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"Cleaner" shrimps?

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ABSTRACT: In the western North Atlantic, some shrimps of the genus *Periclimenes* interact with fishes. According to prevailing wisdom, these shrimps "clean" the fishes (i.e. they remove parasites, diseased tissue, or detritus from their exposed surfaces). With one exception, the numerous literature entries recite anecdotal evidence. The only report based on empirical studies has dismissed the notion that "cleaner" shrimps perform the services attributed to them, leaving the nature of the relationship unresolved.

INTRODUCTION

The scene is a coral reef. A fish approaches a shallow ledge occupied by a sea anemone. Standing among the anemone's tentacles is a shrimp. The shrimp starts to wave its antennae. Having reached the ledge, the fish rolls partway onto its side and remains motionless. Quickly the shrimp abandons the anemone and climbs onto the fish, roaming over its sides and back, even disappearing beneath a flared operculum. The shrimp soon emerges into the fish's open mouth, teeters momentarily on the fish's lower lip, and abruptly ends the association by flipping backward and settling on the anemone. After righting itself, the fish swims away. What has just happened?

According to popular wisdom, the shrimp performed needed services by removing parasites, diseased tissue, and perhaps even detritus particles from the fish's surfaces. Both parties have benefited, the fish by receiving a "cleaning", the shrimp by gaining a meal. An open and shut case of mutualism, or so it seems. In this brief essay I trace the published history of "cleaning symbiosis" as it relates to "cleaner" shrimps of the western North Atlantic, summarize existing evidence in support or refutation of "cleaning", and speculate on why we find the concept of one animal species "cleaning" another so compelling.

HISTORY OF "CLEANING SYMBIOSIS"

Eibl-Eibesfeldt (1955) first observed small fishes "cleaning" larger ones. He proposed the term "Putzsymbiosen" ("cleaning symbiosis") to describe the removal of parasitic crustaceans by "cleaners" from host fishes. Eibl-Eibesfeldt did not actually see parasites being removed and made no direct test of his hypothesis.

Six years later "cleaning symbiosis" was conceptually reborn, cushioned snugly between a teleological interpretation of goal-directed behavior and ecological determinism.

Its leading prophet and provisor was Conrad Limbaugh. Eibl-Eibesfeldt's modest "Putz-symbiosen" was swept aside as Limbaugh et al. (1961:237) boldly declared: "Certain species of small, brightly colored shrimps have been observed to remove and eat parasites, injured tissue, and possibly undesirable food particles from a large variety of cooperating reef fishes." Although data were not presented, this statement – simple and direct – left no room for doubt. In the brief time allotted them – a few minutes at most – "cleaners" had to carry out the garbage, distinguish parasites and foreign items from healthy tissue, make emergency medical decisions, and perform delicate surgery. Such responsibilities required strong mutualistic bonds between "cleaners" and hosts, a fact not lost on Limbaugh et al. (1961) who pronounced "cleaners" to be exempt from predation.

"Cleaning symbiosis" – or rather its absence – was believed to have huge ecological consequences. Limbaugh et al. (1961:237) described the effect of removing "cleaner" fishes and shrimps from sections of a Bahamian reef: "The observed result within a few weeks was a reduced number of reef fishes and a high incidence of fishes with frayed fins and ulcerated sores." Although this statement was purely anecdotal, the "cleaning" station as swim-in clinic nonetheless became dogma. Sefton (1977:37), for example, wrote: "For the cleaners it is a continuing banquet, and for the cleaned it is an essential visit; experiments show that without the benefit of cleaners, fishes may sicken and eventually die from unchecked parasites." No such experiments, of course, had been performed. Limbaugh (1961:45) summed up his proof without evidence with this statement: "Among the organisms I have noted in the stomach contents of cleaners [presumably both fishes and shrimps] are copepods and isopods . . . . "

Following Limbaugh's publications, sightings of "cleaning symbiosis" increased. In the western North Atlantic several species of shrimps were purportedly at work "cleaning" fishes. Literature entries accumulated as new eyewitness accounts were described and later cited uncritically. Putative "cleaners" eventually included *Periclimenes anthophilus* Holthuis & Eibl-Eibesfeldt, 1964 (Sargent & Wagenbach, 1975); *P. pedersoni* Chace, 1958 (Chace, 1958; Collette & Talbot, 1972; Colin, 1972; Criales, 1979; Criales & Corredor, 1977; Feder, 1966; Holthuis & Eibl-Eibesfeldt, 1964; Jonasson, 1987; Johnson & Ruben, 1988; Limbaugh, 1961; Limbaugh et al., 1961; Mahnken, 1972; Roessler & Post, 1972; Ross, 1983; Sargent & Wagenbach, 1975; Sefton, 1977; Smith & Tyler, 1973; Wicksten, 1995; Williams, 1984; Williams & Williams, 1979); *P. yucatanicus* (Ives, 1891) (Feder, 1966; Jonasson, 1987; Limbaugh et al., 1961; Mahnken, 1972; Roessler & Post, 1972; Ross, 1983; Spotte et al., 1991; Wicksten, 1995); *Lysmata grabhami* (Gordon, 1935) (Criales, 1979; Criales & Corredor, 1977; Feder, 1966; Jonasson, 1987; Limbaugh et al., 1961; Roessler & Post, 1972; Ross, 1983; Wicksten, 1995); *Stenopus hispidus* (Olivier, 1811) (Criales & Corredor, 1977; Feder, 1966; Jonasson, 1987; Limbaugh et al., 1961; Roessler & Post, 1972; Ross, 1983; Wicksten, 1995); *S. scutellatus* Rankin, 1898 (Criales & Corredor, 1977; Feder, 1966; Limbaugh et al., 1961; Ross, 1983; Wicksten, 1995); and *Brachycarpus biunguiculatus* (Lucas, 1849) (Corredor, 1978; Criales & Corredor, 1977).

