

Carbon flux on coral reefs: effects of large shifts in community structure

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ABSTRACT: The effect of replacement of live coral cover by epilithic algae on patterns and magnitudes of carbon flux is examined for the shallow front slope of a midshelf reef in the Great Barrier Reef (GBR) complex of Australia. A steady-state network of carbon exchange among 19 trophic compartments is constructed for the coral-dominated state. From this, 2 scenarios for patterns of carbon flux when algae dominate are derived, viz. (1) the increase in algal production is channeled to detrital pathways (grazers do not respond), and (2) grazers utilise the increase in production of algal carbon so that transfers to detritus and grazers are in the same proportion as occurs when coral cover is high. The 3 models summarise current knowledge of carbon flux on GBR reef fronts and are compared using network analysis. Because fluxes in the reef front zone are dominated by exogenous imports and exports as a result of the high volume of water passing around and over the reef, the analyses ignore advective fluxes across the zone that are not internalised. The shift in structure to an algae-dominated system realises lower rates of benthic primary production, and thus system size and activity (i.e. total system throughput, internal throughput, development capacity and ascendancy) are reduced, suggesting a disturbed system. With loss of coral cover, the proportion of the total flow that is recycled and transferred to the detritus pool increases (although the structure of recycling is not affected), and the balance of pathways in the network is changed: average path length increases, while the average trophic level of most of the second order consumers, and trophic efficiencies of most trophic categories, decreases. Also, there are marked changes in dependencies of particular trophic groups on others. The analysis shows that, in the coral-dominated state, carbon fixed by zooxanthellae is used indirectly by most organisms in the system, even those seemingly remotely connected. Differences between the coral- and algae-dominated systems were much greater than differences between the 2 scenarios for the algae-dominated state. However, the exact fate of additional algae-derived carbon in the system is an important consideration since the 2 scenarios for the algae-dominated state yielded dissimilar values for some parameters (e.g. flow diversity, trophic dependencies and effective trophic levels of some compartments, relative importance of recycling, trophic efficiency of some trophic categories).

KEY WORDS: Carbon flux · Coral reef · Coral dominated · Algae dominated · Crown-of-thorns starfish · Network analysis

INTRODUCTION

On a global scale, many natural communities are experiencing large and fundamental changes in structure, often as a result of anthropogenic activities and often manifesting themselves as a decrease in diversity. However, whereas causality can sometimes be identified, there is little understanding of the consequences of large shifts in community structure on the processes and functioning of communities and ecosystems, de-

spite recent interest in this area (Chapin et al. 1992, Done et al. in press). Coral reefs provide a pertinent (and disturbing) marine example in that worldwide there is an increasing number of reefs that are shifting from systems dominated by coral to systems dominated by fleshy and/or turf-forming macroalgae (Wilkinson 1993, Hughes 1994). The transition to an algae-dominated community is often regarded as degradative and may be mediated by outbreaks of crown-of-thorns starfish, bleaching events, pollution, increased sedimentation, removal of grazers from the system (e.g. by overfishing), cyclones, or combinations of any of these

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(e.g. Smith et al. 1981, Moran 1986, Brown 1987, Hughes 1989, 1994, Birkeland & Lucas 1990, Knowlton et al. 1990, Done 1992a, b, c, Glynn & Colgan 1992, Moran et al. 1992, Glynn 1993, Sebens 1994).

Although the consequences of the shift away from reef-building corals to free-living algae are poorly understood, it is clear that changes in state to the lower diversity, algae-dominated configuration may be stable over an extended period (Hughes 1994; see also Hatcher et al. 1989, Knowlton 1992 for comment on stability of state changes) and that the transition represents a major shift in the balance of primary production from domination by zooxanthellae with a significant input from turf algae, to domination by turf algae, calcareous algae, and in many cases fleshy and foliose macroalgae. The question we address here is whether this shift significantly affects patterns of carbon flux and/or production of heterotrophic species, either as a result of changes in overall rates of primary production or in the relative magnitude of flows between different trophic groups.

