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ORIGINAL ARTICLE

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Phytoplankton: a significant trophic source for soft corals?

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Abstract Histological autoradiographs and biochemical analyses show that ^{14}C-labelled microalgae (diatoms, chlorophytes and dinoflagellates) are used by the soft coral *Dendronephthya* sp. Digestion of the algae took place at the point of exit of the pharynx into the coelenteron. Ingestion and assimilation of the labelled algae depended on incubation time, cell density, and to a lesser extent on species-specificity. ^{14}C incorporation into polysaccharides, proteins, lipids and compounds of low molecular weight was analysed. The ^{14}C-labelling patterns of the four classes of substances varied depending on incubation time and cell density. ^{14}C incorporation was highest into lipids and proteins. Dissolved labelled algal metabolites, released during incubation into the medium, contributed between 4% and 25% to the total ^{14}C activity incorporated. The incorporated microalgae contributed a maximum of 26% (average of the four species studied) to the daily organic carbon demand, as calculated from assimilation rates at natural eucaryotic phytoplankton densities and a 1 h incubation period. The calculated contribution to the daily organic carbon demand decreased after prolonged incubation periods to about 5% after 3 h and to 1–3% after 9 h. Thus the main energetic demand of *Dendronephthya* sp. has to be complemented by other components of the seston.

Keywords Carbon budget · ^{14}C-labelled microalgae · *Dendronephthya* sp. · Herbivory · Soft coral

Introduction

Anthozoans are polytrophic organisms, i.e. they simultaneously or alternatively derive nutrients through a variety of mechanisms from different trophic sources. The polytrophic nature of the anthozoans varies greatly among species with respect to morphology, habitats and availability and diversity of food. The lack of reliable information on the total food supply and its constituents for a particular habitat, including interactions of physicochemical, hydrological and biological factors, limits our understanding of the feeding biology of anthozoans.

Heterotrophy includes the uptake of particulate living and dead organic matter (POM) and the absorption of dissolved organic material (DOM). In zooxanthellate species, the phototrophic supply is delivered by endosymbiotic microalgae (zooxanthellae = dinoflagellates of the *Symbiodinium microadriaticum* group; Carlos et al. 1999) living within gastrodermal host cells (e.g. Muscatine and Weis 1992). In a variety of zooxanthellate and azooxanthellate scleractinian species, filamentous algae which colonize the skeletons also contribute to the corals' energy needs (Schlichter et al. 1996, 1997).

The POM supply in a given habitat is highly diverse in quantity and quality and comprises all the different size classes of plankton and organic detritus. Thus partitioning of trophic resources may be necessary to coexist in the same habitat. (Sorokin 1993; Ayukai 1995; Anthony 1999, 2000; Fabricius and Dommisse 2000).

Anthozoans exploit POM through predation, suspension feeding or deposit feeding. The question as to whether or not living phytoplankton or phytodetritus can be used by anthozoans has been the subject of considerable controversy in the literature (Yonge 1930; Johannes et al. 1970; Porter 1974; Lewis and Price 1975; Lewis 1982; Shick 1991; Sebens 1997; Slattery et al. 1997; Bak et al. 1998; Schlichter and Brendelberger 1998; Sebens et al. 1998; Anthony 1999, 2000).

For the alcyonarian *Dendronephthya hemprichi* Fabricius (1995, 1996) and Fabricius et al. (1995a, b, 1998) published several partially conflicting papers, which in the end indicated a significant retention of phytoplankton. The calculations of the authors show that in

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D. hemprichi the gain of organic carbon through herbivory exceeds the daily demand by a factor of 1.3.

We studied the utilisation of phytoplankton by anthozoans with the aid of ^{14}C-labelled microalgae. Our feeding experiments allowed us to quantify the ingestion of algae; however, it is incorrect to equate the retention of algae by suspension feeders with their metabolic utilisation, although this has frequently been done in the past.

Nevertheless, investigations using labelled microalgae allow us to determine the actual metabolic utilisation of phyto-POM and enable us to assess the assimilation of ingested algae and its conversion into different metabolites of soft corals. These quantitative data are substantial enough to use for calculating carbon budgets and for estimating the potential protein supply through herbivory.

The feeding of anthozoans with ^{14}C-labelled microalgae has already been studied by Roushdy and Hansen (1961), Farrant et al. (1987) and Sorokin (1991). Sorokin investigated the ingestion of labelled microalgae by 24 anthozoan species and was able to show a significant retention of algae for the zoantharian *Zoanthus sociatus* and *Mopsella aurantia* (Gorgonacea); for the soft coral *Dendronephthya* sp., algal ingestion was negligible. Farrant et al. (1987) found only very low ^{14}C incorporation after feeding the soft coral *Capnella gaboensis* with ^{14}C algae, thus doubting that phytoplankton is utilized by this species.

For our experiments we chose the azooxanthellate soft coral *Dendronephthya* sp. because Fabricius et al. (1998) had proved that herbivory is a significant trophic source for this species. The azooxanthellate nature of *Dendronephthya* sp. was advantageous to quantify the pure heterotrophic fuelling of the metabolism of an anthozoan species. For comparison we studied the ingestion of microalgae by a temperate soft coral, and three actinian species.

Materials and methods

Anthozoans

Colonies of the azooxanthellate soft coral *Dendronephthya* sp. (Alcyonacea) up to 1 m high grow in shallow areas with moderate water movement as well as in deeper areas at the fringing reef off the Marine Science Station Aqaba, Gulf of Aqaba, Red Sea, Jordan (29°30′N).

Specimens of the temperate alcyonarian *Alcyonium digitatum* were purchased from the Biologische Anstalt Helgoland, Hamburg (Germany) and maintained in a closed system at 15±1°C, 34.5‰ S and under a 12/12 h light/dark cycle.

Microalgae

In the Red Sea, dinoflagellates are the most abundant group of eucaryotic phytoplankton, making up 49% of the total phytoplankton, followed by diatoms with 33.4%. Green algae and cyanobacteria together account for 17.6% (Kimor and Golandsky 1977; Klinker et al. 1978; Levanon-Spanier et al. 1979). Recent analyses show that eucaryotic phytoplankters total about 6,000 cells ml^{-1} (Yahel et al. 1998).

Offered species

These are divided into four groups as follows:

1 Chlorophyta, Prasinophyceae: *Tetraselmis* sp., size: 10–16× 4–8 µm, cell mass 47.67 pg; cell wall: extracellular minute fused scales of acid mucopolysaccharides; storage product: starch. Cells with a high level of unsaturated fatty acids.
2 Eustigmatophyceae: *Nannochloropsis* sp., size: 2–4 µm, cell mass 3.16 pg; cell wall: polysaccharide; storage product: chrysolaminarine, polyunsaturated fatty acids.
3 Chrysophyta, Bacillariophyceae: *Chaetoceros muelleri*, size: 8.1×6.4 µm, without setae, cell mass 63.1 pg. This species frequently forms chains. Cell wall: a siliceous core enveloped by organic layers (mucopolysaccharides), storage product: chrysolaminarine, with a high level of unsaturated fatty acids.
4 Dinophyta, Dinophyceae: *Amphidinium klebsii*, size: 30–36 µm, cell mass 162.3 pg, and an undetermined dinoflagellate (Nr 1407, Institute of Botany, University of Cologne), size 7–9 µm. Cell walls of the dinoflagellates: polysaccharide plates (cellulose), storage products: starch and a high amount of lipids.

Most of the algal cultures were donated by the Institute of Botany (Dr. I. Reize) of the University of Cologne. *A. klebsii* was obtained from the "Institut und Sammlung von Algenkulturen of the University of Göttingen" (Germany). Data were taken in part from R. Peters (personal communication), Institute of Botany, University of Cologne, Strathmann (1967), Hausmann (1985), Schmid (1994) and C. Gallegos (personal communication).

Culture conditions

Chaetoceros muelleri, *Nannochloropsis* sp. and *Tetraselmis* sp. were grown in f/2 medium (Guillard and Ryther 1962; Guillard 1975); the dinoflagellate species in ASP-H medium (Guillard and Ryther 1962) at 50 µE m^{-2} s^{-1} (Li-Cor 18SB quantum radiometer, Li-Cor sensor UWQ 2646) and under a 12/12 h light/dark cycle.

Labelling of microalgae

^{14}C labelling was performed according to Rivkin (1985). The concentration of $NaH^{14}CO_3$ averaged 37 KBq ml^{-1}. The labelled algae were fed after 22 h of continuous illumination at 50 µE m^{-2} s^{-1}.