THE EVIDENCE

Evidence in support of "cleaning symbiosis" by shrimps is inferential, based entirely on observations of association (e.g., Johnson & Ruben, 1988; Jonasson, 1987; Spotte et al., 1991). Williams & Williams (1979) reported that *Periclimenes pedersoni* successfully removed crustacean parasites (juveniles of *Anilocra* sp.) from a live fish under laboratory conditions, but provided no data. Limbaugh et al. (1961:245) wrote: "Parasites are removed as the shrimp moves rapidly over the fish. In this operation it pulls directly at the parasite or opens the tissue surrounding it." F. A. Chace Jr., one of Limbaugh's coauthors, later admitted that this statement was conjectural: the removal of parasites had not been observed (Turnbull, 1981).

Factors that elicit and direct the "cleaning" response are poorly described. According to Colin (1972:2), *P. pedersoni* demonstrates "cleaning behavior towards anesthetized fish, paper fish models, paper fish shapes, and paper rectangles." When the shrimp were satiated with food, "cleaning" behavior was not seen. A model made of white paper with inked features elicited the greatest number of "cleaning" responses, even more than an anesthetized fish, indicating that olfaction might not be important. Sargent & Wagenbach (1975) dissected behavioral aspects of the "cleaning" sequence.

Others have tried to quantify "cleaning" activity by recording the number of "cleaning" events or the number of host fishes (individuals or species) that are "cleaned" (e.g., Criales, 1979; Criales & Corredor, 1977; Johnson & Ruben, 1988; Jonasson, 1987; Mahnken, 1972; Wicksten, 1995). Jonasson (1987) tested "cleaning" efficacy in three species of shrimps and even devised a "Cleaning Efficiency Index" to compare scores. Like others before him, he provided no direct measure of what was monitored.

Only Turnbull (1981) has properly assessed "cleaning symbiosis" by a shrimp. His unpublished dissertation describing interactions of *P. pedersoni* with four species of serranids in the Bahamas set an empirical standard in the attempt to measure any costs or benefits derived from "cleaning symbiosis."

Turnbull spent more than 5 years on the project, including 343 hours of direct observation underwater. He collected serranids by spear, surveyed and identified their external parasites, and made "infestation maps" to determine whereon the fishes parasites were most prevalent. By photographing *P. pedersoni* in the act of "cleaning" he was able to make "feeding maps" for comparison with his "infestation maps". In other experiments involving *P. pedersoni*, Turnbull tested immunity to predation, determined which foods were eaten under different conditions, and examined physical characteristics of the principal feeding structures of the shrimp to evaluate "cleaning" capability.

Turnbull also placed an acrylic hemisphere perforated with tiny holes over an assemblage of 18 *P. pedersoni* occupying a single anemone, preventing the shrimp from potential "cleaning" activities for 42 days. Foregut contents of these "non-interactive" shrimp were compared with those of "interactive" shrimp collected during "cleaning" activities or immediately afterward. Other fishes were captured, stained in situ with alcian blue (selective for mucins), and released to be "cleaned" by shrimp.

Most fishes were infested with parasitic crustaceans, which were thought to be potential prey of *P. pedersoni*. Turnbull (1981:25) wrote: "Although parasitic copepods and isopods were quite commonly encountered on the surfaces of the serranids . . . they were never seized by the shrimp. In fact, caligid copepods were not infrequently observed to dart directly beneath individual *P. pedersoni* . . . ." Nor did parts of any parasite appear in analyses of shrimp foregut contents. Even though Turnbull discovered that his maps of "infestation" and "feeding" overlapped, the shrimp were actually consuming the skin mucus of their hosts, not eating the parasites, as revealed by fish mucus in their foreguts. The mucus was apparently being extruded in greatest quantities near infestation sites, perhaps as a direct result of inflammation induced by parasitism. The shrimp were trapping this material using chelae of the first and second pereopods or the flagella. The shrimp also appeared to feed on tiny detritus clusters present on the skin of host fishes. Despite visible abrasions on many of the fishes, tissue fragments were never removed by shrimp.

