

Heterotrophy in tropical scleractinian corals

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ABSTRACT

The dual character of corals, that they are both auto- and heterotrophs, was recognized early in the twentieth Century. It is generally accepted that the symbiotic association between corals and their endosymbiotic algae (called zooxanthellae) is fundamental to the development of coral reefs in oligotrophic tropical oceans because zooxanthellae transfer the major part of their photosynthates to the coral host (autotrophic nutrition). However, numerous studies have confirmed that many species of corals are also active heterotrophs, ingesting organisms ranging from bacteria to mesozooplankton. Heterotrophy accounts for between 0 and 66% of the fixed carbon incorporated into coral skeletons and can meet from 15 to 35% of daily metabolic requirements in healthy corals and up to 100% in bleached corals. Apart from this carbon input, feeding is likely to be important to most scleractinian corals, since nitrogen, phosphorus, and other nutrients that cannot be supplied from photosynthesis by the coral's symbiotic algae must come from zooplankton capture, particulate matter or dissolved compounds. A recent study showed that during bleaching events some coral species, by increasing their feeding rates, are able to maintain and restore energy reserves.

This review assesses the importance and effects of heterotrophy in tropical scleractinian corals. We first provide background information on the different food sources (from dissolved organic matter to meso- and macrozooplankton). We then consider the nutritional inputs of feeding. Finally, we review feeding effects on the different physiological parameters of corals (tissue composition, photosynthesis and skeletal growth).

Key words: scleractinian corals, heterotrophic nutrition, zooplankton, picoplankton, nanoplankton, photosynthesis, calcification.

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I. INTRODUCTION

The dual character of corals, that they are both auto- and heterotrophs, was recognized early in the twentieth Century (Yonge & Nicholls, 1931), particularly following the scientific reports of the Great Barrier Reef Expedition (1928-1929) of C.M. Yonge. These reports provided detailed information on reef coral physiology, especially on feeding behaviour and nutrition (Yonge, 1930*a,b*; Yonge & Nicholls, 1931) and also reviewed earlier literature on coral physiology (Vaughan, 1919). The role of zooplankton feeding was investigated by Goreau & Goreau (1960) and Goreau, Goreau & Yonge (1971). Since these famous works, numerous studies have confirmed that many species of corals are active heterotrophs (reviewed by Muscatine, 1973; Wellington, 1982; Sebens *et al.*, 1996; Grottoli, 2002; Houlbrèque *et al.* 2004*a,b*; Palardy, Grottoli & Matthews (2005, 2006), and that heterotrophy accounts for between 0 and 66% of the fixed carbon incorporated into coral skeletons (Muscatine *et al.*, 1989; Grottoli & Wellington, 1999). In addition to providing carbon, feeding is likely to be important to most scleractinian corals, since nitrogen, phosphorus, and other nutrients that cannot be supplied from photosynthesis by the coral's symbiotic algae must come from capture of zooplankton, particulate matter or dissolved compounds (Muscatine & Porter, 1977; Porter *et al.*, 1984; Davies, 1991; Ferrier, 1991; Fabricius, Yahel & Genin, 1995; Grottoli & Wellington, 1999; Lesser *et al.*, 2000). Heterotrophic carbon can also become a significant energy source for corals when photosynthetic carbon is unavailable, during bleaching events or in deep and/or turbid waters (Falkowski *et al.*, 1984; Bythell, 1988; Muscatine & Weis, 1992; Anthony & Fabricius, 2000; Leletkin, 2000; Anthony & Connolly, 2004; Anthony, 2006).

This review assesses the importance and effects of heterotrophy in tropical scleractinian corals. We first provide background information on the different food sources (from dissolved organic matter to meso- and macrozooplankton). We then consider the nutritional inputs of feeding. Finally, we review its effects on the different physiological parameters of corals (tissue composition, photosynthesis and skeletal growth).

II. FOOD SOURCES

Reviews on coral nutrition by Goreau *et al.* (1971) and Muscatine (1973) showed the extremely diverse multitrophic pathways of corals, acting as primary producers, carnivores, detritus feeders and also dissolved organic carbon scavengers. Many corals are known to be effective zooplankton feeders

(Sebens, Witting & Helmuth, 1997), capturing particles upon contact by nematocyst discharges, tentacle grabbing, or mucus adhesion (Yonge, 1930*a*; Abe, 1938; Lewis & Price, 1975; Lewis, 1977; Sebens *et al.*, 1998). Corals are also able to ingest particles from a wide size range (Anthony, 1999; DiSalvo, 1992; Sorokin, 1973; Sebens *et al.*, 1996; Ferrier-Pagès *et al.*, 1998; Palardy *et al.*, 2005). This variety of nutrition sources includes dissolved and particulate organic matter (DOM and POM) (Lewis, 1977; Ferrier, 1991; Al-Moghrabi, Allemand & Couret, 1993; Mills & Sebens, 1997; Anthony, 1999; Anthony & Fabricius, 2000), picoplankton (Sorokin, 1973; Bak *et al.*, 1998; Ferrier-Pagès *et al.*, 1998; Houlbrèque *et al.*, 2004*b*), nanoplankton such as ciliates (Ferrier-Pagès *et al.*, 1998; Houlbrèque *et al.*, 2004*b*) and mesomacro-zooplankton (Coles, 1969; Johannes, Cole & Kuenzel, 1970; Johannes & Tepley, 1974; Porter, 1974; Sebens *et al.*, 1996; Palardy *et al.*, 2005, 2006) (Fig 1 illustrates the different plankton size classes included in the diet of scleractinian corals).

(1) Dissolved organic matter

Numerous symbiotic coral species are able to take up dissolved organic matter (DOM), mainly in the form of carbohydrates, dissolved free amino acids (DFAA) and urea, even when DOM is in nanomolar concentrations (Stephens, 1960, 1962; Stephens & Schinske, 1961; Goreau *et al.*, 1971; Al-Moghrabi *et al.*, 1993; Ferrier, 1991, Grover *et al.*, 2006, 2008). Stephens (1960) measured the removal of ¹⁴C-labelled D-glucose from solution in sea water by the coral *Fungia* sp.. He showed that this species was capable of removing glucose from solution even at low concentrations and suggested that by utilizing naturally occurring carbohydrates in sea water, some coral species could obtain sufficient material to meet maintenance requirements in selected locations. Similarly, symbiotic corals have developed adaptations to take up the ammonium or urea by-products of animal metabolism, suggesting a co-evolution process between host and symbionts (Furla *et al.*, 2005).

Studies on DOM uptake rates by corals have mostly concerned urea (Wafar *et al.*, 1985, Wafar, Wafar & Raj Kumar, 1993; Grover *et al.*, 2006) and DFAA (Ferrier, 1991; Al-Moghrabi, *et al.*, 1993; Hoegh-Guldberg & Williamson, 1999; Grover *et al.*, 2008). Urea concentrations in sea water range from 0 to 13 $\mu\text{mol l}^{-1}$, with very low values in open ocean systems (Bronk, 2002). DFAA concentrations are even lower, ranging from 20 nmol l^{-1} to 1 $\mu\text{mol l}^{-1}$ (Palenik & Morel, 1990; Ferrier, 1991). However, since they are continuously recycled in the water column by micro-heterotrophs and also by larger animals such as fish, they are generally considered an important nitrogen source for phytoplankton (Maguer, Lecorre & Madec, 1996; Berman & Bronk, 2003) and zooxanthellae (Grover *et al.*, 2006,

