

Biocommunication of corals

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Abstract

Scleractinian corals are keystone species of tropical reef ecosystems. As with any organism, but corals in particular, the biocommunicative approach regards evolution, development and growth of these organisms as a process that intrinsically relies upon complex and efficient communication patterns. Such patterns are sign-mediated interactions that cannot be reduced to mere exchange of information, but rather require active coordination and active organization mediated via distinctive signs. Communication processes within and among corals take place at varying levels and occur within cells, among cells, between corals of the same species, between corals of different species, and among transspecific organisms that include all phyla of all kingdoms of this tropical ecosystem, from microbes, plants, fungi, and all the way up to higher animal taxa. These processes are most evident when the coral is partly or totally impaired – as is the case with diseased corals. Although corals are almost at the trophic base of shallow tropical reef biota, they are not passive ‘prisoners’ of their environment. Rather the opposite is the case: being at the base, or more appropriately at the centre, of what a reef community is all about, they actively shape their environment and thereby provide other organisms from other taxa with both habitat and substrate.

Keywords: coral communication, semiochemical vocabulary, sign-mediated interactions, coordinated behavior.

INTRODUCTION

Coral research has assembled a wide variety of empirical data on molecular biological, cell biological and ecological aspects which provide a puzzling view of these seawater habitats. The biocommunicative approach also identifies behavioural patterns which are the result of complex organismic actions coordinated by specific signalling processes. Communication processes should not be considered a mere exchange of information; rather, they can be substantiated as diverse and manifold sign-mediated patterns of interaction.

Semiochemicals are used according to three kinds of rules to coordinate actions

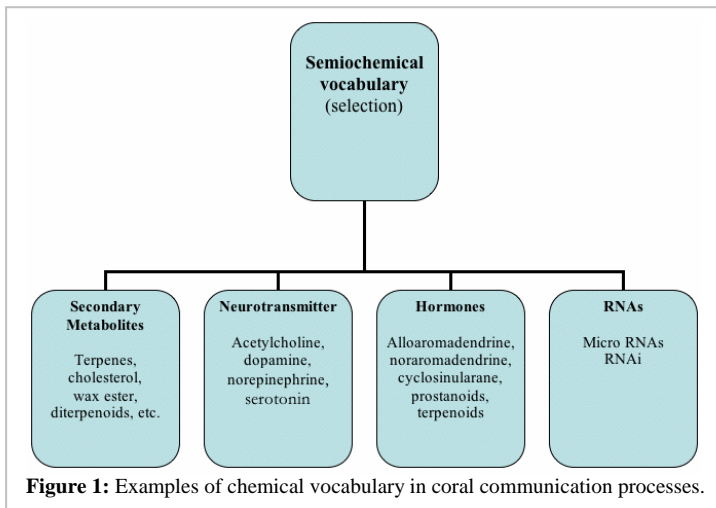
The biocommunicative approach in general investigates communication processes within and between cells, tissues, organs and organisms as *sign-mediated interactions*. Signs in most cases are molecules. Therefore they are called semiochemicals (*semeion* = Greek: sign). Because signs can be combined in various

ways according to combinatorial rules (syntax), a limited number of signs can serve to transport different messages, i.e. different meanings (semantics). Therefore it is possible to identify identical messages which trigger different response behaviours because in different situational contexts identical signs may transport different messages. Which meanings are transported by signs depends on variable situational contexts (pragmatics), as sign-generating organisms are interwoven in real-life habitats (Witzany 2006). Therefore the biocommunicative approach investigates *sign-mediated interactions* within and between organisms according to syntactic, pragmatic and semantic rules.

In contrast with purely behaviouristic observations or molecular biological investigations the biocommunicative approach looks at a great variety of *sign-mediated interactions* which depend on the generation, transmission, uptake and interpretation of messages leading to appropriate response behaviour. (a) Growth and (b) development are different modes of behaviour and need other patterns of signalling than (c) defence or (d) reproductive patterns. Likewise, (e) mutualistic symbioses require different forms of coordination from those of (f) commensalism or (e) parasitism. Additionally, every behavioural pattern may be coordinated within beneficial and prosperous

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environmental conditions or, in contrast, under stress. These different behavioural response patterns have to be generated as a complex communication process within cells, tissues and organs of the coral organism without which no coordinated behaviour could be generated. From this perspective signalling processes are no mere exchange of information but are essential parts of *complex coordinative actions*. The different forms of symbiotic associations, for example, with both their endosymbionts and exosymbionts (on the mucosa of the coral animal) stress the fact that conduct of symbiotic partners is beneficial for both parties as long as they are characterised by the absence of stress factors. As there are altruistic forms of interactions between coral and symbionts so there are defence response patterns, which can also involve life-and death situations.

Transorganismic, interorganismic and intraorganismic communication of corals

In this review we look at current knowledge of corals. As we will see, we can differentiate communication processes of non-related taxa (transorganismic) among the same and related species (interorganismic) and within the animal (intraorganismic).