State transitions to algae-dominated communities have been widespread in the central sector of the Great Barrier Reef (GBR) in Australia since the 1960s as a result of outbreaks of crown-of-thorns starfish *Acanthaster planci*, but not all reefs have been affected adversely (Johnson 1992, Moran et al. 1992). Davies Reef, a typical midshelf platform reef in the central sector and one of the most intensively studied reefs worldwide, suffered minimal damage from starfish until the 1990s when it was moderately affected. Here we construct a steady-state model of carbon flux on the shallow windward slope of a coral-dominated reef based largely on empirical measurements from Davies Reef but augmented with data from other reef systems. From this, we derive 2 scenarios for carbon flux in the algae-dominated state which are also based on empirical measurements of primary production. Using network analysis (Wulff et al. 1989) to make quantitative comparisons among the different models, we address the question of how changes in community structure from coral- to algae-dominated systems affect network properties and patterns of carbon flux.

METHODS

The overall approach was first to assemble a steady-state network of carbon flux on a coral-dominated reef not affected by crown-of-thorns starfish, capturing as much detail in trophic structure as possible from empirical measurements. From this, 2 scenarios of carbon flow for an algae-dominated state were derived and all 3 models were then compared using network analysis. The models do not consider transitional states in the phase shift to the algae-dominated system.

Construction of steady-state models of carbon flux.

In balancing the competing requirements of detail of trophic structure and availability of empirical measurements, a steady-state model of the shallow front slope (5 to 10 m, average depth 7.5 m) of Davies Reef (18° 50' S, 147° 39' E) was developed. Davies Reef is a midshelf platform reef typical of the central region of the GBR and has been studied intensively for over 2 decades. The model is an open system describing flux activity in this shallow zone and is steady state in the sense that net flow through compartments is zero (i.e. total inputs balance total outputs; note that this does not require equilibrium community structure within compartments). The network contained 19 trophic compartments (Fig. 1), which included 2 non-living compartments (water column and sedimentary detritus), 4 categories of primary producers [phytoplankton, zooxanthellae in corals, coralline algae (COA) and filamentous turf-forming algae], 4 sources of exogenous input into the system as a result of oceanic water flowing onto the reef (phytoplankton, zooplankton, water column bacteria, and water column protozoa and microzooplankton), and 5 categories of export out of the front slope zone (same as exogenous inputs, plus piscivorous fish). There was no compartment for fleshy or foliose macroalgae since, unlike other coral reef systems that become dominated by algae (Carpenter 1990, Littler et al. 1993, Hughes 1994), fleshy macroalgae are a rare component of mid- and outer-shelf GBR reefs, irrespective of coral cover.

In calculating exogenous inputs, and therefore the hydrodynamic regime of a platform reef, we ignored water flowing around the reef and considered only the input of inter-reef water that eventually leaves the reef front to flow over the reef into downstream zones. This volume is smaller (by an unknown magnitude) than the amount flowing parallel to the reef front which eventually moves around the reef to exit downstream without flowing over the reef (Hamner & Hauri 1981, Hamner & Wolanski 1988, Hamner et al. 1988). There were several reasons to ignore water flowing around the reef; first, the network analyses considered only the carbon internalised in the system and not that which simply passed through the zone, so ignoring water flowing around the reef had no effect on our results of network analyses. Second, carbon flowing along the slope and around (not over) the reef that is not internalised in this zone is not used by other downstream reef zone assemblages. Finally, there are no empirical estimates of the magnitude of this flux for midshelf GBR reefs.