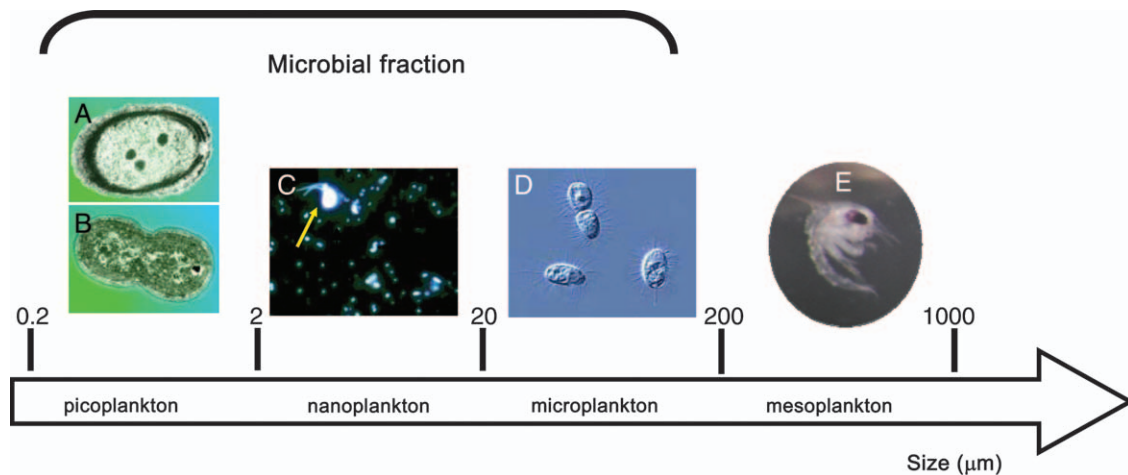


Fig. 1. Plankton size classes: picoplankton, nanoplankton, microplankton and mesozooplankton included in the diet of scleractinian corals. (A, B) Scanning electron micrographs of (A) *Prochlorococcus* sp. (0.6 μm) and (B) *Synechococcus* sp. (1 μm) (<http://www.lbl.gov/Archive/JGI-microbe-clues.html>). (C) Epifluorescence microscope image showing one nano-flagellate cell indicated by a yellow arrow (previously stained with di amino phenyl indol (DAPI) and exposed to ultraviolet excitation). Image of (D) ciliates (mean total length is 100 – 200 μm) taken under phase contrast microscope and (E) crab zoea (mean total length is 1000 μm).

2008). Uptake of urea by the symbiotic association increases when urea concentrations and light levels increase (Grover *et al.*, 2006), although the value of the carrier affinity ($K_m = 1 \mu\text{mol l}^{-1}$) indicates that corals are well adapted to the low levels of urea usually found in sea water. At an *in situ* urea concentration of $0.3 \mu\text{mol l}^{-1}$, the uptake rate is equal to $0.06 \text{ nmol N h}^{-1} \text{ cm}^{-2}$. Several studies presented evidence for DFAA stimulating feeding in corals (Mariscal & Lenhoff, 1968; Goreau, 1961; Goreau *et al.*, 1971; Lehman & Porter, 1973). For example, Goreau *et al.* (1971) discovered that low concentrations of glycine, alanine, phenylalanine and leucine trigger a typical feeding response, including extension of tentacles, swelling of the coenosarc, and sometimes extrusion of mesenterial filaments, in several Caribbean coral species. For the massive reef-building coral *Montastrea cavernosa*, glutamic acid is by far the most successful feeding activator, promoting tentacle extension (Lehman & Porter, 1973). Schlichter (1982) showed that the carbon and nitrogen within DFAA was an important energetic source for corals. More recent studies found that the uptake of DFAA was non-selective (Ferrier, 1991), and was light and concentration dependent (Al-Moghrabi *et al.*, 1993; Grover *et al.*, 2008). It also involves a membrane carrier, with a low affinity of $1.32 \mu\text{mol l}^{-1}$ appropriate to the low concentrations measured in the environment (Al-Moghrabi *et al.*, 1993; Grover *et al.*, 2008). Uptake rates ranged from 4.5 to $100 \text{ nmol cm}^{-2} \text{ h}^{-1}$ (Ferrier, 1991; Grover *et al.*, 2008), suggesting that DFAA represent a non-negligible contribution to the nitrogen input for these invertebrates (Ferrier, 1991; Al-Moghrabi *et al.*, 1993).

(2) Detrital particulate organic matter

Surface sediments on coral reefs contain bacteria, microbial exudates, protozoa, interstitial invertebrates, microalgae and sorbed and detrital organic matter (Lopez & Levinton,

1987) that are all potential food sources to corals. Several recent studies showed that corals can feed on, and benefit from, particles in suspension or trapped in the sediment (Anthony, 1999; Anthony & Fabricius, 2000), especially corals inhabiting turbid near-shore areas (Anthony, 2000). For these corals, rates of sediment ingestion are a linear function of sediment load, with an assimilation efficiency of 50-80% (Anthony, 2000). Active sediment ingestion followed by digestion of its organic content was revealed during experiments using sediment labeled with Fluoresceine or ^{14}C in the corals *Fungia horrida* (Rosenfeld, Bresler & Abelson (1999) and *Acropora millepora* (Anthony, 2000). Mills & Sebens (2004) and Mills, Lipschultz & Sebens (2004) showed that suspended particulate matter or benthic sediments layered onto the surfaces of six different scleractinian coral species (*Montastrea franksi*, *Diploria strigosa*, *Madracis mirabilis*, *Siderastrea siderea*, *Agaricia agaricites*, and *Porites astreoides*) was ingested and nitrogen assimilated.

(3) Live particulate organic matter

For a long time, scientists did not consider zooplankton a major nutritive source for corals. This lack of interest was partially explained by the fact that reef zooplankton densities were underestimated. The majority of zooplankton sampling was conducted during the day and biomass calculations only included oceanic planktonic species (Johannes *et al.*, 1970; Alldredge & King, 1977). Recently, more appropriate zooplankton sampling techniques have provided more accurate information on zooplankton concentrations (Heidelberg, Sebens & Purcell, 2004) suggesting that plankton could play a major role in coral metabolism.

(a) Mesomacro-zooplankton and phytoplankton

Corals are voracious predators of zooplankton (Fig. 2) (Titlyanov *et al.*, 2000a; Grottooli, 2002; Ferrier-Pagès *et al.*,

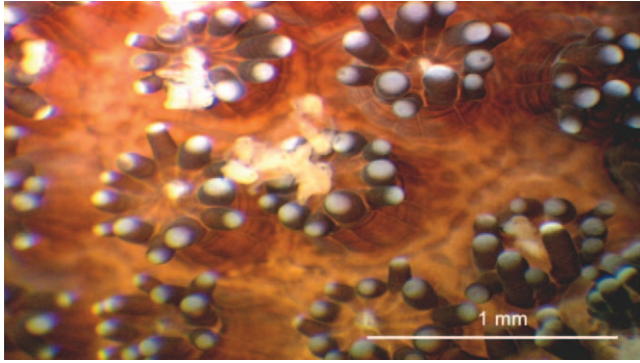


Fig. 2. Polyps of the scleractinian coral *Stylophora pistillata*, catching nauplii of the crustacean *Artemia salina*. (Photo by É. Tambutté, CSM, Monaco)

2003; Fabricius & Metzner, 2004; Palardy *et al.*, 2005, 2006; Grottoli, Rodrigues & Palardy, 2006), they can ingest from 0.5 to two prey items per polyp per hour of ingestion (Sebens *et al.*, 1996). Several studies measured substantial near-bottom depletion of mesozooplankton over different coral reefs, suggesting an intense grazing by benthic organisms, among which corals play a non-negligible role (Glynn, 1973; Hamner *et al.*, 1988; Yahel, Yahel & Genin, 2005b).

