

Cleaning symbioses from the parasites' perspective

A. S. GRUTTER

Department of Zoology and Entomology, School of Life Sciences, University of Queensland, Brisbane, Qld. 4072

SUMMARY

Cleaning behaviour has generally been viewed from the cleaner or client's point of view. Few studies, however, have examined cleaning behaviour from the parasites' perspective, yet they are the equally-important third players in such associations. All three players are likely to have had their evolution affected by the association. As cleaner organisms are important predators of parasites, cleaners are likely to have an important effect on their prey. Little, however, is known of how parasites are affected by cleaning associations and the strategies that parasites use in response to cleaners. I examine here what parasites are involved in cleaning interactions, the effect cleaners have on parasites, the potential counter-adaptations that parasites have evolved against the predatory activities of cleaner organisms, the potential influence of cleaners on the life history traits of parasites, and other factors affected by cleaners. I have found that a wide range of ectoparasites from diverse habitats have been reported to interact with a wide range of cleaner organisms. Some of the life history traits of parasites are consistent with the idea that they are in response to cleaner predation. It is clear, however, that although many cleaning systems exist their ecological role is largely unexplored. This has likely been hindered by our lack of information on the parasites involved in cleaning interactions.

Key words: Cleaning behaviour, cleaner fish, *Labroides dimidiatus*, gnathiidae, evolution.

INTRODUCTION

Cleaning associations involve cleaner organisms that remove ectoparasites and other material, such as mucus, scales and skin, from the body surfaces of other apparently co-operating animals (Feder, 1966). The latter are often referred to as hosts, customers, or clients. Cleaning behaviour is one of the most highly developed inter-specific communication systems known, with clients striking elaborate postures (Feder, 1966) which have generally been assumed to make ectoparasites more accessible to cleaners. A wide range of animals function as cleaners, including crustaceans, ants, birds, fishes, lizards (Nicolette, 1990) and turtles (Krawchuk, Koper & Brooks, 1997).

Although terrestrial examples of cleaning are known, mainly involving cleaner birds (Mooring & Mundy, 1996), most examples are aquatic. Van Tassell, Brito & Bortone (1994) listed 132 fishes and invertebrates, most of which are marine. Cleaning behaviour among fishes occurs in both temperate and tropical waters, with a larger number described for the latter. These are from a wide range of families, with a large proportion belonging to the wrasses (Van Tassell *et al.* 1994). In addition to fish, the clients include octopus (Johnson, 1982), turtles (Vogt, 1979; Losey, Balazs & Privitera, 1994; Krawchuk *et al.* 1997), marine iguanas (Hobson, 1969), and whales (Swartz, 1981).

Cleaner fish are important predators of ectoparasites. They feed on a wide range of ectoparasites in diverse geographic locations. Some cleaners eat large numbers of parasites (Arnal & Morand, 2001; Grutter, 1996*a*, 1997*a*) while others, although they may each eat few parasites due to their small size, are found in large numbers (Arnal & Côté, 2000) and thus may, overall, exert a significant effect on their prey.

Interactions between cleaners and parasites can be considered as interactions between enemies and victims, i.e. a predator-prey system (Hastings, 2000; Keeling, Wilson & Pacala, 2000). Predator-prey interactions are a significant component of ecological communities and raise fundamental questions. For example, given that such interactions are inherently unstable, how is it that the species co-exist? Understanding how the responses of the organisms, for example defence against predators, influence the dynamics of the system can provide information on how such systems function. It can also provide insight into the role of evolution in shaping these relationships.

Cleaners, as predators of parasites, are likely to have an effect on their prey. However to what extent they affect parasite populations is only recently being investigated. Although most studies have focused on the effects of cleaners on local parasite size and abundance on fish (Limbaugh, 1961; Youngbluth, 1968; Losey, 1972; Gorlick, Atkins & Losey, 1987; Grutter, 1996*b*, 1999*a*) the life-history traits and behaviour of parasites may have also been affected over evolutionary time in response to predation pressure.

Tel: 61-7-3365 7386. Fax: 61-7-3365 1655.
E-mail: a.grutter@mailbox.uq.edu.au

Table 1. Parasitic isopods involved in cleaning interactions. Unless otherwise stated, information was obtained from diet analyses. NA = Not available

Family (order)	Parasite identity	Cleaner species	Family	Location	Comment	Reference
Gnathiidae	juveniles	<i>Labroides dimidiatus</i>	Labridae	Lizard Island, Great Barrier Reef (GBR)		Grutter, 1996a, 1997a
	juveniles	<i>L. dimidiatus</i>	Labridae	Heron Island, GBR		Grutter, 1997a
	juveniles	<i>L. dimidiatus</i>	Labridae	New Caledonia		Grutter, 1999c
	juveniles	<i>L. dimidiatus</i>	Labridae	Japan		Sano, Shimizu & Nose, 1984
	juveniles	<i>L. dimidiatus</i>	Labridae	Society Islands		Randall, 1958
	juveniles	<i>L. bicolor</i>	Labridae	Society Islands		Randall, 1958
	juveniles	<i>L. bicolor</i>	Labridae	Heron Island, GBR		Randall, 1958
	juveniles	<i>L. phthiophagus</i>	Labridae	Hawaii		Randall, 1958
	juveniles	<i>L. rubrolabiatus</i>	Labridae	Moorea		Randall, 1958
	juveniles	<i>Oxyjulis californica</i>	Labridae	California		Hobson, 1971
	juveniles	<i>Symphodus melanocercus</i>	Labridae	Mediterranean Sea		Senn, 1979; Arnal & Morand, 2001
	juveniles	<i>Centrolabrus rupestris</i>	Labridae	Portugal		Henriques & Almada, 1997
	juveniles	<i>Ctenolabrus rupestris</i>	Labridae	Plymouth aquarium, United Kingdom (UK)		Potts, 1973
	juveniles	<i>Halichoeres cyanocephalus</i>	Labridae	Brazil		Sazima, Moura & Gasparini, 1998
	juveniles	<i>Crenilabrus melops</i>	Labridae	Plymouth aquarium, UK		Potts, 1973
	juveniles	<i>Centrolabrus exoletus</i>	Labridae	Spain		Galeote & Otero, 1998
	juveniles	<i>Thalassoma bifasciatum</i>	Labridae	Puerto Rico		Losey, 1974

	juveniles	<i>Heniochus monoceros</i>	Chaetodontidae	New Caledonia		Lo, C., unpublished data
	juveniles	<i>Chaetodon citrinellus</i>	Chaetodontidae	Lizard Island, GBR		Cribb, T., unpublished data
	juveniles	<i>Elacatinus prochilos</i>	Gobiidae	Bahamas		Arnal & Côté, 2000
	juveniles	<i>Gobiosoma (Elacatinus) illecebrosus</i>	Gobiidae	Panama		Bohlke & McCosker, 1973
	juveniles	<i>Gobiosoma</i> spp.	Gobiidae	Puerto Rico		Losey, 1974
	juveniles	<i>Entelurus aequoreus</i>	Syngnathidae	Plymouth aquarium, UK		Potts, 1973
	juveniles	<i>Syngnathus typhle</i>	Syngnathidae	Plymouth aquarium, UK		Potts, 1973
	juveniles	<i>S. acus</i>	Syngnathidae	Plymouth aquarium, UK		Potts, 1973
	juveniles	<i>Brachyistius frenatus</i>	Embiotocidae	California		Hobson, 1971
	juveniles	<i>Phanerodon atripes</i>	Embiotocidae	California		Hobson, 1971
Cymothoidae	<i>Anilocra haemuli</i>	<i>Periclimenes pedersoni</i>	Palaemonidae	Puerto Rico	Laboratory experiment. Observed eating isopods	Bunkley-Williams & Williams, 1998
	'cymothoids'	<i>Thalassoma bifasciatum</i>	Labridae	Puerto Rico		Losey, 1974
	<i>Codonophilus</i> sp.	<i>Coris sandageri</i>	Labridae	New Zealand	2 cm parasite removed from mouth of client by cleaner, disabled by repeatedly striking it against rocks, then eaten	Ayling & Grace, 1971
(Isopoda)	'Larval isopods'	<i>Echeneis naucrates</i>	Echenidae	NA		Cressey & Lachner, 1970
	'Parasitic isopods'	<i>Canthidermis maculatus</i>	Balistidae	Hawaii	Observed biting 'parasitic isopods'	Gooding, 1964

Predation events are characterized by the encounter, detection, identification, approach, subjugation, and consumption of the prey (Endler, 1991). Parasites involved in cleaning interactions therefore should have developed defence mechanisms or counter-adaptations to deal with the above sequence of predation events. Adaptations can be defined as traits directly shaped by selection (Ridley, 1993). Counter-adaptations of prey are numerous and include crypsis, polymorphism, spacing themselves out, mimicry, escape flights, weapons of defense, active defense and toxins (Krebs & Davies, 1993).

How the life history traits of parasites evolved is an important question in parasitology. Life-history strategies mainly evolve in response to pressures of different environments on the survival and fecundity of different age-classes (Partridge & Harvey, 1988; Poulin, 1996). Most of the studies on the evolution of life history traits of parasites have been on how parasites evolved from free-living forms (Poulin, 1995a). Factors, other than those directly related to parasitism, however, are also likely to have played a role in the evolution of parasite life history traits.

Adaptation in defence against predators is one of these. Since it is nearly impossible to observe the development of these processes, their evolution can be extrapolated from existing associations. Although adaptations can only be studied in light of phylogeny (Harvey & Pagel, 1991), there is some circumstantial evidence to support some of the predictions below. Further studies, including phylogenetic approaches and experimental studies are, however, needed.