In any case these communication processes are coordinated in an orderly manner, thereby enabling a context-coherent coordination of behavioural patterns. As long as these processes are comprehended, and interactions as well as exchange of information successfully established, the organism will prosper. Once these patterns become corrupted, via natural or anthropogenically-induced alterations, the coral animal faces an interactive uphill struggle. If external disturbances interfere with communication processes, as in the case of chronic events, it will compromise the animal's state of health and ultimately induce disease or even death. In order to understand better the survival strategies of corals it is necessary to work out the underlying interactional pattern—an issue that is of

great relevance, especially when we consider the effects of global climate change (Hoegh-Guldberg *et al.*, 2007).

Chemical Vocabulary

Communication patterns of signalling molecules within and among corals are amazingly complex. Depending on the developmental stage or other situational contexts, e.g. the reproduction process, different molecules are used. Until yet several classes of molecules (Fig. 1) which serve as signs in communicative processes has been identified:

- Secondary metabolites such as terpenes, cholesterol, wax ester diterpenoids
- Neurotransmitter such as acetylcholine, dopamine, norepinephrine, serotonin
- Hormones such as alloaromadendrine, noraromadendrine, cyclosinularane, prostanoids, terpenoids
- RNAs such as microRNAs and RNAi

Varying behavioural patterns lead to the production of different signals with different functions: antimicrobials, antifungals, corresponding secondary metabolites, and hormones (Kim, 1994; Slattery *et al.*, 1995,1999; Ramesh and Venkateswarlu, 1999; Iwashima *et al.*, 2000; Kim *et al.*, 2000a,b; Yasumoto *et al.*, 2000; Roussis *et al.*, 2001; Twan *et al.*, 2003; Watanabe *et al.*, 2003; Iguchi *et al.*, 2004; Zhang *et al.*, 2005).

As will be demonstrated later, corals possess a broad variety of hormonal substances for different behaviours, e.g. reproduction cycles and defence patterns against opportunistic microbes, carnivores, herbivores and fungal infections (Hay *et al.*, 1987; Kim *et al.*, 2000a,b; Slattery *et al.*, 1999).

Interpretation of mechanical influences

In this review we will demonstrate that corals, being predominantly sessile organisms, are an essential part of the manifold communication patterns present within coral reef ecosystems. Thus, internal communication patterns correspond and are co-evolutionarily adapted to external signals of non-coral organisms. The coral animal, therefore, must be able to distinguish between self and non-self. According to their tolerance limits, these animals process and evaluate information in order to adjust their responses adequately. Equipped with appropriate recognition patterns, and in the absence of external interference, coral animals are able to thrive and establish themselves in oligotrophic environments of the tropics.

Hitherto most specialists have considered corals as archaic, sessile animals that are placed at the lower level of organismic complexity. Now, however, it is becoming increasingly obvious that their evolution,

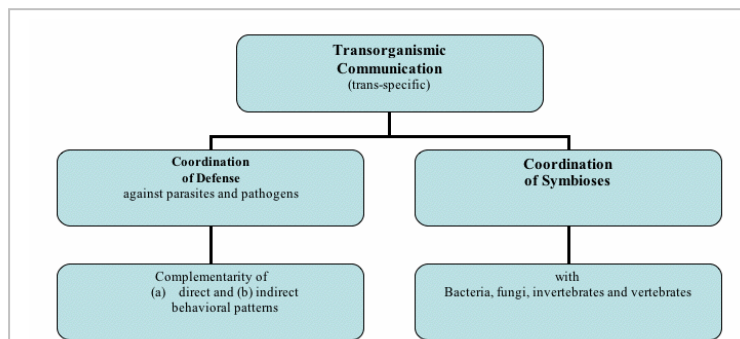


Figure 2: Levels of transorganismic (trans-specific) communication.

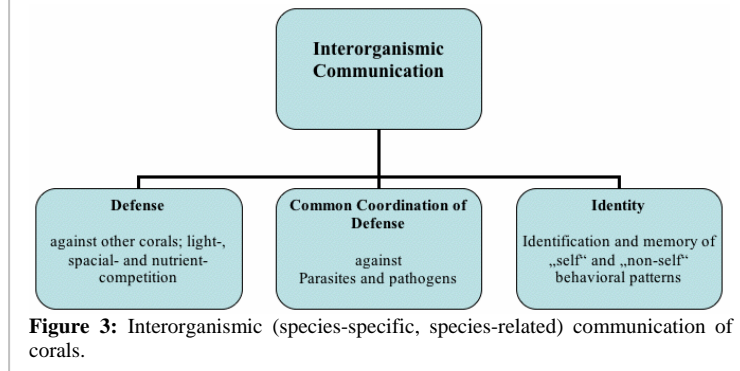


Figure 3: Interorganismic (species-specific, species-related) communication of corals.

growth and development depend upon complex and successful communication processes. This article gives an overview of the manifold levels of coral communication and thereby broadens the understanding of these organisms.

