The Role of Plankton in Coral Trophodynamics

Christine Ferrier-Pagès, Mia Hoogenboom, and Fanny Houlbrèque

Abstract Historically, reef-building corals have been considered to be photoautotrophs due to their symbiosis with dinoflagellates that transfer photosynthetically fixed carbon to the animal tissue. Nevertheless, corals also obtain carbon heterotrophically through capture of plankton, ingestion of suspended particulate matter, and uptake of dissolved organic compounds. This review assesses the effects of heterotrophy on coral physiology, and how strongly feeding on all of these food sources contributes to coral energy budgets. Evidence in the literature demonstrates that feeding has a positive effect on coral tissue, enhancing the growth of both partners of the symbiosis. Nevertheless, the effects of feeding are light dependent: in general, tissue quality (lipid and protein composition) is enhanced in the presence of an adequate food source only under low-light conditions or in bleached corals. On the other hand, growth rates are typically highest under conditions of high light and food availability. However, under low-light conditions, feeding can provide a mechanism to maintain skeletal growth rates even though photosynthesis is reduced. Overall, a strong interaction between autotrophy and heterotrophy is apparent for scleractinian corals. Feeding can play a central role in maintaining physiological function when autotrophy is reduced. Moreover, taking all food sources into account, heterotrophy contributes more strongly to coral energy budgets than was previously thought. Nevertheless, not all symbiotic corals can sufficiently upregulate heterotrophic feeding to compensate for reduced photosynthesis, and identifying which coral species are facultative heterotrophs should be a focus of future research.

Keywords Feeding • heterotrophy • photosynthesis • coral physiology

C. Ferrier-Pagès (✉) and M. Hoogenboom
Centre Scientifique de Monaco, c/o Musée Océanographique, Avenue Saint-Martin, Monaco, MC, 98000
e-mail: ferrier@centrescientifique.mc

F. Houlbrèque
International Atomic Energy Agency, Marine Environment Laboratories, 4 Quai Antoine 1er, Monaco, MC 98000

1 Introduction

Reef-building corals have been considered to be mainly photoautotrophs, because they live in symbiosis with unicellular dinoflagellates (zooxanthellae) that transfer large amounts of photosynthetically fixed carbon to their host (Muscatine and Porter 1977). These photosynthates, often deficient in nitrogen and phosphorus, are thought to be exuded as mucus (Crossland 1987; Wild et al. 2004) or used as fuel for respiration, rather than assimilated into biomass (Falkowski et al. 1984; Davies 1991). Essential nutrients for growth and reproduction must therefore be acquired through heterotrophic feeding (Sebens et al. 1996; Anthony and Fabricius 2000; Ferrier-Pagès et al. 2003). The Scientific Reports of the Great Barrier Reef Expedition (1928–1929) of C.M. Yonge were among the first investigations into heterotrophic behavior of corals (Yonge 1930a,b; Yonge and Nicholls 1931). Since these famous works, numerous studies have confirmed that most coral species can in fact be active heterotrophs (Goreau and Goreau 1960; Goreau et al. 1971; Muscatine 1973; Wellington 1982; Sebens et al. 1996; Grottoli 2002; Houlbrèque et al. 2004a,b; Palardy et al. 2005, 2006).

Heterotrophic feeding by corals takes many forms, ranging from capture of live organic matter (LOM), uptake of dissolved organic material (DOM), and/or ingestion of suspended particulate matter (SPM, Fig. 1). LOM is considered to be the most important of these food sources, and corals are able to capture particles of a wide size range (from 0.4 μm to 2 mm) through nematocyst discharges, tentacle grabbing, or by mucus adhesion (reviewed by Muscatine 1973). Picoplankton are the smallest organisms that corals commonly ingest, both taxa that are free-living in the water column (Sorokin 1973; Farrant et al. 1987; Bak et al. 1998; Ferrier-Pagès et al. 1998; Houlbrèque et al. 2004b), and taxa directly associated with the coral mucus layer (Rohwer et al. 2001). Indeed, it has been suggested that corals develop a bacterial farm around them in order to be continuously fed. Evidence for this phenomenon comes from Herndl and Velimirov (1985) who found a large bacterial population within the coelenteron of four Anthozoan species.

Other forms of LOM that provide a food source for corals include nanoplankton (Ferrier-Pagès et al. 1998; Houlbrèque

Z. Dubinsky and N. Stambler (eds.), *Coral Reefs: An Ecosystem in Transition*,
DOI 10.1007/978-94-007-0114-4_15,

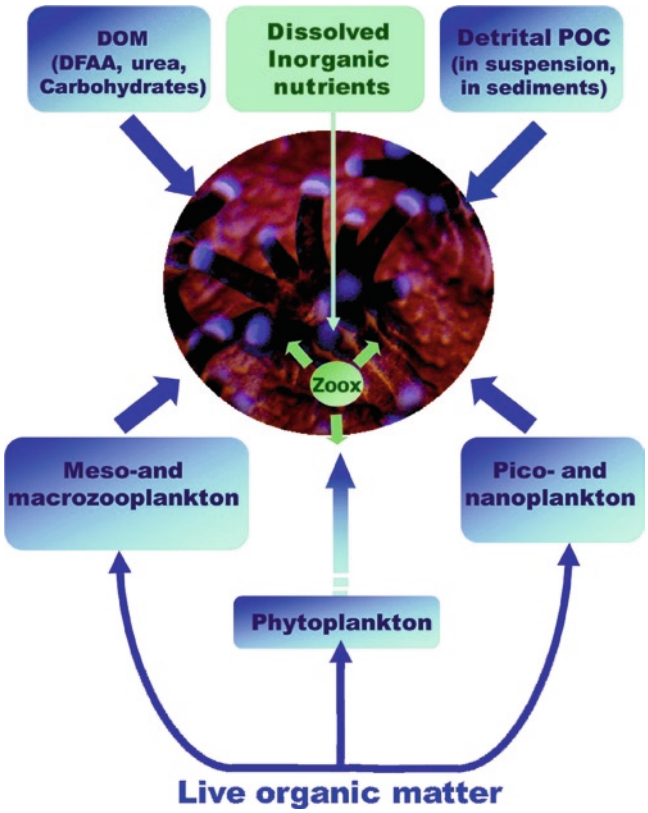

Fig. 1 Corals acquire nutrients through the animal feeding (heterotrophic feeding is represented by blue arrows): on dissolved organic matter (DOM), detrital particulate organic matter (POM), and live organic matter (LOM) (pico- and nanoplankton and meso- and macrozooplankton). The ingestion of phytoplankton has only been shown for soft corals. Corals can acquire nutrients via autotrophy (autotrophic nutrition is represented by green arrows), by transfer of photosynthates produced by the symbiotic dinoflagellates, which pump dissolved inorganic nutrients from seawater

et al. 2004b; Kramarsky-Winter et al. 2006) and meso-/macrozooplankton (Coles 1969; Johannes et al. 1970; Johannes and Tepley 1974; Porter 1974; Sebens et al. 1996; Palardy et al. 2006) (Fig. 1). Most studies on grazing rates have been performed using zooplankton, including copepods, eggs, larvae, and demersal zooplankton (i.e., Titlyanov et al. 2000a; Grottoli 2002; Ferrier-Pagès et al. 2003; Fabricius and Metzner 2004; Palardy et al. 2005, 2006; Grottoli et al. 2006). In general, corals can ingest from 0.5 to 2 prey items per polyp (Sebens et al. 1996) with ingestion rates depending on plankton density (Ferrier-Pagès et al. 2003; Palardy et al. 2005) or species (Palardy et al. 2005) as well as on water flow rates around colonies (Sebens and Johnson 1991; Sebens et al. 1998). The type of zooplankton found in the gut contents of corals is diverse (Sebens et al. 1996; Palardy et al. 2005; 2006) and is more strongly influenced by the feeding effort of coral colonies than by prey availability or polyp size (Palardy et al. 2005, 2006). Finally, although ingestion of phytoplankton has been demonstrated for soft corals (Fabricius et al. 1995), this has not yet been observed among the scleractinia.

