THE ROYAL SOCIETY

Prudent sessile feeding by the corallivore snail *Coralliophila violacea* on coral energy sinks

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Convergence of form and function has accompanied the evolution of modular growth in terrestrial plants and colonial marine invertebrates. Part of this convergence is related to the optimal exploitation of resources (space and light) and the ability to translocate energy products from sources to sink sites. Feeding on the energy pathways and energy sinks of terrestrial plants is a well-known phenomenon. Hermatypic corals, the major organisms constructing tropical reef environments, contain photosynthetic algae (zooxanthellae), energetic products of which are translocated towards sink sites located at the corals' growing tips and regenerating areas. Despite the plant–coral convergence in energy pathways and sinks, there has been no evidence to date that coral energy sinks are exploited by coral predators. Gastropods of the genus *Coralliophila* are found feeding on coral margins, causing small and localized tissue damage. However, the ability of these snails to continue to feed without moving over a long period remains puzzling. Using a ^{14}C labelling technique, we found that colony margins of the stony coral *Porites* function as major energy sinks. When snails inhabited these sites they incorporated significant amounts of ^{14}C, indicating that they had fed on photosynthetic products translocated from the interior of the colony. Furthermore, when snails aggregate in the interior of the colony, thereby causing large surface injuries, they induce the development of significant new sink sites. This mode of prudent sessile feeding maximizes the efficiency of energy exploitation by the predatory snail, while minimizing tissue damage to the coral. The fact that energy sink sites occur in many coral species suggests that the strategy of sink exploitation for nutrition could also occur in many other marine host–symbiont relationships.

Keywords: *Coralliophila violacea*; energy sinks; feeding; integration; *Porites* sp.; Red Sea

1. INTRODUCTION

Carbon transfer between sources (sites that export assimilates) and sinks (sites that import assimilates) and its regulation within colonial organisms are critical aspects in their biology (Dyrynda 1986). In hermatypic corals, photosynthetic products are continuously translocated from the symbiotic zooxanthellae to the host tissue, thereby contributing to a variety of energetic requirements such as maintenance, synthesis of new cells, formation of skeletal matrix, mucus production, deposition of calcium carbonate, and storage of energy-rich compounds for coral reproduction (Muscatine & Cernichiari 1969; Crossland *et al*. 1980*a*,*b*; Muscatine *et al*. 1981, 1984; Rinkevich & Loya 1983, 1984; Kellogg & Patton 1983; Stimson 1987). In a pioneering study on coral–algae symbiosis, Pearse & Muscatine (1971) documented that in *Acropora cervicornis*, organic products, mainly in the form of lipids, glycerol and glucose, are translocated from the branch base to the tip (sink site), contributing to coral calcification. They found that both ethanol–methanol–chloroform-soluble and -insoluble tissue fractions were translocated upwards from the lower parts of the branches. Taylor (1977) further confirmed a strong preferential movement and accumulation of ^{14}C-labelled compounds towards the tips in *A. cervicornis*, and Rinkevich & Loya (1983) recorded a similar pattern of translocation in the branching coral *Stylophora pistillata*.

The energy resources available to an organism are often limited and hence are differentially allocated according to a variety of biological demands (Kozlowski & Wiegert 1986; Oren *et al*. 1998). The paradigm for intracolonial transport of organic compounds within hermatypic corals is not new; Pearse & Muscatine (1971) suggested that intracolonial translocation occurs towards regions of maximal demand. This early hypothesis was recently supported by Oren *et al*. (1997*a*), who documented an orientated intracolonial transport of ^{14}C-labelled photosynthetic products towards regeneration areas in the massive stony corals *Favia favus* and *Platygyra lamellina* in Eilat (Red Sea).

The hermatypic role of scleractinian corals is obviously counteracted by the activities of coral predators. Compared with attacks by *Acanthaster planci* and *Diadema* sp., the harmful effects of the corallivorous gastropods are less widespread. Many gastropods of the genus *Coralliophila* are found feeding on the margins of the living tissues of coral colonies, causing small and localized tissue