Even though tropical coral reefs are embedded in an oligotrophic setting, they are still capable of sustaining a lush environment. The frequent description of reefs as the ‘tropical rainforests of the sea’ is rooted in structural conditions that can be compared to terrestrial ecosystems of the tropics: i.e. growth rates are in tune with autochthonous species and their associated symbionts, ensuring a stable, long-term equilibrium, similar to tropical rain forests (Hubbell, 1997). It is not surprising then that community structures of coral reefs easily cover a developmental time window stretching over thousands of years. The sudden emergence of modern reefs across the globe as we know them today was initiated some 6000 to 9000 years ago (Hallock, 1997; Pandolfi, 2002).

Over the last decades, however, the scientific community has noticed a drastic increase in coral-associated diseases of tropical reefs (Sutherland *et al.*, 2004). Caribbean reefs are hardest-hit, earning this region the title ‘coral disease hot spot’ (Weil, 2004). Abiotic interferences affect all eukaryotic organisms at any cellular level. Corals are particularly affected, as they are keystone species in tropical reef ecosystems (Bak *et al.*, 1982; McClanahan *et al.*, 2003). Natural disasters such as earthquakes, cyclones and tsunamis change and thereby shape reef ecosystems. Under

natural conditions such interference, results in change of species composition, favouring pioneering and faster-growing species, thereby initiating a new cycle of coral succession. Connell’s intermediate-disturbance hypothesis (IDH) gives a good summary of the associated affects of such disturbances (Connell, 1978; Begon *et al.*, 1996; Loya, 2004). Under moderate conditions, abiotic influences enable coral animals to release signalling chemicals via ocean currents (Harrison *et al.*, 1984; Penland *et al.*, 2004). Morphogenesis is yet another characteristic of stony corals that is likewise determined by abiotic conditions, i.e. light intensity, swell and surge patterns, oceanic currents (Geistner, 1977, Horiguchi *et al.*, 1999; Veron *et al.*, 2000; Gleason *et al.*, 2005; Stambler *et al.*, 2005; Vargas-Angel *et al.*, 2006).

In the context of anthropogenic influences, eutrophication owing to land-based intensive farming or mariculture, excessive fishing practices, and other man-made influences also interferes with coral-ecosystem communication, thereby easily tipping the balance towards a filter-feeding community. High phosphate levels in otherwise oligotrophic waters, for example, rapidly shut down the calcification mechanism (phosphate poisoning). In addition, higher nutrient levels favour (macro)-algae and prevent larval settling, with the result of a readily replacement of the coral-symbiont biotope (Tanner, 1995; Loya, 2004). Once filter feeders substitute for the coral carpet and become the dominant organisms, it is almost impossible to re-establish a thriving coral ecosystem within a reasonably short period (Hatcher, 1997; Elmqvist *et al.*, 2003). Closely associated with eutrophication and coastal degradation is the global trend in the decline of mangrove forest cover. Mangroves are an essential part of the wider tropical reef ecosystem, as their numerous prop roots account for a very rich and diverse habitat ranging from algae, sponges, and marine invertebrates to nurseries for young shrimp and coral fishes. Habitat degradation for shrimp farms and other coastal utilisation not only increases coastal erosion, but likewise interferes with the communication processes within the wider reef ecosystem, thereby detrimentally feeding back onto adjacent reefs (Mumby *et al.*, 2004).

Another man-made disturbance originates from chemical interference; just one example is the pesticide Chlorpyrifos used on golf courses. Coral larvae are extremely sensitive to chemical signals at levels that are well below the detectable limits of current human technology. Since crustose coralline algae easily take up this pesticide, coral larvae have lower recruitment rates on substrates exposed to the chemical at concentrations even as low as 5ppb than on untreated controls (Richmond, 1997).

Transorganismic (trans-species) Communication

Both mechanical and chemical sign-mediated interactions of corals with other genera, families, and phyla, as well as with members of other kingdoms, are not only essential for their survival, but are the basis of coordination and organisation (Fig. 2). These interactions cover the entire range—from the mutually supporting over neutral to harmful behaviours. The variety of symbiotic communications, for example, requires very different behaviours from the partners involved (Weis *et al.*, 2001).

Direct and indirect defence mechanisms are manifold and complement each other. Corals possess a ‘non-self’ warning system, especially when confronted with opportunistic microbes (Rohwer *et al.*, 2004). Such microbes include single-celled autotrophic and heterotrophic prokaryotes, autotrophic and heterotrophic eukaryotes, as well as viruses. In fact, these opportunists can be found in all three domains of life on our planet, i.e. bacteria, archaea, and eukarya (Sherr *et al.*, 2000).