Much of the work on cleaning is restricted to tropical, semitropical, and warm-temperate regions most likely due, at least in part, to a lack of observations in other areas. Most of the information on the parasites involved in aquatic cleaning interactions is restricted to fishes. For example, although cleaner shrimps are a popular example of cleaner organisms, evidence that they indeed remove parasites is almost nil (Spotte, 1998). This study, therefore, relies heavily on information available from marine fishes including studies involving the use of cleaner fish in commercial fish farms, and to a lesser degree freshwater fishes. When examining what parasites are involved in interactions with cleaners I have also included cleaners other than fish for completeness. Much of the following is speculative. In general, much more evidence is needed to support the proposed hypotheses.

To explore cleaning behaviour from the parasites' perspective, I examined (1) what parasites are involved in cleaning interactions, (2) the effect cleaners have on parasites, (3) the potential counter-adaptations that parasites have made against the predatory activities of cleaner organisms, (4) the influence of cleaners on the life history traits of parasites, and (5) other factors affected by cleaners.

PARASITES INVOLVED IN CLEANING INTERACTIONS

Crustacea

Isopods. Only examples where gnathiids were actually found in the diet were included in this study. Gnathiids, in addition to caligid copepods, are one of the most common parasite groups found in the diet of cleaner fishes (Table 1). Gnathiids are eaten by 20 fish species which include wrasses, gobies, pipefish, butterflyfish and perch from diverse locations including the Indo-Pacific, the Caribbean, Brazil, Europe, and California (Table 1). For the cleaner fish *Labroides dimidiatus* at Lizard Island, gnathiid isopods make up 95% of the items in the diet (Grutter, 1997a). Butterflyfish occasionally have gnathiids in their diet (Table 1), yet this has, as of yet, not been reported in the literature. The above butterflyfish likely obtained gnathiids by cleaning other fish, as *Heniochus monoceros* at the same location that the diet analyses were made have been observed cleaning other fish (T. Cribb, personal communications) and butterflyfish juveniles are known to act as cleaners (Feder, 1966; Youngbluth, 1968; Hobson, 1969; Allen, Steene & Allen, 1998).

Other isopods in the diet of cleaners are cymothoids which are eaten by a Caribbean cleaner shrimp in the laboratory and by wrasse in Puerto Rico and New Zealand. Seabass in the Canary Islands and diskfishes also eat 'isopods'. In addition, triggerfish off drifting objects in Hawaii have been observed biting 'parasitic isopods' on another triggerfish (Table 1).

Copepods. Caligid copepods have been found in the diet of 15 fish species including wrasses, diskfish, jacks, chubs, and sweeps (Table 2). Other copepods also eaten by cleaner fish include pennellids, bomolochids, pandarids, *Hastchekia* sp., and laerneids. Cleaner fish that eat copepods are geographically diverse and include fish from the Indo-Pacific, California, Argentina, Florida, the Caribbean, Europe, and New Zealand (Table 2).

Other parasitic arthropods

Other parasitic arthropods involved in cleaning interactions include barnacles which are removed by fish from grey whales and by crabs from turtles, amphipods removed by fish from grey whales and by crabs from turtles, argulids removed by fish from other fish and ticks removed by crabs from marine iguanas (Table 2).

Parasitic flatworms

Of the parasitic flatworms, only capsalid monogeneans have been found in the diet of cleaner fish (Table 3). There is some evidence that some monogeneans may be affected by cleaners. Cowell *et*

al. (1993) showed that the marine cleaner fishes *Gobiosoma oceanops* and *G. genie* significantly affected the abundance of *Neobenedenia melleni* on sea-water cultured tilapia while *Thalassoma bifasciatum* did not. Benedeniine monogeneans were also found in the diet of the cleaner fish *Labroides dimidiatus* (Table 3). This cleaner fish also affected the abundance and size-frequency distribution of *Benedenia lolo* on the wrasse *Hemigymmus melapterus* (Labridae), but this effect varied with the size of the client fish (Grutter, Whittington & Deveney, unpublished observations). Other parasitic flatworms involved in 'circumstantial' cleaning interactions include microbothrids, gyrodactylids, and 'encysting trematodes' (Table 3).

Other parasites

Some leeches may also be affected by cleaners. Wrasses have been observed removing leeches from fish and the scarcity of a leech species has been related to the high abundance of the cleaner *Crenilabrus melops* in some areas of Britain (Table 3). Ciliates may also be involved in cleaning interactions. Although the cleaner fish *L. dimidiatus* ingests the trophont stages of the parasitic ciliate *Cryptocaryon irritans*, the agent of white spot disease, from the cultured stenohaline fish *Lates calcarifer* (Centro-pomidae), cleaner did not significantly affect the parasite's abundance (Halliday, unpublished observations). This was likely due to the inaccessibility, the small size and the rapid population growth of *C. irritans* and the uncooperative behaviour of the client. The small number of host epithelial cells in the cleaner's gut suggested that cleaners did not remove trophonts beneath the epithelium but rather those trying to burrow into or leaving the host (Halliday, unpublished observations).

Bacteria

While tissue infected with bacteria has been reported as a target of cleaner fishes (Limbaugh, 1961) and there is some evidence that cleaners may assist with wound healing in fish (Foster, 1985), the effect of cleaners on bacterial infections remains unresolved.

THE EFFECT OF CLEANERS ON PARASITES

Earlier studies found no effect of marine fish cleaners on parasites. Youngbluth (1968) and Losey (1972), both found at the same sites in Hawaii, no effect of cleaners on the abundance of parasites or client fish. Similarly, at Lizard Island on the Great Barrier Reef, Grutter (1996b) found no effect of cleaners on parasites of the damselfish *Pomacentrus moluccensis*. The study examined the size, total abundance and number per taxon of parasites. Although Limbaugh (1961) found that the removal of 'all known cleaning organisms' from 2 reefs in the Bahamas resulted in

increased infection in the form of 'fuzzy white blotches, swelling, and ulcerated sores and frayed fins' and emigration of clients, the study involved no quantitative data or controls.

Gorlick *et al.* (1987) found that the abundance of parasites was not affected by cleaners at Enewetak Atoll. They did, however, find that parasitic copepods *Dissonus* sp. were larger in the absence of cleaners. As *Labroides dimidiatus* selectively feed on the larger parasites (Grutter, 1997b), this result would, at first glance, appear to be due to cleaner feeding preferences. The study, however, also suggested density dependent population regulation by the parasites themselves. In the absence of cleaners, most fish had only one large (ca. 1 mm) copepod. In contrast, on reefs with cleaners, fish had several small copepods. This suggested that a large copepod prevented new copepods from recruiting onto fish (Gorlick *et al.* 1987).

The only study to date to show a quantitative effect of any cleaner on parasite abundance was done using caged fish on reefs with cleaners or with all cleaners removed (Grutter, 1999a). This study found a 3.8 fold increase in gnathiid isopod abundance on reefs without cleaners after 12 days. More interestingly, no differences were found between reefs with and without cleaners when caged fish were sampled at dawn after 12 h. In contrast, when fish were sampled the following sunset after 24 h, there was a 4.5 fold increase in gnathiid abundance on fish from reefs without cleaners. This change in abundance of gnathiids between dawn and sunset is likely due to the fact that cleaners are only active during the day (Grutter, 1996a). It also suggests that cleaner fish predation plays a significant role in the daily decline in gnathiid abundance found on wild fish (Grutter, 1999a, 1999b). Cleaners also affected the abundance of the corallanid isopod *Argathona macronema* on caged fish (Grutter & Lester, in press).

The size of a parasite may influence its likelihood of being eaten by a cleaner. Within the species *L. dimidiatus*, cleaners selectively feed on larger gnathiid isopods thus making larger gnathiids more vulnerable to predation (Grutter, 1997b). However, the maximum size of gnathiids eaten may be limited by the size of the cleaner, or more specifically by its throat width, as more large gnathiids are eaten by large cleaners than by smaller cleaners (Grutter, 2000). Interestingly, cleaners affect parasites (corallanid isopods) that are even larger than gnathiids, but only up to a particular size (< 6 mm). Isopods that are larger, in contrast, are not affected (Grutter, McCallum & Lester, in press). How this occurs is unclear as the smaller corallanids are wider than the throat width of cleaners (Grutter, 2000). The small size of some parasites may explain why they are not affected by cleaners, such as *Cryptocaryon irritans* (350 µm) which are eaten in low numbers while