Specific activity of the algae

After labelling, 100 µl of suspension was placed on a glass-fibre filter (Whatman GF/A, three replicates). The sample was then acidified and rinsed with 50 ml filtered sea water. The ^{14}C activity of the dried filters was measured. The cell number was counted using a haemocytometer in aliquots of the algal suspensions (three replicates). The specific activity was calculated by dividing the radioactivity of the filter through the amount of algae. The conversion of dpm data into cell numbers on the basis of the specific activity is, strictly speaking, correct only for short incubation periods, for which radioactivity correlates with the cell amount; later on, the correlation diverges especially due to dissimilation processes.

Feeding experiments

Incubation of corals

Branches of large colonies of *Dendronephthya* sp. were removed in situ in 1–8 m depth and were then transferred, protected from light, into flow-through tanks, exposed to a natural light/dark cycle at a reduced irradiance of 5 µE m^{-2} s^{-1} at noon; temperature 26±2°C, salinity 41‰. The colonial fragments were mounted with silicon tubes so that they floated freely in the tanks. The colonies

regained their expanded habitus after a few hours. From the large colonial fragments, small terminal branches were cut off for the feeding experiments. After amputation the branches were put in incubation holders. A holder consists of a perforated bottom plate connected by three thin rods to a ring at the top (all plastic). Further handling of the coral fragments could thus be performed with reduced stress, and the fragile construction did not significantly interfere with the water flow within the incubation vessels. Fragments of *Alcyonium digitatum* were incubated under the same conditions.

The amputated terminal branches of *Dendronephthya* sp. remained in running sea water for several hours and were then transferred first into sterile, filtered sea water (SFS) (glass-fibre filter: Machery and Nagel, 0.5 µm) and afterwards into the incubation vessels containing 300 ml SFS.

The media in the incubation vessels were agitated either by a gentle stream of air bubbles producing slightly turbid conditions or by means of a magnetic stirring bar placed below the perforated basal plate of the incubation holder, generating an unidirectional flow (stirrer: Variomac Poly 15). The flow speed averaged 4–5 cm s^{-1}, which is a realistic in situ value (Fabricius 1995) (flow meter: Schiltknecht, Type Mini Air 20, connected to an aquasensor). With the first experimental setup 12 incubations, and with the second setup six incubations, could be performed simultaneously.

^{14}C-labelled microalgae were added to the media, giving final densities of 600, 6,000 and 60,000 cells ml^{-1}, respectively.

After the incubation periods shown in the figures and the table, half of the experimental colonial fragments were either immediately fixed for histology in 3.6% buffered formaldehyde solution or were put into a mixture of chloroform/methanol 2:1 (v/v) for biochemical analyses (Rivkin 1985). This unrinsed sample type comprised both ^{14}C-labelled algae remaining in the gastrovascular system, and labelled material already incorporated into the coral tissues.

The other half of the experimental colonial fragments were placed in either chloroform/methanol or in formaldehyde after several hours of incubation in running sea water. The rinsing procedure was intended to remove free algae adhered to the surface and free algae within the gastrovascular system.

To simulate in situ conditions more accurately, larger colonial fragments (about 15 cm in height) were incubated in 2,800 ml medium, containing either 6,000 or 60,000 cells ml^{-1} (under turbid conditions). After incubation periods of 0.5, 3 and 9 h, the tissue samples were treated according to the procedure given above. Prior to biochemical and histological preservation, the colonial fragments were separated into terminal branches with a high polyp density, and into basal branches with a low polyp density.

Controls for absorption of released ^{14}C photoassimilates

Although the feeding experiments were performed under reduced irradiance, it cannot be excluded that the corals took up dissolved ^{14}C-labelled photoassimilates (DOM) released by the algae during the rather long incubation periods. This means that radioacarbon incorporated into the corals did not necessarily originate from assimilated particulate algal material.

To test for this possibility, control experiments were performed: first the particular algae species was suspended for a given period at a certain density in 300 ml medium. After a certain incubation period, the algae were removed from the SFS by filtration (glass-fibre filter, Machery and Nagel, 0.5 µm). Coral fragments were then incubated in the algae-free media for the same time periods and were treated as described above. Due to filtration stress, it is most likely that in the control experiments DOM concentrations were higher than in the standard experiments. Furthermore, the consumption of ^{14}C-labelled bacterial biomass by the corals cannot be excluded, for the cultures were unialgal but not axenic. The amount of ^{14}C material assimilated by the corals could therefore be influenced by incorporated ^{14}C bacterial biomass labelled through the utilisation of ^{14}C photoassimilates released by the algae during co-incubation.

Incubation of Alcyonium digitatum

The incubation of the temperate soft coral took place according to the same procedure. The incubation volume was 300 ml, the temperature 15±2°C and the salinity 34.5‰.

Respirometry

Respiration by colonial fragments of *Dendronephthya* sp. was measured polarographically in temperature-constant perspex chambers (1,500 ml) at 26±2°C and 41‰ S. Oxygen was determined with a WTW E0–200 electrode connected to a WTW Dig-Oxi 530 (WTW). The respiration rates were calculated on a mg protein baseline. The respiration data were the basis for the carbon budgets listed in Table 1.

Biochemical analyses

Homogenisation

The incubated branches of *Dendronephthya* sp. were homogenised in chloroform/methanol 2:1 (v/v) for 1 min (9,500 rpm) with an Ultra Turrax homogenisator (IKA). In the same way tissue of *Alcyonium digitatum* was treated. Prior to further manipulations the homogenates were shaken for about 12 h to improve extraction.

Fractionation

The separation of the initial homogenates into four main fractions [lipids, polysaccharides, proteins and low molecular weight compounds (LMWC)] was performed according to Rivkin (1985). The protocol in short: the homogenates were filtered through a glass-fibre filter (Whatmann GF/A). To the filtrate 10 ml Aqua dest. was added. After a few hours the separation into a polar and an apolar phase was completed. Both phases were dried and dissolved in chloroform or in Aqua dest. The glass-fibre filter covered with the tissue residue was cut into small pieces and proteins were precipitated with 5% TCA (trichloracetic acid) at 95°C for 1 h. The tissue/glass-fibre filter suspension was filtered through a second glass-fibre filter, on which the precipitated proteins remained. The filtrate contained polysaccharides which were dried and dissolved in Aqua dest.

Determination of protein

The residual proteins on the (second) filter were hydrolysed with 1 N NaOH for 30 min at 95°C. Proteins were determined according to Lowry et al. (1951). Ovalbumin was used for calibration standards.

For comparison with literature data, the ash-free dry weight and the protein contents of polyps and colony fragments were determined according to standard methods.

Separation of lipids

The different constituents of the lipid fractions were separated by thin layer chromatography (TLC) according to Glasl and Pohl (1974) on silica plates (Merck 60F, 0.25 mm). After separation, the plates were covered with X-ray films (Hyperfilm-βmax; Amersham-Buchler). Time of exposition varied between 2 and 12 weeks depending on ^{14}C activity.

For quantification the radioactive spots were scraped off of the plates. The powder was transferred into a scintillation cocktail and shaken for 12 h, then the radioactivity was measured. The amount of incorporated radiocarbon into the different constituents of one line is expressed as a percentage of total radiocarbon.

Determination of radioactivity

The ^{14}C activity of subsamples of all fractions and dried glass-fibre filters was measured in scintillation cocktail (Universol ES;

ICN) in a scintillation counter (Beckman LS 1800; dpm version). The ^{14}C content of the different fractions was calculated on a protein baseline of the initial homogenates.

Histological autoradiography

Terminal branch pieces (about five polyps) were preserved in buffered 3.6% formaldehyde solution either immediately after the incubation periods listed or after about 5 h post-treatment in running sea water (see above). The preserved branches were rinsed in tap water, decalcified for 2 h in 4% salpetric acid (dissolution of the sclerites) and were then treated according to histological standard methods and embedded in paraplast (Roth). The pieces were cut into 15 µm thick sections.

Autoradiographs were produced using the dipping technique (LM-1 photoemulsion; Pharmacia). After 7–9 days of exposition the preparations were developed with Kodak D19.

Statistics

Incorporation of labelled algae as a function of time was tested by the Mann-Whitney *U*-test. Calculations of linear regressions and trends were analysed with the aid of Microsoft Excel 97.