Corals interact with non-related species through their muco-poly-saccharide layer (MPSL). This species-specific layer forms a boundary through which dissolved nutrients and gases diffuse. Hence, the mucus is a barrier against opportunistic pathogens and should be considered the primary immune organ of corals. Beneficial prokaryotic residents living on and within the MPSL are yet another shield against opportunistic settlers (Shnit-Orland *et al.*, 2009) and act as host-associated microbial community (Sunagawa *et al.*, 2009). There are large numbers of mucus-adapted microbes, such as phosphate and nitrogen fixers. It is reported that even cold-water corals actively ‘fish’ the surface layer to obtain additional nutrients (Neulinger *et al.*, 2008). In order to do so, corals encourage growth of specific microbes by the secretion of specialised mucus (Kushmaro *et al.*, 2004). This in turn provides specialised microbiota as the ideal substrate to protect the coral animal from opportunistic settlers by occupying entry niches and/or through the formation of inhibition zones, e.g. prokaryotically-mediated production of antibiotics. Any disruption of the highly diversified microbial density on the MPSL will render the coral holobiont more susceptible to opportunistic pathogens, thereby enabling diseases to become established, and ultimately may result in the decline of the whole organism (Rohwer *et al.*, 2004).

Coordination of defence and regeneration

Being predominantly sessile in lifestyle, corals are equipped with additional defence mechanisms against mechanically-induced damage and microbes (Gunthorpe *et al.*, 1990, Kramarsky-Winter, 2004). It

appears that corals can differentiate between the various modes of inflicted tissue damage, i.e. triggered by viruses, bacteria, fungi and invertebrates as well as damage induced by vertebrates. According to the type of damage, corals secrete different combinations of substances that serve to deal with such lesions.

A localised wound response leads not only to the production of mobile signal molecules, but requires a systematic reaction involving the entire organism – obviously, a mature colony has more reserves than a juvenile recruit (Alker *et al.*, 2004). Reactions to lesions stimulate the transmigration of specific amoeboid wound cells toward the site of injury. The action of amoebocytes can be considered as first-aid measures, as they clean up cellular debris. Necrotic tissue is then sloughed off. Only now will the surrounding tissues stretch to cover as much of the wound as possible. If lesions are too large to be covered by stretching tissues, a much slower process takes over: tissue regrowth over the denuded area. It was observed, however, that corals affected by microbial-induced disease revealed a significant reduction of amoebocytes engaged in tissue repair (Kramarsky-Winter, 2004). Amoebocytes are also involved in coral responses to pathogenic and temperature stress (Mydlarz *et al.*, 2008).

Corals are able to coordinate directly and indirectly their complementing protective measures to varying degrees—according to the intensity of damage inflicted by opportunistic species (Chadwick-Furman *et al.*, 1994; Koh 1997; Rinkevich, 2004). The exposure to parasites or pathogens stimulates the coral organism to produce a specific array of immune substances (Bigger *et al.*, 1993; Rinkevich *et al.*, 1994; Hildemann *et al.*, 1977).

In addition, corals also produce enzymes that render their tissues unpalatable to certain predators (Lindquist *et al.*, 1996; Kelman *et al.*, 1999). Contrary to the predictable succession of developmental phases of individual organisms, modular organisms can proliferate at one end while at the other tissues may be already in the phase of decomposition. Death in such organisms often results from becoming too big or succumbing to disease rather than from programmed senescence. Thus, the body of a modular organism has an age structure – it is composed of young and developing, actively functioning, as well as senescent, parts (Begon *et al.*, 1996; Vytopil *et al.*, 2001). The modular structure enables corals to respond adequately to spatial limitations, predators, and unfavourable environmental conditions. Their morphology, in particular branching species, not only provides shelter for juvenile fish species and other invertebrates, but actively benefits the survivorship of the coral: e.g. the crab *Trapezia* sp. can even deter such vicious corallivorous predators as *Acanthaster planci* (Gosliner *et al.*, 1996; Pratchett, 2001).

The fragility of reef-ecosystems becomes evident, however, when external disturbances such as devastating events, e.g. storms or changes in water quality, result in large deviations from normal modal flux rates that can lead to rapid reef decline. When limited in duration, as briefly mentioned in the context of Connell's IDH, such events can stimulate another cycle of reef accretion (Hatcher, 1997). In healthy reef ecosystems, this balance of production and bioerosion of reef biomass and calcium-carbonate substrate is closely balanced with net accumulation barely ahead of net reef loss. It regulates and influences ecosystem function of growth and decay (Glynn, 1997; Paulay, 1997). Under the influence of global climate change, however, nonlinear effects of long-lasting adverse conditions can easily lead to a situation where a 'catch-' or 'keep up' reef can easily precipitate into a 'give-up' state, where 'permanent' decline sets in (Adey, 1978).