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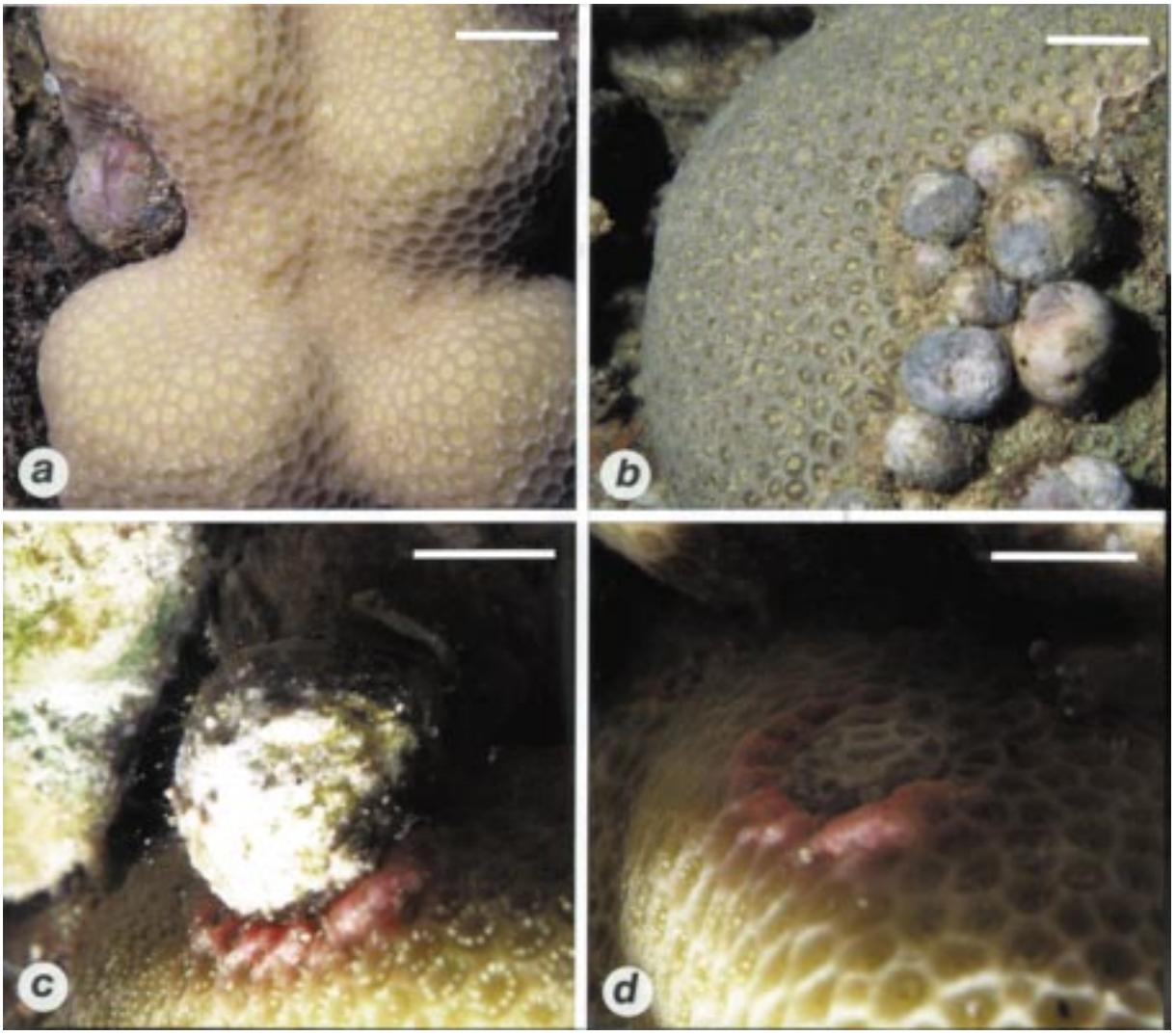

Figure 1. Photographs of *Porites* corals with *C. violacea*. (*a*) A single snail feeding at the margin of the colony (scale bar, 1 cm); (*b*) aggregation of snails feeding in the interior parts of the colony (scale bar, 1 cm); (*c*) close-up of a feeding snail (scale bar, 0.5 cm); (*d*) close-up of the tissue lesion caused by the snail (scale bar, 0.5 cm). The surrounding *Porites* tissue is swollen and pink in response to the injury.

damage (Ott & Lewis 1972; Hayes 1990; Schuhmacher 1992). The tendency of the snails to feed on colony margins has been suggested as a protective strategy, because these basal areas exhibit algal colonization, which disguises the presence of the snail (Brawley & Adey 1982). Corallivores that feed on coral tissues expose the skeleton. Kitting (1975) suggested that molluscs, such as *Coralliophila*, feed without moving to decrease the rate of exposing the white coral skeleton and thus to prevent the 'tracking' of the snail by predatory fish. In addition, a 'food-stealing strategy' was suggested as an explanation for the sessile feeding of *Coralliophila*, because snails were seen with the proboscis inserted into the polyp coelenterons of *Agaricia agaricites* and *Montastrea annularis* (Hayes 1990).