Uptake of DOM mainly concerns carbohydrates, dissolved free amino acids and urea in nanomolar concentrations (Ferrier 1991; Al-Moghrabi et al. 1993; Grover et al. 2006, 2008) (Fig. 1). Uptake rates depend on DOM external concentration as well as on light intensity since photosynthesis enhances DOM uptake (Grover et al. 2006, 2008). Uptake of dissolved organic compounds may occur via diffusion or more certainly via active transport (Grover et al. 2006, 2008). Finally, corals can ingest detrital organic matter either in suspension (SPM, suspended particulate matter), trapped in the sediment (Anthony 1999; Rosenfeld et al. 1999; Anthony and Fabricius 2000; Mills et al. 2004) or in the form of mucus (Wild et al. 2004; Huettel et al. 2006). Generally, massive species with large polyps tend to have higher SPM feeding rates than branching ones with small polyps (Anthony and Fabricius 2000). Conversely to DOM, SPM uptake increases when symbiont photosynthesis decreases (Anthony and Fabricius 2000; Grottoli et al. 2006).

Such a wide diversity of food sources for coral heterotrophy indicates that this feeding mode may account for a large part of the energetic budget of corals, bringing carbon, nitrogen, phosphorus, and other nutrients not supplied by the photosynthesis of the symbionts (Muscatine and Porter 1977; Fitt and Cook 2001; Titlyanov et al. 2000a). Previous papers have reviewed the different methods by which corals can catch their food (Muscatine 1973), as well as the type of prey ingested (i.e., Anthony 1999; DiSalvo 1972; Sorokin 1973; Sebens et al. 1996; Ferrier-Pagès et al. 1998; Palardy et al. 2005). The aim of this review is to assess the effects of heterotrophy on coral physiology and its importance in coral trophodynamics. Indeed, while the importance of autotrophy for the nutritional energy of symbiotic corals has been widely assessed throughout the past 30 years (Muscatine and Porter 1977; Muscatine 1980; Falkowski et al. 1984; Muscatine et al. 1984; Cook et al. 1988; Davies 1991; Muller-Parker et al. 1994a,b; Swanson and Hoegh-Guldberg 1998; Wang and Douglas 1999; Cook and Davy 2001; LaJeunesse 2001), the impact of heterotrophy on coral metabolism has attracted far less attention.

2 Effect of Heterotrophy on Coral Physiology

2.1 Effect of Heterotrophy on Tissue Growth

2.1.1 Animal Tissue Fraction

A common method for identifying food sources (Peterson and Fry 1987) and quantifying carbon and nitrogen fluxes

between trophic levels (Rau et al. 1992) is analysis of the isotopic composition of animal tissue (particularly ^{13}C and ^{15}N). In general, the $\delta^{13}C$ signature of a consumer is similar to that of its diet, while $\delta^{15}N$ is enriched by 3 – 4‰ with each successive trophic level (Rau et al. 1983; Owens 1987). The first general evidence that feeding affects coral tissue comes from changes observed in the $\delta^{13}C$ and $\delta^{15}N$ isotopic signatures. Muscatine et al. (1989) were the first to measure the isotopic signature of coral tissues and found a significant enrichment in both ^{13}C and ^{15}N with depth. This result was explained by a lower photosynthesis to respiration ratio for corals from deep water together with an increase in heterotrophic nutrition. More recently, Reynaud et al. (2002) confirmed these initial findings by experimentally measuring, both for animal tissue and zooxanthellae, a 1.5‰ difference in the $\delta^{13}C$ signature of fed and starved *Stylophora pistillata* colonies. Nevertheless, such isotopic enrichment was not observed for shallow-water corals (Yamamuro et al. 1995), or for corals living in inshore waters and receiving large amounts of $\delta^{15}N$-depleted terrestrial particulate and dissolved organic matter (Sammarco et al. 1999).

In most species, the effect of heterotrophy on animal tissue growth is mainly represented by an increase in protein and/or lipid concentrations per unit skeletal surface area (Anthony and Fabricius 2000; Anthony et al. 2002; Ferrier-Pagès et al. 2003; Houlbrèque et al. 2003). Generally, feeding causes a strong increase in tissue growth compared to skeletal growth. Anthony et al. (2002) suggested that either tissue may react more rapidly than the skeleton to availability of resources, or that the energy content of the tissue may represent the major component of total energy investment in coral growth. Lipids, which represent a major energy reserve for corals (Edmunds and Davies 1986; Harland et al. 1993), are highly influenced by feeding in many coral species. Overall, lipid concentrations are increased in fed corals, both for healthy (Al-Moghrabi et al. 1995; Treignier et al. 2008) and bleached colonies (Grottoli et al. 2006; Rodrigues and Grottoli 2007).

There is increasing evidence that light/photosynthesis and feeding interact to determine tissue properties (Figs. 2 and 3). Firstly, healthy colonies of *Galaxea fascicularis* showed an increase in saturated and mono-unsaturated fatty acids when experimentally maintained under low light and fed *Artemia salina* (Al-Moghrabi et al. 1995). When kept in the dark for 20 days, poly-unsaturated fatty acids also significantly increased in fed colonies but decreased in unfed colonies. Similarly, colonies of *Turbinaria reniformis* doubled all classes of lipids when maintained under low light (100 µmole photons $m^{-2}s^{-1}$) and fed with natural zooplankton (Fig. 2, Treignier et al. 2008). In such fed colonies, fatty acids, sterols, and alcohols increased from 100 to 250, 40 to 120, and 10 to 15 $\mu g\,cm^{-2}$, respectively. However, an increase in lipid stocks was not observed in *T. reniformis* maintained under high light (300 µmoles photons $m^{-2}s^{-1}$), because energy gained by feeding was directed into skeletal growth (Fig. 3, Treignier et al. 2008). Additional evidence for an interaction between photosynthesis and feeding comes from observations made on bleached corals. Feeding has been shown to be very