Results

Autoradiographic studies

Incorporation of ^{14}C-labelled particulate algal material

The ingestion and assimilation of ^{14}C-labelled microalgae by *Dendronephthya* sp. is shown qualitatively in the figures. The different algae species were digested and converted into the corals' biomass almost independently of their taxonomic status, cell wall constituents and cell size.

The algae were retained at the exit of the pharynx into the gastrovascular cavity (Fig. 1). This digesting region of the pharynx lies opposite to the heavily flagellated siphonoglyph (Fig. 2). Algae such as *Chaetoceros muelleri* (8.1×6.4 µm, chain-forming), *Tetraselmis* sp. (10×8×6 µm) and the dinoflagellates (from 7 up to 36 µm) seem to be large enough to be retained at this "check point". Cells of the minute species *Nannochlo-*

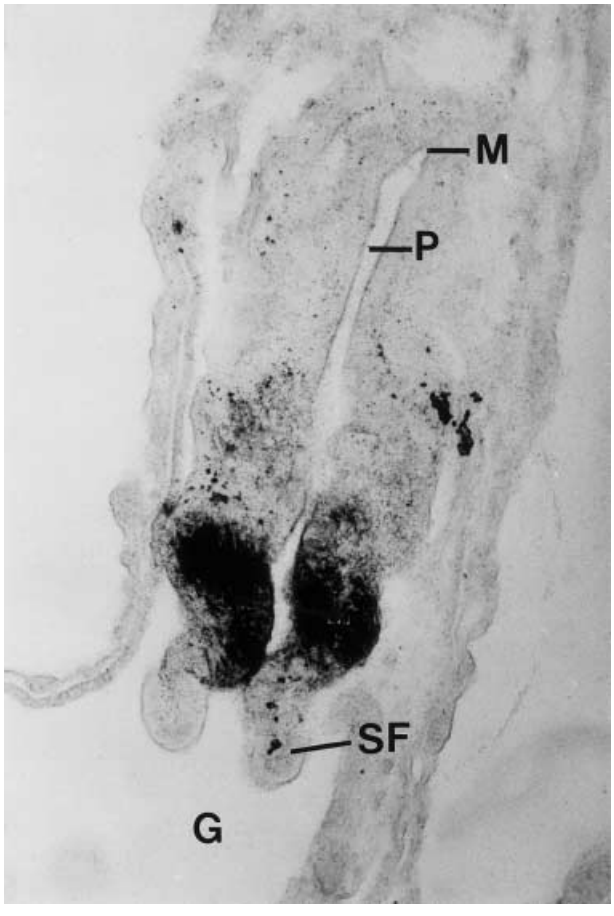

Fig. 1 Incorporation of particulate ^{14}C-labelled algal material (*Chaetoceros muelleri*) into the soft coral *Dendronephthya* sp. Autoradiogram of a histological longitudinal section through a polyp. The coral sample was preserved after 9 h of incubation at an algal density of 60,000 cells ml^{-1}. *M* mouth, *P* pharynx, *SF* septal filament, *G* gastrovascular cavity

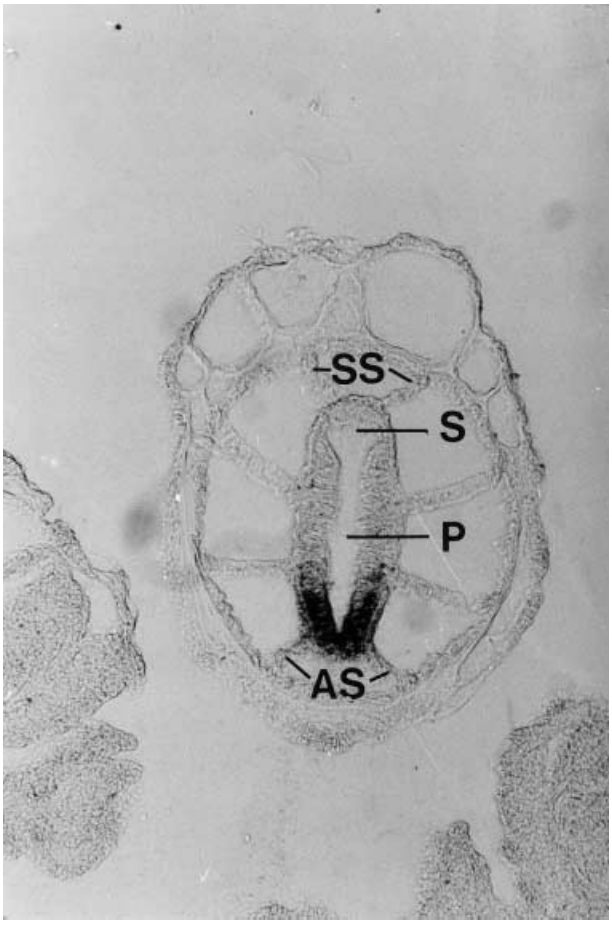

Fig. 2 Incorporation of particulate ^{14}C-labelled algal material (*Chaetoceros muelleri*) into the soft coral *Dendronephthya* sp. Autoradiogram of a histological cross section through a polyp. The coral sample was preserved after 30 min of incubation in water containing 60,000 cells ml^{-1}. *P* pharynx, *S* siphonoglyph, *SS* sulcal septa, *AS* asulcal septa. Longitudinal axis of the pharynx about 200 µm

ropsis sp. (2–4 µm) were occasionally found to be in contact with gastrodermal tissues of the coelenteron at some distance from the pharynx, suggesting that at least some specimens of this algal species had passed through the pharynx unaffected.

The distribution of ^{14}C-labelled particulate algal material from the lower exit of the pharynx to other parts of the colony was rather independent of time during the periods studied (Fig. 3). Due to the long incubation periods and the continuous supply of labelled algae, it is not possible to give exact information about the time course.

Absorption of dissolved ^{14}C labelled algal metabolites

During the experiments the algae released ^{14}C-labelled metabolites into the incubation media. The absorption of these ^{14}C photoassimilates would lead to an accumulation of labelled assimilates in the tissues of *Dendronephthya* sp. due to the well-known capacity of anthozoans for utilising dissolved organic material (Pütter 1911; Schlichter et al. 1986).

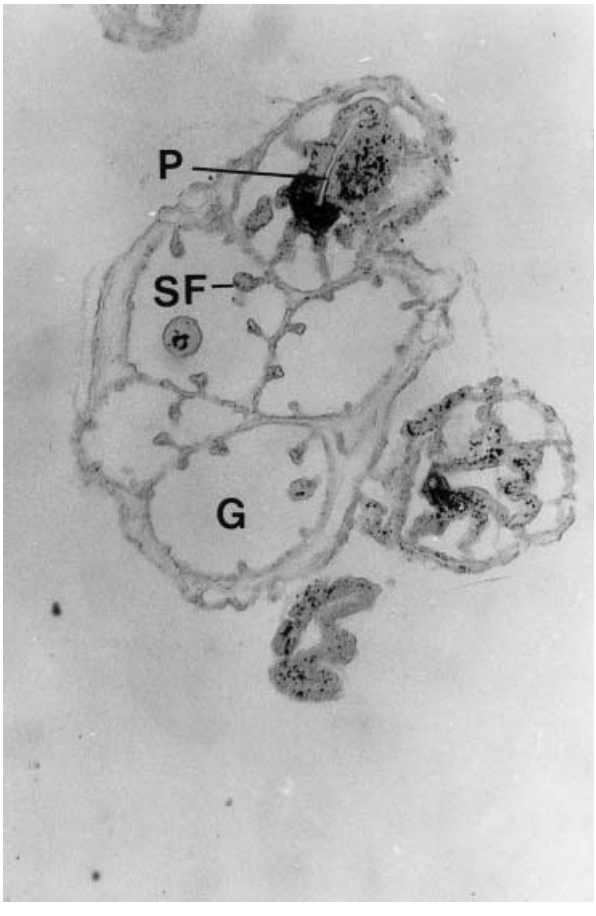

Fig. 3 Histological autoradiograph of a cross-section through a terminal branch of a colony of the soft coral *Dendronephthya* sp. The branch was incubated for 3 h in water containing 60,000 cells ml^{-1} (*Chaetoceros muelleri*). Only a few polyps contained labelled algae and the allocation of labelled material from the place of digestion to adjacent regions was low. *P* pharynx, *SF* septal filaments, *G* gastrovascular cavity

In the control experiments the algae had been removed from the media prior to the incubation of the colonial fragments. Autoradiographs from control incubations showed only a weak ^{14}C accumulation. Absorption of dissolved ^{14}C photoassimilates took place predominantly through gastrodermal cells.