The zooplankton assembly over coral reefs consists of a complex, patchy and highly dynamic mixture of pelagic plankton advected to the reef (Tranter & George, 1969; Glynn, 1973; Sammarco & Crenshaw, 1984; Hamner *et al.*, 1988; Carleton, Brinkman & Doherty, 2001; Heidelberg *et al.*, 2004), eggs and larvae produced by reef inhabitants (Vaissière & Seguin, 1984; Echelman & Fishelson, 1990), and demersal plankton (Alldredge & King, 1977). This last group, consisting of organisms found near or within the substratum during the day and ascending into the water column at night, is especially conspicuous over coral reefs (Alldredge & King, 1977; Porter & Porter, 1977; McWilliam, Sale & Anderson, 1981; Ohlhorst, 1982; Lewis & Boers, 1991; Carleton & Hamner, 2007; Hamner, Colin & Hamner, 2007). At sunset, zooplankton biomass starts to increase rapidly (reviewed by Heidelberg *et al.*, 2004, Yahel, Yahel & Berman, 2005a; Yahel *et al.*, 2005b). The abundance of copepods of 500–700 μm in size, already relatively high during the daytime, is fivefold enhanced during the night (Yahel *et al.*, 2005a). A greater than fourfold augmentation in the abundance of 500–710 μm zoae and other demersal crustaceans as well as larger zooplankton (>710 μm) (e.g. copepods, zoea, tunicates, and polychaetes) also characterizes the transition to nocturnal conditions (Yahel *et al.*, 2005a).

It has therefore been assumed that corals feed primarily during the night, when zooplankton densities at the anthozoans' depth are highest (Sebens & DeRiemer, 1977; Heidelberg *et al.*, 2004; Yahel *et al.*, 2005a,b). Several coral species expand their tentacles only at night (Porter, 1974; Lewis & Price, 1975). In the Gulf of Aqaba, Red Sea, the massive corals *Favites* sp., *Favia fava*, and *Platygyra* spp. begin to expand their tentacles 15–45 min after sunset, reaching full expansion mode 60 min after sunset (Yahel *et al.*, 2005a).

However this does not apply to all coral species; most *Porites* species have tentacles extended for feeding during both the night and day (Johannes & Tepley, 1974).

The ability of different coral species to feed on zooplankton has been quantified using several methodologies (Coles, 1969; Johannes *et al.*, 1970; Porter, 1974, 1976; Lewis & Price, 1975; Lewis, 1976; Sebens & Johnson, 1991; Helmuth & Sebens, 1993; Sebens *et al.*, 1996, 1997, 1998; Palardy *et al.*, 2005, 2006; Grottoli *et al.*, 2006). In laboratory conditions, Coles (1969) measured for the first time the energy provided by *Artemia salina* prey to corals during 10 hr feeding episodes and calculated that the three tropical corals tested were able to ingest several times as many calories daily from *Artemia salina* prey than they lose by respiration. Later, Lewis (1976) tested the ability of 15 species of Atlantic reef corals to act as suspension feeders by removing particles from sea water in culture vessels. He concluded that the rates of particle clearance of the coral *Agaricia agaricites* were influenced by both current velocity and type of food.

According to Porter (1976), the ability of a species to capture zooplankton is determined by its morphology. Species with low surface:volume (S:V) ratios (mounding, solitary, clusters) and large polyps would be zooplankton-capture specialists whereas species with high S:V ratios (branching, plating) and small polyps are more likely to be “light-capture” specialists. However, field observations in the Caribbean Sea (Sebens *et al.*, 1996, 1998) and the Gulf of Panama (Palardy *et al.*, 2005, 2006) contradict the model of Porter (1976). Sebens *et al.* (1996) showed that branching corals with small polyps capture more zooplankton per unit biomass than do mounding corals with much larger polyps. Indeed, small polyp size alone does not appear to limit zooplankton feeding (Sebens *et al.*, 1996), although it may limit the upper size captured for some kinds of prey. The type of tentacles and nematocysts present are likely to be more important for prey capture than polyp size alone. Two studies by Palardy *et al.* (2005, 2006) performed on the feeding rates of three different species of Eastern Pacific corals (*Pocillopora damicornis*, *Pavona clavus* and *Pavona gigantea*) demonstrated that the assemblage of captured zooplankton did not differ among species, depths, or seasons but that feeding rate increased with zooplankton abundance, depth and temperature. In addition, feeding rates were higher as S:V decreased and were independent of polyp size. Thus they concluded that feeding rate variations are due to increased feeding effort and not due to S:V ratio or polyp size.

The type of zooplankton found in the gut contents of corals is diverse (Porter, 1974; Johannes & Tepley, 1974; Johnson & Sebens, 1993; Sebens *et al.*, 1996; Palardy *et al.*, 2005, 2006) and does not seem systematically to reflect prey availability. Porter (1974) found a large percentage of copepods in coelenteron contents of *Montastrea cavernosa* (polyp diameter >10 mm), as did Johnson & Sebens (1993) for the species *Meandrina meandrites* (polyp diameter around 10 mm). On the other hand, despite accounting for at least 61% of individuals in the zooplankton community, no copepods were captured by the investigated corals of a shallow reef at Isla Contadora in the Gulf of Panamá (Palardy *et al.*, 2006). Indeed the two species investigated:

Pocillopora damicornis (1 mm diameter polyps) and *Pavona gigantea* (3 mm diameter polyps) both fed preferentially on isopods, amphipods, and crab zoeae, (200–400 µm length), despite the threefold difference in their polyp size (Palardy *et al.*, 2006). Similarly, Sebens *et al.* (1996) measured high capture rates for relatively uncommon large prey, concluding that small strong-swimming zooplankton such as copepods (especially *Oithona* sp.) are captured much less readily, even when extremely abundant. Such copepods have avoidance or escape behaviours that make them difficult for corals to capture (Sebens *et al.*, 1996).

Studies of pelagic-benthic coupling in coral reefs have focused on zooplankton rather than phytoplankton. Ingestion of phytoplankton has only been demonstrated for soft corals (Fabricius *et al.*, 1995), but not for scleractinian species.

(b) Pico- and nanoplankton

Coral gut content examination does not allow estimation of the grazing rates of small and soft-bodied prey such as pico- and nanoplankton, because they are rapidly digested. Only a limited number of studies have therefore investigated the ability of scleractinian corals to feed on pico- and nanoplankton (<100 µm) including bacteria, cyanobacteria, flagellates and ciliates (Sorokin, 1973, 1991; Farrant *et al.*, 1987; Ferrier-Pagès *et al.*, 1998; Bak *et al.*, 1998; Houlbrèque *et al.*, 2004b). However, these microbial communities play a key role in marine food webs (Pomeroy, 1974) since they are the main contributors to pelagic planktonic communities in terms of biomass (Stockner & Antia, 1986; Ducklow, 1990; Charpy, 2005) and production (Platt, Rao & Irwin, 1983). In reef waters, concentrations may be as high as 10^6 bacteria ml⁻¹, 10^4 – 10^5 cyanobacteria ml⁻¹ and up to 10^4 total flagellates ml⁻¹ (Ducklow, 1990; Sorokin, 1991; Ferrier-Pagès & Gattuso, 1998; Tada *et al.*, 2003). Due to their rapid growth rates, heterotrophic bacterioplankton account for a significant part of the carbon and nitrogen flow to upper trophic levels (Azam *et al.*, 1983).