Table 2. Other parasitic arthropods involved in cleaning interactions

Family (order or class)	Parasite identity	Cleaner species	Family	Location	Comment	Reference
Caligidae	<i>Caligus hobsoni</i> , <i>Lepeophtheirus</i> sp.	<i>Oxyjulus californica</i>	Labridae	California	Nest-guarding male garibaldi, which attacked all fishes including cleaners, had more <i>C. hobsoni</i> during the breeding season than outside the breeding season	Hobson, 1971
	<i>C. hobsoni</i>	<i>Phanerodon atripes</i>	Labridae	California		Hobson, 1971
	<i>Caligus</i> sp.	<i>Centrolabrus exoletus</i>	Labridae	Spain		Galeote & Otero, 1998
	<i>Caligus elongatus</i>	<i>Crenilabrus melops</i>	Labridae	Northern Europe		Costello, 1996; Deady, Varian & Fives, 1995
	'Caligid'	<i>L. dimidiatus</i>	Labridae	Japan		Chikasue, M., personal communication
	<i>Caligus</i> spp.	<i>Symphodus melanocercus</i>	Labridae	Mediterranean Sea		Arnal & Morand, 2001
	'Calagoid copepods'	<i>L. bicolor</i>	Labridae	Society Islands		Randall, 1958
	'Calagoid copepods'	<i>L. phthirophagus</i>	Labridae	Hawaii		Randall, 1958
	'Caligoid copepods'	<i>L. dimidiatus</i>	Labridae	Japan		Sano, Shimizu & Nose, 1984
	'caligid larvae' & 'Caligidae'	<i>L. dimidiatus</i>	Labridae	Lizard Island, Great Barrier Reef		Grutter, 1997a
	'caligid larvae' & 'Caligidae'	<i>L. dimidiatus</i>	Labridae	New Caledonia		Grutter, 1999c
	'calagoid' & 'caligid copepods'	<i>L. dimidiatus</i>	Labridae	Marshall, Phoenix, & Society Islands		Randall, 1958
	<i>Achtheinus dentatus</i>	<i>Remora remora</i>	Echenidae	Argentina		Szidat & Nani, 1951
	<i>Nesippus</i> sp.	'Echeneid fishes'	Echenidae	Central Pacific		Strasburg, 1959
	<i>Gloiopotes</i> sp.	'Echeneid fishes'	Echenidae	Central Pacific		Strasburg, 1959
	'Caligoid copepods'	<i>Oligoplites saurus</i>	Carangidae	Florida, USA		Carr & Adams, 1972; Lucas & Benkert, 1983
	'caligid copepods'	<i>Hermosilla azurea</i>	Kyphosidae	California, USA		DeMartini & Coyer, 1981
	'caligid copepods'	<i>Girella nigricans</i>	Kyphosidae	California, USA		DeMartini & Coyer, 1981
	'caligid copepods'	<i>Thalassoma bifasciatum</i>	Labridae	Puerto Rico		Losey, 1974
	'Caligoids'	<i>Atypichthus strigatus</i>	Scorpididae	Southern Australia		Glasby & Kingsford, 1994

Bomolochidae	'caligid copepods' 'bomolochid'	<i>Elacatinus prochilus</i> <i>L. dimidiatus</i>	Labridae Labridae	Bahamas Japan		Arnal & Côté, 2000 Chikasue, M., personal communication Arnal & Morand, 2001
Pennellidae	<i>Peniculus fistula</i>	<i>Symphodus melanocercus</i>	Labridae	Mediterranean Sea		
Pennellidae	<i>Lernaenicus radiatus</i>	<i>Fundulus heteroclitus</i>	Cyprinodontidae	North Carolina, USA	In laboratory	McCutcheon & McCutcheon, 1964
Pennellidae	'pennellid'	<i>L. dimidiatus</i>	Labridae	Japan		Chikasue, M., personal communication
Pandaridae	<i>Pandarus armatus</i> 'pandarid'	<i>Remora remora</i> 'Echenied fishes'	Echenidae Echenidae	Argentina Central Pacific		Szidat & Nani, 1951 Strasburg, 1959
Hatschekiidae	<i>Hatschekia</i> sp.	<i>Remora</i> spp. <i>Centrolabrus exoletus</i>	Echenidae Labridae	NA Spain		Cressey & Lachner, 1970 Galeote & Otero, 1998
(Copepoda)	'Laerneids'	<i>Thalassoma bifasciatum</i>	Labridae	Puerto Rico		Losey, 1974
	'Laerneids'	<i>L. dimidiatus</i>	Labridae	Society Islands		Randall, 1958
Coronulidae	'Parasitic copepods' <i>Cryptolepas rhachianecti</i>	<i>Coris sandageri</i> <i>Atherinops affinis</i>	Labridae Atherinidae	New Zealand Baja California, Mexico	Barnacles observed being picked off grey whale and in the diet of cleaner	Ayling & Grace, 1971 Swartz, 1981
Lepadidae	'Goose barnacle cyprids'	<i>Planes minutus</i>	Grapsidae	Madeira, Portugal	Removed by crabs from loggerhead turtles <i>Caretta caretta</i>	Davenport, 1994
(Cirripectida)	'Small barnacles'	<i>Thalassoma lunare</i>	Labridae	Fairfax Island, Great Barrier Reef	Removed from green turtle <i>Chelonia mydas</i>	Booth & Peters, 1972
Platylepadidae	<i>Platylepas hexastylus</i>	<i>Thalassoma duperry</i>	Labridae	Hawaii	Barnacles removed from green turtle <i>Chelonia mydas</i>	Losey, Balazs & Privitera, 1994
Amphipoda	<i>Cyamus</i> sp.	<i>Atherinops affinis</i>	Atherinidae	Baja California, Mexico	Observed being picked off grey whales <i>Eschrichtius robustus</i> and in the diet of cleaner fish	Swartz, 1981
Amphipoda	<i>Podoceros chelophilus</i>	<i>Planes minutus</i>	Grapsidae	Madeira, Portugal	Removed from loggerhead turtles <i>Caretta caretta</i>	Davenport, 1994
Arguloidae	<i>Argulus</i> sp.	<i>Oligoplites saurus</i>	Carangidae	Florida		Carr & Adams, 1972
Ixodidae	<i>Amblyomma darwini</i>	<i>Amblyrhynchus cristatus</i>	Grapsidae	Galapagos	Ticks removed by crab from sunbathing marine iguanas	Beebe, 1926

Table 3. Other parasites involved in cleaning interactions

Family (order or class)	Parasite identity	Cleaner species	Family	Location	Comment	Reference
Capsalidae	<i>Neobenedenia melleni</i>	<i>Gobiosoma oceanops</i>	Gobiidae	Bahamas	Laboratory study including diet analysis	Cowell, Watanabe, Head, Grover & Shenker, 1993
Capsalidae	<i>Neobenedenia melleni</i>	<i>G. genie</i>	Gobiidae	Bahamas	Laboratory study including diet analysis	Cowell <i>et al.</i> 1993
Capsalidae	<i>Neobenedenia melleni</i>	<i>Thalassoma bifasciatum</i>	Labridae	Bahamas	Laboratory study including diet analysis	Cowell <i>et al.</i> 1993
Capsalidae	'benedeniine monogeneans'	<i>Labroides dimidiatus</i>	Labridae	Lizard Island, Great Barrier Reef	Accessory sclerites in diet	Deveney, M., unpublished data, see Grutter, 1997a
Capsalidae	<i>Benedenia lolu</i>	<i>L. dimidiatus</i>	Labridae	Australia	Laboratory experiment including diet analysis	Grutter, Whittington & Deveney, unpublished data
Microbothriidae	<i>Pseudoleptobothrium aptychotrema</i>	<i>Paramonacanthus oblongus</i>	Monacanthidae	Australia	Parasitic flatworm found severed off a ray was attributed to the leatherjacket fish	Kearn, 1978
Gyrodactylidae	<i>Swingleus</i>	<i>Cyprinodon variegatus</i>	Cyprinodontidae	Virginia, USA	Infected fish seen chafing and posing for cleaner, parasites not found in diet	Able, 1976
Gyrodactylidae	<i>Gyrodactylus</i>	<i>C. variegatus</i>	Cyprinodontidae	Virginia, USA	Infected fish seen chafing and posing for conspecifics	Able, 1976
Gyrodactylidae	<i>Gyrodactylus</i>	<i>Apeltes quadracus</i>	Gasteroidae	Maryland, USA	Infected fish pose for and are cleaned by stickleback	Tyler, 1963
(Trematoda)	'encysting trematodes'	<i>Thalassoma bifasciatum</i>	Labridae	Belize	Bites by fish from skin and fins may have been directed at parasites found on clients which were subsequently collected	Reinthal & Lewis, 1986
Piscicolidae	<i>Calliobdella lophii</i>	<i>Centrolabris exoletus</i>	Labridae	Germany	Fish observed removing leeches in laboratory	Samuelsen, 1981
Piscicolidae	<i>Sanguinotus pinnarum</i>	<i>Crenilabrus melops</i>	Labridae	Britain	Scarcity of leech has been attributed to high incidence of cleaner fish	Hussein & Knight-Jones, 1995
Hymenostomatidae	<i>Cryptocaryon irritans</i>	<i>Labroides dimidiatus</i>	Labridae	Australia	Trophont stages of ciliate on cultured stenohaline fish <i>Lates calcarifer</i> were eaten by cleaner but parasite's abundance not affected by cleaner	Halliday I.A., unpublished data

larger copepod parasites (*Lernaenicus* sp.) are actively targeted on the same fish (Halliday, unpublished observations).

More information, however, is needed on the long-term effect of cleaners on parasite populations. This is currently being examined for gnathiids using emergence traps on reefs with and without cleaners to sample gnathiids as they emerge from the reef in search of hosts (Murphy and Grutter, unpublished observations).

The above impacts on the local abundance and size of parasites show that some parasites are under pressure to avoid being eaten. Certain strategies, such as counter-adaptations against predators, and altered life-history traits may therefore have evolved to minimize this risk. Surprisingly, this is a relatively little studied area. Some limited information, however, is available to explore these potential strategies.

COUNTER-ADAPTATIONS OF PARASITES AGAINST CLEANERS

Counter-adaptations of prey against predation can be divided into the sequence of events that characterize a predator's behaviour when feeding (see introduction). These are listed below and include the encounter, detection, identification, approach, subjugation and consumption of the prey (Endler, 1991). Prey have a greater advantage in avoiding predation in the early stages of the predation sequence as the probability of getting through all stages is low, the predator is closer in later stages, and defenses used in later stages require more energy expenditure (e.g. toxins, spines) (Endler, 1991).

Encounter

Timing of encounters with predators. During encounters between prey and predators, apparent rarity (Endler, 1991) may be used by prey as an anti-predator defence. This may involve differences in predator and prey activity times (Endler, 1991). Thus, parasites may avoid being eaten by cleaners by infecting fish at times when predators are scarce. Most families to which cleaner species belong, such as labrids and chaetodontids, are diurnal (Hobson, 1965, 1972). Of these, the behaviour of *Labroides dimidiatus* is best studied. They are strictly diurnal, returning to a sleeping hole each night (Grutter, 1995a; Robertson & Choat, 1974). *Gobiosoma evelynae* also only clean during the day (Johnson & Ruben, 1988). Thus the predation risk from many cleaner species should be lower at night.