The most common *Coralliophila* species in the northern parts of the Gulf of Aqaba (Red Sea) is *Coralliophila violacea* (Schuhmacher 1992). Like all members of the gastropod family Coralliophilidae, *C. violacea* lacks both jaws and a radula (Ward 1965; Brawley & Adey 1982), obtaining its food by a special mode of sucking with the proboscis that preserves the polyp for long-term exploitation (Ward 1965). Examining the impact of corallivorous snails on stony corals in the Red Sea, Schuhmacher (1992) found that *C. violacea* only feeds on colonies of *Porites* sp. and *Synarea* sp., often at the margin of the living tissue. The objective of the present study was to test the puzzling ability of *C. violacea* to feed without moving by examining a new feeding hypothesis, which suggests that *C. violacea* is a corallivore that feeds on the coral's energy-sink sites.

2. MATERIALS AND METHODS

From June to November 1997 we examined the feeding behaviour of *C. violacea* (figure 1*a*) on 46 *Porites* colonies at a depth of 6–9 m opposite the Marine Biology Laboratory in Eilat (Red Sea). The surface areas of the lesions caused by the feeding of individual snails, as well as by aggregation feeding, were recorded by analysing underwater photographs of these lesions with a computerized image analyser (Olympus CUE-3). To

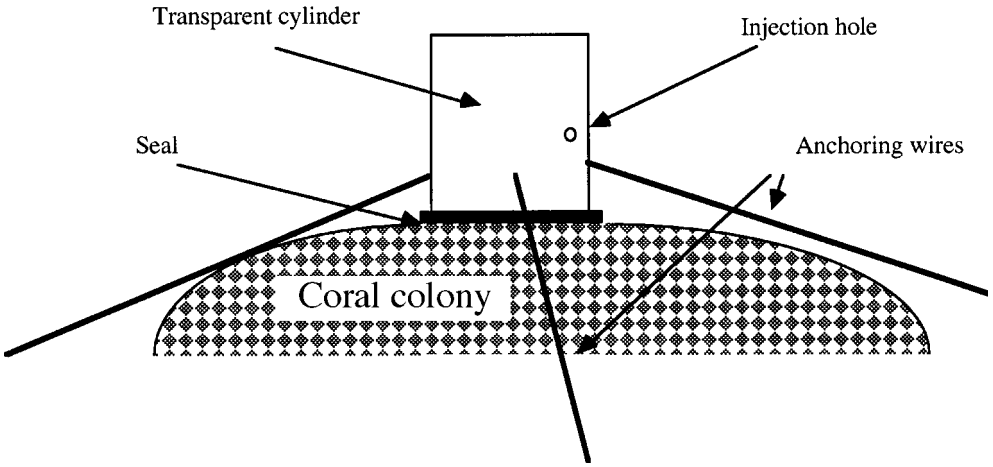

Figure 2. A diagram of the transparent cylinder used to label a restricted tissue area (3 cm^2) with radioactive carbon on the surface of the experimental *Porites* colonies.

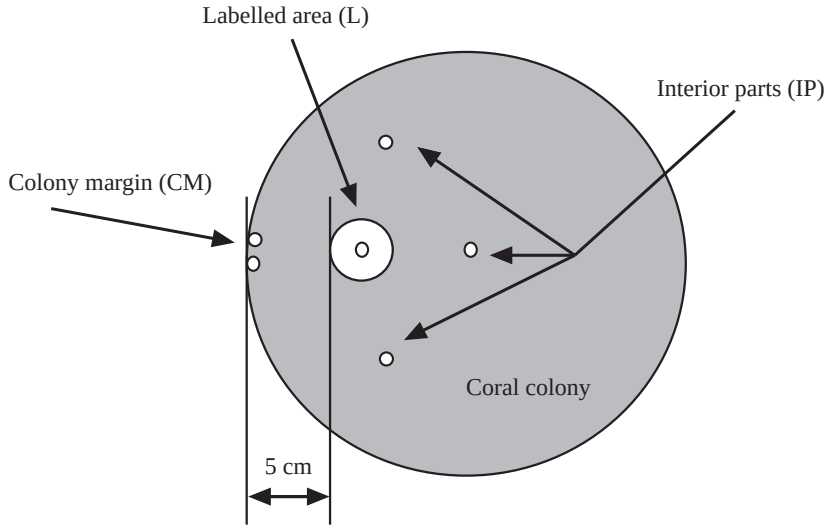

Figure 3. A schematic diagram of the labelling and sampling locations in *Porites* colonies that had no snails ($n=5$). The labelling cylinder was attached 5 cm from the colony margin (CM). White dots represent the locations from which the tissue fragments were taken. L, labelled area; CM, colony margin; IP, interior parts of the colony. Activity of ^{14}C in the tissues of these fragments was determined by liquid scintillation counter.

examine possible energy transfer between the coral host and its snails, we labelled 17 additional *Porites* colonies (all approximately 20 cm^2 in diameter) with radioactive bicarbonate, as described below.

