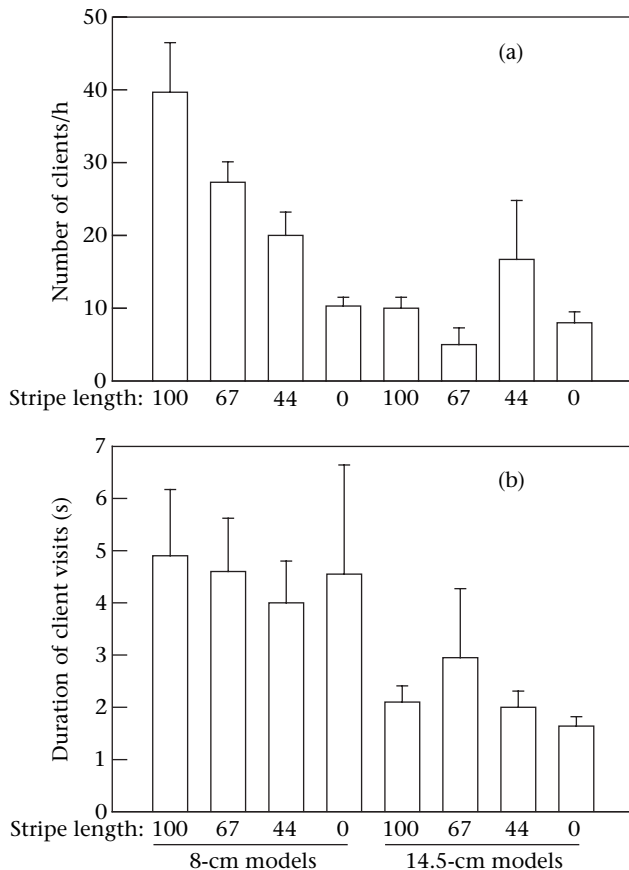


Figure 1. (a) Number of clients visiting cleaner wrasse models per h and (b) duration(s) of visits in relation to model size and stripe length. Stripe length is expressed as a percentage of body length. Means are shown ± 1 SE. $N = 3$ in all cases.

similar-sized models with shorter stripes or super-sized models with lateral stripes of any length. Once clients were attracted to the models, however, the duration of their visit and intensity of interest were no longer linked to the length of the model's stripe, although the life-size models generated more intense interest and longer visits than the super-sized ones. The facts that the composition of the clientele visiting models was similar to that of natural cleaning stations, instead of being biased towards piscivores, and that many clients adopted incitation poses suggest that the clients in our study were genuinely seeking cleaners rather than potential prey. The visual cues signalling cleaning services at close range therefore appear to be different from those providing initial, long-distance information about cleaning.

Super-sized models failed to elicit much interest from potential clients. Our 14.5-cm models were in fact slightly larger than the largest obligate species of cleanerfish present on the reef. The bicolor cleaner wrasse, *L. bicolor*, which sports a full-length yellow lateral stripe as a juvenile but a half-length black stripe interrupted by a bright yellow tail patch as an adult, can reach a maximum length of 14 cm (Myers 1999). Few species larger than this possess the 'picker'-type foraging mode and associated mouth morphology that appear to be required for cleaning

(Hobson 1971, 1976; McCourt & Thomson 1984). A large body size may therefore be a signal that is incompatible with cleaning behaviour.

The presence of a full-length lateral stripe is important for recognition among *L. dimidiatus* individuals. Potts (1973) found that *L. dimidiatus* models with a lateral stripe elicited a greater response from conspecifics than models with alternative or no patterns. Our results suggest that stripes are also important in cleaner–client communication, but only in conjunction with a small cleaner body size, and only when considering the initial approach made to the models by clients. The visual system of reef fish is characterized by a relatively poor resolving power such that the fine-grain colour patterns of most reef fish become blurred to other fish at between 1 and 5 m (Marshall 2000). However, this is not true of bolder stripe markings, which fish can detect over larger distances (Marshall 2000). The black stripe on a white background of our models, or black stripe on a yellow or blue background of most cleanerfish, would therefore provide highly contrasting combinations which would attenuate little over distance or depth (Lythgoe 1968, cited in Marshall 2000) and which would remain conspicuous to client fish over relatively large distances (i.e. more than 5 m).