In California, gnathiids emerge from the reef in search of hosts mainly at night (Hobson & Chess, 1976; Stepien & Brusca, 1985) with fewer emerging during the day (Hobson & Chess, 1976). At Lizard Island, where cleaners are numerous (Green, 1996), some life-stages or species of gnathiids only emerge from the reef at night, indicating they are nocturnal;

diurnal gnathiids are only found during the new and full moon (Grutter, Morgan & Adlard, 2000). More importantly, some gnathiid species only infect fish at night (Grutter, 1999b; Paperna & Por, 1977; Potts, 1973), although some are diurnal, but to a lesser degree (Grutter, 1999b). For some of these species, such nocturnal tactics should reduce predation from diurnal cleaners and other diurnal predators such as planktivores. It has been suggested that some shrimp may engage in nocturnal cleaning (Corredor, 1978). Laboratory experiments, however, found that only one cleaner shrimp (*Periclimenes pedersoni*) out of 4 species tested ate cymothoid isopods (Bunkley-Williams & Williams, 1998). Whether it also cleans at night is unknown. Due to the lack of information on the feeding habits of cleaner shrimp the possibility that cleaner shrimp eat gnathiid isopods at night cannot be excluded.

Exposure to predators. One way of reducing the rate of encounter with a predator is to reduce the time prey are exposed to predators. When apparently sampling the host for an appropriate place to feed, gnathiids often land on the host for a few seconds then return to the benthos before re-sampling the fish (Grutter, unpublished observations). Gnathiids also only require up to an hour to feed and then leave the host (Grutter, unpublished observations). Such behaviour reduces the time they are exposed to cleaners. These behaviours are possible because of their high mobility (see below).

Hiding from predators. Another tactic of apparent rarity is the use of hiding or inconspicuous resting places (Endler, 1991). After quickly feeding and leaving the host, gnathiids then return to the benthos and hide in the benthos, most likely in dead coral and sponges (Holdich & Harrison, 1980) where they digest and moult to the next larval stage (Upton, 1987). Again, such behaviour is possible because of their high mobility (see below).

Detection and identification

Immobility. Immobility of prey at certain times is often used as an antipredator defence (Endler, 1991). Observations of gnathiid isopods reveal that when on host fish they often remain immobile and rarely move to other sites by crawling over the body surface (Grutter, unpublished observations).

Cryptic locations (site-specificity). Some of the cryptic lifestyles of some fish parasites may have evolved, in part, as a response to cleaning. Some microhabitats of fish are less likely to be cleaned than others. The copepod *Caligus minimus*, for example, lives inside the opercula and mouth cavity of seabass *Dicentrarchus labrax* and thus may be inaccessible to Mediterranean cleaners (Costello *et al.* 1996). Similarly, the copepod *Leposiphilus labrei*, which dwells

within the skin of fish and is thus inaccessible to cleaners, is common on corkwing wrasse that engage in intraspecific cleaning (Costello *et al.* 1996). The parasites eaten by the cleaner fish *Oxyjulis californica* consist mainly of mobile forms, such as gnathiid isopods and caligid copepods, while more specialized forms such as dichelesteiid, chondracanthid, and lerneopodid copepods in the branchial and oral cavities escape predation (Hobson, 1971). The former are more similar to the free-living forms requiring few changes in the feeding behaviour of cleaners compared to feeding on the more specialized species (Hobson, 1971).

The potential role of predation in monogenean biology was reviewed by Kearn (1999). Kearn (1994) proposed that predation was likely more significant in the ecology and evolution of monogeneans than previously thought and that predation may have provided the selective pressure which led to the colonization of sites, other than the skin, by ancestral monogeneans. Most likely this would have included the use of sites which are cryptic. For example, benedeniine monogeneans are found in cryptic areas such as the branchial cavity, lip folds, pharyngeal tooth pads, pelvic fins, and branchiostegal membranes of fish (Whittington, 1996; Whittington & Kearn, 1990). On elasmobranchs, the body chambers with external openings, such as the branchial cavity, nasal fossae, cloaca, rectal gland, and coelum of elasmobranch are regularly examined when surveyed for monocytilid monogeneans (Whittington, 1996; Whittington & Kearn, 1990).

The cleaners *Remora* spp. are rarely found on the fins of fish, possibly because of the disturbances of the host's movements (Cressey & Lachner, 1970). Interestingly, the copepods *Pandarus* are abundant on the fins but are not found in the diet of *Remoras* (Cressey & Lachner, 1970). This suggests that the fins may serve as a refuge from predation by diskfishes (Cressey & Lachner, 1970).

Client posing behaviour, such as the opening of mouths and operculae or extension of fins, increases the likelihood that clients are cleaned (Côté, Arnal & Reynolds, 1998) and most likely serves to increase the accessibility of parasites by exposing them to cleaners. For example, sea bass *Centropristes striatus* expose their gills to topminnows *Fundulus heteroclitus* in the laboratory so they can access their parasitic copepods (McCutcheon & McCutcheon, 1964). Whether or not clients engage in posing behaviour and the types of postures they use are likely to affect a parasite's choice of habitat. Finally, cryptic sites may also protect the parasite from the client's own attempts to clean itself, such as by chafing.

Cryptic colour patterns. The colour of prey is cryptic if it resembles a random sample of the visual background as perceived by the predator at the time

and place where the prey is most vulnerable to predation (Endler, 1991). It has been suggested that such crypsis in some parasites may reduce predation from cleaners. Pigmentation has been reported in many monogeneans (Deveney & Whittington, 2001) and may serve as camouflage from predators (Kearn, 1976, 1979, 1994; Roubal & Quartararo, 1992; Whittington, 1996). Some cleaner fish eat monogeneans in aquaria (Cowell *et al.* 1993; Kearn, 1976, 1978) and in the wild (Grutter, 1997a). Laboratory experiments show that pigmented monogeneans *Benedenia* spp. suffer decreased predation from *L. dimidiatus* compared with unpigmented species (Deveney, Whittington, & Grutter, unpublished observations). Pigments in the dendritic gut of the monogenean *Dendromonocotyle kuhlii* may serve as a dorsal screen for reproductive organs (Kearn, 1979). An ideal camouflage would be to match pigments with the site of attachment. This appears to occur in *Benedenia lutjani* which can contain yellow pigment that matches the colour of the site of attachment (Whittington, 1996). Pigmentation also varies on the body of some parasites, for example, gnathiids have more pigmentation on their dorsal side, the side more exposed to potential predators (Grutter, unpublished observations). Fishes sometimes alter their colouration while being cleaned (Feder, 1966 and references therein). Possibly, this may make parasites more visible to cleaners, such as in the case of white fungi which were accentuated by a darkening of the fish (Wyman & Ward, 1972). Parasites, in turn, may also have to adjust their camouflage in response to client colour changes.

Many parasites, such as copepods, gnathiid isopods and helminths, also have wholly or partly translucent bodies which may possibly also serve to camouflage the parasite. *Benedenia seriola*, found on the sides of the fish *Seriola quinqueradiata*, have a highly transparent vitellarium compared to *Entobdella soleae* which are found on the lower side of sole and thus are unlikely to be exposed to predation (Kearn, 1994). Some *Anoplodiscus* monogeneans found on fish fins are also translucent while others are not (Roubal & Quartararo, 1992). It has been suggested that some *Anoplodiscus* may use a combination of pigmentation and translucence to help them blend into the background of the hosts which may reduce predation from cleaners (Roubal & Quartararo, 1992). These authors also pointed out that worms and copepods on the gills or in the buccal cavity of the sparid hosts, areas likely less accessible by predators, tended to be more opaque. Wahlert & Wahlert (1961) proposed that the differences in the colours of copepods of the Mediterranean and North Sea (opaque versus coloured) may be due to fewer potential known cleaners (perciform fishes) in the latter.

The response of the monogenean *Encotyllabe caballeroi* to light may reduce predation from

cleaners (Kearn & Whittington, 1992). The rapid contraction of the body in response to brief illumination to light may occur in response to the increase in illumination that occurs when host fishes pose for cleaner fishes by opening their opercula and mouths. If this is the case, then invasion into gill and oral cavities by monogeneans has not necessarily prevented predation by cleaners (Whittington, 1996). Interestingly, benedeniines from the gills of fishes on the Great Barrier Reef do not contain pigments (Whittington, 1996). As benedeniines most likely ingest pigments from pigmented host tissue, gill parasites are unlikely to obtain such pigments, as pigmentation is not common in fish gill chambers (Whittington, 1996). In addition, pigmentation would likely make parasites more conspicuous on gills (Whittington, 1996).

Approach

Mode of fleeing. Speed and high mobility to avoid the approach of predators may be used by prey to avoid predation (Endler, 1991). Such tactics may be adopted by some parasites. Gnathiids readily leave teleost hosts when disturbed (Grutter, 1995*b*) and are rapid swimmers, swimming an estimated 10 to 20 cm.sec⁻¹ (Grutter, unpublished observations). Interestingly, gnathiids on sharks and rays (Grutter & Poulin, 1998) are not as mobile as those found on teleosts. They often remain on host gills, even after they have been dissected (Grutter, unpublished observations) or in the case of epaulette sharks, remain on fish in the laboratory for days (Grutter, unpublished observations) and even when disturbed (Heupel & Bennett, 1999). Although there are some reports of cleaning in sharks (Keyes, 1982; Sazima & Moura, 2000), no information on the parasites involved is available.