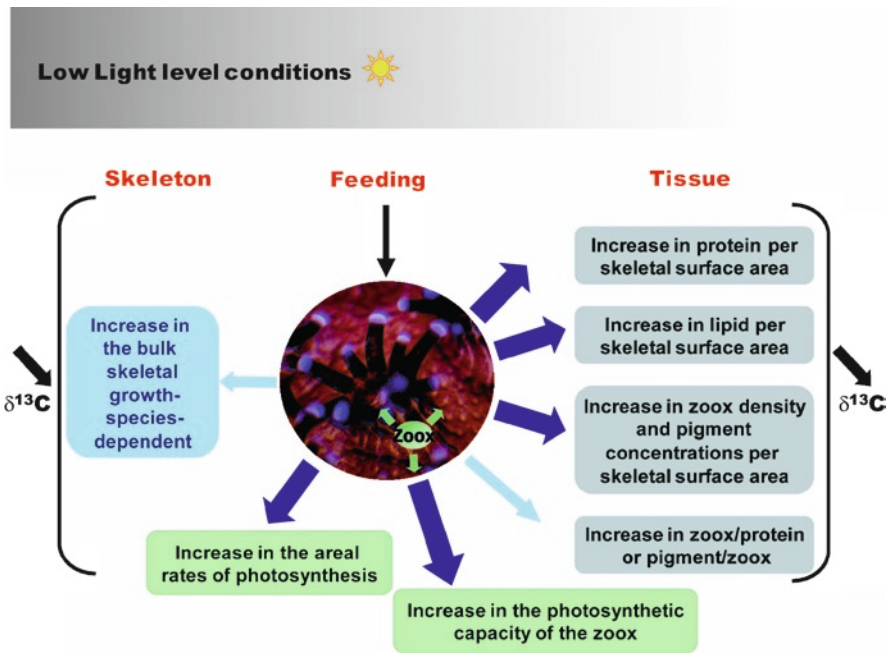

Fig. 2 Effects of feeding on corals maintained under low-light levels. Information was obtained with experiments performed either on *Stylophora pistillata* for most parameters, or *Turbinaria reniformis* for lipids. Zoox = zooxanthellae. Thick arrows represent a large effect of feeding, while small arrows represent a small effect of feeding

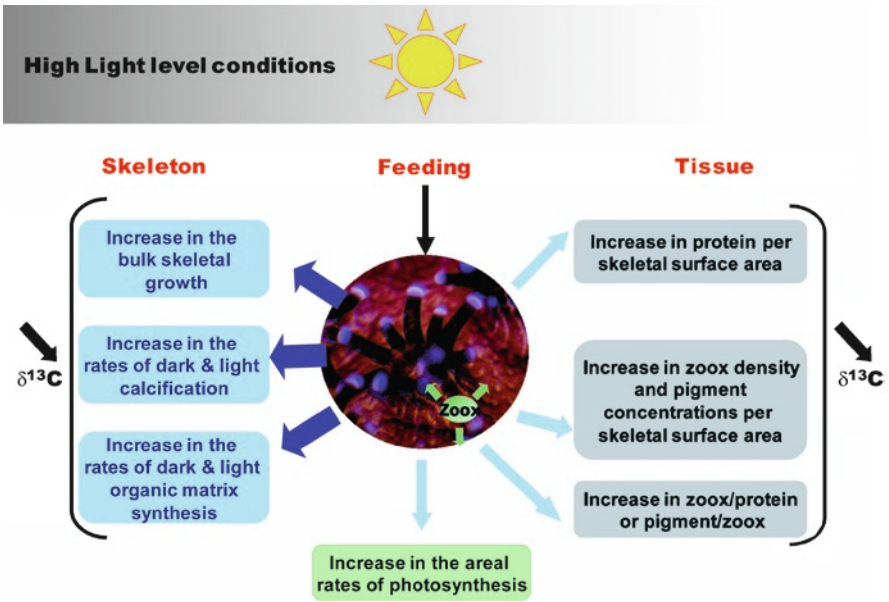

Fig. 3 Effects of feeding on corals maintained under high-light levels. Information was obtained with experiments performed either on *Stylophora pistillata* for most parameters, or *Turbinaria reniformis* for lipids. Zoox = zooxanthellae. Thick arrows represent a large effect of feeding, while small arrows represent a small effect of feeding

important for lipid stocks when corals bleach and translocation of algal photosynthates is greatly reduced. Although it is not the rule for all coral species (Grottoli et al. 2004), a decrease in storage lipids (i.e., wax esters, triacylglycerols, and polyunsaturated fatty acids) has been measured in thermally bleached corals (Grottoli et al. 2004; Yamashiro et al. 2005; Bachok et al. 2006; Papina et al. 2007). This suggests that the animal draws from its energy reserves to compensate for the decrease in the photosynthetic lipid production. However, corals able to catch zooplankton, and thus able to replenish their energy reserves, are less likely to die from bleaching than poor plankton consumers (Grottoli et al. 2006). This is the case for *Montipora capitata*, which increased its grazing rates more than fivefold when bleached and was thus able to acquire sufficient carbon from heterotrophy to meet its metabolic energy requirements, and to restore its lipid reserves (Grottoli et al. 2006). For this coral, the average percent contribution of heterotrophically acquired carbon to daily animal respiration (CHAR) therefore increased from 20 to 100%, demonstrating that heterotrophy played a central role in resilience to bleaching.

Feeding also results in higher protein concentration per unit surface area, both for healthy (Szmant-Froelich and Pilson 1980; Kim and Lasker 1998; Ferrier-Pagès et al. 2003; Houlbrèque et al. 2003, 2004a), and bleached corals (Rodrigues and Grottoli 2007). Indeed, it has been suggested that the major role of zooplankton capture could be to provide the symbiosis with essential amino acids, (Rahav et al. 1989), since animals were thought to be incapable of synthesizing them de novo. In the coral *Oculina arbuscula*, the ingested ^{15}N-labeled brine shrimp was indeed recovered in the protein fraction after 4 h for the zooxanthellae, and in the amino-acid pool that was then converted into protein for the animal fraction (Piniak et al. 2003). In the branching tropical coral *Stylophora pistillata*, a twofold increase in protein per surface area (from 0.42 to 0.73 mg cm^{-2}) was observed after 4 weeks of experimental feeding with *Artemia salina* prey (Houlbrèque et al. 2003, 2004a) or with natural zooplankton (Ferrier-Pagès et al. 2003). For this species, an interaction between light and feeding on the tissue growth rate was again observed. Estimates of tissue growth rates, based on the protein and weight values, ranged from 0.1 to 0.3% day^{-1} in starved and fed corals maintained under low light, respectively, and from 0.4 to 0.6% day^{-1} for the same corals maintained under high light. For healthy corals, feeding had a stronger impact on protein under low light, when carbon from photosynthesis is not sufficient for metabolic requirements (Ferrier-Pagès et al. 2003). For bleached corals, protein contents decrease in parallel with lipids during the stress (e.g., *Montipora capitata*, Rodrigues and Grottoli 2007). As was the case for lipids, particulate feeding by bleached corals of this species lead to increased protein concentrations within 2 months (from 0.2 to 0.3 g DW^{-1}, Rodrigues and Grottoli 2007). Moreover, stable isotope analyses (^{13}C) of host tissue and zooxanthellae indicated that fixed carbon was heterotrophically acquired during the first month of recovery from bleaching, before photoautotrophic acquisition resumed after 4–8 months (Rodrigues and Grottoli 2007).