Size and stripes thus provide initial information about cleaning services that attracts clients. Subsequent levels of client interest, however, appear to be based on other cues, which may include other visual or tactile signals. For example, cleaner wrasses often perform a zigzag dance which seems to attract clients (Potts 1973). It is not known whether the natural rate of dancing is constant or whether cleaners modify their dancing rates as clients approach. Our models did dance, but at a constant rate and perhaps not in a completely realistic manner. Colour, rather than pattern, may also convey further close-range information. The reflectance spectra of the colour pattern of many coral reef fish include ultraviolet (UV) wavelengths (Losey et al. 1999), and many reef fish species have ocular media that permit the perception of UV light (Siebert & Marshall 2001). It is not yet known whether cleanerfish have UV patterns, but N. J. Marshall & A. S. Grutter (unpublished data) have discovered the existence of an unusually long wavelength component in the blue colouration of cleanerfish and cleaner shrimp. Such 'cleaner blue' colour, which our models were lacking, may confirm cleaning activity at close range. Finally, physical contact between cleaner and client usually follows the initial approach by clients and is an important determinant of the length of client visits at natural cleaning stations (Bshary & Würtz 2001). Contact between client and model occurred only five times in our trials (i.e. in less than 1% of visits), and contact was always initiated by clients.

The fact that stripes signal cleaning activity in *L. dimidiatus* (this study) as well as in Caribbean cleaning gobies (Côté 2000) suggests convergence, either towards an identical pattern (Eibl-Eibesfeldt 1955; Wickler 1963; Potts 1973) or more broadly towards a generally conspicuous pattern (G. Losey, personal communication). Whether the pattern and colour of cleaners have evolved to signal cleaning per se is open to debate. There have been some suggestions that bright colouration in obligate

cleaners may indicate toxicity or unpalatability (Feder 1966; Hobson 1971). Colin (1975), for example, has shown that the cleaning goby *Gobiosoma evelynae* is noxious to predatory fish, although not as much as the noncleaning gobies *G. chancei* and *G. horsti*. However, although there have been no reports to date of predation on cleaners during cleaning, cleanerfish are sometimes found in the gut contents of predatory fish, suggesting that they are palatable (Côté 2000). More likely, there has been selection for standardization of cleaning signals to increase communication efficiency. The latter could be achieved through a number of mechanisms equivalent to those that have been shown to be important in the design and evolution of warning signals. These could include, for example, innate attraction to the cleaning colour and pattern and rapid learning by naïve clients as well as more rapid recognition and increased memorability by experienced clients (Guilford 1990; Speed 2000). Indeed, Losey et al. (1995) have shown innate recognition of cleaner wrasses by some laboratory-bred clients.

In conclusion, we have demonstrated that small body size and the presence of lateral stripes both contribute as long-distance signals of cleaning services for fish clients. However, the cues conveying further close-range information on cleaning behaviour remain elusive. The potential interaction between the 'cleaner blue' colour discovered by N. J. Marshall & A. S. Grutter (unpublished data) and a striped pattern should be explored. It is possible that the colour amplifies the stripe pattern, or vice versa, thus creating a more easily recognizable signal, but our results suggest that stripes can act independently of colour. Convergent signalling among cleaners, using size, stripes and colour, should facilitate their recognition by fish clients. Since there is a low level of mutual interdependence of cleaners and clients, with individual cleaners servicing a variety of clients (e.g. Grutter 1996) and individual clients potentially using a number of cleaners (Bshary & Schaeffer 2002), such convergence may be the hallmark of poorly coevolved mutualisms.