For the coral-dominated state, coral cover was assumed to be 55% at 5 to 10 m, where corals are the principal filter-feeding organisms (Daniel et al. 1985). The derivation of flow magnitudes is given in Appendix 1. Where empirical data for Davies Reef were not

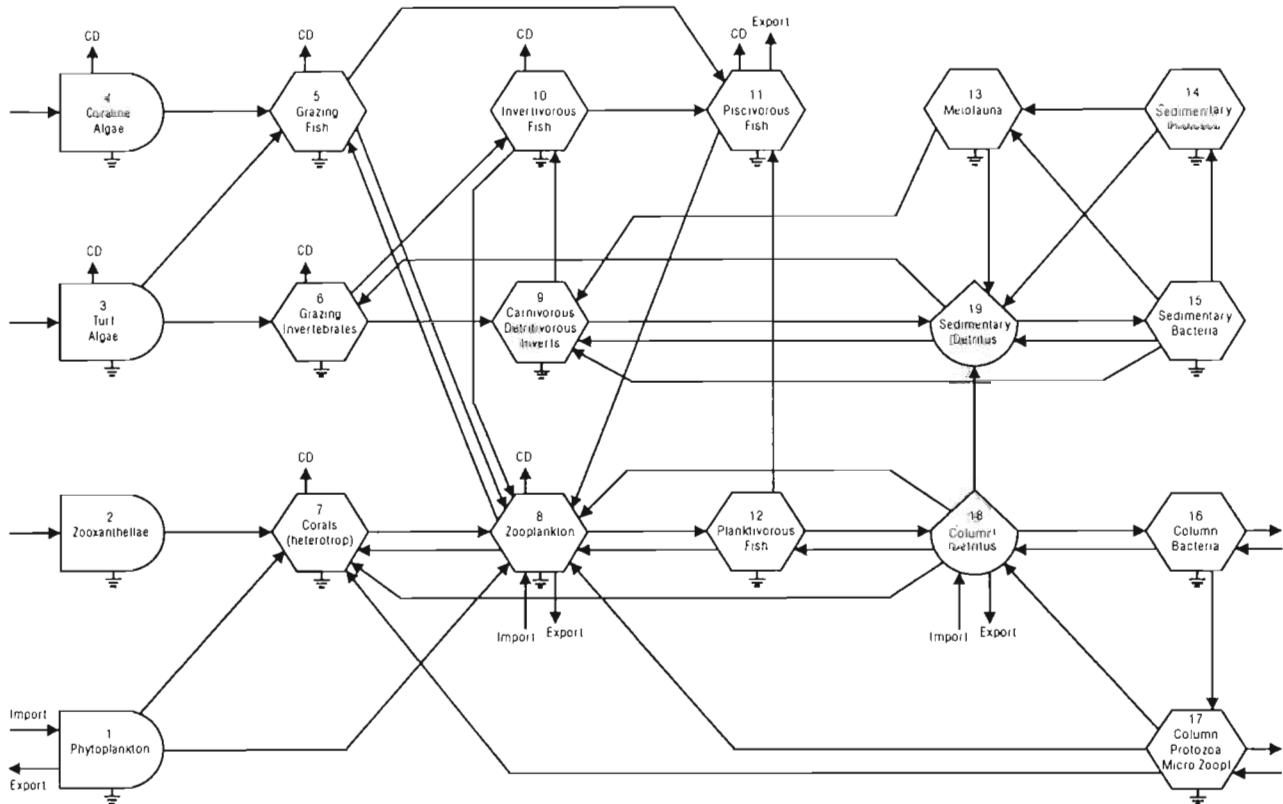


Fig. 1 Basic structure of the network representing carbon flux on the shallow front slope of Davies Reef, Australia. Flows are among 4 autotrophic, 13 heterotrophic, and 2 non-living trophic compartments. (⊕) Respiration. CD: water column detritus; Corals (heterotrop): heterotrophic component of corals; Micro Zoopl: microzooplankton

available, data were used from other reefs, or flows were derived by difference assuming steady state in trophic compartments or assuming allometric behaviour of physiological parameters (Peters 1983).