2.1.2 Algal Fraction

In addition to its effects on coral tissue, heterotrophic feeding influences the symbiont population. Indeed, since nutrients are continuously exchanged between the host and its symbionts, feeding affects zooxanthellae metabolism. Several authors have observed translocation of nutrients from the coral animal to the symbionts (D'Elia and Cook 1988; Dubinsky et al. 1990; Piniak et al. 2003). A depression of N uptake by symbionts was observed in colonies of the hermatypic coral *Madracis mirabilis* when fed zooplankton to repletion (D'Elia and Cook 1988). Transfer of ^{15}N-labeled prey from the animal to the symbionts was also shown to occur in less than 10 min in the coral *Oculina arbuscula* (Piniak et al. 2003). Such transfer of nutrients explains the general increase in zooxanthellae densities per skeletal surface area that has been observed in healthy fed colonies (Muscatine et al. 1989; Dubinsky et al. 1990; Titlyanov et al. 2000a,b, 2001; Ferrier-Pagès et al. 2003; Houlbrèque et al. 2003, 2004a). Similarly, during a bleaching event, colonies of *Montipora capitata* that presented a high feeding rate were able to maintain symbionts at the same density as unbleached colonies, whereas zooxanthellae densities for a species with a lower feeding capacity (*Porites compressa*) rapidly decreased. The increase in zooxanthellae density in response to feeding lends support to the hypothesis that zooxanthellae are nitrogen limited (Dubinsky et al. 1990). A comparable increase in density is also observed when dissolved inorganic nitrogen is supplied to the corals (Dubinsky et al. 1990). Overall, whenever corals are enriched in inorganic or organic nutrients, there is an increase in the nitrogen content of the zooxanthellae and a corresponding decrease in the C/N ratio (Snidvongs and Kinzie III, 1994; Grover et al. 2002).

Due to the general increase in zooxanthellae densities per skeletal surface area in fed corals, chlorophyll concentrations per square centimeter are often higher in fed *versus* starved corals (Dubinsky et al. 1990; Stambler et al. 1991; Titlyanov et al. 1999) maintaining chlorophyll per algal cell constant. However, a feeding-related increase in chlorophyll per zooxanthellae has also been observed (Titlyanov et al. 2000a, 2001; Ferrier-Pagès et al. 2003; Houlbrèque et al. 2003). It must be noted that the zooxanthellae increase per skeletal surface area after feeding is partially due to the general thickening of the tissue above the skeleton. When algal densities are expressed per amount of animal tissue protein, data show that the animal protein/algal density ratio is either maintained constant (Fitt et al. 1982; Houlbrèque et al. 2003), decreases (Muller-Parker 1985; Al-Moghrabi et al. 1995), or increases in favor of the algal component (Clayton and Lasker 1984; Ferrier-Pagès et al. 2003; Houlbrèque et al. 2004a). In the latter situation, growth of the symbionts can be higher than the growth of the animal cells, leading to the occurrence of multiple symbionts within the same animal cell. This number of symbionts per host cell has been called the cell-specific density or CSD (Muscatine et al. 1998). Most corals collected in the field are characterized by a predominance of host cells containing a single dinoflagellate (singlets, 62.3–80.4% of cells) followed in decreasing frequency by those containing two (doublets, 28–34%), and three (triplets, 3.0–0.7%) dinoflagellates. However, some species, such as *Acropora palmata* and *Madracis mirabilis* present 20–50% of doublets, respectively, suggesting a higher capacity for heterotrophy (Sebens et al. 1996; Muscatine et al. 1998). Several authors (Titlyanov et al. 2000a, 2001; Houlbrèque et al. 2003) have also noted that the influence of heterotrophy on algal growth is light dependent, with the biggest effect of feeding observed under low light (Fig. 2). In such cases, the positive effect of feeding on algal density may be a strategy to increase rates of photosynthesis and energy production. In temperate corals, the few studies performed have also shown a temperature-feeding interaction on zooxanthellae density but the direction of this effect requires further investigation (Howe and Marshall 2001; Miller 1995; Rodolfo-Metalpa et al. 2008).

In conclusion, feeding has a positive effect on coral tissue, enhancing the growth of both partners of the symbiosis. This means that nutrients ingested by the coral animal also benefit the algal partner (e.g., Piniak et al. 2003). Nutrient exchanges between both partners are also observed with inorganic nutrients, which are first taken up by the zooxanthellae and then transferred to the coral host (Hoegh-Guldberg and Smith 1989; Dubinsky and Stambler 1996; Marubini and Davies 1996; Grover et al. 2002, 2003). Finally, the effect of feeding on coral tissue is light dependent and affected by zooxanthellae densities: feeding has the greatest impact on symbiont dynamics either under low-light conditions or in bleached corals.

2.2 *Effect of Heterotrophy on Rates of Photosynthesis*

The effect of heterotrophy on rates of photosynthesis has not been well investigated and further research is needed to understand all aspects of this relationship. There is some experimental evidence that indicates an increase in areal rates of photosynthesis in fed corals, due to increased zooxanthellae density and chlorophyll content per skeletal surface area (Dubinsky et al. 1990; Titlyanov et al. 2000a,b, 2001; Houlbrèque et al. 2003, 2004a). Houlbrèque et al. (2004a) measured both a change in the maximum net photosynthetic rate and in the light intensity at which photosynthesis approaches saturation. Nevertheless, the literature gives contradictory results regarding the effects of feeding on the

photosynthetic capacity of zooxanthellae (i.e., photosynthesis per cell or per chlorophyll). While some studies showed no change in rates of photosynthesis per cell with feeding (Houlbrèque et al. 2003, 2004a) or even a decrease (Dubinsky et al. 1990), others demonstrate the opposite effect (Titlyanov et al. 2001; Davy et al. 2006). Titlyanov et al. (2001) showed that zooxanthellae photosynthetic capacity was enhanced by feeding under low light due to increased photoacclimation potential compared to that of starved corals. A very recent study (Griffin et al. sbm) performed on *Pocillopora damicornis* confirms that feeding increases zooxanthellae viability and improves their photosynthetic efficiency (ΦPSII), indicating that photosynthetic activity is constrained in the absence of a heterotrophic supplement to nutrition (Houlbrèque et al. 2003, 2004a). It is generally thought that nitrogen supply through heterotrophy drives the enhancement of symbiont photosynthetic capacities. Nitrogen is required for photo-adaptation or photoacclimation (Dubinsky et al. 1990; Titlyanov et al. 2001), and starvation induces an increase in the ratio of glutamine/glutamate suggesting a lack of nitrogen (for *Plesiastrea versipora*, Davy et al. 2006). Differences in the effects of feeding on the rates of photosynthesis of different coral species might therefore originate from species-specific differences in internal stores of nitrogen, either from the host or the zooxanthellae themselves. An alternative explanation is that the photobiological response to heterotrophy is mainly due to improved host–symbiont coupling (Furla et al. 2005), since pigment content and the ratio of chlorophyll-a to chlorophyll-c_2 did not change.

Recent studies (Griffin et al. sbm) also indicate that heterotrophic feeding increases bleaching resilience: colonies of *P. damicornis* fed brine shrimp and experiencing a heat shock did not show a decline in zooxanthellae photosynthetic function. However, such a decline was observed in starved corals and was consistent with previous studies showing photosynthetic impairment at temperatures above 31 °C (Hill and Ralph 2006). This suggests that either the fed host provided nutritional support to prevent damage to the photosynthetic apparatus of the zooxanthellae, or the host's demand for photosynthate was reduced allowing the symbiont to use these energy sources for their own survival.