Consumption

Large size of prey. Some prey may evade or slow down their consumption by predators through large body size. The larger parasitic corallanid isopods escape predation from *Labroides dimidiatus*, most likely because their widths are up to 4 times the throat width (Grutter, 2000) of the cleaner (Grutter & Lester, in press).

Unpalatability. Whether some parasites are unpalatable is yet to be determined. Some parasites, such as gnathiid isopods of the elasmobranchs *Carcharhinus melanopterus*, and *Rhynchobatus djiddensis* from Heron Island, and *Carcharias taurus*, from Umghlanga Rocks, South Africa have bizarre colouration consisting of swirling or banded colour patterns, colourful 'eyes' marked on the dorsal surface and bright yellow pigments (B. Moore, I.

Whittington, N. Smit, respectively, personal communications). Monogeneans also often have brilliant colours (Whittington, 1996). The possibility exists that these colours may be aposematic (I. Whittington, personal communications), whereby the colours are 'warnings' indicating the organism is noxious or at least unpalatable due to distasteful chemicals (Mallet & Joron, 1999).

INFLUENCE OF CLEANERS ON THE LIFE HISTORY TRAITS OF PARASITES

The major factors influencing parasite life history traits, particularly virulence, are transmission rate, transmission mode and host immunity (Clayton & Tompkins, 1994; Ewald, 1995; Frank, 1996; Koella & Agnew, 1999; Koella & Doebeli, 1999). However, little is known about the impact of ecological factors, such as predation risk, on the evolution of ectoparasite life-traits. There is some evidence that predation risk may affect the body size and age at maturity of some parasites. Whether predation risk affects the fecundity and generation time of parasites eaten by cleaners needs to be explored. In gnathiids, both fecundity and generation time vary (Grutter, unpublished observations), but how this relates to predation risk has not been explored.

Body size of parasites

For isopods, in addition to the effect of habitat characteristics on the evolution of body size (Poulin, 1995*b*), the effect of predators may be important. Isopods in higher latitudes have larger body sizes (Poulin, 1995*b*). For some non-parasitic isopods, this has been explained as due to lower predation intensity by fish at high latitudes (Wallerstein & Brusca, 1982). The cleaner *L. dimidiatus* selectively preys on larger gnathiid isopods (Grutter, 1997*b*). Interestingly, Gnathidae have smaller body sizes than their closest free-living relatives (Poulin, 1995*b*). Selection pressure from cleaners could thus have resulted in gnathiids adopting small size as a refuge from predators.

Conversely, cleaners may also have some difficulty in eating very large parasites. The maximum prey size the cleaner *L. dimidiatus* can exploit appears to be limited by their throat size (Grutter, 2000). This may explain why cleaners only affected the smaller corallanid isopods found on caged fish (Grutter & Lester, in press). Interestingly, parasitic cymothoids and corallanids, in contrast to gnathiids, generally attain larger body sizes than free-living relatives (Poulin, 1995*b*).

Some gnathiids, at first glance, may appear to escape predation through large size. Gnathiids on the benthic epaulette shark *Hemiscyllium ocellatum* are much larger (Heupel & Bennett, 1999) than those

found in the diet of *L. dimidiatus* (Grutter, 1997b). They are also found mainly on exposed areas of the fish, such as the cloaca and lips, and do not readily leave the fish when disturbed (Heupel & Bennett, 1999). Although common in shallow coral reefs (Last & Stevens, 1994) where cleaners such as *L. dimidiatus* are prevalent (Green, 1996), epaulette sharks are, however, nocturnal (Heupel & Bennett, 1999). They are thus unlikely to encounter cleaner fish that are mainly active during the day (Grutter, 1996a). Thus the behaviour of the host may play a more important role than parasite size in the parasite's vulnerability to cleaners.

Age at maturity

Arnal, Charles, Grutter, & Morand (unpublished observations) developed a model that predicted the age of maturity of ectoparasites, a trait that influences the size at maturity and hence the fecundity of ectoparasites, as a function of cleaner fish abundance. There are great local and regional variations in cleaner density (Green, 1996; Losey, 1987; Arnal, Morand & Kulbiki, 1999). Thus, depending on the location, predation pressure on ectoparasite populations should differ: i.e. there should be a high predation risk where cleaner fishes are abundant and a low predation risk where cleaner density is low. Arnal *et al.* (unpublished observations) hypothesised that the evolution of the life history traits of ectoparasites should thus vary as a function of cleaner density. A relationship between age at maturity, body size and fecundity in parasites, has been shown in the case of helminth parasites (Gemmill & Read, 1998; Morand & Sorci, 1998; Read & Allen, 2000) and between body size and fecundity in the case of gnathiids (Tanaka & Aoki, 2000). Arnal *et al.* (unpublished observations) therefore assumed that the fecundity of gnathiid isopods is related to age at maturity. Their model predicts that a high density of cleaner fish selects for an early age in maturity in ectoparasites and thus that fish cleaning behaviour is a selective factor acting on ectoparasites. This is supported by observations showing that gnathiids eaten by *L. dimidiatus* in lower latitude areas where cleaners appear to be more abundant (Côté, 2000) moult earlier and mature earlier (Grutter, 1999a; Grutter & Hendrikz, 1999; Paperna & Por, 1977; Tanaka & Aoki, 2000) than do gnathiids in other areas (Klitgaard, 1991; Stoll, 1962; Wägele, 1987). Whether this is just due to geographic and/or temperature variation, however, needs to be tested.

It should be noted, however, that most of the above studies on gnathiids have only dealt with unidentified juvenile stages (gnathiids are generally only identified from males (Cohen & Poore, 1994)). As there is evidence that several gnathiid species are found on a single host (Grutter *et al.* 2000), the

juveniles exhibit a wide range of different colour patterns (Murphy & Grutter, unpublished observations) which has been linked to their species identity (Grutter *et al.* 2000), their size range is large (Grutter, unpublished observations), and their mobility and life-cycle (moult rates) differ between fish groups (e.g. teleosts and elasmobranchs) (Grutter, unpublished observations) it is highly likely that numerous species are involved in cleaning interactions. This raises the possibility that some cleaners may prefer some species over others which may in turn explain some of the patterns discussed above. Clearly, more precise information is needed on the identity of the parasites involved in cleaning interactions.

OTHER FACTORS AFFECTED BY CLEANERS

Parasite transmission

Cleaners may become infected with the parasites and diseases of their clients. The intimate contact between cleaners and clients may increase their transmission, particularly for parasites with direct transmission between hosts. There is some evidence that cleaners become infected with client parasites. Individual *Oxyjulis californica* engaged in cleaning have similar parasitic copepods to the client species they clean (Hobson, 1971) implying they may get them from their clients. *L. dimidiatus* become infected with gnathiid isopods, their main food source, in the laboratory (Grutter, unpublished observations).

Whether cleaners transmit parasites or diseases is of great concern for cleaners used in fish farms (Costello *et al.* 1996). Corkwing cleaners became infected when held with salmon infected with the bacterium *Vibrio* sp. (Costello *et al.* 1996). Similarly, *Aeromonas salmonicida* has been transmitted from farmed Atlantic salmon (most likely dead) to cleaners *Centrolabrus exoletus* and *C. rupestris* in salmon cages (Treasurer & Cox, 1991; Treasurer & Laidler, 1994). *Centrolabrus rupestris* become infected with infectious pancreatic necrosis virus from salmon (Gibson, Smail & Sommerville, 1998).

However, most cleaners clean conspecifics which may explain the low number of parasites on some cleaners (Costello, 1996; Costello *et al.* 1996). Of 5 species of cleaners, 2 that do not engage in intraspecific cleaning had a greater proportion of external parasites (Costello, 1996; Costello *et al.* 1996).

Less is known of the transmission of disease by cleaners to clients. Parasites on temperate cleaners are common (Costello, 1991; Karlsbakk, Hodneland & Nylund, 1996). The probability of their transmission to farmed salmon is low as most parasites are either specific to labrid fish or require that the host be eaten or be passed on to an invertebrate to complete its life-cycle (Costello *et al.* 1996). One of

these cleaners, *Centrolabrus rupestris* may be a source of re-infection of infectious pancreatic necrosis virus in farmed salmon (Gibson *et al.* 1998).

These raise the issue of the host specificity of the parasite infecting the cleaner and whether such parasites actually persist on the cleaner. Interestingly, some cleaners appear to be immune to particular parasites. For example, *L. dimidiatus* avoided infection by the parasitic ciliate *Cryptocaryon irritans*, the agent of white spot disease, even after 3 weeks of exposure in captivity (Halliday, unpublished observations). Whether this was due to host specificity is unclear.

Finally, parasites often have parasites themselves. Cleaners may therefore also play a role in their transmission. For example, gnathiids have hyper-parasites such as haemogregarines and larval nematodes (Davies, Eiras & Austin, 1994; Davies & Johnston, 2000; Monod, 1926; Smit, 2000; Smit & Davies, 1999). By eating gnathiids, cleaners may either transmit these or alternatively, reduce their populations.

Predation avoidance in parasites

Some parasites appear to avoid being eaten by cleaners as they make no attempt to conceal themselves. Lernaean and penellid copepods on the external surface of fish often have trailing egg cases or body parts (Kabata, 1992). Although fish cleaned by the cleaner fish *Oxyjulis californica* have lernaean, none were found in their diet (Hobson, 1971). Why such highly visible parasites are not eaten is unknown. Losey (1987) proposed that this practice may invite predation of eggs to increase dispersal or infection of an intermediate host. Some lernaean are, however, eaten by *Labroides phthirophagus* (Randall, 1958; Youngbluth, 1968) and topminnows *Fundulus heteroclitus* (McCutcheon & McCutcheon, 1964). Such behaviours also raise questions about the parasite's palatability. Cymothoid isopods are often also highly exposed; Losey (1987) proposed their armour and size, however, may provide them with some form of protection against predators. Such 'immunity' from predation in parasites may also be linked to the parasite's host specificity.