Sorokin (1973) was one of the first to suggest that corals consume organic phosphorus in the form of planktonic bacteria rather than taking up inorganic phosphorus at the same concentrations. Herndl & Velimirov (1985) found a large bacterial population within the coelenteron of four anthozoan species, suggesting that corals farm and feed on bacteria. This has been confirmed under culture conditions (Farrant *et al.*, 1987; Sorokin, 1991; Ferrier-Pagès *et al.*, 1998). In particular, the importance of pico- and nanoplankton as a nutrient source for scleractinian corals has been highlighted in flume studies (Houlbrèque *et al.*, 2004b), where three different scleractinian species, symbiotic and asymbiotic, with small or large polyps, showed a significant uptake of microorganisms. Among these microorganisms, nanoflagellates seemed to be a major food source in terms of carbon and nitrogen content. For the model species *Stylophora pistillata*, the ingestion of pico- and nanoplankton was shown to bring three times more nitrogen than dissolved sources (ammonium, nitrate and DFAA) (Fig. 3) (Ferrier, 1991; Hoegh-Guldberg & Williamson, 1999; Grover *et al.*, 2002, 2003). *In situ* studies showed that pico-nanoplankton as well as phytoplankton were actively removed from waters flowing above reef flats

(Bak *et al.*, 1998; Moriarty *et al.*, 1985; Ayukai, 1995; Gast *et al.*, 1998; Yahel *et al.*, 1998; Genin *et al.*, 2002; Houlbrèque *et al.*, 2006), suggesting a potential role of corals in this ingestion although other potential grazers such as sponges, bivalves, tunicates and soft corals will also be involved (Fabricius *et al.*, 1995; Ribes *et al.*, 2005; Houlbrèque *et al.*, 2006; Ribes & Atkinson, 2007).

For scleractinian corals, the major mechanism involved in the uptake of protozoans, microplankton and other small prey is the production of mucus nets (Muscatine, 1973; Ferrier-Pagès *et al.*, 1998). Many corals feed on fine particles caught in mucus films or strands which are drawn by cilia into the polyp's mouth (Lewis & Price, 1975; Lewis, 1978). Kramarsky-Winter *et al.* (2006) showed that the surfaces of the large-polyped coral species *Favia fava* and *Fungia granulosa* were covered by a layer of aggregate-like microorganisms. The highest density of microorganisms occurred in the region of the polyp mouth, suggesting their utilisation by the coral host as a food source. Particle trapping and bacterial colonization may further enhance the value of mucus aggregates as a food source (Ferrier-Pagès *et al.*, 2000; Wild *et al.*, 2004; Huettel, Wild & Gonelli, 2006) for corals. For example, in the reef waters of Heron Island it has been shown that within only 2–3 h, bacterial density in the mucus exceeded that of ambient sea water by four orders of magnitude (Huettel *et al.*, 2006).

III. HETEROTROPHIC NUTRIENT INPUTS

The photosynthates translocated by the zooxanthellae are sometimes considered “junk food” (Falkowski *et al.*, 1984) deficient in nitrogen, phosphorus and amino acids (Battey & Patton, 1987), which are essential nutrients for growth (Falkowski *et al.*, 1984; Rinkevitch, 1989; Davies, 1991). External food supplies are considered to be a major nutritive source of nitrogen, phosphorus (Farrant *et al.*, 1987; Sorokin, 1991; Ayukai, 1995; Sebens *et al.*, 1996), and also carbon for corals (Porter, 1976; Sorokin, 1993; Grottoli *et al.*, 2006).

(1) Organic nitrogen input

Ingestion of dissolved and particulate organic matter represents an important source of nitrogen for the symbiotic association (Rees & Allard, 1989; Szmant, Ferrier & Fitzgerald, 1990), especially for deep corals (Muscatine & Kaplan, 1994) or those living in inshore waters (Sammarco *et al.*, 1999). Indeed, the analysis of the stable isotopes of nitrogen ($\delta^{15}\text{N}$) in coral tissue revealed a tendency for depletion in $\delta^{15}\text{N}$ in many coral species as depth increases, following the pattern of depletion in $\delta^{15}\text{N}$ of the zooplankton prey (Muscatine & Kaplan, 1994). It suggests that deep corals rely mainly on heterotrophy for their acquisition of nutrients. This is not a general rule for surface corals, for which no depletion in $\delta^{15}\text{N}$ was measured (Yamamuro, Kayanne & Minagawa, 1995), except for those living in inshore waters and receiving large amounts of $\delta^{15}\text{N}$ depleted terrestrial particulate and dissolved organic matter (Sammarco *et al.*, 1999).

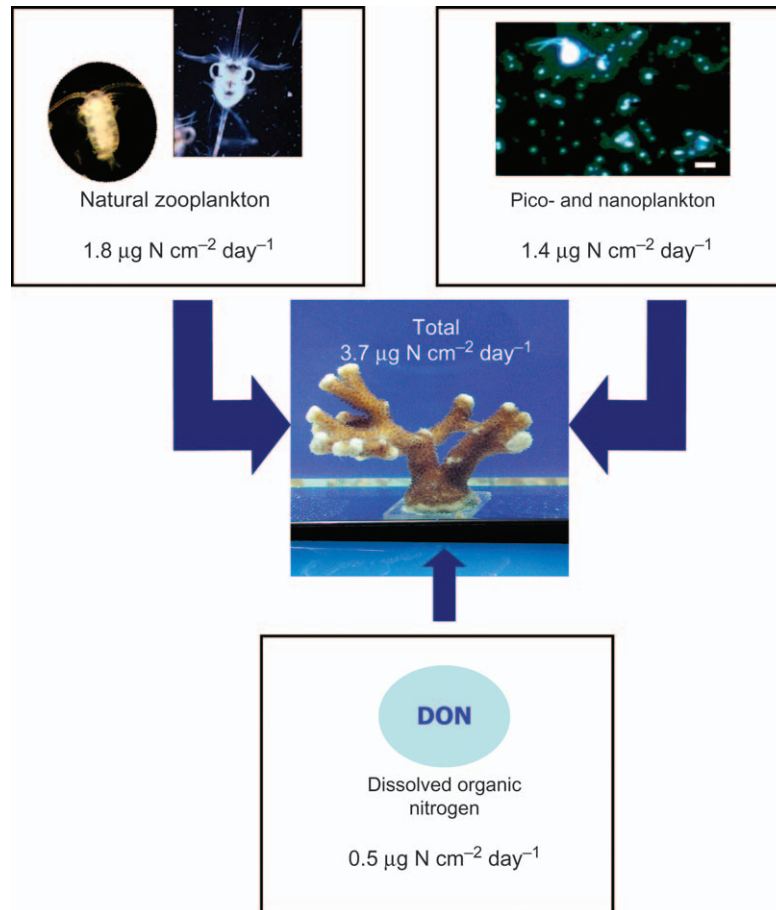


Fig. 3. Daily nitrogen inputs in the scleractinian coral *Stylophora pistillata*. For all following estimations, we took an average of 50 polyps per cm^{-2} for this species. *S. pistillata* fed on natural zooplankton (approximately 1500 prey l^{-1}) can gain more than $1.8 \mu\text{g N cm}^{-2} \text{day}^{-1}$ (Ferrier-Pagès *et al.*, 2003). According to Houlbrèque *et al.* (2004b), ingestion of pico- and nanoplankton by this species provides up to $1.4 \mu\text{g N cm}^{-2} \text{day}^{-1}$. Dissolved organic nitrogen, at the lowest concentrations found in seawater (approximately $0.2\text{--}0.3 \mu\text{mol l}^{-1}$) contributes $0.5 \mu\text{g N cm}^{-2} \text{day}^{-1}$ (Grover *et al.*, 2008). So in total, feeding can provide up to $3.7 \mu\text{g N cm}^{-2} \text{day}^{-1}$ to the colonies of *S. pistillata*, depending on environmental conditions.