Round transparent cylinders were constructed to enable ^{14}C labelling of small (3 cm^2) restricted tissue areas on the surface of the colonies examined (figure 2). The opening of each cylinder was glued to an artificial sponge, achieving a firmly sealed contact with the coral tissue. Each cylinder was tightly attached to the surface of the colony by three steel wires anchored to a hard substrate near the colony. After sealing the cylinder to the coral surface, ^{14}C was injected through a hole, 3 mm in diameter and covered with rubber (figure 2). The injected radioactive carbon (final concentration 0.1 μCi ml^{-1}) left a volume of 10 ml of air for water stirring and the exchange of gas. Colonies were labelled at 07.00 to allow 10 h of daylight for active photosynthesis. At the end of this labelling procedure, the cylinders were carefully removed from the experimental colonies.

Four different ^{14}C-labelling treatments (i.e. labelling locations) were used to determine the possible transfer of photosynthetic products from the *Porites* tissues to their host snails. In the first treatment we labelled five *Porites* colonies with no snails. The labelling cylinders were attached to the surface of these colonies at a distance of 5 cm from the colony margin (CM, figure 3). The second treatment labelled four additional *Porites* colonies, each bearing one to two snails at its margin. Again, the cylinders were attached to the surface of the colonies at a distance of 5 cm from their margins and 5–7 cm from the margin snails (MS, figure 4). The third treatment labelled four *Porites* colonies, each bearing one snail in its interior. The cylinders were attached 5 cm from each interior snail (IPS, figure 5). This labelling treatment was additionally used to determine possible energy translocations towards margins located at distances greater than 5 cm. The fourth treatment labelled four *Porites* colonies bearing aggregations of snails (8–13 snails in each patch) in their interiors. The cylinders were attached to the coral surface 5 cm from the border line of the lesion caused by the aggregating snails (AS, figure 6).

Coral fragments (tissue + skeleton) were taken from the experimental colonies 48 h after labelling, by means of a round stainless steel corer, enabling collection of similarly sized fragments (1 cm^2). From each labelled colony we sampled 5–6 tissue fragments (sampling locations in each treatment are presented in figures 3–6, respectively). For controls we sampled fragments and snails from ten unlabelled *Porites* colonies. The samples were placed individually in plastic vials and brought to the laboratory. The sea water was drained from each vial and 8 ml of hydrogen peroxide (30%) was added to digest the tissues. After complete digestion (24 h), the remaining skeletons were removed and two replicates of 0.5 ml from each vial were sampled. Five millilitres of Biodegradable Counting Scintillation cocktail (BCS, Amersham) were added to each sample. Activity of ^{14}C in *Porites*

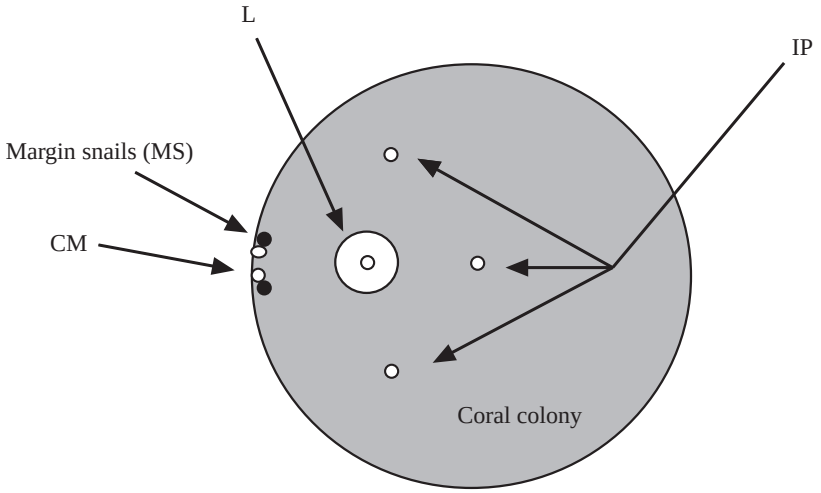

Figure 4. Schematic diagram of the labelling and sampling locations in *Porites* colonies that bore 1–2 snails at their margins ($n=4$). White dots represent the locations from which the tissue fragments were taken; black dots represent the snails. MS, marginal snails (for other abbreviations see figure 3).