CONCLUSIONS

A wide range of parasites are involved in cleaning interactions. There is some support for counter-adaptations of parasites against predation from cleaners. The evidence is, however, mainly circumstantial indicating that more studies are needed. It is also clear that in most examples above, the ecological role of parasites in cleaning interactions is little understood. In most of these cases, reports where parasites were involved in cleaning interactions were not studied further. Yet, the diversity of

parasites and wide range of hosts from diverse environments suggest that cleaning may be more common and widespread than previously thought. More observations are needed in temperate and polar seas.

Of these, gnathiid isopods and caligid copepods stand out as common parasites eaten by cleaner fishes. Why these parasites are so commonly eaten deserves attention and would increase our understanding of cleaning behaviour.

When evaluating 'adaptations', it should be noted that adaptations present in one organism are not necessarily adaptations in another organism (Poulin, 1995c). As Poulin (1995c) proposed for the supposed 'adaptive' changes in behaviour of parasitized animals, many of the 'adaptations' of parasites against predators proposed in this study are based only on intuition and not on rigorous criteria. A similar set of conditions used for host behaviour (Poulin, 1995c) could be applied to the 'adaptive' changes in parasites in response to predators: these include complexity, purposive design, convergence among different lineages and fitness benefits to the parasites.

Finally, the role of parasites in cleaning interactions is not one-way, with cleaners only affecting the parasites. Complex interactions between the three main players, the parasites, the cleaners, and the clients occur (Losey, 1987). For example, these include the effect of parasites on the client's cleaning behaviour (Grutter, 2001) and schooling behaviour (Reinthal & Lewis, 1986), the effect of cleaning behaviour on the feeding behaviour of clients (Grutter *et al.* in press), and the effect of cleaners on the parasites of the parasites they feed on (see above). In addition, there are other participants which are affected by cleaning interactions including aggressive mimics (Wickler, 1968) and Batesian mimics of cleaners (Zander & Nieder, 1997).

REFERENCES

- ABLE, K. W. (1976). Cleaning behaviour in the cyprinodontid fishes: *Fundulus majalis*, *Cyprinodon variegatus*, and *Lucania parva*. *Chesapeake Science* **17**, 35–39.
- ALLEN, G. R., STEENE, R. & ALLEN, M. (1998). *A Guide to Angel Fishes and Butterflyfishes*. Perth, Australia, Van Guard Press.
- ARNAL, C. & CÔTÉ, I. M. (2000). Diet of broadstripe cleaning gobies on a Barbadian reef. *Journal of Fish Biology* **57**, 1075–1082.
- ARNAL, C. & MORAND, S. (2001). Importance of ectoparasites and mucus in cleaning interactions in the Mediterranean Sea. *Marine Biology* **138**, 777–784.
- ARNAL, C., MORAND, S. & KULBICKI, M. (1999). Patterns of cleaner wrasse density among three regions of the Pacific. *Marine Ecology Progress Series* **177**, 213–220.
- AYLING, A. M. & GRACE, R. V. (1971). Cleaning symbiosis among New Zealand fishes. *New Zealand Journal of Marine and Freshwater Research* **5**, 205–218.

- BEEBE, W. (1926). *Galapagos World End*. New York, G. P. Putnam's Sons.
- BOHLKE, J. E. & MCCOSKER, J. E. (1973). Two additional West Atlantic gobies (genus *Gobiosoma*) that remove ectoparasites from other fishes. *Copeia* **1973**, 609–610.
- BOOTH, J. & PETERS, J. A. (1972). Behavioural studies on the green turtle (*Chelonia mydas*) in the sea. *Animal Behaviour* **20**, 808–812.
- BUNKLEY-WILLIAMS, L. & WILLIAMS JR, E. H. (1998). Ability of Pederson cleaner shrimp to remove juveniles of the parasitic cymothoid isopod, *Anilocra haemuli*, from the host. *Crustaceana* **71**, 862–869.
- CARR, W. E. & ADAMS, C. A. (1972). Food habits of juvenile marine fishes: evidence of the cleaning habit in the leatherjacket, *Oligoplites saurus*, and the spottail pinfish, *Diplodus holbrooki*. *Fishery Bulletin* **70**, 1111–1120.
- CLAYTON, D. H. & TOMPKINS, D. M. (1994). Ectoparasite virulence is linked to mode of transmission. *Proceedings of the Royal Society of London. Series B* **246**, 211–217.
- COHEN, G. F. & POORE, G. C. B. (1994). Phylogeny and biogeography of the Gnathiidae (Crustacea: Isopoda) with descriptions of new genera and species, most from south-eastern Australia. *Memoirs of the Museum of Victoria* **54**, 271–397.
- CORREDOR, L. (1978). Notes on the behaviour and ecology of the new fish cleaner shrimp *Brachycarpus biunguiculatus* (Lucas) (Decapoda natantia, Palaemonidae). *Crustaceana* **35**, 35–40.
- COSTELLO, M. J. (1991). Review of the biology of wrasse (Labridae: Pisces) in Northern Europe. *Progress in Underwater Science* **16**, 29–51.
- COSTELLO, M. J. (1996). Development and future of cleaner-fish technology and other biological control techniques in fish farming. In *Wrasse: Biology and Use in Aquaculture* (ed. Sayer, M. D. J., Treasurer, J. W. and Costello, M. J.), pp. 171–184. Oxford, Fishing News Books.
- COSTELLO, M. J., DEADY, S., PIKE, A. & FIVES, J. M. (1996). Parasites and diseases of wrasse being used as cleaner-fish on salmon farms in Ireland and Scotland. In *Wrasse: Biology and Use in Aquaculture* (ed. Sayer, M. D. J., Treasurer, J. W. and Costello, M. J.), pp. 211–227. Oxford, Fishing News Books.
- CÔTÉ, I. (2000). Evolution and ecology of cleaning symbioses in the sea. *Oceanography and Marine Biology: An 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**, 256–266.
- COWELL, L. E., WATANABE, W. O., HEAD, W. D., GROVER, J. J. & SHENKER, J. M. (1993). Use of tropical cleaner fish to control the ectoparasite *Neobenedenia melleni* (Monogenea: Capsalidae) on seawater-cultured Florida red tilapia. *Aquaculture* **113**, 189–200.
- CRESSEY, R. F. & LACHNER, E. A. (1970). The parasitic copepod diet and life history of diskfishes (Echeneidae). *Copeia* **1970**, 310–318.
- DAVENPORT, J. (1994). A cleaning association between the Oceanic Crab *Planes minutus* and the Loggerhead Sea Turtle *Caretta caretta*. *Journal of the Marine Biological Association of the United Kingdom* **74**, 735–737.
- DAVIES, A. J., EIRAS, J. C. & AUSTIN, R. T. E. (1994). Investigations into the transmission of *Haemogregarina bigemina* Laveran & Mesnil, 1901 (Apicomplexa: Adeleorina) between intertidal fishes in Portugal. *Journal of Fish Diseases* **17**, 283–289.
- DAVIES, A. J. & JOHNSTON, M. R. L. (2000). The biology of some intraerythrocytic parasites of fishes, amphibia and reptiles. *Advances in Parasitology* **45**, 1–107.
- DEADY, S., VARIAN, S. J. A. & FIVES, J. M. (1995). The use of cleaner-fish to control sea lice on two Irish salmon (*Salmo salar*) farms with particular reference to wrasse behaviour in salmon cages. *Aquaculture* **131**, 73–90.
- DEMARTINI, E. E. & COYER, J. A. (1981). Cleaning and scale-eating in juveniles of the Kyphosid fishes, *Hermosilla azurea* and *Girella nigricans*. *Copeia* **1981**, 785–789.
- DEVENEY, M. R. & WHITTINGTON, I. D. (2001). A technique for preserving pigmentation in some capsalid monogeneans for taxonomic purposes. *Systematic Parasitology* **48**, 31–35.
- ENDLER, J. A. (1991). Interactions between predator and prey. In *Behavioural Ecology: An Evolutionary Approach*, 3rd edn., (ed. Krebs, J. R. and Davies, N. B.), pp. 169–196. Oxford, Blackwell Science Publications.
- EWALD, P. W. (1995). The evolution of virulence: a unifying link between parasitology and ecology. *Journal of Parasitology* **81**, 659–669.
- FEDER, H. M. (1966). Cleaning symbiosis in the marine environment. In *Symbiosis* (ed. Henry, S. M.), pp. 327–380. New York, Academic Press.
- FOSTER, S. A. (1985). Wound healing: a possible role of cleaning stations. *Copeia* **1985**, 875–880.
- FRANK, S. A. (1996). Models of parasite virulence. *Quarterly Review of Biology* **71**, 37–78.
- GALEOTE, M. D. & OTERO, J. G. (1998). Cleaning behaviour of rock cook, *Centrolabrus exoletus* (Labridae), in Tarifa (Gibraltar Strait Area). *Cybio* **22**, 57–68.
- GIBSON, D. I., SMAIL, D. A. & SOMMERVILLE, C. (1998). Infectious pancreatic necrosis virus: experimental infection of goldsinny wrasse, *Ctenolabrus rupestris* L. (Labridae). *Journal of Fish Diseases* **21**, 399–406.
- GEMMILL, A. W. & READ, A. F. (1998). Counting the cost of disease resistance. *Trends in Ecology and Evolution* **13**, 8–9.
- GLASBY, T. M. & KINGSFORD, M. J. (1994). *Atypichthys strigatus* (Pisces: Scorpididae): An opportunistic planktivore that responds to benthic disturbances and cleans other fishes. *Australian Journal of Ecology* **19**, 385–394.
- GOODING, R. M. (1964). Observations of fish from a floating observation raft at sea. *Proceedings of the Hawaiian Academy of Science* **39**, 27.
- GORLICK, D. L., ATKINS, P. D. & LOSEY, G. S. (1987). Effect of cleaning by *Labroides dimidiatus* (Labridae) on an ectoparasite population infecting *Pomacentrus vaiuli* (Pomacentridae) at Enewetak Atoll. *Copeia* **1987**, 41–45.
- GREEN, A. L. (1996). Spatial, temporal and ontogenetic patterns of habitat use by coral reef fishes (Family Labridae). *Marine Ecology Progress Series* **133**, 1–11.
- GRUTTER, A. S. (1995a). Relationship between cleaning rates and ectoparasite loads in coral reef fishes. *Marine Ecology Progress Series* **118**, 51–58.