Direct uptake of nitrogen from natural particulate matter (PM) was demonstrated experimentally by Mills *et al.* (2004), using ^{15}N -labelled PM in the mounding species *Siderastrea radians*, *Montastrea franksi* and *Diploria strigosa*; uptake rates ranged from $0.80 \mu\text{g Particulate Nitrogen (PN) cm}^{-2} \text{h}^{-1}$ in *S. radians* to as high as $13 \mu\text{g PN cm}^{-2} \text{h}^{-1}$ in *M. franksi*. Houlbrèque *et al.* (2004b) also estimated that the ingestion of small planktonic cells (pico- and nanoplanktonic cells) by *Stylophora pistillata* can provide up to $1.2 \text{ ng N polyp}^{-1} \text{ h}^{-1}$ (Fig. 3). For this species, it has been calculated that heterotrophic nutrition can provide up to $3.7 \mu\text{g N cm}^{-2} \text{day}^{-1}$. Relatively few studies however have examined nitrogen assimilation efficiencies for the different types of prey ingested by tropical scleractinian corals. Nitrogen assimilation rates of 40–100% and 80–100% have been reported for deposited and fine suspended particulate matter, respectively (Mills, 2000; Mills & Sebens, 2004). Bythell (1988) calculated that particulate feeding is required to satisfy 70% of the nitrogen demand in *Acropora palmata* and Anthony (1999) estimated stoichiometrically, from carbon assimilation, that suspended particulate matter

could provide up to 33% of the nitrogen required for growth in *Pocillopora damicornis*.

With the exception of Mills *et al.* (2004), who did not find nitrogen transfer to the symbiotic zooxanthellae, it is now widely established that both partners of the symbiosis benefit from the input of particulate nitrogen. This transfer was, for example, measured in a tropical scleractinian coral, *Oculina diffusa*, using *Artemia salina* nauplii labeled with the stable isotope tracer ^{15}N (Piniak & Lipschultz, 2004). In this study, zooxanthellae were strongly labeled with ^{15}N approximately 4 h after feeding; an insufficient period for recycling of ^{15}N to occur (i.e. via host digestion, synthesis into host macromolecules, catabolism, excretion and uptake by zooxanthellae). This rapid appearance of prey nitrogen in zooxanthellae was thought to be due to direct uptake of prey nitrogen digested within the coelenteron, probably as NH_4^+ , rather than following host assimilation. An estimation of nitrogen fluxes in the zooxanthellae, taking into account their growth rates and dissolved inorganic nitrogen input showed that 90% of the nitrogen used by zooxanthellae in *Stylophora pistillata* is recycled from the host

(Rahav *et al.*, 1989). In the same way, Rodrigues & Grottoli (2006) demonstrated that increases in $\delta^{15}\text{N}$ of zooxanthellae following bleaching were consistent with increases in nitrogen uptake by corals to support zooxanthellae recovery and mitotic cell division. Thus corals can upregulate dissolved inorganic nitrogen acquisition to stimulate zooxanthellae growth when needed.

(2) Organic phosphorus input

Few studies have focused on phosphorus input by feeding. It is widely known that zooxanthellae contribute to phosphorus acquisition by recycling it from the metabolic waste products of the host (Yonge & Nicholls, 1931). However, by measuring fluxes of dissolved phosphorus into un-fed corals, D'Elia (1977) showed that this uptake was low and suggested that hermatypic corals would require some particulate phosphorus, in the form of meso- or micro-zooplankton, to satisfy their requirements for maintenance and growth. This was also suggested by Sorokin (1973), who had demonstrated previously that corals were able to consume organic phosphorus in the form of planktonic bacteria (around $3 \mu\text{g day}^{-1}$).

(3) Organic carbon input

It is generally accepted that the symbiotic association between corals and zooxanthellae is fundamental to the development of coral reefs in oligotrophic tropical oceans (Muscatine & Porter, 1977; Davies, 1991; Grottoli & Wellington, 1999; Lesser *et al.*, 2000), because zooxanthellae transfer the major part of their photosynthates (carbohydrate products) to the coral host (Muscatine, 1990). The debate within the literature however concentrates on whether heterotrophy or autotrophy is the major source of carbon (Coles, 1969; Johannes *et al.*, 1970; Goreau *et al.*, 1971; Johannes, 1974; Lewis & Price, 1975; Porter, 1976; Lewis, 1977; Edmunds & Davies, 1986; Sorokin, 1993; Anthony, 1999; Leletkin, 2000; Grottoli *et al.*, 2006). Different estimations concerning heterotrophic carbon supply vary from a non-significant contribution (Johannes *et al.*, 1970; Edmunds & Davies, 1986), through meeting 15–35% of daily metabolic demand (DME) in healthy corals (Porter, 1976; Sorokin, 1993; Grottoli *et al.*, 2006) to up to 100% in bleached corals (Grottoli *et al.*, 2006). It was first suggested that heterotrophic carbon does not represent a significant energy source for corals living in shallow waters but becomes important for corals inhabiting deep or turbid waters or in low-light environments (Falkowski *et al.*, 1984; Bythell, 1988; Muscatine & Weis, 1992; Anthony & Fabricius, 2000; Leletkin, 2000; Anthony & Connolly, 2004; Anthony, 2006). This theory was partially confirmed by Muscatine *et al.* (1989), who showed that as depth increased, the difference between zooxanthellae and animal tissue $\delta^{13}\text{C}$ increased and the latter approached the $\delta^{13}\text{C}$ of oceanic particulate organic carbon. The fact that coral feeding increases with depth has been demonstrated directly by Palardy *et al.* (2005) and indirectly using isotope analyses by Grottoli & Wellington (1999).

Other observations however tend to support the idea that heterotrophy can be important at all depths. Based on plankton capture rates, and considering an energy equivalent of 20.8 kJ g^{-1} per ingested holoplanktonic copepods (Webber & Roff, 1995), Witting (1999) calculated that zooplankton ingestion represented a non-negligible energy input (from 0.8 to $1.8 \text{ J cm}^{-2}\text{day}^{-1}$) for the growth of two scleractinian corals, *Montastrea annularis* and *Porites furcata*. Finally, Grottoli *et al.* (2006) showed that feeding rates on zooplankton can increase dramatically in bleached corals and can provide corals with up to 100% of their daily metabolic demand (daily animal respiration rate). This was a conservative estimate of the role of heterotrophy in the coral diet as it did not include anything smaller than $50 \mu\text{m}$ or possible feeding rates during the day for corals with continuous polyp extension. Thus the role of heterotrophy in the coral metabolic budget is probably much higher than current calculations show.

(4) Compensation heterotrophy/autotrophy

Photosynthesis processes and prey capture have long been considered as two independent nutritional modes but it has now been demonstrated that they are closely linked. Indeed, each partner of the symbiotic association is able to use nutrients obtained by auto- or heterotrophy (Anthony & Fabricius, 2000).

Several studies have investigated the ability of corals to shift from phototrophy to heterotrophy (Clayton & Lasker, 1982; Anthony, 1999; Anthony & Fabricius, 2000; Piniak, 2002; Palardy *et al.*, 2005; Grottoli *et al.*, 2006; Rodrigues & Grottoli, 2007). Clayton & Lasker (1982) concluded that the quantity of ingested plankton directly depended on photosynthate availability while Piniak (2002) found symbiotic and asymmetric forms of the temperate coral *Oculina arbuscula* to have equivalent prey-capture rates, independent of their symbiotic condition and of the energy derived from photosynthesis.

Nevertheless, it is now widely thought that the ability to switch from autotrophic to heterotrophic carbon sources is species-specific. Anthony (1999) and Anthony & Fabricius (2000) revealed that only certain symbiotic coral species show heterotrophic plasticity and demonstrated that the ability to change trophic mode of some coral species is a mechanism for sustaining a positive energy balance in turbid environments. Two zooxanthellate coral species (*Goniastrea retiformis* and *Porites cylindrica*) were exposed for two months to shaded and unshaded conditions and a range of suspended particulate matter (SPM) levels. In response to prolonged shading, *G. retiformis* more than doubled its rate of particle feeding and gained tissue and skeletal mass at all experimental light and SPM levels while for *P. cylindrica*, carbon loss due to shading was not compensated by particle feeding and resulted in energy deficiency.