The network for the coral-dominated reef was used to derive 2 models of carbon flux for the algae-dominated state (Appendix 2), viz. (1) where coral cover is reduced to 2% by crown-of-thorns starfish (Keesing 1990) and dead coral skeletons are colonised by COA and turf algae, but where grazing fish and invertebrates do not respond to the increased abundance of algae (e.g. Williams 1986, T Hart unpubl. data; see 'Discussion') and the excess in production of algal carbon is exported as detritus in the water column, and (2) where coral cover is reduced to 2% and grazers respond to the increased availability of algae (e.g. Robertson 1991) so that losses of algal carbon to grazers and losses to detritus are in the same proportion as occurs in the coral-dominated state (ca 1:1). In these models it was assumed that production of epilithic algae (COA + turf algae) per unit area of algae-covered substratum on starfish-affected reefs was identical to that on algae-covered substratum on coral-dominated reefs. This may be conservative in that preliminary data (from a single reef at a single time) suggest that algal biomass per

unit area of algae-covered substratum may be up to 1.8 times higher in crown-of-thorns impacted areas (D. Klumpp unpubl. data). However, given that the area affected by starfish in Klumpp's pilot study supported a high cover of transient bluegreen algae, we favour a conservative interpretation of these preliminary measurements. Furthermore, exploratory sensitivity analyses (not presented here) for the scenario where additional algal production is lost to detritus showed that changes in gross production of autotrophs of this magnitude did not qualitatively affect comparisons. Similarly, we assumed similar productivity of turf algae for both scenarios of the algae-dominated state based on identical productivity per unit biomass of grazed (uncaged) and ungrazed turf at Davies Reef (Klumpp et al. 1987). Higher rates of algal production per unit biomass at higher standing biomass of algae appear to be a unique property of damselfish territories (Klumpp et al. 1987). On Davies Reef there is no evidence of reduced productivity of turf algae per unit biomass with reduced grazing pressure as has been reported elsewhere (see Carpenter 1990).

Despite the need for some assumptions and difficulties associated with assembling disparate measurements from a variety of sources into a system scheme,

we contend that our values are within range for Davies Reef and preserve sensible physiological ratios and, accordingly, that our models adequately describe the flow structures in the shallow front zone of a typical midshelf platform reef in the GBR system. The appendices outline the assumptions in obtaining flux patterns; discrepancies with other systems are noted therein and in the 'Discussion'.

Network analysis (NA). A detailed comparison of the 3 models was undertaken using the NA software NETWRK3 produced by R. E. Ulanowicz (see Wulff et al. 1989). This technique allows for quantitative comparison of different network systems that have the same general structure of flows among the same kind of trophic compartments. Thus, different ecosystems of similar trophic structure (e.g. Wulff & Ulanowicz 1989), or temporal sequences in a single system (e.g. Baird & Ulanowicz 1989, Field et al. 1989b), can be compared. To help the reader interpret output presented here, a brief description of NA output is given below.

Total system properties

- Total System Throughput (TST) = Σ (all flows), including inputs and outputs, and is a measure of the 'size' of the system
- Internal Throughput (IT) = Σ (all flows), not including inputs (inputs include gross production of autotrophs)
- overall Finn cycling index is the proportion of TST that is cycled = $[\Sigma(\text{cycled flows})]/TST$
- Finn cycling index for 'feeding cycles' is the proportion of total flow that is cycled in cycles where all components are living
- Detritivory (Dt) is the flow from detritus \rightarrow trophic category II
- Herbivory (H) is the flow from trophic category I \rightarrow II
- relative importance of recycling = Dt/H
- Flow Diversity (D) is an information measure (on a log scale) of the 'organisation' of flows based on the number and evenness of inputs to compartments. There are several definitions of D (cf. Field et al. 1989a, b, Kay et al. 1989), and here we define D *sensu* Ulanowicz (NETWRK3 software), i.e. $D = A/TST$, where A = ascendancy
- Average Path Length (APL) is the average (or expected) number of steps (transfers) a unit of medium (in this case, carbon) experiences in passing through the network; $APL = (TST - EI)/EI = IT/EI$, where EI is the total of exogenous inputs (and includes the gross production of autotrophs)
- Ascendancy ($A = TST \times D$) is an information-based measure of both size and organisation of flows. A tends to increase with increasing trophic specialisation, successional stage towards 'maturity' of a system, internalisation, and increased cycling. De-

creases in A are usually interpreted as indicative of stress

- Development Capacity (DC) defines the potential for a network to develop, i.e. defines the maximum possible value of A . DC can be viewed as a measure of the 'total uncertainty' of the network, and A as the amount of uncertainty resolved by knowing the flow structure
- Overheads ($DC - A$) define residual uncertainty in flow structure and are partitioned into components due to respiration, inputs, exports and redundancy (Rd), where Rd is the residual uncertainty associated with multiple or parallel pathways