Increased areal rates of photosynthesis do not always result in higher transfer of photosynthates from the zooxanthellae to the coral host. The first studies of this phenomenon were performed with inorganic nitrogen supply, and demonstrated an inverse relationship between nitrogen enrichment (which enhanced zooxanthellae growth) and carbon excretion in the coral *Porites astreoides* (McGuire and Szmant 1997) and in another anthozoan (green hydra, McAuley 1992). Davy and Cook (2001) also demonstrated lower carbon translocation in *Artemia salina* fed sea anemones compared to starved ones for *Aiptasia pallida*. The lower transfer of zooxanthellate photosynthates in fed animals has been explained by retention of photosynthates for the symbiont's own requirements (Davy and Cook 2001). Another factor to take into account is the quality of the photosynthates transferred. Nutrient-replete zooxanthellae mainly transfer amino acids to the host in addition to glucose and glycerol (Swanson and Hoegh-Guldberg 1998; Wang and Douglas 1999). Nutrient limitation (i.e., reduced feeding) might reduce amino-acid synthesis and induce a shift toward translocation of carbon-enriched compounds. Clearly, the effects of feeding on photosynthetic efficiency and carbon translocation require further research.

2.3 Effect of Heterotrophy on Skeletal Growth

In addition to its effects on coral tissue, heterotrophic feeding influences skeleton formation. General evidence for this comes firstly from the observed correlation between the $\delta^{13}C$ isotopic signature of tissue and skeleton (Heikoop et al. 2000). Usually, corals deposit a calcium carbonate skeleton that is depleted in ^{13}C relative to ambient seawater, as a result of kinetic and metabolic fractionation (McConnaughey 1989). However, physiological processes can alter the skeletal $\delta^{13}C$ signature. Elevated photosynthesis generally results in $\delta^{13}C$ depletion (Swart et al. 1996; Juillet-Leclerc et al. 1997) whereas respiration, as well as coral spawning, causes an enrichment (Swart et al. 1996; Kramer et al. 1993; Gagan et al. 1996). Theoretically, increased heterotrophic feeding by corals should lead to a decrease in skeletal $\delta^{13}C$ because zooplankton is depleted in ^{13}C relative to seawater (Rau et al. 1992). However, studies of this effect have produced conflicting results. Using a 19-year seasonal skeletal record of *Porites*, Felis et al. (1998) measured ^{13}C depletions that coincided with large, interannual plankton blooms, and suggested that corals have increased heterotrophy during these events. Reynaud et al. (2002) found no effect of feeding on the skeletal $\delta^{13}C$ signature of *Stylophora pistillata* potentially due to the fact that the *Artemia salina* prey used during the experiment were not as depleted in ^{13}C as natural zooplankton. Conversely, Muscatine et al. (2005) showed higher $\delta^{13}C$ of the skeletal organic matrix of non-symbiotic corals, which rely on heterotrophy, compared to symbiotic ones. Grottoli (2002) also observed an increase in skeletal $\delta^{13}C$ for colonies of *Porites compressa* fed with brine shrimps in high concentrations. In the latter study, it was hypothesized that an increase in zooxanthellae and rates of photosynthesis following input of nitrogen from feeding drove the increase in skeletal $\delta^{13}C$ (Grottoli 2002). Overall, although it is clear that feeding influences skeleton formation, how the interaction between photosynthesis and feeding moderates this effect warrants further investigation.

Different terms can be used to describe skeletal growth in corals. The first term is linear extension rate (LER), which is most often expressed in millimeters of skeleton accreted. LER can be measured from skeletal banding seen on X-radiographs of thin slices of coral skeleton cut along the growth axis (Lough and Barnes 1997), or by staining the skeleton with a dye (usually Sodium Alizarin Sulfonate) and measuring the amount of calcium carbonate deposited above the stain line (Barnes and Crossland 1980). The buoyant weight technique (Jokiel et al. 1978; Spencer-Davies 1989) is another method that measures bulk skeletal growth rate (most often expressed in% day^{-1} or in $mg\,g^{-1}$). This growth rate is the product of skeletal density and extension rate and is obtained by weighing the coral in seawater where the skeletal and seawater densities are known. Finally, calcification (most often expressed as nmoles Ca^{2+} mg $protein^{-1}$ d^{-1}) is the term employed for skeletal growth when the incorporation of the radiotracer ^{45}Ca is measured in the skeleton (Tambutté et al. 1995). All these different techniques for measurements of skeletal growth rates have been employed to assess the effect of heterotrophy on coral calcification.

Of the above techniques, bulk skeletal weight increases have most often been used to investigate the effects of feeding on calcification. Johannes (1974) was one of the first to work on this subject and found that corals grew equally fast in 1 µm-filtered seawater as in unfiltered seawater. Although the amount of food in the two water types was not assessed, this result suggests that food availability had a negligible effect on skeletal growth. Later Wellington (1982) used field manipulations of light and zooplankton concentrations to show that reduced feeding decreased skeletal growth for only one of three study species (*Pavona clavus*) but had no effect on two other coral species. In agreement with this result, a study of the effects of light intensity and suspended particulate matter (SPM) concentrations showed that a coral with a high capacity to utilize SPM as a food source (*Goniastrea retiformis*) had slightly (10%) higher growth rates when grown under high SPM concentrations and high light (Anthony and Fabricius 2000). Conversely to the above observations, bulk skeletal growth of the coral *Stylophora pistillata* was highly enhanced (30%) when colonies were experimentally fed during 8 weeks with natural zooplankton, although the effect of feeding was light dependent (Ferrier-Pagès et al. 2003; Houlbrèque et al. 2003, 2004a). In the latter studies, fed corals kept at low light maintained a constant growth rate over time, growth was strongly suppressed in starved corals and the highest growth rates were observed for fed corals maintained under high light (as previously noticed for *G. retiformis*, Anthony and Fabricius 2000). Collectively, these studies indicate that feeding has a positive effect on growth rates for certain coral species, but that light intensity is also an important factor (Figs. 2 and 3). Nevertheless, this effect is by no means apparent for all species: feeding may have no effect on skeletal growth (e.g., Wellington 1982; Anthony and Fabricius 2000), or may even reduce growth rates (Grottoli 2002). In the latter example, linear extension rates of the coral *Porites compressa* decreased when colonies were exposed to very high plankton concentrations (5–60 times greater than those measured on the reef). Grottoli (2002) hypothesized that very high feeding rates overstimulate zooxanthellae growth and decouple the coral–algal symbiosis.

More recently, an interaction between light and feeding was confirmed using experiments on ^{45}Ca incorporation into the skeleton of the coral *Stylophora pistillata* (Houlbrèque et al. 2003, 2004a) (Figs. 2 and 3). The use of this radioisotope allows short-term measurements of dark and light calcification rates, which were both two to three times higher in corals fed during 5 weeks with natural zooplankton and *Artemia salina* nauplii. Light calcification rates ranged from 100 to 250 nmoles Ca^{2+} $cm^{-2}\,h^{-1}$ in starved and fed corals, respectively, and dark calcification rates ranged from 40 to 80 nmoles Ca^{2+} $cm^{-2}\,h^{-1}$ for the same corals. The increase in calcium carbonate deposition was linked to an increase in organic matrix synthesis (Houlbrèque et al. 2004a). Calcification indeed consists of two processes: deposition of an organic matrix layer followed by deposition of a calcium carbonate ($CaCO_3$) layer (Allemand et al. 1998). This organic matrix potentially plays a key role in processes such as crystal size, growth and orientation, and regulation of skeletal formation (Weiner and Addadi 1991; Falini et al. 1996; Belcher et al. 1996), and is composed of various amino acids with a composition that differs between symbiotic and non-symbiotic species (Cuif and Gautret 1995). Houlbrèque et al. (2004a) demonstrated that dark calcification rates were more strongly enhanced by feeding than were light calcification rates. This is due to the fact that, under illumination, there is a close coupling between deposition of the organic matrix and the $CaCO_3$ layers, whereas in darkness organic matrix deposition is usually depressed compared to the deposition of calcium carbonate.