Emerging work clearly shows that shifts from photoautotrophy to heterotrophy also occur with depth (Palardy *et al.*, 2005) and bleaching (Grottoli *et al.*, 2006). Grottoli *et al.* (2006) demonstrated that in the absence of zooxanthellae (during bleaching events), *Montipora capitata* colonies increased feeding rates and acquired large quantities of heterotrophic carbon in excess of daily metabolic energy requirements. It

has been concluded that species that can significantly increase their heterotrophic input of carbon during bleaching and recovery have a significantly better capacity to maintain and restore energy reserves (as lipids, carbohydrates and proteins) (Grottoli *et al.*, 2006, Rodrigues & Grottoli, 2007) compared to species like *Porites compressa*, which are largely dependent on photosynthetically fixed carbon (Rodrigues & Grottoli, 2007). It is important to note that even healthy *P. compressa* and *P. lobata* meet 20-40% of their daily metabolic demands heterotrophically (Grottoli *et al.*, 2006), meaning that zooplankton represents a non-trivial carbon input.

IV. EFFECTS OF HETEROTROPHY ON CORAL PHYSIOLOGY

The importance of autotrophy for coral metabolism has been widely studied during the last thirty years (Muscatine

& Porter, 1977; Muscatine, 1980; Falkowski *et al.*, 1984; Muscatine *et al.*, 1984; Cook, D'Elia & Muller-Parker, 1988; Davies, 1991; Muller-Parker, Cook & D'Elia, 1994a; Muller-Parker *et al.*, 1994b; Marubini, 1996; Swanson & Hoegh-Guldberg, 1998; Wang & Douglas, 1998; Cook & Davy, 2001; LaJeunesse, 2001). On the contrary, the number of studies which have focused on the effects of feeding on coral metabolism (photosynthesis, respiration, skeletal and tissue growth) is much more limited. Nevertheless, it has been clearly demonstrated that feeding induces significant changes in many physiological parameters and that both host and algal symbionts respond rapidly to changes in food availability (Fitt, 2000; Houlbrèque, Tambutté & Ferrier-Pagès, 2003; Houlbrèque *et al.*, 2004a,b). Fig 4 summarises these effects of feeding on the main physiological parameters of scleractinian corals. While it is well known that nutrients are continuously exchanged between the two symbiotic partners (Muscatine, 1990), only six studies have focused on the simultaneous effects of heterotrophy on the algal and

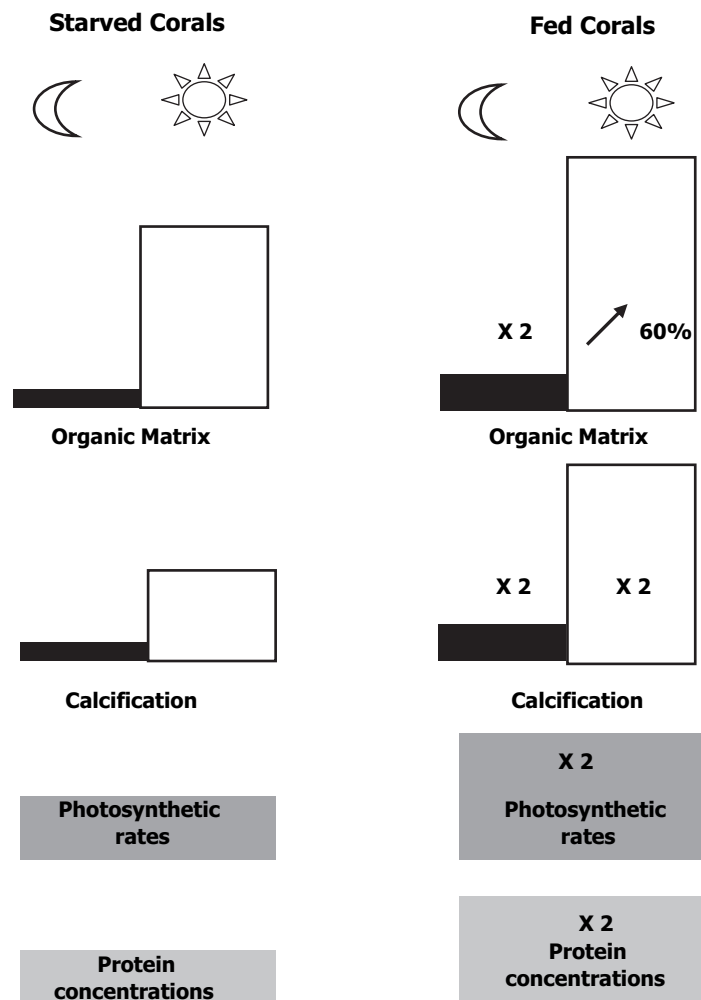


Fig. 4. Summary of studies on Scleractinian corals (Dubinsky *et al.*, 1990; Witting, 1999; Titlyanov *et al.*, 2000a,b, 2001; Ferrier-Pagès *et al.*, 2003; Houlbrèque *et al.*, 2003, 2004a) showing that feeding induces significant changes in many physiological parameters. Compared to starved corals, fed corals showed: (1) twofold greater protein concentrations and photosynthetic rates per unit skeletal surface area; (2) twofold higher dark and light calcification rates; (3) twofold greater organic matrix synthesis in the dark and a 60% increase in the light.

animal components (Witting, 1999; Ferrier-Pagès *et al.*, 2003; Houlbrèque *et al.*, 2003, 2004a; Rodrigues & Grotoli, 2006, 2007) and the relative importance of phototrophy *versus* heterotrophy remains only partially understood.

(1) Effects of heterotrophy on coral tissue

Heterotrophy tends to increase tissue synthesis levels (Jacques & Pilon, 1980; Sebens & Johnson, 1991; Al-Moghrabi, Allemand & Couret, 1995; Kim & Lasker, 1998; Anthony & Fabricius, 2000; Ferrier-Pagès *et al.*, 2003; Houlbrèque *et al.*, 2003, 2004a). Indeed, an increase in protein concentration with feeding has been reported for numerous tropical corals (Clayton & Lasker, 1984; Al-Moghrabi *et al.*, 1995). In laboratory experiments with *Stylophora pistillata*, Ferrier-Pagès *et al.* (2003) and Houlbrèque *et al.* (2003, 2004a) highlighted a two to eightfold increase in protein concentration in fed *versus* starved corals. This increase (significant after three weeks of feeding) appeared faster than the increase in skeletal growth (significant only after eight weeks) (Ferrier-Pagès *et al.*, 2003; Houlbrèque *et al.*, 2003, 2004a), resulting in thicker tissue over each calyx (Lough & Barnes, 2000) and thus more biomass per polyp. Anthony, Connolly & Willis (2002) suggested that either tissue reacts more rapidly than skeleton to availability of resources, or that tissue energy content represents a major component of the total energy investment in coral growth. Not only protein but also lipid content is increased by feeding in healthy corals (Al-Moghrabi *et al.*, 1995; Treignier *et al.*, 2008). Indeed Al-Moghrabi *et al.* (1995) found, in the coral *Galaxea fascicularis*, an increase in the proportion of saturated and mono-saturated fatty acids (C16 and C16:1 n-7) in fed corals maintained in the light, as well as an increase in levels of some polyunsaturated fatty acids in fed corals maintained in the dark, compared to starved corals. They related this increase to feeding on *Artemia salina*, as they are rich in those compounds. Treignier *et al.* (2008) found that energy storage in the form of lipid was light dependent. Under low light levels, and therefore a low photosynthate input, feeding increased the concentrations of storage lipids, such as saturated fatty acids, membrane constituents such as polyunsaturated fatty acids, and sterols, either in the host or in the symbionts. Conversely, under high light levels, the lipid energy provided by feeding was directed towards an increase in calcification, as well as in chlorophyll and protein content. At both light levels, however, the isotopic signature of the lipids was affected by feeding, which significantly enriched some fatty acids of the host tissue and of the zooxanthellae in ^{13}C .