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References

- Agrawal, A. A. 1998. Leaf damage and associated cues induce aggressive ant recruitment in a Neotropical ant-plant. *Ecology*, **79**, 2100–2112.
- Boucher, D. H. (Ed.). 1985. *The Biology of Mutualism: Ecology and Evolution*. New York: Oxford University Press.
- Boucher, D. H., James, S. & Keeler, K. H. 1982. The ecology of mutualisms. *Annual Reviews of Ecology and Systematics*, **13**, 315–347.
- Bshary, R. & Schaeffer, D. 2002. Choosy reef fish select cleanerfish that provide high-quality service. *Animal Behaviour*, **63**, 557–564.
- Bshary, R. & Würtz, M. 2001. Cleanerfish *Labroides dimidiatus* manipulate client reef fish by providing tactile stimulation. *Proceedings of the Royal Society of London, Series B*, **268**, 1495–1501.
- Clarke, K. R. & Warwick, R. M. 1994. *Change in Marine Communities: An Approach to Statistical Analysis and Interpretation*. Swindon: Natural Environmental Research Council, U.K.
- Colin, P. L. 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*. Neptune City: TFH Publications.
- Côté, I. M. 2000. Evolution and ecology of cleaning symbioses in the sea. *Marine Biology and Oceanography Annual Review*, **38**, 311–355.
- Côté, I. M., Arnal, C. & Reynolds, J. D. 1998. Variation in posing behaviour among fish species visiting cleaning stations. *Journal of Fish Biology*, **53** (Supplement A), 256–266.
- Dodson, C. H., Dressler, R. L., Hills, H. G., Adams, R. M. & Williams, N. H. 1969. Biologically active compounds in orchid fragrances. *Science*, **164**, 1243–1249.
- Eibl-Eibesfeldt, I. 1955. Über Symbiosen, Parasitismus und andere zwischenartliche Beziehungen bei tropischen Meeresfischen. *Zeitschrift für Tierpsychologie*, **12**, 203–219.
- Feder, H. M. 1966. Cleaning symbiosis in the marine environment. In: *Symbiosis* (Ed. by S. M. Henry), pp. 327–380. New York: Academic Press.
- Fricke, H. 1966. Zum Verhalten des Putzerfisches, *Labroides dimidiatus*. *Zeitschrift für Tierpsychologie*, **23**, 1–3.
- Grutter, A. S. 1996. Parasite removal rates by the cleaner wrasse *Labroides dimidiatus*. *Marine Ecology Progress Series*, **130**, 61–70.
- Guilford, T. 1990. The evolution of aposematism. In: *Insect Defenses: Adaptive Mechanisms and Strategies of Prey and Predators* (Ed. by D. L. Evans & J. O. Schmidt), pp. 23–61. New York: State University of New York Press.
- Hobson, E. S. 1969. Comments on certain recent generalisations regarding cleaning symbiosis in fishes. *Pacific Science*, **23**, 35–39.
- Hobson, E. S. 1971. Cleaning symbiosis among California inshore fishes. *Fishery Bulletin*, **69**, 491–523.
- Hobson, E. S. 1976. The rock wrasse, *Halichoeres semicinctus*, as a cleaner fish. *California Fish and Game*, **62**, 73–78.
- Janzen, D. H. 1979. How to be a fig. *Annual Reviews of Ecology and Systematics*, **10**, 13–52.
- Losey, G. S. 1979. Fish cleaning symbiosis: proximate causes of host behaviour. *Animal Behaviour*, **27**, 669–685.
- Losey, G. S., Mahon, J. L. & Danilowicz, B. S. 1995. Innate recognition by host fish of their cleaning symbionts. *Ethology*, **100**, 277–283.
- Losey, G. S., Cronin, T. W., Goldsmith, T. H., David, H., Marshall, N. J. & McFarland, W. N. 1999. The UV visual world of fishes: a review. *Journal of Fish Biology*, **54**, 921–943.
- McCourt, R. M. & Thomson, D. A. 1984. Cleaning behavior of the juvenile Panamic sergeant major, *Abudefduf troschelii* (Gill), with a résumé of cleaning associations in the Gulf of California and adjacent waters. *California Fish and Game*, **70**, 234–239.
- Marshall, N. J. 2000. Communication and camouflage with the same 'bright' colours in reef fishes. *Philosophical Transactions of the Royal Society of London, Series B*, **355**, 1243–1248.
- May, R. M. 1982. Mutualistic interactions among species. *Nature*, **296**, 803–804.

- Myers, R. F.** 1999. *Micronesian Reef Fishes*. Guam: Coral Graphics.
- Potts, G. W.** 1968. The ethology of *Crenilabrus melanocercus*, with notes on cleaning symbiosis. *Journal of the Marine Biological Association, U.K.*, **48**, 279–293.
- Potts, G. W.** 1973. The ethology of *Labroides dimidiatus* (Cuv. and Val.) (Labridae; Pisces) on Aldabra. *Animal Behaviour*, **21**, 250–291.
- Siebert, U. E. & Marshall, N. J.** 2001. Ocular media transmission of coral reef fish: can coral reef fish see ultraviolet light? *Vision Research*, **41**, 133–149.
- Smith, D. C. & Douglas, A. E.** 1987. *The Biology of Symbiosis*. London: Edward Arnold.
- Speed, M. P.** 2000. Warning signals, receiver psychology and predator memory. *Animal Behaviour*, **60**, 269–278.
- Wickler, W.** 1963. Zum Problem der Signalbildung, am Beispiel der Verhaltens: Mimikry zwischen *Aspidontus* und *Labroides*. *Zeitschrift für Tierpsychologie*, **20**, 657–679.
- Youngbluth, M. J.** 1968. Aspects of the ecology and ethology of the cleaning fish, *Labroides phthirophagus* Randall. *Zeitschrift für Tierpsychologie*, **25**, 915–932.