Communicative Coordination of Symbioses

Generally, there are multiple symbiotic interactions, which can be clearly differentiated into mutualistic, aggressive and defensive properties (Van Veghel *et al.*, 1996; Hay, 1997). Corals serve as symbiotic hosts for algae, protists, fungi, and a variety of bacterial and archaeal communities as well as viruses (Marhaver *et al.*, 2008). Owing to the gradual increase in global sea-surface temperatures, communication processes between endosymbionts and coral hosts are increasingly disturbed (Baird *et al.*, 2009; Rosenberg *et al.*, 2009). In such cases, the coral's ability to neutralise endosymbiotic production of radicals is compromised (Lesser 2004). Hence thermal stress combined with high irradiance pushes the host into the distress phase which leads to ever more frequent expulsion of endosymbiotic algae as temperature extremes exceed thermal threshold levels (Hoegh-Guldberg, 1999, 2004). During extended bleaching events coral communities of entire reef sections lose their ability to regenerate and ultimately fade out, giving rise to a completely altered ecosystem (Edmunds *et al.*, 2003; Rowan, 2004; Jones *et al.*, 2008). There are, however, some clades of Symbiodinium that are better adapted to the higher temperatures and therefore develop different symbiotic interactions (Stat *et al.*, 2008). Under certain circumstances corals are able to swap less temperature-tolerant clades for better-adapted ones (Buddemeier *et al.*, 2004; Sampayo *et al.*, 2008), thereby enabling corals to partly regain their vitality (Rowan, 2004). The most marked differences among clades of Symbiodinium can be found between corals of the Caribbean and those in the Indo-Pacific region, while lesser differences exist among clades along a depth gradient within a given region (Toller *et al.*, 2001). Tropical reef corals are ecologically important examples of mutually helpful associations, whose success depends on the intrinsically interwoven webs of

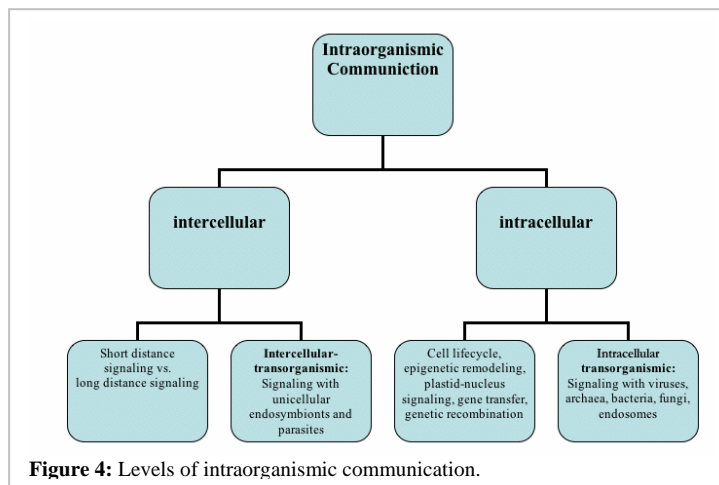
life. This network of complex communicative interactions shapes a sensitive dynamic equilibrium. Yet, as illustrated previously, this balance can far too easily be disturbed by outside influences, thereby triggering the collapse of entire reef sections. Besides active conservation efforts, only an exact analysis of the communication patterns of all the partners involved can aid a better understanding of coral physiology, disease patterns, and biotic and abiotic stress-factors (Edmunds *et al.*, 2003).

Interorganismic (species-specific and species-related) communication

Species-specific and species-related sign-mediated interactions are termed inter-organismic communication (Fig. 3). Hermatypic reef corals are social organisms and with few exceptions, such as some members of Fungiidae, they are predominantly colonial and modular in appearance. This social capacity implies a species-specific sign-mediated interaction process, which enables corals of the same or a similar species, as well as distantly related relatives, to coordinate their behaviour. This coordination is most obvious during reproduction.

While some corals reproduce sexually, which requires synchronisation of opposite sexes, such as in cases of mass spawning, others do so asexually via budding or fragmentation. Most corals employ both modes of reproduction (Miller *et al.*, 2004). Gametogenesis is a time- and resource-dependent process, so each method depends on favourable environmental conditions and developmental stages. Laboratory breeding experiments with some *Acropora* species have shown that pre-mating barriers are not strong. This indicates that chemical messengers are almost absent or not recognised in some of these species, in order to prevent merger of gametes from different species. The effect of such hybridisation can range from sterile individuals to introgression, speciation and even extinction (Wallace, 1999). Hence it comes as no surprise that species involved in mass spawning overcome this limitation by expelling their gametes at precisely different time-windows of the lunar cycle coupled with solar insolation, and/or sea-surface temperatures (Harrison *et al.*, 1984; Penland *et al.*, 2004; Twan *et al.*, 2006).

Evolutionary processes are also induced via hybridisation (Márquez *et al.*, 2002; Miller *et al.*, 2003). In situ observations along the GBR revealed that in a single night up to 150 species of the highly cross-fertile genus *Acropora* spawn within hours of each other. High cross-fertilisation rates were documented in vivo, while molecular tree topologies confirmed non-monophyletic patterns. These bore little similarity to cladistic analysis based on skeletal morphology or to the fossil record, leading to the conclusion that hybridisation does contribute to the enormous success



of these species (Ryan 2006; Van Oppen *et al.*, 2001). Indeed, hybridisation and polyploidy are recognised not only in other coral genera but also among a wide variety of marine invertebrates (Pfenninger *et al.*, 2002). Similarly, recombinational crosses between directly and indirectly developing species of sea urchin have resulted in novel gene expression (Nielsen *et al.*, 2000) and novel ontogenetic pathways (Raff *et al.*, 1999), leading to the creation of new larval morphologies (Ryan, 2006). According to Williamson (2003), interphyletic hybridisation of marine invertebrates must be a major transfer route of marine larval forms between taxa through a wide variety of hybridisations (Ryan 2006; Combosch *et al.*, 2008).