Numerous studies have shown enhancement of zooxanthellae concentration (per cm^2 of surface skeleton) in fed corals (Muscatine *et al.*, 1989; Dubinsky *et al.*, 1990; Titlyanov *et al.*, 2000a,b, 2001; Houlbrèque *et al.*, 2003, 2004a) (Fig. 5). In Houlbrèque *et al.* (2003), colonies of *Stylophora pistillata* fed with freshly collected zooplankton and submitted to low light levels ($< 200 \mu\text{moles photons m}^{-2} \text{s}^{-1}$) underwent a doubling of zooxanthellae concentration compared to starved corals. The evidence of an interaction between light and feeding for the algal population is

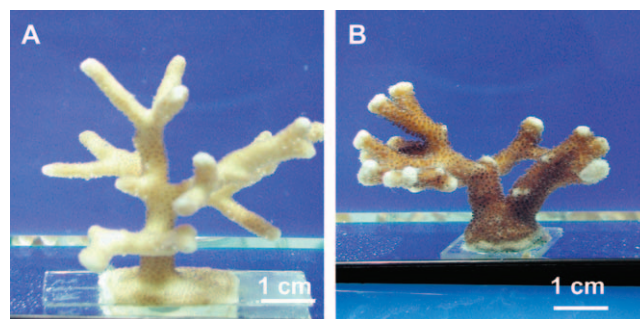


Fig. 5. (A) Starved and (B) fed colonies of *Stylophora pistillata* showing the difference in tissue pigmentation due to a simultaneous increase in zooxanthellae density and chlorophyll concentration per algal cell in fed corals (Grotoli, 2002; Titlyanov *et al.*, 2000a,b, 2001).

consistent with other reports (Titlyanov *et al.*, 2000a; 2001) where it was concluded that the zooxanthellae density of well-fed corals was able to increase under low light levels. This increase matched an increase in the cell-specific density (CSD), which represents the number of zooxanthellae contained in each individual host cell. Most corals (Muscatine *et al.*, 1998) are characterized by a predominance of host cells containing a single dinoflagellate (singlet, 62.3 - 70.4% of the total cells) followed in decreasing frequency by those containing two (doublet; 28.3% to 34.3%), three (triplet; 0.7% to 3.0%) and above four symbionts (quadrupelet; 0.4 to 0.7%). In fed corals, the number of doublets and triplets was significantly increased compared to starved corals (Houlbrèque *et al.*, 2004a). It therefore appears that feeding disproportionally enhances the growth of the algae relative to the animal cells. A similar increase in CSD was observed in an environment enriched with inorganic nitrogen (Muscatine *et al.*, 1998) and *Artemia salina* (Grotoli, 2002), suggesting that the algae are nitrogen limited. When collected *in situ* in the same environment, different coral species do not display the same CSD, which ranged from approximately 50% for doublets in *Madracis mirabilis* to 20% for doublets in *Acropora palmata* (Muscatine *et al.*, 1998). This may suggest different feeding capacities for different species, with “effective” predator, such as *M. mirabilis* (Sebens *et al.*, 1996), displaying a higher CSD than “poor” predators.

Concentrations of chlorophyll a and c₂ per square centimetre are often higher in fed *versus* starved corals (Dubinsky *et al.*, 1990; Stambler *et al.*, 1991; Titlyanov *et al.*, 1999; Ferrier-Pagès *et al.*, 2003; Houlbrèque *et al.*, 2003), either due to an increase in zooxanthellae density as described above or to an increase in the amount of chlorophyll content per algal cell (Titlyanov *et al.*, 2000a,b, 2001; Ferrier-Pagès *et al.*, 2003; Houlbrèque *et al.*, 2003).

The simultaneous increase in the concentration of protein, lipids and chlorophyll in fed coral colonies suggests that nutrients, incorporated in particulate form, were used both by the host and the symbionts (Clayton & Lasker, 1984; D’Elia & Cook, 1988; Cook *et al.*, 1988). The same effect on zooxanthellae was achieved when sea water was enriched with dissolved inorganic nitrogen such as nitrate

and ammonium (Hoegh-Guldberg & Smith, 1989; Dubinsky & Stambler, 1996; Marubini & Davies, 1996).

(2) Effects of heterotrophy on photosynthesis

At elevated feeding rates, enhanced rates of photosynthesis normalized per unit surface area are recorded, due to the simultaneous increases in zooxanthellae density and the amount of chlorophyll per zooxanthellae (Dubinsky *et al.*, 1990; Titlyanov *et al.*, 2000*a,b*, 2001; Houlbrèque *et al.*, 2003, 2004*a*). For *S. pistillata*, changes in photosynthetic parameters such as maximal net photosynthetic rate (P_{max}^n) and talling index (the light intensity for which maximal photosynthesis is reached; I_k) have been observed (Titlyanov *et al.*, 2001; Houlbrèque *et al.*, 2004*a*). The increase in P_{max}^n generally corresponds to an increase in the number of photosynthetic units (Prézelin, 1987).

This feeding enhancement of photosynthesis does not always correspond to higher transfer of photosynthates if the algae retain the surplus for their own requirements (Davy & Cook, 2001), but may be related to better quality of photosynthates transferred (Swanson & Hoegh-Guldberg, 1998; Wang & Douglas, 1998). Since the supply of nitrogen directly influences the zooxanthellar C:N ratio (Snidvongs & Kinzie, 1994; Grover *et al.*, 2002), feeding might increase amino acid synthesis compared to the production of non-nitrogenous compounds such as glycerol and glucose (Swanson & Hoegh-Guldberg, 1998; Wang & Douglas, 1998).

(3) Effects of heterotrophy on skeletal growth

Heterotrophy plays a significant role in coral skeletal growth, because scleractinian corals allocate a high proportion of the energy brought by food to it. Coral growth can be measured in several ways: linear extension rate, global skeletal growth (determined by following the weight of the coral colony using, for example, the buoyant weight technique) and calcification rate (measured using the alkalinity technique or by ^{45}Ca incorporation).

Wellington (1982) was one of the first to use field manipulations of light and zooplankton levels to assess the effect of feeding on the growth rates of three tropical corals: *Pavona clavus*, *Pavona gigantea* and *Pocillopora damicornis*. Among these three species, only *Pavona clavus* minimized the negative effect of shading when zooplankton were present. *Pocillopora damicornis* grew independent of zooplankton supply while *Pavona gigantea* appeared highly dependent on both light and zooplankton levels but was unable to compensate for the effects of shading with zooplankton feeding. In laboratory conditions, a feeding-induced increase in the global skeletal growth rate was demonstrated for some scleractinian corals maintained under shaded conditions (Anthony & Fabricius, 2000). Five other laboratory studies investigated the effects of natural zooplankton feeding on both skeletal and tissue growth rates of tropical corals (Witting, 1999; Grottoli, 2002; Ferrier-Pagès *et al.*, 2003; Houlbrèque *et al.*, 2003, 2004*a*) of which only Grottoli (2002) reported decreases in skeletal extension rates with increases in feeding. However in this case feeding rates were stimulated with plankton concen-

trations that were 5-60 times greater than that measured on the reef and it was hypothesized that at very high feeding rates, unregulated high levels of nutrients over-stimulated zooxanthellae growth and decoupled the coral-algal symbiosis. Conversely, Ferrier-Pagès *et al.* (2003) recorded for the species *Stylophora pistillata*, global skeletal growth rates 30% higher in fed colonies than in starved ones. In this study, fed corals grown under low-light conditions were able to maintain their growth rates, while the growth rates of starved corals dramatically decreased during the incubation. Using the same species, Houlbrèque *et al.* (2003) showed that calcification rates in both dark and light conditions were greatly enhanced by feeding, with rates two to three times higher in fed than in control corals.

Several explanations can be considered to explain this skeletal enhancement.