Biochemical studies

Accumulation of ^{14}C-labelled algal metabolites and the labelling patterns of coral biomass in relation to incubation time, cell density and species specificity

The accumulation of ^{14}C-labelled algal metabolites within tissues of *Dendronephthya* sp. is shown in the figures for a diatom (*Chaetoceros muelleri*), a green alga (*Nannochloropsis* sp.), and for dinoflagellates (*Amphidinium klebsii* and an undetermined species).

The amount of accumulated radiocarbon (cell number) as well as the pattern of incorporated ^{14}C-labelled algal material with respect to the four classes of substances (lipids, low molecular weight compounds, polysaccharides, proteins) of *Dendronephthya* sp. depends on cell density, incubation time and to a lesser extent upon the species studied. The ^{14}C-labelling patterns of the four molecular fractions of the algae (after 22 h of continuous labelling) and those of the coral differ (Figs. 4, 5).

Algal density

The total radiocarbon accumulation after incubation in 600 cells ml^{-1} averaged only about 16% of that recorded after incubation in 6,000 cells ml^{-1}, and the accumulation of ^{14}C-labelled algal metabolites increased by the factor 2–8 when a 10-fold higher algal density was used (Figs. 4, 5 and Table 1). At low algal concentrations ^{14}C accumulation remained low up to 9 h of incubation, whereas at a higher algal concentration (60,000 cells ml^{-1}) ^{14}C accumulation increased significantly with incubation time.

At low concentrations (600 and 6,000 cells ml^{-1}) the protein fraction showed the highest ^{14}C incorporation, followed by lipids and LMWCs. ^{14}C incorporation into polysaccharides was very low. After incubation at high cell density (60,000 cells ml^{-1}), the ^{14}C incorporation was strongest into the lipid fractions, correlating with the fact that anthozoans generally use lipids for storage (Patton et al. 1977; Shick 1991). A different pattern was recorded when *Tetraselmis* sp. was used: ^{14}C incorporation into lipids and proteins increased with incubation time, following the general trend, but incorporation into the LMWC fraction was also high (data not shown).

Incubation time and species specificity

The accumulation of ^{14}C-labelled algal metabolites in the four molecular fractions of the coral tissue

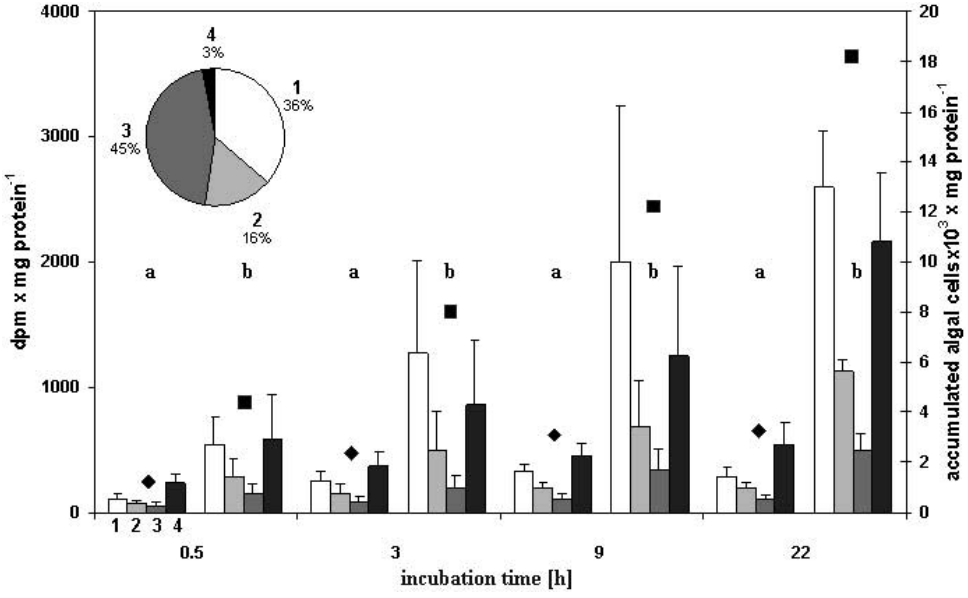

Fig. 4 Ingestion and assimilation of ^{14}C-labelled *Chaetoceros muelleri* (size: 8.1×6.4 µm) by the soft coral *Dendronephthya* sp. Accumulation of ^{14}C-labelled algal metabolites in the coral as a function of feeding (=incubation) time and algal density. Experiments at a density of 6,000 (*a*) and experiments at 60,000 cells ml^{-1} (*b*). Temperature 26±2°C, salinity 41‰, natural light/dark cycle at reduced irradiance of 5 µE m^{-2} s^{-1}. Incubation volume 300 ml. Means ±SD of *n*=4–9. *Columns*: incorporated radiocarbon into the four fractions in dpm per mg protein (*left side ordinate*): *1* lipids, *2* low molecular weight compounds, *3* polysaccharides, *4* proteins. *Diamonds and squares*: Total amount of ingested algae at the initial cell densities *a* or *b*, respectively (*right side ordinate*). *Inset*: ^{14}C pattern of the four fractions (1–4) of the algae after 22 h of continuous labelling

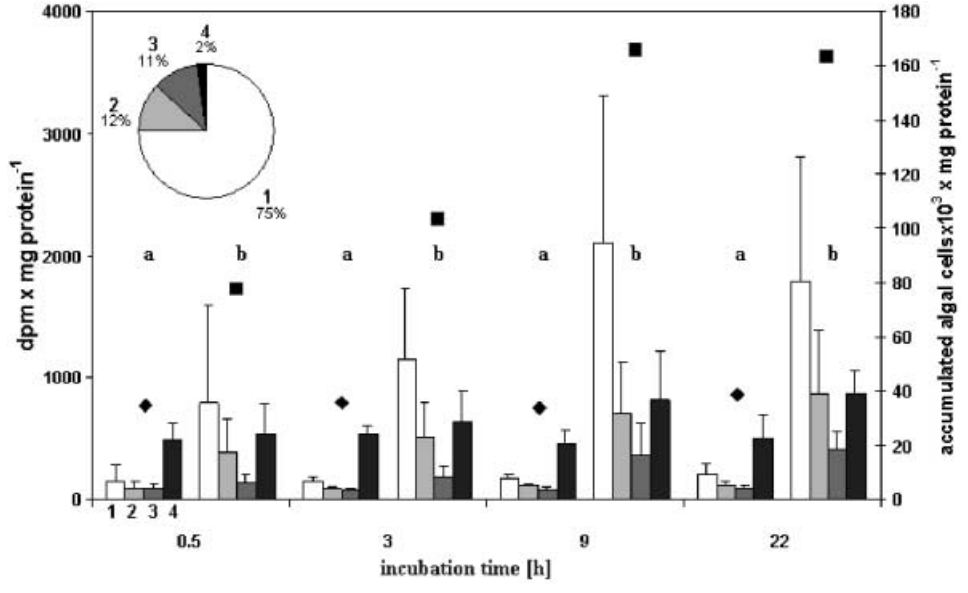

Fig. 5 Ingestion and assimilation of ^{14}C-labelled *Nannochloropsis* sp. (2–4 µm) by the soft coral *Dendronephthya* sp. Accumulation of ^{14}C-labelled algal metabolites in the coral as a function of feeding (=incubation) time and algal density. Experiments at a density of 6,000 (*a*) and experiments at 60,000 cells ml^{-1} (*b*). Temperature 26±2°C, salinity 41‰, natural light/dark cycle at reduced irradiance of 5 µE m^{-2} s^{-1}. Incubation volume 300 ml. Means ±SD of *n*=5–9. *Columns*: incorporated radiocarbon into the four fractions in dpm per mg protein (*left side ordinate*): *1* lipids, *2* low molecular weight compounds, *3* polysaccharides, *4* proteins. *Diamonds and squares*: Total amount of ingested algae at the initial cell densities **a** or **b**, respectively (*right side ordinate*). *Inset*: ^{14}C pattern of the four fractions (1–4) of the algae after 22 h of continuous labelling

increased and the labelling patterns changed with incubation time (Figs. 4–6; Table 1). For *Chaetoceros muelleri* and the dinoflagellate species, the increase was statistically significant at all densities, for *Nannochloropsis* sp., however, only at high cell densities (*U*-test). At low cell density, the labelling pattern established after 30 min remained virtually constant over 22 h (*U*-test).