Trophic analysis and compartmental attributes

- Dependency Coefficients are the fraction of total flow leaving one compartment that enters another compartment (including direct, indirect and recycled flows)
- the Effective Trophic Level of a compartment is a weighted average of the compartment's trophic level, where weightings are the relative amounts of total inflow into the compartment at different trophic levels; by convention the trophic level of autotrophs and detritus = 1
- Trophic Efficiency is the comparison of inflow into a trophic category with outflow available to the next trophic category (= ecological efficiency)

In addition, network analysis (1) extracts all biogeochemical cycles and identifies subgroups of cycles, referred to as nexuses, that share the same smallest, or limiting, transfer and (2) enables derivation of a Lindeman spine, which is an abstract food chain in which the network is collapsed and the system summarised by describing fluxes between successive trophic categories or levels (note that a single trophic compartment or 'trophic guild' may be represented in several trophic categories).

RESULTS

Total system properties

General

Carbon flux in the shallow (5 to 10 m) front zone of Davies Reef is dominated by exogenous inputs and exports as a result of transport of particulate organic carbon (POC) in water moving onto the reef (see Compartments 1, 8, 16, 17, 18, Appendix 1). The flow velocity and amount of POC carried generates inflows and outflows of carbon several orders of magnitude greater than individual transfers within the zone. However, since the great majority of exogenous carbon in

the water column is swept into and out of the front reef zone without being internalised (i.e. most transport is across the reef front and then around the reef to exit downstream, while a smaller volume flows into the reef flat zone; see Hamner & Hauri 1981, Hamner & Wolanski 1988, Hamner et al. 1988), the network analyses were undertaken ignoring the high throughflow of exogenous carbon.

System size and overall flow structure

In the transition from a coral- to an algae-dominated system, the amount of carbon fixed in benthic primary production decreases from ca 15.9 to 3.0 g C m⁻² d⁻¹ (= 13.17 and 1.81 g C m⁻² d⁻¹ net primary production, NPP) since in this system live coral is more productive than an equivalent area of dead coral covered with epilithic algae (see 'Discussion'). This effects a decrease in the total system measures that are based on absolute magnitudes of flows (i.e. internal and total system throughputs, ascendancy, development capacity and overheads; see Table 1, Fig. 2, Appendices 1 & 2). Similarly, the transfer of carbon between trophic categories I→II, ..., IV→V is ~4 to 14 times lower in the algae-dominated system, depending on the particular transfer (Fig. 2). Not surprisingly, overall flow magnitudes for the algae-dominated state are slightly greater when a proportion of the increased biomass of algae is consumed by grazers and passed on through the food web instead of being channeled to the detritus pool (Table 1).

The greatest diversity of flows is realised in the algae-dominated configuration where grazers respond to the increase in algal production (Table 1), which reflects a greater evenness of flows, particularly from primary producers → first order consumers → second order consumers. In the coral-dominated state, primary production and flux of plant carbon to consumers is dominated by zooxanthellae and transfer from zooxanthellae to coral tissue (93 and 98% respectively for the coral-dominated state, versus 18 and 40% for depleted coral cover where grazers respond to the increase in algae). The greater average path length in the algae-dominated configurations (Table 1) is also attributable to turf and coralline algae accounting for a greater proportion of the primary production after loss of coral cover. In the coral-dominated state, a greater amount of carbon fixed by zooxanthellae travels only 2 steps before being lost via export

of zooplankton, whereas when turf and coralline algae account for most of the primary production, a unit of flux will, on average, travel more steps before exiting the system (Fig. 1, Appendices 1 & 2; note that in balancing models in which 'exogenous' carbon is ignored, there is no export of water-column detritus in any state of the system and export of zooplankton only occurs when coral dominates).

