

Review

Animal Symbioses in Coral Reef Communities: a Review

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Received November 1, 1987; Accepted April 27, 1988

Abstract

Symbioses, close heterospecific associations representing many types of adaptive interactions, are very common in coral reef communities. Of special significance are those associations involving reef-building corals, themselves common hosts for symbioses. Although many of the animal symbioses surveyed can be classified according to the traditional categories of commensalism, mutualism, and parasitism, others are difficult to categorize, especially since little is known about their biology. Terms and definitions used in their description are reviewed in an effort to standardize their usage. Of potential value is the application of the concepts of cost and fitness to the analysis and classification of symbiosis.

Keywords: symbiosis, commensalism, mutualism, parasitism, behavioral symbiosis, coral reefs, review

1. Introduction

The establishment of a close association between two species as an alternative to direct competition is an important strategy for survival in biotic communities. This can be especially significant in highly diverse communities, such as coral reefs, where selection for survival in the face of strong competition is at a premium. The term *symbiosis* is used here to designate these close heterospecific associations irrespective of harm or benefit to the partners. This designation is in accordance with the original definition of

the term by de Bary (1879) as "phenomena of dissimilar organisms living together". Unfortunately, the term has also been used as a synonym of mutualism, which is only one of several types of heterospecific associations.

Coral reef communities include the largest assemblage of symbiotic associations in the marine environment and possibly in the biosphere. Some of the reef coral species are hosts to probably the largest variety of symbionts in the community. These range from obligate zooxanthellae essential to the survival of the host (including calcification and therefore crucial to reef formation) to numerous types of external associates. Corals provide a large surface area, shelter among branches, potential food (tissue, mucus and its associated detritus, food caught by ciliary-mucoid activity) and a hard skeleton used as a substratum by specialized burrowers and gall-forming forms. The defense mechanisms of the coral host (especially nematocysts and extruded mesenterial filaments), although a barrier to symbionts particularly during larval settlement, may be used by established symbionts to their advantage. Although dead coral colonies are utilized as temporary habitats by a diverse group of non-specialists, only live corals provide a more stable environment to symbiotic specialists (see Coles, 1980).

This review has developed from an earlier one written during a research training program held at the Hawaii Institute of Marine Biology (Castro, 1986). It attempts to clarify terms and concepts used in the description of the various types of animal symbioses recorded from coral reef communities. It is not intended as a catalogue of these associations. Algae-invertebrate symbioses, although animal symbioses in the strict sense, are excluded since numerous reviews of the subject already exist (for example Büchner, 1965 and Trench, 1979). References given for examples listed emphasize surveys and reviews, if available, rather than by the more voluminous original literature. It is hoped that this review will help investigators standardize usage of terminology and prevent the confusing ambiguity and redundancy often seen when heterospecific associations are referred to in the literature.

2. The Meaning of Symbiosis

Symbioses are perhaps best recognized as a broad category of heterospecific associations embracing various degrees of adaptive interaction. The nature and significance of the interactions between the partners are very diverse and difficult to categorize. As a result, numerous terms and definitions have been coined to describe symbioses. The literature abounds with discussions of the terminology used in designating these associations. Among the numerous

reviews the following contain valuable treatments of the subject: Baer (1952), Caullery (1952), Cameron (1956), Dogiel (1962), Lincicome (1963), Geiman (1964), Croll (1966), Henry (1966), Cheng (1967), Nicol (1967), Matthes (1967), Read (1970), Starr (1975), Odening (1976), Nobel and Nobel (1982), Lewin (1982), and Lewis (1985). Unfortunately, no general agreement exists as to the use of terms, particularly the term symbiosis.

The American Society of Parasitologists has recommended the use of the term symbiosis as a collective category that includes commensalism, mutualism, and parasitism (Hertig et al., 1937). Although the term was used in this context by de Bary (1879), it remained associated with his investigations of the mutualistic relationship between algae and fungi in lichens. This misinterpretation has been responsible in part for the widespread use of symbiosis as a synonym of mutualism.