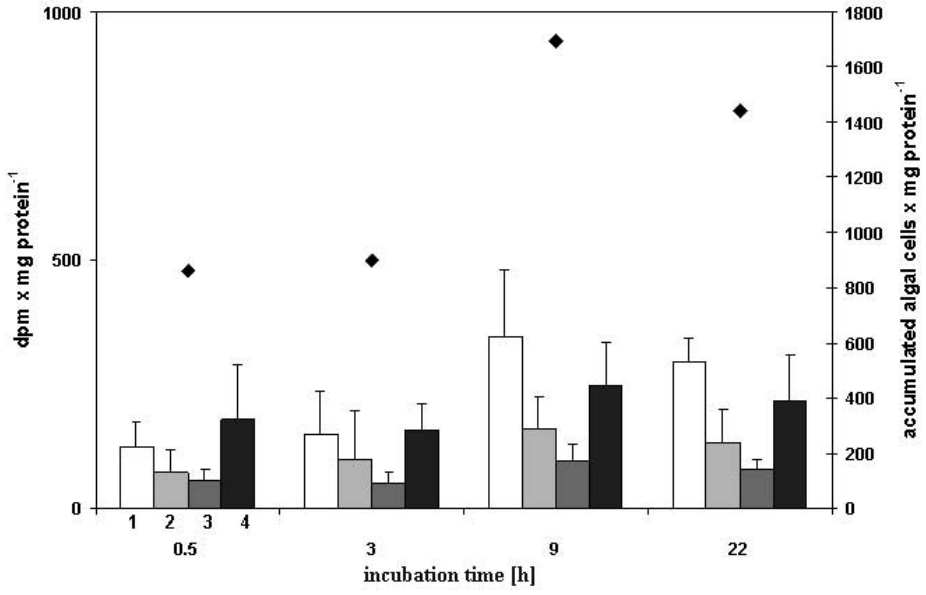

Fig. 6 Ingestion and assimilation of ^{14}C-labelled dinoflagellates (*Amphidinium klebsii* and an undetermined species) by the soft coral *Dendronephthya* sp. Accumulation of ^{14}C algal compounds into the coral as a function of feeding (=incubation) time and at an algal density of 6,000 cells ml^{-1}. Temperature 26±2°C, salinity 41‰, natural light/dark cycle at reduced irradiance of 5 µE $m^{-2}s^{-1}$. Incubation volume 300 ml. Means ±SD of *n*=6. *Columns*: incorporated radiocarbon into the four fractions in dpm per mg protein (*left side ordinate*): *1* lipids, *2* low molecular weight compounds, *3* polysaccharides, *4* proteins. *Diamonds*: Total amount of ingested algae (*right side ordinate*)

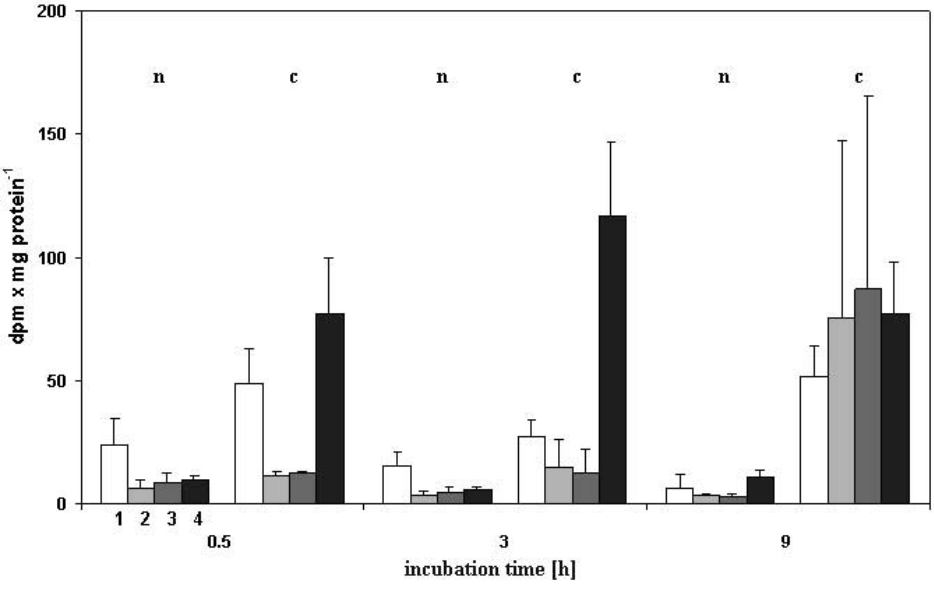

Fig. 7 Absorption of dissolved ^{14}C-labelled algal assimilates by *Dendronephthya* sp. The algae were removed from the media prior to the incubation of the colonial fragments; *Nannochloropsis* sp. (*n*), *Chaetoceros muelleri* (*c*). Concentration of algae: 6,000 cells ml^{-1}, three replicates. *Columns*: incorporated radiocarbon into the four fractions in dpm per mg protein: *1* lipids, *2* low molecular weight compounds, *3* polysaccharides, *4* proteins

Contribution of dissolved labelled photoassimilates (DOM) to the total ^{14}C accumulation

Though the feeding experiments were performed under strongly reduced irradiance (5 µE m^{-2} s^{-1}), it is possible that the algae released ^{14}C-labelled assimilates during incubation, which were used by the corals. Control experiments, in which coral fragments were incubated in media from which the algae had been removed previously, indicate that DOM absorption is low (Fig. 7). The amount of ^{14}C absorbed did not exceed 4% in *Nannochloropsis* sp. and 25% in *Chaetoceros muelleri*, compared with that absorbed from media with complete algae still inside.

The algae cultures used were unialgal but not axenic. Bacteria growing in the media and utilising ^{14}C algal material could become incorporated by the corals and thus contribute to the total accumulated radiocarbon. However, the low ^{14}C incorporation of dissolved algal metabolites after incubation in algae-free media does not indicate an important trophic role of bacteria.

Methodological effects upon the results of the feeding experiments

Post-treatment of incubated colony fragments

In addition to those subsamples which were treated immediately after incubation, other subsamples from the same experimental setup were maintained for several hours in running sea water before biochemical or histological preservation. This was done to distinguish between ^{14}C activity of algal material being already incorporated into the corals' polymers and activity originating

from ingested algae still floating within the gastrovascular system. However, in experiments with *Chaetoceros muelleri*, *Nannochloropsis* sp. and the undetermined dinoflagellate species, the post-rinsing treatment had only a slight influence on the results, and thus the data from both types of subsamples were pooled. This finding corresponds to the autoradiographic studies, which indicated that free algal cells (with the possible exception of *Nannochloropsis* sp.) are not accumulated within the gastrovascular cavity.

Agitation of the media during incubation

The ingestion of microalgae by *Dendronephthya* sp. was influenced by the way in which the incubation media were agitated. The retention of algae under turbid conditions was about 2.5 times higher than under flow conditions, where the algae drifted to the periphery of the incubation vessels, diminishing the probability of ingestion.

Retention and assimilation of ^{14}C-labelled algae as a function of polyp density

To simulate the natural trophic situation for *Dendronephthya* sp. more realistically, feeding experiments were performed with larger colonial fragments (about 15 cm in height). Incubation took place in 2,800 ml media at a natural density of 6,000 cells ml^{-1} of *Chaetoceros muelleri* and *Nannochloropsis* sp., respectively, under turbid conditions.

Prior to homogenisation and fractionation, the incubated colonial fragments were separated into terminal branches with a high polyp density and into basal parts bearing fewer polyps.

With respect to the time-dependent uptake of *Chaetoceros muelleri* (size: 8.1×6.4 µm, chain-forming), the ^{14}C accumulation in the terminal branches was about twice as high as those in the basal parts of the same colony. The ^{14}C accumulation rates in terminal branches of large colony fragments corresponded to those determined in the standard feeding experiments in which isolated terminal branches were incubated.

As to the ingestion and assimilation of *Nannochloropsis* sp. (size: 2–4 µm) by large colonial fragments, the accumulated ^{14}C activity in terminal branches of the colony was about 1.5 times higher than that in the basal parts of the same colony. A comparison of terminal branches remained on larger colony fragments during incubation with those of isolated ones (standard feeding experiments) shows that accumulation rates of the former were about 4 times higher (Table 1, tall fragments).