Recycling

The structure of recycling is similar in all models and is relatively complex. All models contain 78 cycles, there are only 12 single-cycle nexuses (15.4% of all cycles), and there are 2 large nexuses, one containing 20 cycles and one containing 16 cycles. All cycles in both large nexuses include transfers via sedimentary and/or water column detritus, and the largest cycles (up to 10 transfers in the circuit loop) also include flows through both detritus categories. Flows via detritus are also important in many of the smaller nexuses, with 88.5% (69) of all cycles involving water column detritus and 66.7% (52) involving sedimentary detritus. However, despite the importance of both forms of detritus in recycling, bacteria play a relatively minor role since water column bacteria are involved in only 16.7% (13) of cycles and sedimentary bacteria in only 35.9% (28). Moreover, the magnitude of flows via bacteria is small (Appendices 1 & 2), and transfers involving bacteria are the critical or limiting transfer in

Table 1 Comparison of total system properties of network models of coral- and algae-dominated states of the shallow reef slope of Davies Reef. Exogenous inputs not internalised in the system are not included in these analyses. † ↑ in algal C: increase in algal carbon in the shift from a coral- to an algae-dominated state. *Units of g C m⁻² d⁻¹

Parameter	Coral dominated	Algae dominated	
		↑ in algal C to detritus	↑ in algal C to grazers & detritus
Total system throughput*	82.97	26.62	27.38
Internal throughput*	64.64	21.73	22.32
Full development capacity	233.2	77.0	81.1
Full ascendancy	155.7	50.0	52.7
Overhead (inputs)	4.21	1.86	1.78
Overhead (exports)	0.71	0.11	0.16
Overhead (respiration)	26.78	10.00	10.74
Redundancy	45.84	15.03	15.70
Flow diversity	1.88	1.88	1.93
Average path length	3.53	4.44	4.41
Finn cycling index (feeding cycles only)	0.033	0.0038	0.0038
Overall Finn cycling index	0.258	0.324	0.316
Relative import. of recycling	0.98	7.39	5.31
Detritivory*	13.47	7.11	7.11
Herbivory*	13.7	0.96	1.34