Predator-prey relationships should not be considered instances of symbiosis. Predators can be differentiated from symbionts (particularly parasites) by their momentary association with a smaller prey and by their rapid and destructive consumption of whole individuals or fragments (see Cheng, 1967; Nobel and Nobel, 1982). An absolute demarcation between predation and parasitism, however, is sometimes impossible, and some authors prefer not to make a distinction (for example Watt, 1968; Gilbert et al., 1976). Examples of such intermediate situations among marine organisms are the "micropredatory" gastropod molluscs associated with cnidarians (Graham, 1955; Rees, 1967; Robertson, 1970; Salvini-Plawen, 1972; Yonge, 1974; Hadfield, 1976).

The adaptive interaction between the members of a symbiosis results in the establishment of a dynamic equilibrium between the partners. Relative benefit or harm is the consequence of such interaction. Symbioses have, therefore, been classified according to the presence or absence of harm or benefit in the partners. Parasitism has been traditionally said to occur when the larger member of the association (the host) is harmed or diseased, mutualism when both members obtain benefit, and commensalism when no harm or benefit to the host occurs. The use of these criteria in categorizing symbioses, however, has been unfortunate. The concepts of benefit and harmfulness tend to be anthropomorphic in their interpretation and are usually difficult to analyze. Furthermore, very little is known about the biology of most symbioses and first-hand observations of the presence of harm or benefit may be deceptive. On the other hand, "benefit" as an outcome of a heterospecific interaction may be useful in understanding the evolution of symbioses (for example Keeler, 1985).

A more recent concept used in categorizing symbioses is the presence or absence of metabolic dependency, an idea developed by Cameron (1956) and Smyth (1962). Parasites are accordingly defined as being metabolically dependent on their host, whereas commensal are associated with their host without exhibiting any metabolic dependency. Mutual metabolic dependency is characteristic of mutualism. Metabolic (biochemical) dependency in the form of nutrients, enzymes, or even developmental stimuli (Cheng, 1967) can be experimentally demonstrated or quantified and used in a more objective context. Unfortunately, our inadequate knowledge of most symbioses, particularly the associations often described as commensalistic, prevents the application of these criteria to all heterospecific associations. It is also difficult to apply this concept when dealing with symbioses where behavioral (rather than biochemical) adaptations are predominantly involved.

Relative fitness, although not always easy to quantify, may be useful in categorizing symbioses (see Roughgarden, 1975). In this context a commensal can be considered an associate which increases its fitness as a result of the symbiosis without changing the fitness of its host, a parasite as an associate which likewise increases its fitness while decreasing that of its host, and a mutualistic associate as that which increases its fitness as well as that of its host.

A growing number of investigators has opted to surmount the difficulties of categorizing symbioses by minimizing the need of classifying the association in question and merely referring to it as an instance of symbiosis. This is particularly advantageous in those cases where the nature of the association is not adequately understood. The boundaries of what encompasses these almost limited systems of coexistence are often unimportant and meaningless. In practice and for descriptive purposes, however, it is desirable to at least use the term symbiosis and to indicate that it is used following its original definition as a broad category embracing various types of close heterospecific associations.

I have opted to use the traditional classification of symbioses (i.e. commensalism, mutualism, and parasitism) as the most convenient way of organizing the material. Classification of some of the associations follows traditional or most current treatment in the literature, again for the sake of convenience.

3. Commensal Symbioses

Instances of commensalism are the most difficult to demarcate among the three major categories of symbioses. Borderline cases between parasitism and commensalism can be recognized in numerous symbioses. Many symbionts have been classified as commensals on the assumption that there is no metabolic dependency on their host or that the host does not appear to be harmed by the symbiont. Our knowledge of most of these associations, however, remains restricted to descriptive accounts of the distribution, morphological adaptations, and general behavior of the partners. It will not be surprising to find that metabolic dependency in one or both partners has evolved in many of these associations.