"Non-interactive" shrimp fed extensively on detritus, algae, and their own anemones. Their foreguts contained calcareous sediment and algae from the substratum in addition to nematocysts and zooxanthellae from anemone tissues. These shrimp were never observed to pursue or seize free-living crustaceans. Foregut contents of "interactive" shrimp contained only fish skin mucus or small amounts of detritus.

Shrimp were occasionally swallowed by their host fishes, which refuted the immunity-to-predation hypothesis. Shrimp imprisoned inside the acrylic hemisphere survived without apparent harm, demonstrating that their livelihood was not dependent on food obtained during "cleaning." As Turnbull (1981:37) stated, ". . . the removal of mucus and detrital particles from the surfaces of serranids represents only one facet of the overall trophic position of *Periclimenes pedersoni* as an omnivore." Scanning electron microscopy indicated a structural basis for nonprehensile feeding, perhaps by entrapment of food items (including fish mucus) in setae of the principal feeding appendages. From Turnbull's findings, *P. pedersoni* appears to lack a mechanism for capturing and then grasping prey, and its first two pereopods seem incapable of performing "surgery."

Turnbull therefore rejected the notion that "cleaning symbiosis" is commensal (i.e., host fishes neither shelter the shrimp nor share food with them). The quantities of mucus removed were minimal, causing no discernible injury to the hosts. Parasitism on host fishes could therefore be eliminated, although the shrimp were clearly preying on their anemones. Without direct evidence of benefit to the host, mutualism could be rejected too. Turnbull was left with de Bary's original definition of symbiosis (de Bary, 1879:5); that is, ". . . des Zusammenlebens ungleichnamiger Organismen" (the living together of two dissimilarly named organisms). This is symbiosis defined in an unrestricted sense without costs or benefits (Saffo, 1992). As Saffo (1992:18) noted, de Bary's definition ". . . is an association by intimacy of interaction, rather than by the consequences of that interaction."

DISCUSSION

Ross (1983:193) wrote, "Cleaning symbiosis is surely one of the most remarkable of all ecological and behavioral adaptations." Where "cleaner" shrimps are concerned, the concept seems all the more astonishing for having endured so long without an empirical foundation. We tell ourselves that something must be going on. Why else does a shrimp climb onto a fish? And why does the fish permit this to happen? These are reasonable questions. As Mayr (1992:131) pointed out, "More than anything else it is the existence of adapted features that led biologists to ask 'why?' questions." For example, when asked how he came upon the discovery that blood circulates, Sir William Harvey answered because he wondered why veins had valves (see Mayr, 1992:131–132).

According to Mayr (1992), adapted features are characterized in part by their capacity to perform teleonomic activities; that is, to function as somatic programs. Mayr (1992:127) defined a teleonomic process as ". . . one that owes its goal-directedness to the operation of a program." He emphasized that the goal-directedness of a teleonomic activity lies not in the future (in which case it would be teleological) but within the code of the program itself. Adapted features such as cleaning symbiosis should be predictable analogs of Harvey's valves and veins. Any such program must be compatible with Mayr's framework, divested as it is not just from teleology but from anthropomorphism, teleology's philosophical derivative.

Does "cleaning" behavior by a shrimp qualify? A shrimp in the process of "cleaning" a fish presumably displays certain elements of its behavioral repertoire in this direction. A program, if present, requires it. But even if "cleaning" is teleonomic, its adapted features in terms of costs and benefits remain unclear, especially from the standpoint of the host. Tactile stimulation from the "cleaner" might be a fish's only reward (Sargent & Wagenbach, 1975).

Early reports of "cleaning" symbiosis suggested nuances of interspecific cooperation and ecological utility that were difficult to resist from a teleological perspective. The images conveyed were of nature in balance, of animals cooperating to keep it so. It was a scene of goal-directed behavior reflecting back the future instead of the program: with the naturalist as provocateur, life in coral seas was unabashedly teleological. Limbaugh (1961:42), for example, wrote of *Periclimenes pedersoni*: "The fish usually presents its head or a gill cover for cleaning, but if it is bothered by something out of the ordinary, such as an injury near its tail, it presents its tail first. The shrimp . . . walks rapidly over the fish, checking irregularities, tugging at parasites with its claws and cleaning injured areas. The fish remains almost motionless during this inspection and allows the shrimp to make minor incisions in order to get at subcutaneous parasites."

Such appealing interpretations of nature are usually sticky quagmires cleverly disguised. "Cleaning symbiosis" might better have been seen as discontinuous activity with no predetermined endpoint, just as the milling of people on a street corner infers nothing about ultimate destinations. It might have been prudent, in other words, to accept initially the null hypothesis of no association. Admitting that falsification of the null must precede acceptance of the alternative hypothesis has always been difficult. Campbell (1993:93) wrote: "As social animals, we acquire confident beliefs through the reports of others. The layers of equivocality are then more numerous . . . ." In science, as in other endeavors, a layer called "objectivity" is always the thickest and most uncertain.

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