Utilisation of microalgae by Alcyonium digitatum

Alcyonium digitatum accumulated an average of 30% fewer microalgae than *Dendronephthya* sp., calculated on a mg protein baseline (data not shown).

Discussion

Histological autoradiography

Incorporation of particulate ^{14}C-labelled algal material in Dendronephthya *sp*

Incorporated ^{14}C-labelled particulate algal material was mainly observed at the exit of the pharynx into the coelenteron. Autoradiographs showing several polyps cut in the pharynx region, demonstrate that only a few polyps contained labelled material at a time, even after 22 h of incubation. The finding that only a few polyps were found to ingest algae is supported by the inspection of hundreds of histological sections.

When discussing the amount and the distribution of ^{14}C-labelled metabolites in the histological autoradiographs, one has to bear in mind that during preparation of the histological sections some alterations had taken place. The silver grains of the autoradiographs originate from ^{14}C incorporation into formaldehyde-precipitable molecules. Lipids and most of the intracellular low molecular weight compounds had already been removed prior to the final preparation of the autoradiographs.

The total concentration of eucaryotic phytoplankters in the Gulf of Aqaba is about 6,000 cells ml^{-1} (Yahel et al. 1998). Special mechanisms are required to obtain microalgae from such a low in situ cell density. According to Fabricius (1995) the pinnulate tentacles of *Dendronephthya hemprichi* produce sieving structures with a mesh size of about 60–80 µm. Filtration on a purely physical basis therefore seems insufficient for keeping back microalgae. Lewis (1982) did not find any indication for the involvement of mucus in the feeding activity of octocorals. Our histochemical studies support this observation (data not shown). For *Corallium rubrum*, Abel (1970) described particles caught by the tentacles and then stuffed into the stomodaeum through tentacle contraction or coordinated mouthward strokes of the tentacles. However, for the studied microalgae and all other microsize POM components, it is most likely that particles are transported by ciliary activity into the pharynx of *Dendronephthya* sp. Larger algae or condensed algal packages were retained at the exit of the pharynx where digestion starts. The idea that the pharynx is involved in digestion has already been suggested by Kükenthal (1925).

The blockage of the basal exit of the pharynx is the decisive event in controlling further particle retention, thus influencing the filtration efficiency and having a severe impact upon the calculation of energy budgets (Table 1). The ingestion rates are therefore also controlled by internal feeding structures and not only by the flow regime and the particle concentration, which are in general the main factors controlling passive suspension feeding (Anthony 1999).

The autoradiographs give evidence of the assimilation of algal material, although it is not clear whether the incorporated compounds are cell wall polymers or intracel-

lular components including storage products. The digestion of cell wall polymers would be crucial for maximal energetic utilisation of algal biomass.

Nevertheless, the histological autoradiographs give an incorrect impression of the trophic importance of phytoplankton. The energy calculations based on the biochemical investigations indicate that the actual contribution is low. The wrong impression of the autoradiographs results from the high sensitivity of the ^{14}C technique.

Reports about the equipment of anthozoans with enzymes which digest cell wall polymers of algae are rare. Ishida (1936) investigated enzymes of a sea anemone and did not find any carbohydrate-degradating enzymes. A low activity of cellulolytic enzymes was reported for a soft coral species by Elyakova (1972) and Elyakova et al. (1981) and for a sea anemone by van Praët (1984). These reports might indicate a low capacity of anthozoans for digesting algal cell walls. However, it cannot be excluded that the measured enzymatic activities originated from ingested herbivorous zooplankton or ingested algae, and not from the anthozoans themselves. Fabricius (1996) reports on the intracellular digestion of algae by *Dendronephthya hemprichi* at an electron-microscope level, but did not present any information on where this occurred. To be able to use intracellular algal cell components, cell walls need not necessarily be digested by coral enzymes (see below).

The allocation of labelled algal material from the place of digestion to other parts of the colony could be managed (1) through cell to cell transport, (2) extracellularly within the fluid-filled gastrovascular system, or (3) by mobile amoebocytes which are abundant within the mesogloea. This layer between the epidermis and the gastrodermis could speculatively function as a path for well-directed intracolonial food transport. The transport of foodstuffs within the gastrovascular system seems to be problematic and less effective due to inevitable losses caused by permanent dilution by the surrounding water.

The content of the gastrovascular cavity of *Dendronephthya hemprichi* was analysed by Fabricius (1995). Her studies revealed eucaryotic phytoplankton and a small amount of cyanobacteria in the coelenteron, although the density of cyanobacteria in the sea is five times higher (Yahel et al. 1998).

Utilisation of dissolved ^{14}C-labelled algal compounds released during incubation

Experiments were performed to assess the importance of algal substances released into the medium during incubation of the corals. Colonial fragments were incubated in media from which the algae had been removed previously. The autoradiographs indicate a low level absorption of labelled DOM; uptake occurred particularly by gastrodermal cells. The quantitative data for the corresponding biochemical analyses of the same experiments indicate that the ^{14}C accumulation rates of dissolved assimilates are low on an absolute scale (see below).

Physiological aspects

Accumulation of ^{14}C-labelled algal metabolites in Dendronephthya *sp. as a function of incubation time, cell density and species specificity*

Not unexpectedly, the accumulation of ^{14}C-labelled algae increased with time and as a function of cell density. The assimilation of algal material by the corals is indicated by a continuous increase of ^{14}C metabolites incorporated into the constituents of the four molecular fractions. However, the intensity of ^{14}C incorporation into lipids, LMWCs, polysaccharides and proteins varied considerably.

According to Rivkin (1985), the ^{14}C-labelling patterns of the four fractions differ even among specimens of the same algal species, depending on their origin and history. Therefore, general explanations about the fate of ^{14}C-labelled algal metabolites incorporated by corals are unreliable. A long-lasting feeding with ^{14}C-labelled algae (up to 22 h) leads to an unspecific "contamination" of the corals' biomass with ^{14}C-labelled algal metabolites via joint precursors of the intermediary metabolism. The conversion of algal into coral metabolites depends not only on algal properties but also on internal processes of the corals (e.g. the stage of energetisation) influencing the labelling intensity of the four fractions.

If we compare the ^{14}C patterns of the four fractions in the algae with the patterns of the four fractions in *Dendronephthya* sp. after ingestion of labelled algae, the quantity of incorporated ^{14}C in the four fractions differed considerably.

The different cell wall polymers and storage products of the different algal species used as food, had only a weak influence on the labelling patterns of the four molecular fractions in *Dendronephthya* sp., with one exception (see below). When feeding with *Chaetoceros muelleri*, *Nannochloropsis* sp., *Amphidinium klebsii* and the undetermined dinoflagellate species the labelling patterns showed similar trends: At low cell densities, ^{14}C incorporation took place mainly into proteins, followed by lipids. At a high cell density, lipids were most strongly labelled, followed by proteins. ^{14}C incorporation and its increase in time in the LMWC fractions was low, which may be explained by the high turnover of constituents of the LMWC fractions in the intermediary metabolism.

The labelling pattern of the four fractions after feeding with *Tetraselmis* sp. varied with respect to a high ^{14}C incorporation into the LMWC fractions. These results should not be overinterpreted, however, for investigations were performed on only one replicate each at 6,000 and at 60,000 cells ml^{-1}.

Two mechanisms could be involved in the breakdown of the algae, working either separately or synergistically: (1) the digestion of the algae could be accomplished by the coral's own enzymes; digestion might start when algal cells get into contact with the septal filaments, and might continue intracellular after endocytosis: (2) Berges and Falkowski (1998) studied the autocatalysed cell

death of unicellular algae (a diatom and a chlorophyte species). Under suboptimal conditions the authors measured a strong increase of protease activity leading to cell lysis. By analogy, algae ingested by *Dendronephthya* sp. could become utilisable by an autocatalysed breakdown without involvement of the coral's own enzymes. The contact with the pharyngeal tissue could start autolysis. In situ or in the algae cultures, a certain amount of the cell population is just in the stage of lysis. One might speculatively argue that it was mainly these algal cells just in the stage of lysis that were ingested. Together with the control mechanism in the pharynx, this could explain the low ingestion rates.

The trophic importance of the algae could be enhanced, however, if cell wall polymers and storage products could finally be enzymatically broken down into utilisable monomers.