- (i) Calcification results from the delivery of calcium and inorganic carbon to the site of calcification with removal of protons. Calcium is acquired from sea water and delivered to the site of calcification through the calciblastic epithelium *via* transcellular active transport (McConnaughey, 1988, 1989; Tambutté *et al.*, 1996; Marshall, 1996). Dissolved inorganic carbon (DIC) is acquired from two different sources: sea water DIC, transported as bicarbonate across the calciblastic cells (Gattuso, Allemand & Frankignoulle, 1999; Marubini & Thake, 1999) and respired CO_2 (Erez, 1978; Furla, Allemand & Orsenigo, 2000). According to the different studies already cited (Al-Moghrabi *et al.*, 1995, Ferrier-Pagès *et al.*, 2003; Houlbrèque *et al.*, 2003, 2004*a*), feeding clearly resulted in increased tissue growth and tissue thickening, with a proportional increase in the zooxanthellae density expressed per unit surface area. The addition of coral biomass could therefore stimulate calcification by increasing the supply of external DIC, *via* an increased number of transporting molecules or by increasing the internal DIC *via* an increase in respiration rate. These rates are indeed often higher in fed corals (Houlbrèque *et al.*, 2003). Heterotrophy could therefore stimulate calcification through tissue growth and supply of metabolic inorganic carbon (Furla *et al.*, 2000). Barnes (1973) was one of the first to underscore the essential relationship between tissue and skeletal growth, and Barnes & Lough (1993) suggested that such tissue thickening might serve as a storage strategy when prey are available. At a later time, skeletal growth may continue at a high rate combined with thinning of the tissue.
- (ii) Feeding could enhance calcification indirectly by increasing the photosynthetic rate. Photosynthesis increases the supply of Ca^{2+} needed for calcification by increasing the ATP production needed for proton pump, which in turns favors carbonate precipitation (McConnaughey, 1989).
- (iii) Skeletal growth in corals involves at least two different processes: the secretion of an organic matrix and the deposition of calcium carbonate (Barnes & Crossland, 1980). At night, the coral lays down an organic matrix that allows the deposition of a CaCO_3 crystalline framework (Vago, Gill & Collingwood, 1997). This

process is followed the next day by the nucleation of new crystals, resulting in increased skeletal density. The presence of an organic matrix in coral skeletons is widely documented (Goreau & Goreau, 1959; Wainwright, 1963; Young, 1971; Constantz & Weiner, 1988; Cuif & Gautret, 1995; Dauphin & Cuif, 1997) and is considered as an essential prerequisite in the formation of a biomineral structure (Goreau & Goreau, 1959; Cuif, Dauphin & Gautret, 1997; Allemand *et al.*, 1998). This matrix potentially plays key roles in various processes such as crystal nucleation and growth, crystal size and orientation and regulation of skeletal formation (Weiner & Addadi, 1991; Falini *et al.*, 1996; Belcher *et al.*, 1996). Cuif *et al.* (1999) demonstrated that the composition of the organic matrix differed depending on whether it was synthesized by symbiotic or asymbiotic corals and Allemand *et al.* (1998) suggested that heterotrophy was a source of aspartic acid, one of the major components of the coral matrix.

Higher incorporation of aspartic acid, one of the major amino acids in the organic matrix of scleractinian corals (Allemand *et al.*, 1998), was observed in the organic matrix of fed corals (Houlbrèque *et al.*, 2004a). Feeding enhanced both dark and light incorporation rates, with greater enhancement in the dark. The authors considered several hypotheses to explain this feeding enhancement (Fig. 6). Feeding might enhance the construction of the organic matrix by (1) providing external amino acids necessary for the construction of the organic matrix; (2) supplying additional energy, especially for processes such as for the $\text{Ca}^{2+}/\text{H}^{+}$ pump, which quantity is increased through high

tissue biomass above the skeleton (McConnaughey, 1988, 1989; McConnaughey & Whelan, 1997; Anthony *et al.*, 2002); or (3) increasing the production of autotrophic amino acids by increasing photosynthesis rate.

V. CONCLUSIONS

(1) The establishment and maintenance of scleractinian corals in nutrient-poor conditions was previously explained solely by their symbiosis with zooxanthellae, which translocate a large fraction of their photosynthates to the host but it is now known that corals have adaptable and varied trophic abilities. Even with a variable zooplankton input in coral reefs, planktonic microorganisms available in reef waters can represent an important source of nitrogen and carbon for scleractinian corals. Therefore, the ability of corals to consume microorganisms is suggested to be one of the major mechanisms sustaining reefs in impoverished environments.

(2) Recent studies on coral physiology demonstrate that corals benefit greatly from zooplankton feeding. Several studies have shown enhancement of the areal pigmentation and zooxanthellae density in fed corals, allowing an increase in areal photosynthesis. Coral calcification and organic matrix synthesis are also greatly enhanced by feeding.

(3) This nutrition mode may be advantageous during episodes of stress since some coral species are able to increase their feeding rates during bleaching events and recovery periods, allowing them greater long-term resilience and therefore to dominate the species composition of the reef.

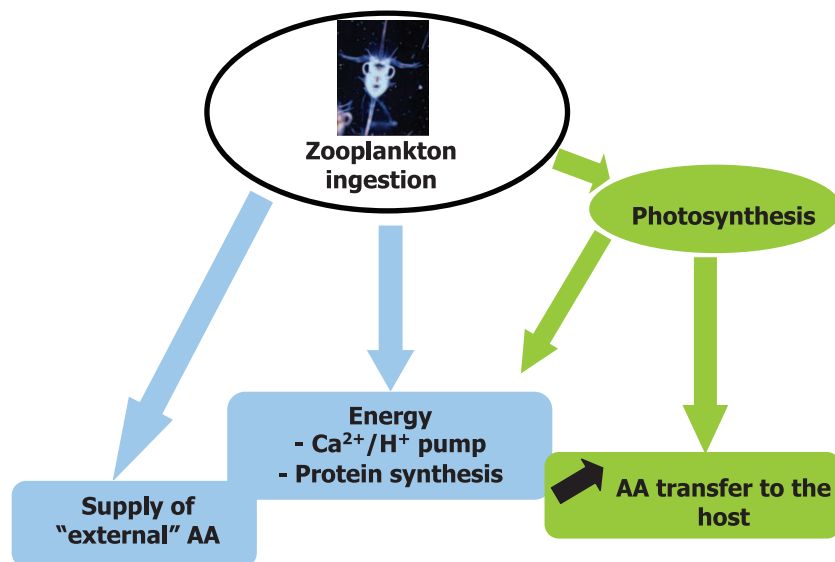


Fig. 6. Hypotheses suggested to explain the closely coupled stimulation of calcification and organic matrix synthesis following zooplankton ingestion in scleractinian corals. Feeding might act directly by providing external amino acids (AA) necessary for organic matrix synthesis or by supplying additional energy for the $\text{Ca}^{2+}/\text{H}^{+}$ pump and protein synthesis. Another possibility is that feeding might act indirectly by increasing photosynthesis rate, which in turn might increase the supply of autotrophic amino acids or the energy input.

(4) Coral energy acquisition and the relative importance of hetero- *versus* autotrophy in corals is still hotly debated in the literature. However, rather than being viewed as either autotrophic or heterotrophic, scleractinian corals should probably be considered polytrophic, using both ingested and translocated carbon as energy sources. An emerging model is that the dependence of corals on heterotrophic nutrition varies with species, depth, plankton abundance, and bleaching. Considerable work still needs to be done in this research area. The establishment of an accurate carbon balance that quantifies the amount of carbon transferred by the zooxanthellae *versus* the amount supplied by heterotrophy (taking into account the absorption of dissolved organic matter and the predation of small planktonic prey) at the scale of a single scleractinian coral colony would be of great interest to biologists.

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