- GRUTTER, A. S. (1995*b*). Comparison of methods for sampling ectoparasites from coral reef fishes. *Marine and Freshwater Research* **46**, 897–903.
- GRUTTER, A. S. (1996*a*). Parasite removal rates by the cleaner wrasse *Labroides dimidiatus*. *Marine Ecology Progress Series* **130**, 61–70.
- GRUTTER, A. S. (1996*b*). Experimental demonstration of no effect by the cleaner wrasse *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*a*). Spatio-temporal variation and feeding selectivity in the diet of the cleaner fish *Labroides dimidiatus*. *Copeia* **1997**, 346–355.
- GRUTTER, A. S. (1997*b*). Size-selective predation by the cleaner fish *Labroides dimidiatus*. *Journal of Fish Biology* **50**, 1303–1308.
- GRUTTER, A. S. (1999*a*). Cleaner fish really do clean. *Nature* **398**, 672–673.
- GRUTTER, A. S. (1999*b*). Infestation dynamics of parasitic gnathiid isopod juveniles on a coral reef fish *Hemigymnus melapterus*. *Marine Biology* **135**, 545–552.
- GRUTTER, A. S. (1999*c*). Fish cleaning behaviour in Noumea, New Caledonia. *Marine and freshwater Research* **50**, 209–212.
- GRUTTER, A. S. (2000). Ontogenetic variation in the diet of the cleaner fish *Labroides dimidiatus* and its ecological consequences. *Marine Ecology Progress Series* **197**, 241–246.
- GRUTTER, A. S. (2001). Parasite infection rather than tactile stimulation is the proximate cause of cleaning behaviour in reef fish. *Proceedings of the Royal Society of London. Series B* **268**, 1361–1365.
- GRUTTER, A. S. & HENDRIKZ, J. (1999). Diurnal variation in the abundance of parasitic gnathiid isopod larvae on coral reef fish: its implications in cleaning interactions. *Coral Reefs* **18**, 187–191.
- GRUTTER, A. S. & LESTER, R. J. G. (in press). Cleaner fish *Labroides dimidiatus* reduce *Argathona macronema* (Corallanidae) isopod infection on the coral reef fish *Hemigymnus melapterus*. *Marine Ecology Progress Series*.
- GRUTTER, A. S., McCALLUM, H. I. & LESTER, R. J. G. (in press). Optimising cleaning behaviour: minimising the costs and maximising ectoparasite removal. *Marine Ecology Progress Series*.
- GRUTTER, A. S., MORGAN, J. A. T. & ADLARD, R. D. (2000). Characterising parasitic gnathiid isopod species and matching life stages using ribosomal DNA ITS2 sequences. *Marine Biology* **136**, 201–205.
- GRUTTER, A. S. & POULIN, R. (1998). Intraspecific and interspecific relationships between host size and the abundance of parasitic larval gnathiid isopods on coral reef fishes. *Marine Ecology Progress Series* **164**, 263–271.
- HARVEY, P. H. & PAGEL, M. D. (1991). *The Comparative Method in Evolutionary Biology*. Oxford, Oxford University Press.
- HASTINGS, A. (2000). The lion and the lamb find closure. *Science* **290**, 712–713.
- HENRIQUES, M. & ALMADA, V. C. (1997). Relative importance of cleaning behaviour in *Centrolabrus exoletus* and other wrasse at Arrabida, Portugal. *Journal of the Marine Biological Association of the United Kingdom* **77**, 891–898.
- HEUPEL, M. R. & BENNETT, M. B. (1999). The occurrence, distribution and pathology associated with gnathiid isopod larvae infecting the epaulette shark, *Hemiscyllium ocellatum*. *International Journal for Parasitology* **29**, 321–330.
- HOBSON, E. S. (1965). Diurnal-nocturnal activity of some inshore fishes in the Gulf of California. *Copeia* **1965**, 291–302.
- HOBSON, E. S. (1969). Remarks on aquatic habits of the Galapagos marine iguana, including submergence times, cleaning symbiosis, and the shark threat. *Copeia* **1969**, 401–402.
- HOBSON, E. S. (1971). Cleaning symbiosis among California inshore fishes. *Fishery Bulletin* **69**, 491–523.
- HOBSON, E. S. (1972). Activity of Hawaiian reef fishes during the evening and morning transitions between daylight and darkness. *Fishery Bulletin* **70**, 715–740.
- HOBSON, E. S. & CHESS, J. R. (1976). Trophic interactions among fishes and zooplankters near shore at Santa Catalina Island, California. *Fishery Bulletin* **74**, 567–598.
- HOLDICH, D. M. & HARRISON, K. (1980). The crustacean isopod genus *Gnathia* Leach from Queensland waters with descriptions of nine new species. *Australian Journal of Marine and Freshwater Research* **31**, 215–240.
- HUSSAIN, N. A. & KNIGHT-JONES, E. W. (1995). Fish and fish-lice on rocky shores around Britain. *Journal of the Marine Biological Association of the United Kingdom* **75**, 311–322.
- JOHNSON, W. S. (1982). A record of cleaning symbiosis involving *Gobiosoma* sp. and a large Caribbean octopus. *Copeia* **1982**, 712–714.
- JOHNSON, W. S. & RUBEN, P. (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.
- KABATA, Z. (1992). *Copepods Parasitic on Fishes*, Oegstgeest, The Netherlands, Universal Book Services/Dr W. Backhuys.
- KARLSBAKK, E., HODNELAND, K. & NYLUND, A. (1996). Health status of goldsinny wrasse, including a detailed examination of the parasite community at Flodevigen, Southern Norway. In *Wrasse: Biology and Use in Aquaculture* (ed. Sayer, M. D. J., Treasurer, J. W. and Costello, M. J.), pp. 228–239. Oxford, Fishing News Books.
- KEARN, G. C. (1976). *Body Surface of Fishes*. Amsterdam, North-Holland Publishing Company.
- KEARN, G. C. (1978). Predation on a skin-parasitic monogenean by a fish. *Journal of Parasitology* **64**, 1129–1130.
- KEARN, G. C. (1979). Studies on gut pigmentation in skin-parasitic monogeneans, with special reference to the monocotylid *Dendromonocotyle kuhlii*. *International Journal for Parasitology* **9**, 545–552.
- KEARN, G. C. (1994). Evolutionary expansion of the Monogenea. *International Journal for Parasitology* **24**, 1227–1271.