In the context of ingestion and assimilation of algae by *Dendronephthya* sp., several questions which have consequences for the calculation of energy budgets remain unanswered. These questions concern the dynamics of ingestion, digestion, assimilation, dissimilation, the exocytosis of energy-rich waste products and undigestible cell wall polymers. Furthermore, the conversion of radioactivity data (dpm × mg protein^{-1}) into cell or cell-mass data restrained by the uncertainty in transforming organic carbon data (cell-mass) into energy equivalents, in that the organic carbon of the cells is never completely used by the consumer. All these aspects ultimately lead to the question of the assimilation efficiency of the ingested algae.

Anthony (1999) studied the incorporation of fine organic particulate matter by scleractinians, and calculated an assimilation efficiency of about 90% at low substrate concentrations, whereas at high substrate concentrations the efficiency dropped down to 40–50%.

One drawback to our studies was that we were unable to measure the degree of dissimilation of ^{14}C-labelled algal metabolites by the corals. However, this did not affect energy calculations based on short-time ingestion/assimilation rates.

The contribution of microalgae to the daily organic carbon demand of Dendronephthya *sp*

The contribution of the algae to the daily carbon demand of *Dendronephthya* sp. was calculated according to standard procedures and on different baselines (Table 1). Basically the energetic gain by assimilated ^{14}C-labelled algae over a certain period of time was correlated with the energetic demand (respiration) for the same period.

Nannochloropsis sp., when offered at natural cell densities (600–6,000 cells ml^{-1}) over a 1 h incubation period, contributed a maximum of 34% to the daily carbon demand (Table 1). However, the calculated contribution to the daily organic carbon demand decreased after prolonged incubation periods to about 5% after 3 h and 1–3% after 9 h. The conspicuous decrease of the high initial rates seems to be influenced by the "digesting blockage" within the pharynx.

The budgets calculated on the basis of a density of 60,000 cells ml^{-1} are, although completely unrealistic, an indication that even under such conditions (e.g. algal blooms) the energy contributed by phytoplankton remains low.

Due to the suboptimal incubation conditions in the standard feeding experiments, the real contribution through herbivory might be higher in situ. The ingestion and assimilation rates calculated for larger algae species (*Chaetoceros muelleri*, *Tetraselmis* sp., Dinoflagellates) on the basis of results obtained under standard conditions and of those simulating in situ conditions were found to be similar. However, for the minute *Nannochloropsis* sp., the incorporation rates under simulated in situ conditions were about 3.5 times higher than in the standard feeding experiments.

The low trophic contribution through herbivory, suggests that there are further heterotrophic resources used by the azooxanthellate *Dendronephthya* sp. Besides DOM, all categories of zooplankton and dead organic materials such as phytodetritus and zoodetritus might be used to meet the energetic demands.

We used the contribution value of 26% to the daily organic carbon demand by herbivory as the basis for a comparison with data published by Fabricius (1995, 1996) and Fabricius et al. (1995a, b, 1998). The value of 26% is based on the incorporation rates (1 h incubation) of the algal species investigated and on their relative abundance in the Gulf of Aqaba (Yahel et al. 1998).

To compare the data listed in the above publications with our data, it was necessary to express biomass or metabolic data of *Dendronephthya* sp. on a common basis. We tried to recalculate data from the literature (respiration/O_2 production/biomass data and the conversion into energy equivalents) on a mg protein basis instead of ash-free dry weight (AFDW) or individual polyp biomass or vice versa.

Fabricius et al. (1995a, b) calculated a daily organic carbon demand of 6.46 mg C × g AFDW^{-1} × 24 h^{-1} for *D. hemprichi*, which is in good agreement with our value of 6.05 mg C × g AFDW^{-1} × 24 h^{-1}, calculated from our measurement of 22.83 µg C × mg protein^{-1} × 24 h^{-1} being equivalent to an oxygen consumption of 0.761 mg O_2 × mg protein^{-1} × 24 h^{-1}.

For *D. hemprichi*, Fabricius (1995) and Fabricius et al. (1995a, b) calculated an important trophic contribution of herbivory, exceeding the basal metabolism by a factor of 2–10. The authors concluded that phytoplankton is the most important trophic resource for *D. hemprichi*. Due to miscalculations while converting chlorophyll measurements into organic carbon data, however, the orginal µg C-rates had to be corrected by the authors to ng C-rates. Based on the new data, the amount of organic carbon derived from herbivory has to be recalculated and the trophic contribution of phytoplankton, depending on flow speed, drops down to 0.33–1.50% (Fabricius 1996). These values conform with our calculations based on long-term incubations.

Table 1 Incorporation of different microalgae species by *Dendronephthya* sp. in relation to cell density and incubation time. The contribution of microalgae to the daily organic carbon demand of *Dendronephthya* sp. varied considerably depending on conditions. A realistic contribution is 26% as it is recorded at 600–6,000 cells ml^{-1} and during a short incubation time (1 h). When offered *Nannochloropsis* sp., considerable differences were found between the ingestion rates for isolated terminal branches and for branches which remained on larger colonial fragments during incubation (tall fragments). Respiration: 0.761 mg $O_2 \times$ mg $protein^{-1} \times 24\ h^{-1}$ which is equivalent to 22.83 µg orgC × mg $protein^{-1} \times 24\ h^{-1}$, on the basis of RQ=0.8. Conversion factors were taken from Strathmann (1967) and C. Gallegos (personal communication)

Offered algal species and organic C content per cell (pg)	Initial algal concentration (cells × ml^{-1})	Incubation time (h) and replicates [*n*]	Amount of incorporated cells × mg $protein^{-1}$	Uptake rates (cells × mg $protein^{-1} \times h^{-1}$)	Regression of algal cell uptake rates	Amount of organic C by algal biomass assimilation (µgC × mg $protein^{-1} \times 24\ h^{-1}$)	Contribution to the daily demand of organic C by algal biomass (%)
Chaetoceros muelleri	600	0.5 [3]	301±177	602±354		0.912±0.536	3.99±2.35
63.1		3 [3]	501±448	167±149		0.253±0.226	1.11±0.99
Chaetoceros muelleri	6,000	0.5 [7]	1,370±463	2,740±926	$y=1721.4\ x^{-0.7647}$	4.149±1.402	18.18±6.14
63.1		3 [6]	2,448±915	816±305		1.236±0.462	5.41±2.02
		9 [4]	3,086±689	342±77		0.519±0.116	2.27±0.51
		22 [6]	3,238±923	147±42		0.223±0.064	0.98±0.28
Chaetoceros muelleri	60,000	0.5 [8]	4,482±2,306	8,946±4,612	$y=5611.4\ x^{-0.6323}$	13.575±6.984	59.46±30.59
63.1		3 [9]	8,037±4,797	2,679±1,599		4.057±2.422	17.77±10.61
		9 [8]	12,244±7,156	1,360±795		2.060±1.204	9.02±5.27
		22 [6]	18,242±3,457	829±157		1.256±0.238	5.50±1.04
Nannochloropsis sp.	600	0.5 [3]	4,902±1,890	9,804±3,780		0.744±0.287	3.26±1.26
3.16		3 [3]	4,755±4,489	1,585±1,496		0.120±0.113	0.53±0.50
Nannochloropsis sp.	6,000	0.5 [6]	34,575±15,279	69,150±30,558	$y=34601\ x^{-0.981}$	5.244±2.318	22.97±10.15
3.16		3 [6]	35,629±5,697	11,876±1,899		0.901±0.144	3.95±0.63
		9 [6]	33,958±8,801	3,773±977		0.286±0.074	1.25±0.32
		22 [5]	38,581±14,284	1,753±649		0.133±0.049	0.58±0.22
Nannochloropsis sp.	60,000	0.5 [9]	77,971±57,703	155,942±115,406	$y=89411x-0.7825$	11.827±8.752	51.80±38.34
3.16		3 [9]	103,776±50,131	34,592±16,710		2.623±1.459	11.49±6.39
		9 [9]	166,162±94,981	18,462±10,553		1.400±0.800	6.13±3.51
		22 [6]	163,988±78,793	7,454±3,581		0.565±0.272	2.48±1.19
Nannochloropsis sp. (Tall fragments)	6,000	0.5 [1]	50,388	100,776	$y=74297x-0.5717$	7.643	33.48
3.16		3 [1]	151,284	50,428		3.824	16.75
		9 [1]	164,087	18,231		1.383	6.06
Tetraselmis sp.	6,000	0.5 [1]	333	666	$y=375.34x-0.7737$	0.762	3.34
47.67		3 [1]	499	166		0.190	0.83
		9 [1]	485	54		0.062	0.27
		22 [1]	893	41		0.046	0.20
Amphidinium klebsii + U-Dino	6,000	0.5 [6]	861±459	1,722±918	$y=918.93x-0.828$	6.708±3.576	29.38±15.66
162.3		3 [6]	902±525	301±175		1.171±0.682	5.13±2.99
		9 [6]	1,696±646	188±72		0.734±0.280	3.22±1.22
		22 [6]	1,442±450	66±22		0.255±0.080	1.12±0.35