Corals can differentiate between ‘self’ and ‘non-self’ (Rinkevich *et al.*, 1994; Rinkevich *et al.*, 2001). In order to protect their own growth range against proliferating opportunists, corals take defensive measures against ‘non-self’ tissues. Allelopathic reactions, such as the production of chemicals to signal presence and to limit excessive proliferation of neighbouring coral species, occur in very complex ways and in various combinations and gradations (Yamazato *et al.*, 1986). There are some completely different and complementary defence mechanisms, e.g. escape by growth, aggressive behaviour, allelochemicals and aggregation (Bruno *et al.*, 1996). Aggressive and defensive behavioural patterns reciprocally depend on the extent of physical contact (Bak *et al.*, 1982; Ferriz-Dominguez *et al.*, 2001). Such responses can be quite broad, in that they can involve complete rejection of other coral colonies (use of sweeper and or stinging tentacles) or in the opposite case can result in complete merger of both colonies (Connell, 1976; Cope, 1982; Chadwick-Furman *et al.*, 1994). Research employing various juvenile coral species showed that there are three kinds of response patterns: fusion, non-fusion and incompatible fusion. In the case of incompatible fusion, the junction of merging tissues lacks endosymbiotic algae. Slow-growing polyps characterise such an interfacial region. Over prolonged periods of time and as a result of this

incompatibility, a skeletal barrier forms (Veron, 1986; Hidaka *et al.*, 1997).

Encounters of different coral species quite often result in subduing of the succumbing species by a dominant species. Overgrowth is simply one strategy to overcome spatial restriction in a flourishing reef community (Veron 1986; Frank *et al.*, 2001).

Spatial and nutritional competition among corals and the concomitant stress factor do affect their fitness (Tanner, 1997; Idjadi *et al.*, 2007). Once resource limitations and habitat constraints are encountered, corals can become very aggressive and even kill competitors. It is well-known that sweeper tentacles, extrusions from the polyp’s gut – up to five times the length of the polyp’s tentacle and equipped with batteries of nematocysts – literally digest competitors. These extended mesenterial filaments are part of the macroscopic defence capabilities (Barnes *et al.*, 1999). In addition, some corals generate considerable amounts of mucus loaded with nematocysts, which spreads out and over into the nearby environment to harm neighbouring colonies. Prolonged mucus production can significantly damage and even kill affected colonies. Other corals kill via the excretion of chemical poisons into the adjacent water body, while others again secrete substances which render larval settlement of potential competitors unfavourable (Lang, 1971, 1973; Logan, 1984, 1986; Lang *et al.*, 1990; Geffen *et al.*, 2005).

Once a coral detects the presence of a nearby species with its ability for non-self recognition, it reacts with the production of finely graded antibacterial/cytotoxic substances that will be used against potential intruders, or even against related coral species. This is an acquired response pattern and becomes engrained as a result of continuous stimulation. Corals are able to learn, in that they compare a given stimulation pattern with bodily stored stimulation patterns of the past (Hildemann *et al.*, 1977; Rinkevich, 2004).

Hence, corals are capable of differentiating between tissues and chemicals of kin species and those of ‘non-related’ species. This is essential in order to avoid repercussions that negatively affect the survival rate of nearby individuals of the same species. Fitted with such tools of discrimination, corals are even able to differentiate the sex of their opponents (Ates, 1989).

Along with their symbiotic partners, each colony must have some kind of sphere of individuality in order to survive and prosper. Once intruders compromise these preconditions, substances are produced and released into the water body that hamper growth and proliferation of nearby competitors (Kim, 1994; Wilsanand *et al.*, 1999; Kim *et al.*, 2000 a,b; Roussis *et*

al., 2001; Slattery *et al.*, 1995). For the same purpose, even sturdy coral species can produce and release fast-acting antibacterial agents into the environment (Geffen *et al.*, 2005).

Intraorganismic communication

As we will see, intra-organismic communication processes are sign-mediated interactions within cells (intracellular) and between other cells of the same organisms (intercellular) (Fig. 4). Both communication processes are of crucial importance for the coordination of growth and development. Similarly to multi-cellular organisms the exchange of information must be assured on a local scale as well as on a spatially larger scale. Only by responding as a whole and in a coherent fashion can coral organisms react to the corresponding developmental challenges and physiological influences.

Intercellular communication

Intercellular communication serves to communicate events within coral tissues or compartments to remotely located cells or tissues. An injured coral, for example, organises an integrated molecular, biochemical and cell-biological response. This also includes immunological reactions (Bigger *et al.*, 1993; Hildemann *et al.*, 1977; Rinkevich, 2004).