Most commensals inhabit the surface of their host. The sharing of food by both partners can be a further adaptation, hence the literal meaning of commensalism as "eating at the same table." Several authors have made a distinction between commensalism and associations where no food appears to be shared. These associates are often described as *phoretic*, *epizoitic*, or *epiphytic*. These terms are often restricted to facultative, non host specific inhabitants of the external surfaces or other animals and plants. Strong host specificity, however, may be an indication of a true symbiotic association. The term *endoecism* has been used to describe associates which inhabit the burrows, tubes, or shelters of their host, whereas, *inquilinism* describes associates which find shelter within (but not inside) the body of the host. *Synocious* associates have been described as those inhabiting the surface or shelter of their host, a combination of phoresis and endoecism.

Discussions on the terminology which has regrettably developed by efforts of classifying commensalism have been given by several authors (for example Caullery, 1952; Henry, 1966; Matthes, 1967; Gotto, 1969).

As expected, there is a great diversity in the types of commensal symbioses found in coral reefs and other marine communities. General reviews of commensalism among marine organisms, have been given, for example Dales (1957, 1966), Nicol (1967), and Gotto (1969). Table 1 summarizes references which list, catalogue, review, or discuss those animal symbioses among inhabitants of coral reefs traditionally referred to as instances of commensalism. The crustacean symbionts of reef corals are treated in the section on mutualistic symbioses.

Table 1. Selected reviews and lists of commensal symbioses in the marine environment including coral reef communities

Commensals	Hosts	References	Remarks
Most groups	Most groups	Caulley, 1952 Dales, 1957, 1966 Nicol, 1967 Gotto, 1969 Read, 1970	
Many groups	Sponges	Fishelson, 1966 Westinga and Hoetjes, 1981	
Most groups	Reef corals	Patton, 1976	Symbionts of live corals
Most groups	Molluscs (commercially important species)	Cheng, 1967	Survey of parasites which includes commensals
Most groups	Crustaceans	Ross, 1983	Comprehensive survey of all types of symbioses
Many groups	Holothurians	Changeux, 1960	
Protozoans	Crustaceans	Sprague and Couch, 1971	
Cnidarians	Molluscs	Rees, 1967	
Hydroids	Hermit crabs	Mills, 1976	
Sea anemones	Hermit crabs and brachyuran crabs	Dales, 1957	Table by J.W. Hedgepeth; also see section on mutualism (behavioral symbioses)
		Ross, 1967, 1974, 1983	Also see section on mutualism (behavioral symbioses)
Sea anemones	Molluscs	Ross, 1967	
Turbellarians	Most groups	Jennings, 1974	
Sipunculans	Corals	Rice, 1976	Associates of coral skeleton

Table 1. (Cont'd.)

Commensals	Hosts	References	Remarks
Polychaetes	Most groups	Clark, 1956	
Molluscs	Cnidarians	Rees, 1967	Includes micropredatory associates
Gastropods	Corals	Robertson, 1970 Hadfield, 1976	Includes micropredatory associates Includes micropredatory associates
Bivalves	Most groups	Boss, 1965 Purchon, 1977	
Bivalves	Corals	Morton, 1983	
Crustaceans	Most groups	Balss, 1956 Patton, 1967 Ross, 1983	Comprehensive survey of all types of symbioses
Crustaceans	Sponges	Arndt, 1933	
Crustaceans	Corals	Dojiri, 1988	Gall-forming species
Copepods	Most groups	Gotto, 1979	Includes parasitic symbioses
Copepods	Sea anemones	Humes, 1982	Includes parasitic symbioses
Copepods	Stony corals	Humes, 1979	Includes parasitic symbioses
Copepods	Holothurians	Humes, 1980	Includes parasitic symbioses
Barnacles	Stony corals	Ross and Newman, 1973 Newman et al., 1976	Associates of coral skeleton Associates of coral skeleton

Table 1. (Cont'd.)