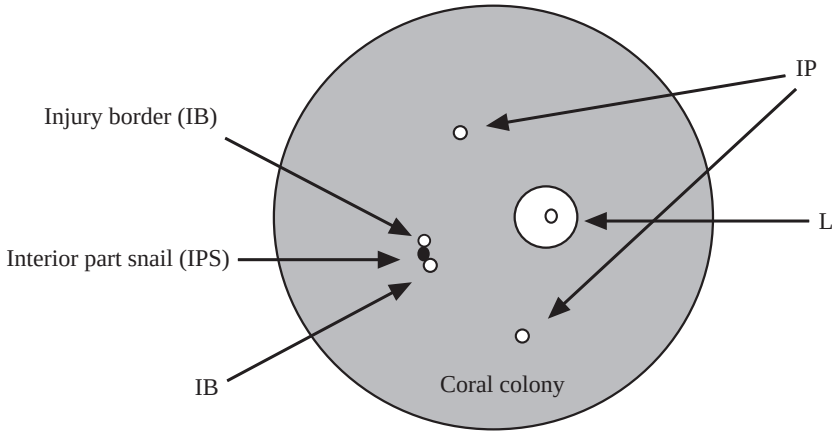

Figure 5. A schematic diagram of the labelling and sampling locations in *Porites* colonies that bore one snail in the interior part ($n=4$). White dots represent the locations from which the tissue fragments were taken and the black dot represents the snail. IPS, interior-part snail; IB, tissues taken from the border line of the lesion caused by the feeding activity of the snail (for other abbreviations see figure 3).

tissues (counts per min (cpm) cm^{-2}) and *Coralliophila* tissues (cpm per snail) was determined by liquid scintillation counter (Packard, Tri-Carb 1500).

3. RESULTS

Eighty-six per cent of the snails examined in this study (total number of snails=156) fed on colony margins (figure 1*a*) or on the borderlines of injuries caused by snail aggregations (figure 1*b*). All these snails remained permanently attached to their feeding sites throughout the four-month study period. Only 14% of the snails examined fed on the interiors of the colonies examined. The total shell length of *C. violacea* ranged between 6 mm and 18 mm and the size of the tissue lesion caused by the feeding activity of an individual average-sized snail was less than 0.25 cm^2 (figure 1*d*). However, snail aggregations in the interior parts of the colony were found to cause relatively larger tissue lesions since in these cases the small individual lesions were combined. *Porites* tissue surrounding the feeding snails frequently became swollen and pink (figure 1*c*,*d*).

Forty-eight hours after the four different ^{14}C labelling treatments, the labelled areas (L) in all experimental colonies (see tables 1–4) demonstrated high ^{14}C activity compared with the natural ^{14}C activity of *Porites* tissues (^{14}C activity in unlabelled randomly sampled *Porites* colonies, i.e. control colonies=23.1 ± 3.63 cpm cm^{-2}, $n=10$). The high ^{14}C activity of *Porites* tissues confined within the labelled areas indicates that our method of restricted tissue labelling was efficient.

(a) Porites *colonies with no snails*

Coral tissues taken from the CM in the five *Porites* colonies that had no snails (see figure 3) exhibited significantly high ^{14}C activity compared with the interior tissues ($p<0.01$, one-way ANOVA, Fisher LSD (Sokal & Rohlf 1969); see CM and IP, table 1). Moreover, the ^{14}C activity of the tissues taken from the interior parts of these colonies did not differ significantly from the ^{14}C activity of tissues taken from the unlabelled control colonies ($p>0.05$, one-way ANOVA, Fisher LSD). The results of this labelling treatment indicate that colony margins function as energy sinks even in the absence of snails and, furthermore, that the translocation of photosynthetic products from the labelled area towards the margin is orientated.

(b) Porites *colonies bearing snails at their margins*

The coral tissues taken from the colony margins of four colonies that bore one to two snails at their margins (see figure 4) demonstrated significantly higher ^{14}C activity compared with the interior tissues ($p<0.01$, one-way ANOVA, Fisher LSD; see CM and IP, table 2). The tissues of the snails that inhabited these margins demonstrated significantly higher ^{14}C activity ($p<0.01$, one-way ANOVA, Fisher LSD; table 2) compared with the ^{14}C activity of snails randomly sampled from unlabelled control colonies (^{14}C activity of control snails=25.2 ± 3.5