In summary, feeding can enhance skeletal growth through three mechanisms:

1. Heterotrophy can stimulate calcification through tissue growth and enhanced supply of dissolved inorganic carbon (DIC). DIC necessary for calcification can be acquired from seawater bicarbonate (Gattuso et al. 1999; Marubini and Thake 1999) or from respired CO_2 (Erez 1978; Furla et al. 2000). Since feeding clearly enhances tissue growth and biomass, calcification can be stimulated by an increased supply of external DIC, via additional transporting molecules or of internal DIC, via enhanced respiration rates (Houlbrèque et al. 2003). Such tissue thickening might serve as a storage strategy when prey is available, allowing a subsequent skeletal growth followed

by thinning of the tissue (Barnes and Lough 1993). High tissue biomass can also supply additional energy, especially for the dark processes such as for the calcium/proton pump (McConnaughey 1989; McConnaughey and Whelan 1997; Anthony et al. 2002).
2. Feeding can indirectly enhance calcification by increasing the photosynthetic process. Photosynthesis supplies ATP for the proton pump, which in turn facilitates transport of carbon for calcification (McConnaughey 1989).
3. Feeding can enhance the construction of the organic matrix by providing some necessary external amino acids. As seen earlier, there is a tight coupling between organic matrix synthesis and calcification, the enhancement of the first process leading to a parallel enhancement of the second one.

In conclusion, the effect of feeding on skeletal growth is species dependent with some species having higher heterotrophic capacities than others. The effect is also light dependent since the highest skeletal growth rates are obtained for fed corals incubated under high light (Fig. 3). Under low light, feeding can maintain, or even enhance, skeletal growth rates that would otherwise be reduced due to lower photosynthetic energy acquisition (Fig. 2). It therefore appears that skeletal growth has a high-energy demand: growth is enhanced when both autotrophy and heterotrophy supply energy to the symbiosis.

3 Energetic Inputs from Heterotrophy

The contribution of heterotrophic feeding to the energy budgets of corals in their natural habitat is not well understood. Due to the difficulty of monitoring *in situ* rates of predation, most studies of coral feeding are experimental and field-based estimates of the energetic input from feeding are therefore rare. Moreover, to date no model has taken into account the potential energy acquisition summed over all types of food available to corals: typically, studies of coral feeding have only considered one type of prey at a time. Finally, nutrient assimilation efficiencies for the different types of food that corals can ingest are not well known because they are mainly deduced from the "egesta" method (Conover 1966; Anthony 1999), which assumes that only the organic component of the food is significantly affected by digestion. Only one study (Piniak et al. 2003) has used the more precise ^{15}N method. All of these factors mean that the relative contributions of autotrophy and heterotrophy to carbon budgets of corals are unknown. In this section, we draw together data from the literature to quantify the magnitude of carbon acquisition from different food sources for several coral species, and from all food sources for a single coral species for which data is available (*Stylophora pistillata*).

Based on experimental work using *Artemia salina* (at a feeding density of 100 Artemia l^{-1}) or natural zooplankton (at 1,500 cells l^{-1}), estimates of carbon acquisition from plankton feeding range from 24 to 600 μg C cm^{-2} d^{-1} (Fig. 4, based on a carbon content of 0.15 μg C per zooplankton prey, Ribes et al. 1998). This broad range of values indicates that feeding capacity is highly species specific, with individual polyps of different coral species capturing between 2 and 50 prey items per hour (see Clayton and Lasker 1982; Sebens and Johnson 1991; Johnson and Sebens 1993; Sebens et al. 1998; Ferrier-Pagès et al. 2003). Although experimental work indicates that zooplankton feeding can make a substantial contribution to daily carbon input, estimates based on field measurements yield much lower values. Indeed, the only study performed on corals maintained under natural conditions has estimated that zooplankton generates approximately 5 μg C cm^{-2} d^{-1} for colonies of *Pavona cactus*, *Pavona gigantea*, and *Pocillopora damicornis* (Palardy et al. 2005). Although experimental measurements of feeding in *Pavona* sp. are not available, these field estimates of feeding for *P. damicornis* are 50-fold lower than experimental estimates (Fig. 4). This inconsistency is most likely due to the fact that the field study did not include predation on the demersal zooplankton community, which migrates near corals during the night and is generally present at a much greater density than planktonic zooplankton (more than 3,000 cells l^{-1}, Heidelberg et al. 2004; Holzman et al. 2005). In fact, a 40% depletion (or 2.60 mg l^{-1}) of demersal zooplankton by reef organisms has been observed during the night (Yahel et al. 2005; Heidelberg et al. 2004). Although no studies have assessed carbon gain by corals at such plankton densities, natural rates of plankton feeding are likely to be higher than previously observed.

In addition to zooplankton, corals also prey on pico- and nanoplankton. Although studies of this feeding mode are rare, pico- and nanoplankton feeding is estimated to yield carbon uptake of approximately 3 μg C cm^{-2} d^{-1} for *S. pistillata* and 30 μg C cm^{-2} d^{-1} for *G. fascicularis* (Houlbrèque et al. 2004b, based on a polyp density of 360 and 1.2 polyps cm^{-2}, respectively). Finally, ingestion of dissolved organic carbon (DOC, Houlbrèque et al. 2004b) and suspended particulate matter (SPM, Anthony 1999) yields from 3 to 580 μg C cm^{-2} d^{-1} (Mills et al. 2004; Anthony 1999; Anthony and Fabricius 2000; Anthony and Connolly 2004). As is the case for zooplankton feeding, SPM ingestion rates are highly species specific (Fig. 4). Very high ingestion rates have been measured for the species *Montastrea franski*, and *Siderastrea radians* (from 474 to 584 μg C cm^{-2} d^{-1}), whereas values for a range of other species are in the vicinity of 10–100 μg C