- KEARN, G. C. (1999). The survival of monogenean (platyhelminth) parasites on fish skin. *Parasitology* **119** (Suppl.), S57–S88.
- KEARN, G. C. & WHITTINGTON, I. D. (1992). A response to light in an adult encyrtellabine (Capsalid) monogenean from the pharyngeal tooth pads of some marine teleost fishes. *International Journal for Parasitology* **22**, 119–121.
- KEELING, M. J., WILSON, H. B. & PACALA, S. W. (2000). Reinterpreting space, time lags, and functional responses in ecological models. *Science* **290**, 1758–1761.
- KEYES, R. S. (1982). Sharks: an unusual example of cleaning symbiosis. *Copeia* **1982**, 225–227.
- KLITGAARD, A. B. (1991). *Gnathia abyssorum* (G. O. Sars, 1872) (Crustacea, Isopoda) associated with sponges. *SARSIA* **76**, 33–40.
- KOELLA, J. C. & AGNEW, P. (1999). A correlated response of a parasite's virulence and life cycle to selection on its host's life history. *Journal of Evolutionary Biology* **21**, 70–79.
- KOELLA, J. C. & DOEBELI, M. (1999). Population dynamics and the evolution of virulence in epidemiological models with discrete host generations. *Journal of Theoretical Biology* **198**, 461–475.
- KRAWCHUK, M. A., KOPER, N. & BROOKS, R. J. (1997). Observations of a possible cleaning symbiosis between painted turtles, *Chrysemys picta*, and snapping turtles, *Chelydra serpentina*, in Central Ontario. *The Canadian Field-Naturalist* **111**, 315–317.
- KREBS, J. R. & DAVIES, N. B. (1993). *An Introduction to Behavioural Ecology*. Third edition. Oxford, UK, Blackwell Science.
- LAST, P. R. & STEVENS, J. D. (1994). *Sharks and Rays of Australia*. Melbourne, CSIRO Australia.
- LIMBAUGH, C. (1961). Cleaning Symbiosis. *Scientific American* **205**, 42–49.
- LOSEY, G. S. (1972). The ecological importance of cleaning symbiosis. *Copeia* **1972**, 820–833.
- LOSEY, G. S. (1974). Cleaning symbiosis in Puerto Rico with comparison to the tropical pacific. *Copeia* **1974**, 960–970.
- LOSEY, G. S. (1987). Cleaning Symbiosis. *Symbiosis* **4**, 229–258.
- LOSEY, G. S., BALAZS, G. H. & PRIVITERA, L. A. (1994). Cleaning symbiosis between the wrasse, *Thalassoma duperry*, and the green turtle, *Chelonia mydas*. *Copeia* **1994**, 684–690.
- LUCAS, J. R. & BENKERT, K. A. (1983). Variable foraging and cleaning behavior by juvenile leatherjackets, *Oligoplites saurus* (Carangidae). *Estuaries* **6**, 247–250.
- MALLET, J. & JORON, M. (1999). Evolution of diversity in warning color and mimicry: polymorphisms, shifting balance, and speciation. *Annual Review of Ecology and Systematics* **30**, 201–233.
- MCCUTCHEON, R. H. & MCCUTCHEON, A. E. (1964). Symbiotic behavior among fishes from temperate ocean waters. *Science* **145**, 948–949.
- MONOD, T. (1926). Les gnathiidae. Essai monographique (morphologie, biologie, systématique). *Mémoires de la Société des Sciences Naturelles du Maroc* **13**, 1–661.
- MOORING, M. S. & MUNDY, P. J. (1996). Interactions between impala and oxpeckers at Matobo National Park, Zimbabwe. *African Journal of Ecology* **34**, 54–65.
- MORAND, S. & SORCI, G. (1998). Determinants of life-history evolution in nematodes. *Parasitology Today* **14**, 193–196.
- NICOLETTE, P. (1990). *Symbiosis: Nature in Partnership*. London, Blandford.
- PAPERNA, I. & POR, F. D. (1977). Preliminary data on the Gnathiidae (Isopoda) of the Northern Red Sea, the Bitter Lakes and the Eastern Mediterranean and the Biology of *Gnathia piscivora* n. sp. *Rapports de la Commission Internationale pour la Mer Méditerranée* **24**, 195–197.
- PARTRIDGE, L. & HARVEY, P. H. (1988). The ecological context of life history evolution. *Science* **241**, 1449–1454.
- POTTS, G. W. (1973). 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.
- POULIN, R. (1995a). Evolution of parasite life history traits: Myths and reality. *Parasitology Today* **11**, 342–345.
- POULIN, R. (1995b). Evolutionary influences on body size in free-living and parasitic isopods. *Biological Journal of the Linnean Society* **54**, 231–244.
- POULIN, R. (1995c). “Adaptive” changes in the behaviour of parasitized animals: A critical review. *International Journal for Parasitology* **25**, 1371–1383.
- POULIN, R. (1996). The evolution of life history strategies in parasitic animals. *Advances in Parasitology* **37**, 107–134.
- RANDALL, J. E. (1958). A review of the labrid fish genus *Labroides*, with description of two new species and notes on ecology. *Pacific Science* **12**, 327–347.
- READ, A. F. & ALLEN, J. E. (2000). The economics of immunity. *Science* **290**, 1104–1105.
- REINTHAL, P. N. & LEWIS, S. M. (1986). Social behaviour, foraging efficiency and habitat utilization in a group of tropical herbivorous fish. *Animal Behaviour* **34**, 1687–1693.
- RIDLEY, M. (1993). *Evolution*. Oxford, Blackwell Scientific Publications.
- ROBERTSON, D. R. & CHOAT, J. H. (1974). Protogynous hermaphroditism and social systems in labrid fish. *Proceedings of the Second International Coral Reef Symposium 1. Great Barrier Reef Committee*, 217–225.
- ROUBAL, F. R. & QUARTARARO, N. (1992). Observations on the pigmentation of the monogeneans, *Anoplodiscus* spp. (Family Anoplodiscidae) in different microhabitats on their sparid teleost hosts. *International Journal for Parasitology* **22**, 459–464.
- SAMEULSEN, T. J. (1981). Der seeteufel (*Lophius piscatorius* L.) in Gefangenschaft. *Zeitschrift Kolner Zoo* **24**, 17–19.
- SANO, M., SHIMIZU, M. & NOSE, Y. (1984). Food habits of teleostean reef fishes in Okinawa Island, southern Japan. *The University Museum, The University of Tokyo, Bulletin* **25**, 1–128.
- SAZIMA, I. & MOURA, R. L. (2000). Shark (*Carcharhinus perezi*), cleaned by the goby (*Elacatinus randalli*), at Fernando de Noronha Archipelago, Western South Atlantic. *Copeia* **2000**, 297–299.
- SAZIMA, I., MOURA, R. L. & GASPARINI, J. L. (1998). The wrasse *Halichoeres cyanocephalus* (Labridae) as a

- specialized cleaner fish. *Bulletin of Marine Science* **63**, 605–610.
- SENN, D. G. (1979). Zur Biologie des Putzerfisches *Crenilabrus melanocercus* (Risso). *Senckenbergiana maritima* **11**, 23–38.
- SMIT, N. J. (2000). A trypanosome from the silver catfish (*Schilbe intermedius*) in the Okavango Delta, Botswana. *Bulletin of the European Association of Fish Pathologists* **20**, 116–119.
- SMIT, N. J. & DAVIES, A. J. (1999). New host records for *Haemogregarina bigemina* from the coast of southern Africa. *Journal of the Marine Biological Association of the United Kingdom* **79**, 933–935.
- SPOTTE, S. (1998). “Cleaner” shrimps? *Helgolander Meeresuntersuchungen* **52**, 59–64.
- STEPIEN, C. A. & BRUSCA, R. C. (1985). Nocturnal attacks on nearshore fishes in southern California by crustacean zooplankton. *Marine Ecology Progress Series* **25**, 91–105.
- STOLL, C. (1962). Cycle évolutif de *Paragnathia formica* (Hesse) (Isopode – Gnathiidae). *Cahiers de Biologie Marine* **3**, 401–416.
- STRASBURG, D. W. (1959). Notes on the diet and correlating structures of some central Pacific echeneid fishes. *Copeia* **1959**, 244–248.
- SWARTZ, S. L. (1981). Cleaning symbiosis between topmelt, *Atherinops affinis*, and Gray Whale, *Eschrichtius robustus*, in Laguana San Ignacio, Baja California Sur, Mexico. *Fishery Bulletin* **79**, 360.
- SZIDAT, L. & NANI, A. (1951). Las remoras del Atlántico Austral con un estudio de su nutrición natural y de parasitos (Pisc. Echeneidae). *Revista del Museo Argentino de Ciencias Naturales* **2**, 385–417.
- TANAKA, K. & AOKI, M. (2000). Seasonal traits of reproduction in a gnathiid isopod *Elaphognathia cornigera* (Nunomura, 1992). *Zoological Science* **17**, 467–475.
- TREASURER, J. W. & COX, D. (1991). The occurrence of *Aeromonas salmonicida* in wrasse (Labridae) and implications for Atlantic salmon farming. *Bulletin of the European Association for Fish Pathology* **11**, 208–210.
- TREASURER, J. W. & LAIDLER, L. A. (1994). *Aeromonas salmonicida* infection in wrasse (Labridae), used as cleaner fish, on an Atlantic salmon, *Salmo salar* L., farm. *Journal of Fish Diseases* **17**, 155–161.
- TYLER, A. V. (1963). A cleaning symbiosis between the rainwater fish, *Lucania parva* and the stickleback, *Apeltes quadracus*. *Chesapeake Science* **4**, 105–106.
- UPTON, N. P. D. (1987). Asynchronous male and female life cycles in the sexually dimorphic, harem-forming isopod *Paragnathia formica* (Crustacea: Isopoda). *Journal of Zoology* **212**, 677–690.
- VAN TASSELL, J. L., BRITO, A. & BORTONE, S. A. (1994). Cleaning behavior among marine fishes and invertebrates in the Canary Islands. *Cybius* **18**, 117–127.
- VOGT, R. C. (1979). Cleaning/feeding symbiosis between grackles (*Quiscalus*: Icteridae) and map turtles (*Graptemys*: Emydidae). *Auk* **96**, 608–609.
- WÄGELE, J. W. (1987). Description of the postembryonal stages of the Antarctic Fish Parasite *Gnathia calva* Vanhoffen (Crustacea: Isopoda) and synonymy with *Heterognathia* Amar & Roman. *Polar Biology* **7**, 77–92.
- WAHLERT, G. V. & WAHLERT, H. V. (1961). Le comportement de nettoyage de *Crenilabrus melanocercus* (Labridae, Pisces) en Méditerranée. *Vie et Milieu* **12**, 1–10.
- WALLERSTEIN, B. R. & BRUSCA, R. C. (1982). Fish predation: a preliminary study of its role in the zoogeography and evolution in shallow water idoteid isopods (Crustacea: Isopoda: Idoteidae). *Journal of Biogeography* **9**, 135–150.
- WHITTINGTON, I. D. (1996). Benedeniine capsalid monogeneans from Australian fishes: pathogenic species, site-specificity and camouflage. *Journal of Helminthology* **70**, 177–184.
- WHITTINGTON, I. D. & KEARN, G. C. (1990). Effects of urea analogs on egg hatching and movement of unhatched larvae of monogenean parasite *Acanthocotyle lobianchi* from skin of *Raja montagui*. *Journal of Chemical Ecology* **16**, 3523–3529.
- WICKLER, W. (1968). The origin of the cleaner mimic. In *Mimicry in Plants and Animals* (ed. Wickler, W.), pp. 157–176. London, Weidenfeld and Nicolson.
- WYMAN, R. L. & WARD, J. A. (1972). A cleaning symbiosis between the cichlid fishes *Etilopplus maculatus* and *Etilopplus suratensis*. I. Description and possible evolution. *Copeia* **1972**, 834–838.
- YOUNGBLUTH, M. J. (1968). Aspects of the ecology and ethology of the cleaning fish, *Labroides phthirophagus* Randall. *Zeitschrift für Tierpsychologie* **25**, 915–932.
- ZANDER, C. D. & NIEDER, J. (1997). Interspecific associations in Mediterranean fishes: feeding communities, cleaning symbioses and cleaner mimics. *Vie et Milieu* **47**, 203–212.