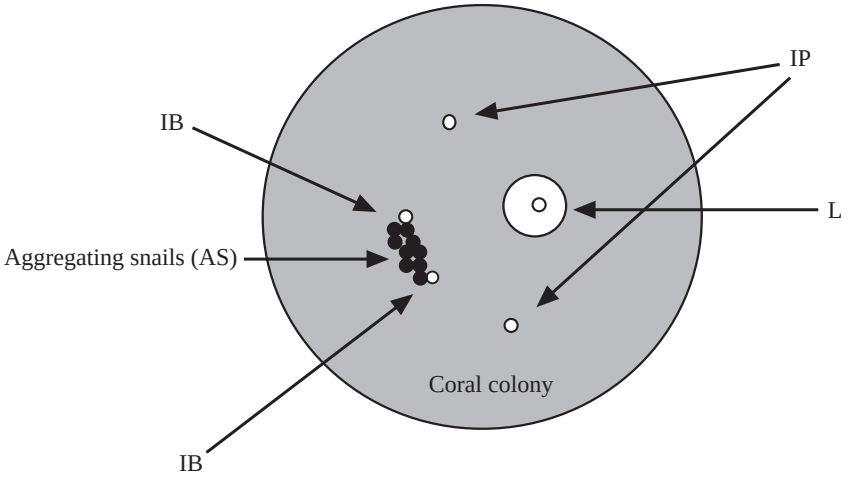

Figure 6. A schematic diagram of the labelling and sampling locations in *Porites* colonies bearing aggregations of snails in their interior parts ($n=4$). AS, aggregating snails; IB, tissues taken from the borderline of the lesion caused by the feeding activity of the aggregating snails (for other abbreviations see figure 3).

cpm per snail, $n=10$). As in the first treatment, the ^{14}C activity of the interior tissues did not differ significantly from those obtained in the control colonies ($p>0.05$, one-way ANOVA, Fisher LSD). The results of this labelling treatment indicate, again, that colony margins act as significant energy sink sites and, furthermore, they reveal the ability of the margin snails to feed on photosynthetic products that are transferred from the interior parts of the colony.

(c) Porites *colonies bearing one snail in their interiors*

Fourteen per cent of the snails were found attached to the interior parts of the 46 colonies examined. The ^{14}C activity of these snails (see figure 5) did not differ significantly from that of snails taken from the control colonies ($p>0.05$, one-way ANOVA, Fisher LSD; table 3). Coral tissues taken from the injury borders (IBs) of the lesions caused by the feeding activity and the tissues taken from the interior parts of these colonies (IP) did not differ significantly in their ^{14}C activity from the tissues taken from the control colonies ($p>0.05$, one-way ANOVA, Fisher LSD; see IB and IP, table 3). The results of this labelling treatment indicate that the small lesion caused by the feeding of an interior snail (projected area $<0.25\,cm^2$) does not induce the development of energy sinks.

In addition, this treatment (figure 5) was used to determine possible energy translocations towards margins located at distances greater than 5 cm. Coral tissues taken from CM located at distances of 8–10 cm from the labelled area showed ^{14}C activity similar to that of control tissues ($p>0.05$, one-way ANOVA, Fisher LSD). This indicates that the strength of the energy sinks located at the CMs is limited to a distance of up to approximately 5 cm; in other words, the colony fraction that donates and transfers photosynthetic products towards the margins lies within about 5 cm of the margin.

(d) Porites *colonies bearing snail aggregations in their interior parts*

The coral tissues taken from the IBs of the lesions caused by aggregation feeding in the IPs (see figure 6) demonstrated significantly high ^{14}C activity compared with the interior tissues ($p<0.01$, one-way ANOVA, Fisher LSD; see IP and IB, table 4). Furthermore, the ^{14}C activity of the snails taken from the aggregation sites was significantly higher then those recorded in the control snails ($p<0.01$, one-way ANOVA, Fisher LSD). The fact that the ^{14}C activity of the IP tissues did not differ significantly from the ^{14}C activity of the control tissues ($p>0.05$, one-way ANOVA, Fisher LSD) indicates that translocation of the photosynthetic products from the labelled area towards the AS was orientated. It is important to note that the size of the tissue injury caused by this feeding activity was greater than $2\,cm^2$ ($n=4$). The results of this labelling treatment indicate that by feeding in aggregations, and by causing large tissue lesions in the IP, snails may induce the development of significant new sink sites.

4. DISCUSSION

Intracolonial transport of materials and metabolites in hermatypic corals provides a means of transferring resources and concentrating them in zones of maximal demand (Pearse & Muscatine 1971). Most of the knowledge regarding the intracolonial translocation of ^{14}C-labelled materials in corals was recorded for branching forms (Muscatine & Cernichiari 1969; Pearse & Muscatine 1971; Rinkevich & Loya 1983, 1984; Fang *et al*. 1989), whereas massive forms were overlooked. The present work is, to our knowledge, the first quantitative study to document an orientated intracolonial transport of ^{14}C-labelled materials towards the growing margins of the massive coral *Porites* (table 1). Moreover, our results suggest that the translocation of photosynthetic products towards the margins (energy sinks) may be exploited prudently (*sensu* Slobodkin 1961) for nutrition, by the corallivore snail *C. violacea* (tables 2, 4).