Commensals	Hosts	References	Remarks
Natantian shrimps	Echinoderms	Bruce, 1982	
Caridean shrimps	Most groups	Bruce, 1976a, 1976b	
Caridean shrimps	Sea anemones	Suzuki and Hayashi, 1977	
Caridean shrimps	Sea urchins	Bruce, 1974	
Pontonine shrimps	Scleractinian corals	Bruce, 1972, 1977	Symbionts of live corals
Pontonine shrimps	Crinoids	Bruce, 1971	
Alpheid shrimps	Gobiid fishes	Harada, 1969	Also see section on mutualism (behavioral symbioses)
Brachyuran crabs	Scleractinian corals	Castro, 1976	Symbionts of live corals
Eumedonid crabs	Echinoderms, cnidarians	Štević, in press	Some considered parasites
Pinnotherid crabs	Most groups	Schmitt et al., 1973	Some considered parasites
Echinoderms	Most groups	Clark, 1976	Non-specific external associates (possibly non-symbiotic)

4. Mutualistic Symbioses

It can be hypothesized that commensal or even parasitic symbioses may evolve toward a mutual exchange of metabolites or an increase in the fitness of both partners as a result of their association. Such is the case of mutualism, the "symbiosis" of most European workers. In zooxanthellae symbiotic with reef corals and in other mutualistic symbioses the host not only provides a habitat to the symbiont but there is a mutual metabolic dependency which is often obligatory. Although a similar exchange of metabolites has been used by some to define parasitism (Smyth, 1962; Lincicome, 1971), the possible utilization of metabolites by the parasitized host is typically a transient, non-obligatory by-product of the parasite. Some theoretical aspects of the significance, evolution, and ecology of mutualistic symbioses are discussed in a collection of papers on the subject (Boucher, 1985) and by Addicott (1986).

Classified here under mutualism are also associations where behavioral rather than physiological adaptations dominate the interaction between the partners. Cleaning symbiosis, for example, has been traditionally classified as mutualistic due to an apparent benefit to the associates. Although food and even other metabolites are sometimes part of these associations (see Trager, 1970), it is difficult to apply the concept of metabolic dependency in their classification. An increase in the fitness of the partners as a result of the association, however, may be used to consider them as mutualistic. The term *behavioral symbioses* may be used to embrace cleaning symbioses and similar heterospecific behavioral interactions.

Complex behavioral patterns have evolved in fishes which remove ectoparasites, injured tissues, and food particles from other fishes, mostly in coral reefs (Feder, 1966; Losey, 1971, 1972, 1978). Similar patterns have been studied in several cleaner shrimps (Limbaugh et al., 1961; recent review by Jonasson, 1986). Visual communication between cleaners and their hosts allows the cleaners to derive nutrition as well as a relative immunity from predation. Physical contact during interactions is transitory. It represents a symbiosis between populations rather than between individuals. A similar communication between symbiotic partners has evolved in the associations between some alpheid shrimps and gobiid fishes (Karplus et al., 1972a, 1972b; Preston, 1978) and between several pomacenrid fishes and sea anemones (Mariscal, 1971; Allen, 1975; Roughgarden, 1975; Schlichter, 1976). These and other types of behavioral symbioses such as the "feeding commensalism" involving goatfishes and other fishes and the associations between several species of fish and shrimp that live among the spines of sea urchins are reviewed by

Fricke (1975).