In a recent paper, Fabricius et al. (1998) again calculated a considerable energy contribution by herbivory for *D. hemprichi*, exceeding the basal metabolism by about 1.3 times. The recent calculations were based on depletion rates of chlorophyll in water passing colonies of *D. hemprichi*, mounted in water flowing at different speeds. The amount of chlorophyll depleted within 20 s was calculated and was the basis for the carbon budget. Depletion rates, as mentioned in the Introduction, are unsuitable for proving metabolic utilisation of algae and are a weak basis for the calculation of carbon budgets. The algae/chlorophyll depletion of a certain water volume is not equivalent to the metabolic utilisation of phytoplankton through a suspension feeder. Pigment depletion might also originate from algae removed by herbivorous zooplankton or epizoans; in addition, algae depletion might be caused by pure adsorption to the colony surface. Furthermore, energy calculations on the basis of unstable cell properties – such as chlorophylls – seem to be problematic in general (Ayukai 1995).

In addition to the chlorophyll depletion of water passing the colonies, Fabricius et al. (1998) studied the accumulation of chlorophyll/phaeopigments inside the gastrovascular cavity (fluorescence method). Energy calculations made on this basis revealed a contribution of 11–29% by herbivory to the daily demand of organic carbon of *D. hemprichi*. This percentage is almost identical to the results of our calculations based on short time incubations.

The finding that eucaryotic algae play only a secondary role in the nutrition of soft coral species (Alcyonacea) has already been reported by Farrant et al. (1987) and Sorokin (1991). Sorokin (1991) studied 24 species of anthozoans and did not find a retention of ^{14}C-labelled microalgae except for the zoantharian species *Zoanthus sociatus* and *Mopsella aurantiaca* (Gorgonacea). Both species ingested algae, but unfortunately assimilation was not tested. Farrant et al. (1987) have also been unsuccessful in demonstrating herbivory by the zooxanthellate soft coral *Capnella gaboensis*. After feeding with ^{14}C-labelled microalgae, the authors concluded that the trophic contribution by herbivory is insignificant for that species.

As early as 1961, Roushdy and Hansen had qualitatively demonstrated the ingestion of ^{14}C-labelled microalgae by the temperate, azooxanthellate soft coral *Alcyonium digitatum*. Our data support this result. The incorporation rates of *Alcyonium digitatum* amounted to about 70% of those of *Dendronephthya* sp.

We also studied the capacity of three actinian species (*Actinia equina, Metridium senile, Urticina felina*) to retain ^{14}C-labelled microalgae (data not shown). The incorporation rates were insignificant and amounted to only about 0.1% of the incorporation rates of *Dendronephthya* sp.

The transfer of ^{14}C-labelled algal metabolites into the storage lipids of corals

TLC separations of the lipid fractions demonstrated up to 11 constituents (data not shown). From the total ^{14}C-labelling of the lipid fractions, a varying percentage was incorporated to the wax ester and di-/triglyceride fractions. After feeding *Chaetoceros muelleri* continuously over 3 h, about 60% of the total ^{14}C incorporation into lipids could be detected in the storage lipids; after feeding *Nannochloropsis* sp. and *Tetraselmis* sp., respectively, the corresponding values were 40% and 30%. Due to experimental misfortune the data for dinoflagellates is not available. The transfer of algal metabolites into the corals' lipid pool underlines the importance of lipids in the metabolism of corals and of anthozoans in general (Patton et al. 1977; Schlichter et al. 1983; Shick 1991).

Previous work has been concerned with the role of sugars and lipids in fuelling the corals' metabolism by herbivory. The increase of radiocarbon in the protein fraction indicates that algal amino acids become incorporated into corals' proteins, thus supporting the nitrogen metabolism continuously, although at a very low rate.

Conclusions and perspectives

The different particulate foodstuffs within and around reefs originate from pelagic and benthic production and include all categories of plankton, zoodetritus and phytodetritus. Larger zooplankters are captured by mobile predators visually while hunting during the day. This reduces the probability for sessile suspension feeders to catch those particles.

Table 2 A comparison of the organic carbon content of different food items for suspension feeders

Taxon		Organic C per individual
Metazoa		
Nauplii (Cyclopoida)[a]	NI	0.048 µg
	NVI	0.202 µg
Nauplii (Calanoidea)[a]	NI	0.033 µg
	NVI	0.225 µg
Protists		
Photoautotrophic	*Chaetoceros muelleri*[b]	63 pg
	Tetraselmis sp.[b]	48 pg
	Nannochloropsis sp.[b]	3 pg
	Amphidinium klebsii[b]	163 pg
Heterotrophic	*Monas* sp.[c]	1.5 pg
Bacteria		
Photoautotrophic	Cyanobacteria[d]	150 fg
Heterotrophic	*Escherichia coli*[e]	0.21 pg

[a] Culver et al. (1985); [b] Strathmann (1967); [c] Borsheim and Bratbak (1987); [d] Waterbury et al. (1986); [e] Watson et al. (1977)

In terms of fulfilling energy needs, the consumption of larger plankters would be of greater benefit (see Table 2): a calanoid nauplius contains 0.225 µg organic carbon compared to a heterotrophic flagellate with 1.45 pg; i.e. the "energy content" of the crustacean larva exceeds that of the protist by a factor of about 155,000. Passive suspension feeding depends on many uncertainties and eventualities. Species which obtain their food in this way require strategies for collecting and accumulating microsize POM, particularly bacteria, protists, phytodetritus and zoodetritus.

In the Gulf of Aqaba, the concentration of bacterioplankton and protozooplankton (up to 15–60 mg C m^{-3}) exceeds the biomass of eucaryotic phytoplankton by many times (Yahel et al. 1998). Thus the question arises as to whether or not the actual biomass of phytoplankton found in the reef system is high enough to substantially contribute to the nutrition of sessile heterotrophs such as corals. The same question has been discussed in the past for the supply of reefal organisms with zooplankton in general (Johannes et al. 1970). We performed feeding experiments with different algal cell densities, including densities of 600/6,000 cells ml^{-1}, corresponding to the natural total density of eucaryotic phytoplankton in the Gulf of Aqaba (Yahel et al. 1998). Our results, and indeed the phytoplankton *ingestion* data of Fabricius et al. (1998), suggest that the natural supply of eucaryotic phytoplankton contributes 34% of the organic daily carbon demand of *Dendronephthya* sp., at a maximum. However, even under completely unrealistic cell densities (60,000 cells ml^{-1}), the energy contribution would not exceed about 60%.

The trophic utilisation of microPOM (including phytoplankton) does not seem to be primarily a question of whether or not algae can be digested by corals, but rather a problem in the collection and accumulation of minute

particles out of a highly diluted suspension. The energy content of microPOM is low, thus these food components are of trophic importance only for those suspension feeders which possess effective mechanisms for collecting and accumulating protists, bacteria and/or detritus. The scleractinian coral *Mycedium elephantotus*, lacking tentacles, catches and accumulates microscopic particles with the aid of mucus nets (Schlichter and Brendelberger 1998).

The zooxanthellate and azooxanthellate alcyonarians (approx. 1,000 species worldwide) exemplify the trophic flexibility/plasticity of one taxon for successfully settling different habitats in high abundance. The majority of subtropical and tropical zooxanthellate species seem to be totally independent of POM, fuelling their metabolism phototrophically by assimilates of their symbionts and by DOM absorption, e.g. *Heteroxenia fuscescens* (Schlichter et al. 1983). Other species exhibit intermediate characteristics, requiring POM to complement their energy demands, e.g. *Capnella gaboensis* (Farrant et al. 1987). Finally, the azooxanthellate species depend totally on heterotrophy and the various species utilise the different POM components according to their trophic specialisation.

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