In a previous study, Oren *et al*. (1997*a*) recorded an orientated translocation of ^{14}C-labelled materials towards large tissue lesions that were inflicted on the surface of the massive corals *Favia favus* and *Platygyra lamellina*. The results of that work were, to our knowledge, the first to show that massive corals transfer energy products towards regenerating areas, and that these injured sites function as strong energy sinks. The fact that *Porites* margins function as energy sinks even in the absence of

Table 1. *Average activity of ^{14}C in* Porites *tissues* (cpm cm^{-2} ±s.d.) *recorded in labelled colonies that had no snails*

(L, coral tissue from labelled area located 5 cm from the colony margin; CM, coral tissue from colony margin; IP, coral tissue from interior parts of the colony also 5 cm from the labelled area. Numbers in parentheses refer to the sample sizes. Each tissue sample was divided into two replicates for measurement of ^{14}C activity. Average background activity of *Porites* tissues = 23.1 ± 3.63 cpm cm^{-2} (control colonies, $n = 10$). Average background activity of snail tissues = 25.2 ± 3.5 cpm per snail (control snails, $n = 10$).)

	tissue type		
coral no.	L	CM	IP
1	8508–8705 (1)	217 ± 14 (2)	24 ± 2 (3)
2	16 481–18 941 (1)	1265 ± 23 (2)	19 ± 6 (3)
3	32 563–35 523 (1)	170 ± 9 (2)	26 ± 8 (3)
4	2957–3147 (1)	111 ± 17 (2)	22 ± 4 (3)
5	5272–5412 (1)	409 ± 31 (2)	28 ± 7 (3)

Table 2. *Average activity of ^{14}C in* Porites *tissues* (cpm cm^{-2} ± s.d.) *and snail tissues* (cpm per snail ± s.d.) *recorded in labelled colonies that bore one to two snails at their margins*

(MS, tissue of the snails taken from CM. For background activities and other notations see table 1.)

	tissue type			
coral no.	L	CM	IP	MS
1	21 445–24 659 (1)	230 ± 38 (2)	28 ± 3 (3)	124 ± 16 (2)
2	1485–1629 (1)	156 ± 19 (2)	21 ± 6 (3)	231 ± 13 (1)
3	16 567–16 849 (1)	276 ± 8 (2)	31 ± 3 (3)	99 ± 11 (1)
4	6567–6747 (1)	403 ± 29 (2)	18 ± 3 (3)	421 ± 35 (2)

snails (table 1) provides an indication that energy transfer may also occur in uninjured coral colonies.

Space for settlement on a coral reef has been shown to be one of the most important limiting factors in this ecosystem (Chornesky 1989). The CMs of *Porites* colonies, as in many other massive corals, are the sites most involved in the competition for space (Chornesky 1989). In addition, *Porites* margins are frequently shaded owing to the spherical shape of the colony (Highsmith 1980), resulting in a lower photosynthetic ability of these sites. The tips of many branching forms of stony corals are white, indicating that they are free of zooxanthellae (Fang *et al.* 1989). Nevertheless, these tips still have a very high calcification rate, indicating that they are fuelled energetically by the lower parts of the branches (Fang *et al.* 1989). In *Porites*, the margin tissues are also whiter than the inner colony tissues, probably owing to their having fewer zooxanthellae, and thus, like the tips of branching forms, they are likely to have lower photosynthetic abilities. We assume that the orientated energy translocation recorded towards the *Porites* margins occurs continually so as to maintain the energetic requirements of these particular sites. In other words, *Porites* margins, like tissue injuries in other massive corals, function as significant energy sinks.

An individual snail, feeding from the IP (figure 5), does not induce the development of a significant sink (table 4). However, it is important to note that the size of the tissue lesion caused by the feeding of a single snail was less than 0.25 cm^2. A previous study on coral regeneration found that large tissue lesions (over 3 cm^2) inflicted on the surface of the massive corals *F. favus* and *Platygyra lamellina* induced the development of significant sinks, in contrast to lesions smaller than 1 cm^2 (Oren *et al.* 1997*a*,*b*). This may explain why the relatively small tissue lesions located in the interior parts of the *Porites* colonies (figure 5) do not act as sinks (table 3). The significant energy sinks located at the margins of the *Porites* colonies (figure 3; table 1) and the fact that snails that fed at these sites incorporated significant amounts of ^{14}C products (figure 4; table 2), reveals the snails' ability to feed on photosynthetic products that were fixed in the IP and then transferred to the margins. These findings provide an explanation for the puzzling sessile feeding ability of *C. violacea*.