Crustacean symbionts of reef corals

The decapod crustaceans associated with scleractinian corals have generated much interest (reviews by Castro, 1976 and Patton, 1976). These shrimps and crabs are host-specific, obligate symbionts of live corals, particularly pocilloporid and acroporid species. Various aspects of community structure of these associations have been analyzed more recently by Abele (1976, 1979, 1984), Abele and Patton (1976), Austin et al. (1980), Coles (1980), Edwards and Emberton (1980), Black and Prince (1983), and Gotelli and Abele (1983). In the case of *Trapezia*, a xanthoid crab, numerous species are distributed throughout the Indo-west and eastern Pacific. The systematic position of some of these has been revised by Galil and Lewinsohn (1984, 1985a, 1985b) and Odinetz (1984a). Our knowledge, however, is incomplete since numerous color variants (and others that remain to be identified) most probably represent separate species. This has been confirmed by the electrophoretic analysis of eight species by Huber (1985b, 1987b), work that strongly suggests fairly recent radiation. Additional investigations on the ecology and behavior of *Trapezia* and other crustacean symbionts of corals include Lassig (1977), Castro (1978), Finney and Abele (1981), Kropp and Birkeland (1981), Odinetz (1984b), Adams et al. (1985), Gotelli et al. (1985), Huber (1985a, 1985c, 1987a, 1987b), Vannini (1985), Huber and Coles (1986), and Galil (1987). *Trapezia* species, together with the shrimp *Alpheus lottini*, increase fitness of their coral hosts by reducing predation, particularly by the starfish *Acanthaster* (Glynn, 1980, 1983b, 1987) and by aiding in the removal of potential settling organisms (Glynn, 1983a). Utilization of host lipids by *Trapezia* has been indirectly confirmed by Glynn et al. (1985). Species of *Tetralia*, a xanthoid crab symbiotic with Indo-west Pacific species of the coral *Acropora*, also appear to protect their host against predation (Glynn, 1983b, 1987).

5. Parasitic Symbioses

Parasites exploit their host not only as a habitat but as a source of nutrition and other essential metabolites. The evolution of this type of relationship necessitates the establishment and maintenance of a dynamic equilibrium between the partners. Although the adaptive significance to the parasite may be obvious, the host is not necessarily "harmed" as a result of the association. Smith (1968) and Lincicome (1971) have presented evidence which suggests that some parasites even increase fitness of the host.

Parasitism is a widespread phenomenon in all biotic communities. Most major groups include species considered to lead a parasitic existence and all free-living species most probably serve as hosts to parasites at one time or another. General reviews of parasitism among marine animals, including those inhabiting coral reefs, have been given by Hopkins (1957), Nicol (1967), and Rohde (1982). Cheng (1967) has extensively surveyed the parasites of numerous marine molluscs some of which inhabit coral reefs. In addition, instances of parasitism among coral reef animals are included in several general surveys (for example Baer, 1952; Caullery, 1952; Nobel and Nobel, 1982; Cheng, 1986).

Protozoa

Numerous species of protozoans have been recorded as external or internal parasites of marine animals. Flagellates, amebas, and ciliates are ubiquitous associates of the digestive tract of most coral reef animals. Although usually considered parasites, the significance of most of these associations remains unknown. All protozoans traditionally classified as sporozoans are parasites. Gregarines, for example, are common parasites of cells and body cavities of invertebrates. Marine vertebrates, especially fishes, are parasitized by numerous species of coccidians, microsporidans, and myxosporidans (Lom, 1984). The first two groups are also found in invertebrates.

Platyhelminthes

This phylum includes the trematodes (flukes) and cestodes (tapeworms), two large and important groups of parasites of vertebrates. Most monogenetic trematodes are ectoparasites (skin and gills) of bony fishes but some species parasitize elasmobranchs, crustaceans, and cephalopods (see Hargis, 1969). Digenetic trematodes are second only to the nematodes as the most common helminth parasites of marine vertebrates and are found in most if not all coral reef fishes. Their complex life cycle always involves a first intermediate host, a mollusc, rarely a polychaete. The vast literature on the systematics and biology of digenetic trematodes has been reviewed by several authors (see Yamaguti, 1971; Erasmus, 1972; Cable, 1974; Rohde, 1984). All cestodes are intestinal parasites of vertebrates and may be found in coral reef fishes (Yamaguti, 1959). Their larval stages can be found in molluscs, crustaceans, fishes and other groups. Although most turbellarians are free-living predators, numerous species are associated with echinoderms, molluscs, crustaceans, and other coral reef invertebrates. One has been reported as an ectoparasite of a reef coral in Hawaii (Jokiel and Townsley, 1974). A few

species have been recorded from fishes. Some symbiotic turbellarians inhabit the body cavity or digestive tract of their hosts and are, therefore, regarded as parasites by some workers (see review by Jennings, 1974).