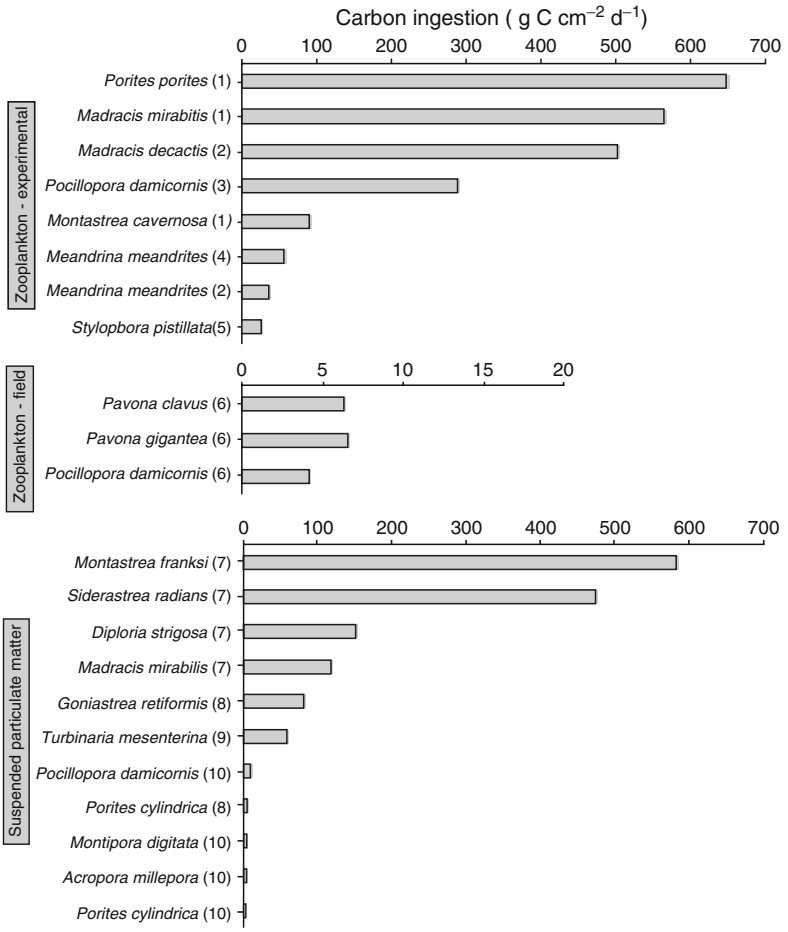

Fig. 4 Carbon gain through various feeding modes for different coral species

NOTES: Values converted to g cm^{-2} d^{-1} based on: carbon content of zooplankton =0.15 g C prey–1 (11), carbon content of SPM = 5% by weight (8). Plankton feeding rates were converted to surface area using polyp densities of 14,15,1,2 and 20 polyps cm^{-2} for *M. decatis, M. mirabilis, M. cevernosa* and *M. meandrites* (based on images in 12) and for *p.pontes* (13).

REFERENCES: (1) Sebens et al. 1998, (2) Sebens & Johnson 1991, (3) Clayton & Lasker 1982, (4) Johnson & Sebens 1993 (5)Femier-Pages et al. 2003, (6)Palardy et al. 2005, (7) Mills et al. 2004, (8)Anthony & Fabricius 2000, (9)Anthony & Connolly 2004, (10) Anthony 1999, (11) Ribes et al. 1998, (12) Veron 2000, (13) Edmunds & Davies 19689.

cm^{-2} d^{-1}. Based on these ingestion rates, studies of SPM feeding have therefore concluded that heterotrophic carbon supply varies from 15 to 35% of the daily metabolic demand in healthy corals (Porter 1976; Sorokin 1993; Grottoli et al. 2006) and may reach 100% in bleached corals (Grottoli et al. 2006). Clearly, a considerable body of evidence now disputes the early view that heterotrophic feeding makes only a minor contribution to the carbon budgets of scleractinian corals (e.g., Muscatine and Porter 1977; Davies 1991).

In fact, relative to carbon acquisition via photosynthesis, it can be demonstrated that heterotrophic feeding contributes significantly to coral energy budgets: even under conditions that have traditionally been considered autotrophic. For the species *Stylophora pistillata*, which has been well studied by many authors, estimates of the daily net carbon fixed by zooxanthellae range from 25 to 123 μg C cm^{-2} d^{-1} in shade- and light-adapted colonies, respectively (Muscatine et al. 1984). Taking all forms of feeding into account, daily carbon acquisition via heterotrophy reaches 18 μg C cm^{-2} d^{-1} at the minimum (Fig. 5). This value is based on the lowest observed measurements of carbon acquired from zooplankton feeding (5 μg C cm^{-2} d^{-1} for zooplankton, Palardy et al. 2005), 8 μg C cm^{-2} d^{-1} for pico- and nanoplankton (Houlbrèque et al. 2004b) and 5 μg C cm^{-2} d^{-1} for DOC/SPM (Anthony 1999; Houlbrèque et al. 2004b). Therefore, the lower bound of estimates of heterotrophically acquired carbon is in fact more than 70% of the value for carbon acquired through symbiont photosynthesis for shade-adapted corals. If predation on demersal zooplankton is included into this estimate, an additional gain of 24 μg C cm^{-2} d^{-1} (Ferrier-Pagès et al. 2003), total daily heterotrophically acquired carbon reaches a maximum estimate of 42 μg C cm^{-2} d^{-1}. This represents more than one-third of the total carbon brought by photosynthesis in light-adapted colonies.

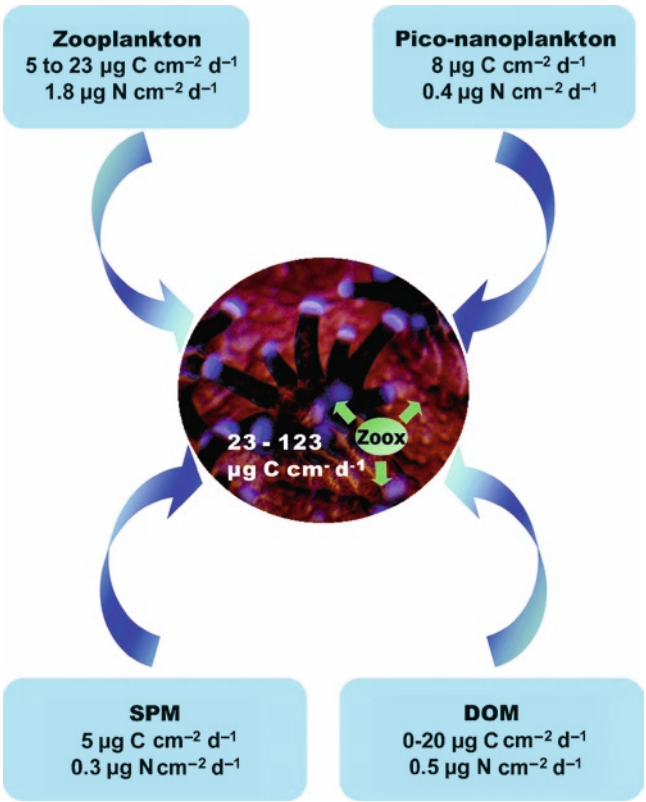

Fig. 5 Auto- and heterotrophic acquisition of carbon and nitrogen in the species *Stylophora pistillata*. *DOC*: dissolved organic carbon; *SPM*: suspended particulate matter. See "Energetic inputs from heterotrophy" for calculations