The status information about the coral's current state is constantly monitored. This kind of information is to some extent suppressed, however, when the organism undergoes periods of growth. Doing so enables expression of the pre-processed intermediate steps necessary to accommodate such phase transitions. Embryonic development in particular and its subsequent transition into the larval stage as well as the metamorphosis to a juvenile polyp require finely-tuned coordination of growth and development (Okubo *et al.*, 2007). Special signalling pathways initiate these steps. Neuropeptides, for example, are hormone-like substances that coordinate metamorphosis (Iwao *et al.*, 2002).

Acquisition of environmental parameters is part of the coral's lifecycle. This kind of information is even passed on to later generations. This pattern becomes most evident during asexual reproduction when offspring respond by establishing an extensive carpet of juvenile thickets, while others show preferences for high irradiance, and yet others again cope well with shadier conditions (Bak *et al.*, 1979).

Intracellular communication

Intracellular merger of symbiotic dinoflagellates with marine cnidarians is the most important prerequisite to ensure a highly productive and diverse reef ecosystem (Santos *et al.*, 2002; Takabayashia *et al.*, 2004). To assert that the effects of symbiosis are long-lasting, this

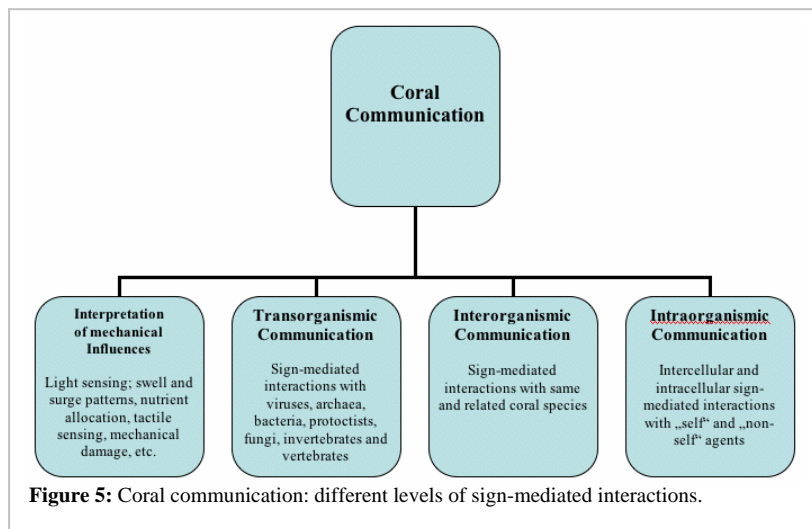
endocytotic process is coordinated by the ApRab5 gene. If, however, expression of this gene is disturbed, it leads to sudden separation and expulsion of the symbionts (Chen *et al.*, 2004, 2005).

Therefore, successful intracellular communication between the symbiogenetically assimilated unicellular eukaryotic cells must take place. It makes sure that external messages are transformed and forwarded to the endosymbionts. This information epigenetically influences the genetic expression of algal DNA. This in turn triggers a particular genetic reply, which leads to the production of signal molecules and generates an adequate response behaviour (Chen *et al.*, 2000).

It seems quite obvious that viroids, viruses and bacteria do interfere in this kind of intracellular communication. Under extreme circumstances, this interference can disturb or even cause the collapse of the coral host – as in the case of induced tissue bleaching by *Vibrio shiloi* in *Oculina patagonica* or *V. coralliilyticus* in *Pocillopora damicornis* (Rosenberg, 2004; Rozenblat *et al.*, 2004). Indeed most Symbiodinium species are infected with icosahedral double-stranded DNA-containing viruses. Under normal conditions they replicate without harming the host. Nonetheless, their latent virulence turns lytic (lethal to Symbiodinium) once water temperatures rise, thereby forcing the coral to expel their death endosymbionts, which also leads to tissue bleaching (Villarreal, 2005). The elimination of the symbiont from the host tissue can vary between exocytosis, host cell detachment and host cell apoptosis (Weis, 2008).

Microbial interactions on the other hand are reciprocal; this enables incorporation of specific genetic features into the intruder's genome as well as the export of microbial datasets into those of the host organism. It is very likely that the ability to incorporate different traits in each other is a key principle of symbiogenetic processes (Shackelton *et al.*, 2004).

On a macroscopic scale, corals possess a decentralised neural network (Westfall *et al.*, 1997). Alignment of this network is never static, but implies neuronal-like plasticity. According to the animal's past experiences, it is the capacity to modify (increase or decrease) the magnitude of their connections. Both memory-functions and long-lasting neuronal plasticity require new RNAs for the appropriate protein synthesis. Such neuronal plasticity implies that signals are relayed via the synapse to the nucleus. Therein, these signals are converted in order to evoke a change in gene transcription. Only then can the resulting changes (RNAs, proteins) be converted and sent back to the synapse to enable long-lasting change (Moccia *et al.*, 2003; Martin, 2004; Thompson *et al.*, 2004). It would be quite interesting to observe investigative efforts that



tackle the decoding functions responsible for intracellular communication processes within corals.