Some of the colonies bore snails that fed in aggregations located in the IPs. This feeding behaviour caused relatively large tissue lesions resulting from the merging of several small individual lesions. When these interior lesions were greater than 2 cm^2 (an aggregation of more than eight snails) they functioned as significant energy sinks (table 3). This interesting finding indicates that *C. violacea* is able to induce the development of new sink sites by inflicting large tissue lesions in the interiors of the colonies. The fact that large tissue lesions on the surface of *Porites* colonies act as significant sinks, unlike small ones (compare table 4 with table 3) indicates that the size of the lesion reflects the strength of the energetic sink, as previously found for the massive stony corals *F. favus* (Oren *et al.* 1997*a*,*b*) and *Platygyra lamellina* (Oren *et al.* 1997*a*). Many members of the genus *Coralliophila* were documented feeding in aggregation (Ward 1965; Miller 1981; Hayes 1990; Soong & Chen 1991). The ability of *C. violacea* to induce the development of major sink sites through aggregation feeding reveals the energetic benefit of this sessile feeding behaviour.

In addition to the previously suggested advantages of the sessile feeding behaviour of *Coralliophila,* which mainly address protective strategies (Kitting 1975; Brawley & Adey 1982; Hayes 1990), the current study indicates that *C. violacea* may be regarded as a prudent predator (Slobodkin 1961). Such sessile feeding maximizes the efficiency of energy exploitation by the predatory snail, while minimizing tissue damage to the coral.

Convergence of form and function has accompanied the evolution of modular growth in terrestrial plants and colonial marine invertebrates (Dyrynda 1986). Part of this convergence is related to optimal exploitation of resources (space and light) and the ability to translocate energy products from sources to sinks. In plants, the sink organs are lateral meristems, developing buds, young leaves, fruits, roots and storage organs (see the review in Ho (1988)). Feeding on the energy pathways and energy sinks of terrestrial plants is a well-known phenomenon, demonstrated by various organisms such as pathogenic

Table 3. *Average activity of ^{14}C in* Porites *tissues* (cpm $cm^{-2} \pm$ s.d.) *and snail tissues* (cpm per snail $\pm$ s.d.) *recorded in colonies that bore one snail in the interior part of the colony*

(L, coral tissue from labelled area located 5 cm from the interior snail; IB, coral tissue from the border line of the injury caused by the interior snail; IPS, tissue of the interior part snail. For background activities and other notations see table 1.)

coral no.	tissue type			
	L	IB	IP	IPS
1	3033–3323 (1)	24±3 (2)	28±7 (2)	28±5 (1)
2	1818–2724 (1)	27±5 (2)	25±4 (2)	24±3 (1)
3	2999–3123 (1)	20±2 (2)	21±5 (2)	33±6 (1)
4	3596–3764 (1)	25±4 (2)	26±2 (2)	21±2 (1)

Table 4. *Average activity of ^{14}C in* Porites *tissues* (cpm $cm^{-2} \pm$s.d.) *and snail tissues* (cpm per snail±s.d.) *taken from labelled colonies that bore snail aggregations in the interior part of the colony*

(L, coral tissue from labelled area located 5 cm from the aggregating snails; IB, coral tissue from the border line of the injury caused by the aggregating snails; AS, aggregating snails from which tissue samples were collected. For background activities and other notations see table 1.)

coral no.	tissue type			
	L	IB	IP	AS
1	15 183–15 403 (1)	383±19 (2)	19±2 (2)	413±32 (4)
2	25 418–27 124 (1)	488±31 (2)	29±7 (2)	179±37 (5)
3	4939–5063 (1)	161±35 (2)	25±5 (2)	233±68 (3)
4	4596–4764 (1)	473±43 (2)	26±2 (2)	123±20 (4)

viruses (Burdon 1987), bacteria (Mani 1964), fungi (Hall *et al.* 1992), parasitic plants (Seel *et al.* 1992) and many gall-forming invertebrates (Mani 1964; Larson & Whitham 1991; Inbar *et al.* 1995). These organisms compete with host-plant sinks and may also alter carbon allocation (Inbar *et al.* 1995). Despite the convergence of plants and hermatypic corals in form and function, the present study is thought to be the first to show a convergence between phloem-feeding insects and a corallivore snail. The ability of the aggregating snails to induce the development of new energy sinks, by forming large tissue lesions, is highly convergent to a previously described pattern of sink development in plants infested with aggregations of free-living aphids (Peel & Ho 1970; Way & Cammell 1970; Dixon 1975; Veen 1985; Hawkins *et al.* 1987; Thomas & Lombard 1991).

Energy-sink sites have been documented for many branching forms of stony corals (Pearse & Muscatine 1971; Taylor 1977; Rinkevich & Loya 1983, 1984) and also for several massive forms (Taylor 1977; Oren *et al.* 1997*a*), indicating the generality of this phenomenon. The sessile sink feeding by *C. violacea* demonstrated in this study affirms the development of this feeding method in the coral reef environment. The widespread phenomenon of feeding on energy pathways and energy sinks by various organisms in terrestrial plants suggests that this feeding method may also be typical of many other marine host–symbiont relationships.

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