In addition to providing a supplementary source of carbon, heterotrophy is a vital source of nitrogen, phosphorus, and other limiting nutrients for the coral symbiosis (Houlbrèque et al. 2004b; Grover et al. 2006, 2008). This is evidenced by the fact that efficiency with which heterotrophically acquired nutrients are assimilated into tissue varies between 33% and 100% for suspended particulate matter (Anthony 1999; Mills 2000; Mills et al. 2004), and reaches 70–100% for zooplankton (Bythell 1988; Piniak et al. 2003). Among the total amount of nutrient acquired, the proportion of ingested prey materials utilized by the symbiotic algae is fairly consistent, ranging from 15 to 25% (Cook 1972; Szmant-Froelich 1981; Piniak et al. 2003). Based on these values, the coral *Stylophora pistillata* fed with natural zooplankton (ca. 1,500 prey l^{-1}) can therefore gain more than 1.8 µg N cm^{-2} d^{-1} (Ferrier-Pagès et al. 2003), representing approximately one-third of the nitrogen required for tissue growth. In addition to zooplankton feeding, ingestion of pico- and nanoplankton together with dissolved and particulate organic matter can be more than sufficient to sustain tissue growth in several coral species (Hoegh-Guldberg and Williamson 1999; Ferrier-Pagès et al. 2003). Depending on species-specific feeding rates, SPM can deliver between 0.3 and 48 µg N cm^{-2} d^{-1} (Mills 2000; Mills et al. 2004; Anthony 1999; Anthony and Fabricius 2000; Anthony and Connolly 2004), based on sediment nitrogen content of 0.41% by weight (Anthony and Fabricius 2000). Pico- and nanoplankton ingestion can yield 0.8–6 µg N cm^{-2} d^{-1} (Houlbrèque et al. 2004b), while dissolved organic matter can contribute between 0.1 and 16 µg N cm^{-2} d^{-1} (Ferrier 1991; Badgley et al. 2006; Hoegh-Guldberg and Williamson 1999; Grover et al. 2006, 2008). Indeed, for the species *Stylophora pistillata* it has been estimated that even at the lower range of the concentrations commonly found in seawater (approximately 0.2–0.3 µM), dissolved organic nitrogen can contribute at least 11% of the total daily nitrogen required for tissue growth (0.5 µg N cm^{-2} d^{-1}, Grover et al. 2008). Drawing together all of these sources of nutrient acquisition, it is evident that nitrogen uptake can exceed 3 µg N cm^{-2} d^{-1} (based on values for *Stylophora pistillata*, Fig. 5). Unfortunately, there is insufficient data available to document the uptake of other major nutrients (e.g., phosphorus) contributed by the different feeding modes. Although some studies agree that corals need to take up organic phosphorus from an external source (D'Elia 1977), studies of nutrient uptake and utilization are lacking. What limited evidence there is indicates that feeding on bacteria would yield approximately 3 µg P d^{-1} (Sorokin 1973), a value comparable to uptake of nitrogen.

4 Perspectives and Directions for Future Research

Although investigation of the importance of heterotrophic feeding for coral metabolism has a long history (Yonge 1930a,b; Goreau et al. 1971), interest in this subject has only recently been regained. It is now evident that, taking into account feeding on all possible sources, heterotrophy contributes more to the carbon budget of corals than previously expected. However, many questions regarding the interactions between heterotrophy, autotrophy, energy allocation, and environmental conditions remain unanswered. To resolve these questions, we need first to have a better quantification of the amount of carbon translocated by the zooxanthellae to the host in different environmental conditions. Most estimates of carbon translocation are based on the "contribution of zooxanthellae to animal respiration" or "CZAR" equation presented by Muscatine et al. (1981). However, this equation is based on several assumptions, in particular, that the respiration of the coral host compared to symbionts is based upon the relative biomass of the two partners (Muscatine et al. 1981; Smith and Muscatine 1986; Verde and McCloskey 1996). Moreover, estimates of translocation from this method tend to be higher than those based on direct measurements (using ^{14}C labeling techniques, Trench 1979). Therefore, new

techniques need to be developed to improve our understanding of CZAR.

Secondly, we need to better define the importance of the different food sources for corals, how the dependence on particular sources may vary across different environmental conditions, and which specific nutrient (carbon, nitrogen, phosphorus) is mainly derived from feeding. Even though some studies have individually assessed the grazing rates on zooplankton (Sebens et al. 1996), pico- and nanoplankton (Houlbrèque et al. 2004b), dissolved/particulate organic matter (Anthony 1999) or sediment (Anthony 1999), none of them have measured, or even estimated, the total amount of energy gained by feeding on all potential sources for a given coral species in a given environment. Therefore, it is not known on which food source corals are most reliant, let alone the capacity of coral species to switch between nutrition modes depending on their habitat. Once feeding rates on the different prey have been accurately measured, both under laboratory and field conditions, it will be possible to estimate how strongly heterotrophic feeding varies seasonally due to changes in plankton concentration, water flow, and turbidity.

Another key question that is poorly understood is how energy acquired through photosynthesis compared to heterotrophy is allocated between symbiont population growth, coral tissue growth, skeletal growth, and reproduction. Indeed, some studies have shown that corals used heterotrophic energy differently depending on the light level under which they were grown (i.e., depending on energy gain through photosynthesis). For example, in *T. reniformis* feeding increased lipid stocks under low light, whereas it enhanced growth under high light (Treignier et al. 2008). Similarly, for *S. pistillata* feeding enhanced growth more strongly under high light compared with low light (Houlbrèque et al. 2003). These few observations provide compelling evidence that corals adopt different energy allocation strategies depending on light and food availability. However, more research is needed to understand how corals use their energy sources to cope with environmental constraints, and what mechanisms are involved in the enhancement of growth by feeding. Furthermore, it remains unclear precisely how feeding enhances photosynthesis, and under which environmental conditions such enhancement occurs. In other words, we need to know when corals allocate food to the zooxanthellae to enhance their photosynthetic capacities, and when they sequester nutrients for use by the host tissue. All these questions can first be investigated under experimental laboratory conditions, but such studies must also be extended to natural conditions.

Recent work has highlighted the importance of heterotrophic feeding as a source of carbon for corals during bleaching events (Grottoli et al. 2006). There is now clear evidence that feeding rates on zooplankton can increase dramatically in bleached corals and provide them with up to 100% of their daily metabolic demand (Grottoli et al. 2006). Nevertheless, not all species are capable of upregulating heterotrophy sufficiently to compensate for reduced photosynthesis. In the Grottoli et al. (2006) study only one of three study species was able to do so (*Montipora capitata* compared with *Porites compressa* and *Porites lobata*). Similarly, Anthony and Fabricius (2000) found that where *Goniastrea retiformis* was able to increase sediment feeding sufficiently to compensate for lower photosynthesis in shaded conditions, the same was not observed for another species (*Porites cylindrica*). Clearly, more research needs to be done to determine which corals are more "heterotrophic" as they are probably the species most resistant to bleaching.

Finally, from a broader perspective, further research must be conducted into the trophic links between plankton, corals, and other organisms. It is well known that there is tight recycling of nutrients within reef ecosystems, for example, coral-dwelling fishes excrete waste nutrients that are subsequently taken up by corals (e.g., Meyer and Schultz 1985). Moreover, mucus released by corals functions as a trap for LOM and SPM (Wild et al. 2004), and can form an important food source for other reef-dwelling organisms (Richman et al. 1975). Numerous species of reef fish also rely on coral tissue and/or coral larvae as a food source (Pratchett 1995; Pratchett et al. 2001). Few of these trophic interactions have been quantified and therefore little is known about the importance of coral heterotrophy for the overall health of reef ecosystems.

5 Conclusions

A strong interaction between autotrophy and heterotrophy is apparent for scleractinian corals. Feeding plays a central role in maintaining coral physiological functioning whenever autotrophy is insufficient, such as for corals living in shaded conditions or experiencing a bleaching event (Anthony and Fabricius 2000; Grottoli et al. 2006). Moreover, the available literature indicates that heterotrophy contributes a larger proportion of total carbon acquisition than was previously expected. In light of the predicted increase in the frequency and severity of bleaching events (Hoegh-Guldberg 1999), this indicates that corals able to increase their feeding effort when necessary will be more resilient to stresses and may come to dominate the reef community. Nevertheless, the available experimental evidence indicates that most symbiotic corals cannot rely solely heterotrophic nutrition (Clayton and Lasker 1982; Grottoli et al. 2006). Therefore, predictive models of climate impacts on reef-building corals should take into account the potential for heterotrophic feeding to mitigate environmental stressors. Identifying which coral species are facultative heterotrophs should be a focus of future research.

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