Variation in pigmentation among corals is primarily the result of a few genes and their associated proteins in the endosymbionts. It is worth noting that the various colour patterns are the result of phenotypic plasticity rather than species diversity, as previously thought (Kelmanson *et al.*, 2003).

The simple organismic structure of Cnidaria phylum groups them almost into the ‘archaic’ section of the animal line as they share most characteristics with a common ancestor as well as those of modern animals of higher taxa, i.e. large-scale coral-algal-sponge bioherms emerged some 450 million years ago (Hallock, 1997). It is worth mentioning that evolution, growth and development of the most important coral endosymbionts, i.e. members of the dinoflagellate genus *Symbiodinium*, assign to them a similar age. In this respect and based on the emergence of the first cnidarian precursors, the coral animal can be regarded as a ‘window into the past’ (Margulis *et al.*, 1988). Despite their simplicity, these animals have nearly as many genes as higher animal taxa – including vertebrates. Genome analysis has shown that most genes in Cnidaria can also be found in higher animals. This suggests that selective gene loss, or restriction of gene expression, rather than massive gene enrichment must be the main trigger for the emergence and evolution of higher animal taxa. This also implies that a selective decrease of the genes contributed to the sheer variety of animal species and paved the way for differentiation of the current known diversity in families, genera and species.

DISCUSSION

There is compelling evidence that evolution, growth and development of scleractinian corals largely depend

on successful trans-, inter- and intra-organismic communication processes (Fig. 5). Indeed, it is not the individual coral organism that accounts for prosperous long-term establishment within the wider coral reef ecosystem, but rather the relationship and exchange of information with its surrounding that enables the coral to survive in the long run. Only once these processes are successfully established can coordination and organisation within the coral animal and with other corals take place in a controlled manner. These processes enable corals to proliferate along with other organisms within the tropical reef ecosystem.

Communication processes should not be considered a mere exchange of information; rather they can be substantiated as diverse and manifold sign-mediated patterns of interaction. The use of such signs is subject to semiotic rules (Witzany, 2006). The underlying rules are quite reliable and conservative.

Proliferation of corals depends on successful communication, which means the communication processes may even fail. The response of a particular interaction can be misleading, e.g. interaction between the coral and its endo- and exosymbionts pretends to be mutualistic, only to draw a temporary advantage from a given interaction and/or even to damage the exploited organism substantially once a shift in environmental conditions takes place. It is obvious that this cannot be the general form of communication. If all symbionts were to behave in this way, no individual species could survive in the long run. In the majority of cases, there must be efficient and successful interactions that are beneficial or at least not harmful for all the participants involved. Anything else leads to unsuccessful communication, disease, and decay of the coral organism. Hence, large-scale inefficiency in communication inevitably leads to long-lasting decline of the entire reef ecosystem. From this perspective we suggest that a beneficial behaviour exists among corals that serves to warn neighbouring organisms of the same species, as has already been observed in many other sessile taxa (Kobayashi *et al.*, 2006).

Successful communication processes are guaranteed once all participants obey the semiotic rules in signal production and combination as well as transduction and interpretation-induced response behaviour. This does not imply, however, that these rules are devoid of errors or distortions. In contrast with natural laws, the rules of sign-usage are in principle subject to change. Violation of this kind leads to distorted messages, which induce missing or even erratic response behaviours. There are various ways in which a message can be misinterpreted:

(a) the sender incorrectly uses signs, they are mutilated and thereby miss the recipient, with the result that it hinders the receiver to respond to them appropriately; e.g. production of secondary metabolites or hormones or neurotransmitter at unusual times caused by stress. (b) the signs continuously encode messages which do not match with reality, e.g. messages indicating the settlement of opportunistic bacteria on the MPSL, increase in sea-surface temperature, etc; the receiver will become aware of the inappropriate content and over extended periods of time will ignore it and eventually adapt to this reality; (c) the signs continuously express a message which encodes for something else rather than what it is normally used for, e.g. ill corals generate semiochemicals which indicate e.g. nutrient availability although no nutrients are available. In the context of chronic violation of the underlying rules, however, the organisation of life-processes is no longer possible, i.e. communicative coordination of evolution, reproduction, growth and development, in and among organisms, is chronically disturbed.

If communication processes in trans-, inter- and intra-organismic levels can be discerned in the future, then the various levels of rules in which signs are used can be differentiated. It is obvious that the 'molecular syntax' (Witzany, 1995) of intracellular sign-usage is different from that of intercellular usage. Similarly, syntactic rules, which determine combinations of signalling molecules, differ in species-specific interactions from those used in trans-specific interactions. Embedded in the pragmatic level, i.e. in the ecological contexts and according to the behavioural contexts, different grammars are used. That is why a structurally identical message attains a partially different meaning when used in another context (Witzany 2005 a,b; Bresgen, 2007). In the future, the integration of this perspective could help to decipher coral-specific meanings of semiochemical messages in their entirety. The more we understand these communication processes and the meaning of the used signs, the deeper our understanding of the entire symbiology of corals will be.

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