Nematoda

Nematodes, commonly known as roundworms, are common parasites of many marine groups. They encyst in tissues or inhabit the digestive tract, body cavity, blood vessels, and other organ systems of the host. Thousands of species are known but many more remain undescribed. Parasitic nematodes are particularly common in fishes (see reviews by Yamaguti, 1961 and Rohde, 1984).

Annelida

All myzostomid annelids are associates of echinoderms, especially comatulids in coral reefs (general treatment by Prenant, 1959). Some species form galls on the body wall of the host while others invade the coelomic cavity or digestive tract. Several species of polychaetes and leeches have been described as parasites of other marine invertebrates and fishes (see Baer, 1952 and Clark, 1956).

Mollusca

Numerous species of prosobranch gastropods show various degrees of heterospecific interactions with cnidarians, including reef corals (Graham, 1955; Rees, 1967; Robertson, 1970; Salvini-Plawen, 1972; Yonge, 1974; Hadfield, 1976) and echinoderms (Baer, 1952; Caullery, 1952; Robertson and Orr, 1961; Lützen, 1968). These range from predation to highly specialized endoparasites. Some of the bivalves associated with invertebrates have been classified as parasites (Boss, 1965).

Crustacea

The parasiteic way of life has evolved in a wide variety of marine crustaceans, including coral reef forms. Baer (1952), Caullery (1952), Ross (1983) and Kabata (1984), among others, have reviewed the occurrence of parasitism among the Crustacea. Numerous species of copepods, for example, are associated with most marine groups. Many are loosely associated with the external surfaces of the host and show few specializations to their symbiotic way of life. A gradation between predation, commensalism, and parasitism, however, is observed in many families of copepods (reviews by Bocquet and

Stock, 1963 and Gotto, 1979). Some have even become highly specialized endoparasites. Parasitic copepods are associated with many groups of coral reef animals, but molluscs, echinoderms, and fishes are among the most common hosts. Similar adaptations from predation to endoparasitism are observed among isopods associated with other crustaceans and fishes. Barnacles often live on the surface of a wide variety of invertebrates and vertebrates without showing any apparent specializations for a parasitic existence. Many species, however, show a high degree of host specificity and some even appear to absorb nutrients from their hosts. The highly specialized ascothoracic cirripedes parasitize soft corals and echinoderms; the rhizocephalids are even more specialized and are responsible for parasitic castration in decapod crustaceans (Rheinhard, 1956). Parasitism among the decapod crustaceans has been described only in brachyuran crabs. All members of the family Pinnotheridae (pea crabs) are symbionts of molluscs, echinoderms, and other invertebrates in coral reefs (see review by Schmitt et al., 1973). Similarly, all eumedonid crabs are symbionts of coral reef echinoderms and cnidarians. These associations may be best described as parasitic but little is known about their biology (Štević et al., in press).

Other groups

Stages in the life cycle of some hydroids and sea anemones appear to be parasites of other cnidarians. Dales (1957) lists several hydroids which appear to be parasites of fishes. Rees (1967) reviews symbioses between cnidarians and molluscs, some of which may be parasitic in nature. Several nemerteans (ribbon worms) are commonly referred to as parasites of bivalves. Cheng (1967), however, reviews these associations and classifies them as commensals. Carapid (pearl) fishes, inhabitants of the body cavity of sea cucumbers, sea stars, tunicates, and bivalves, are sometimes classified as parasites due to their ingestion of some host tissue (review by Trott, 1981)

Acknowledgements

I gratefully acknowledge Drs. Peter W. Glynn and Debbie L. Zmarzly for their comments to earlier versions of the manuscript. The final version was much improved by suggestions from an anonymous reviewer.

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