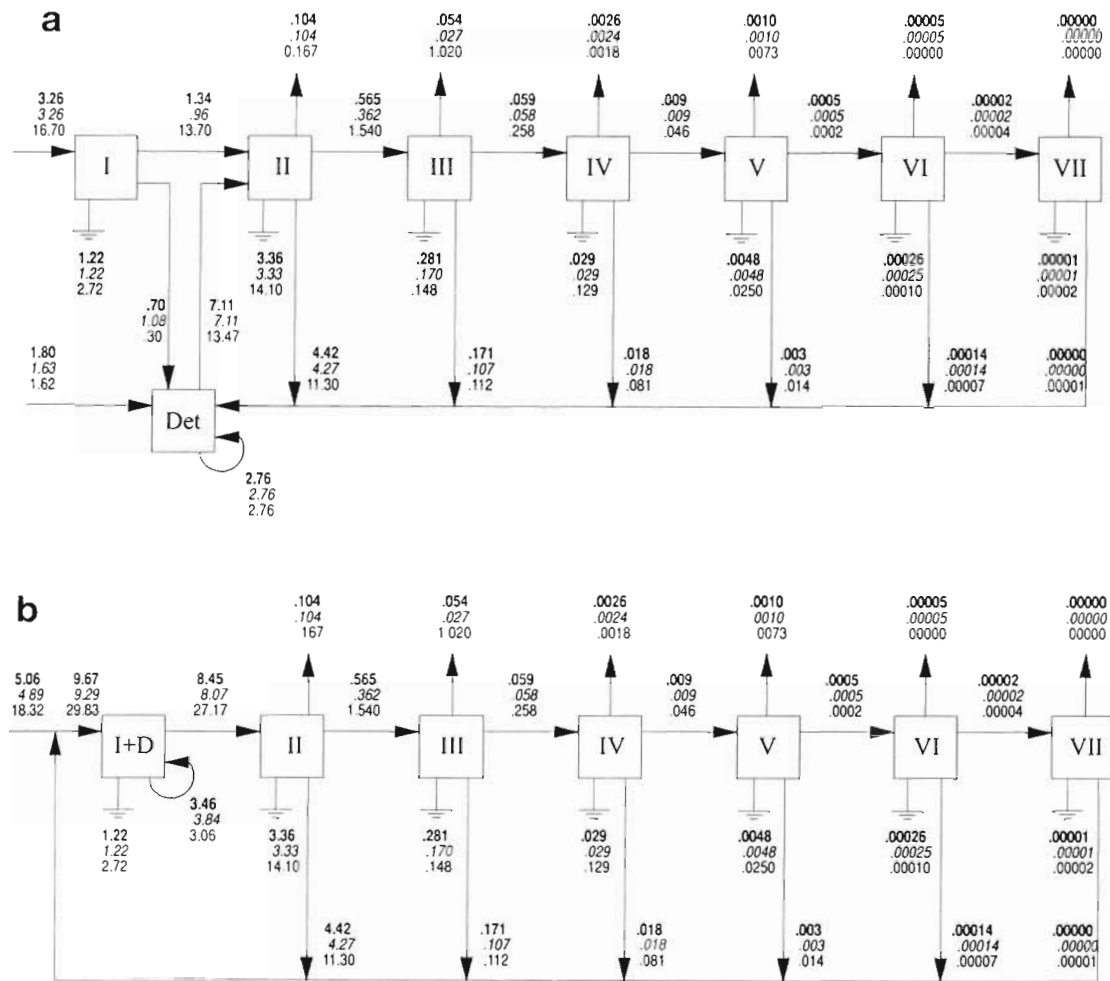


Fig. 2. Lindeman spines summarising trophic structure in which (a) detritus and autotrophs are separate compartments, and (b) where detritus and autotrophs are pooled in the same compartment. Bottom values (normal print) are for the coral-dominated state, middle values (italics) are for the algae-dominated state where the increase in algal production goes entirely to detritus (Scenario 1), and top values (bold) are for the algae-dominated state where grazers consume a proportion of the increase in algal production (Scenario 2). Member compartments of trophic categories I to VII can be determined from Fig. 1 by following network pathways and counting the number of transfers from detritus and primary producer compartments; we adopted the standard convention that primary producers and detritus are at trophic category I

6 cycles. The only qualitative difference in overall flow structure among the models is that in the algae-dominated configuration where grazers increase their consumption of algae, there is only 1 nexus of 2 cycles and 2 containing 4 cycles, whereas the other models have 3 nexuses of 2 cycles and only 1 containing 4 cycles.

The amount of total flow activity that is recycled is high in all models but varies from 25.8% in the coral-dominated state to 32.4% in the algae-dominated state when the increase in algal production is transferred to detritus (overall Finn cycling index, Table 1). The overall increase in the proportion of recycled material with loss of coral cover is indicative of the reduced total system throughput but also suggests that recycling among non-coral components is greater than that

among trophic groups interacting directly with corals. The relative importance of recycling (= ratio of detritivory:herbivory) increases dramatically with loss of coral cover because of the large decrease in 'herbivory'; note that for the purposes of network analysis, corals utilising carbon fixed by zooxanthellae are classified as 'herbivores'. The importance of recycling is greatest when increases in algal production following depletion of corals are channeled to detritus, since in this scenario herbivory is lowest.

In contrast to the trend in the overall cycling index, the Finn cycling index for feeding cycles is an order of magnitude lower when algae dominate (Table 1). This reflects that cycling among living trophic compartments is dominated by exchanges between corals and zooplankton when coral cover is high.

Trophic analysis

Trophic structure

The analysis identified 9 trophic categories (e.g. piscivorous fish are at trophic level IX in transfers from sedimentary detritus → sedimentary bacteria → sedimentary protozoa → meiofauna → detritivorous invertebrates → invertivorous fish → zooplankton → planktivorous fish → piscivores). However, flows associated with trophic categories VIII and IX are minimal, and are therefore not considered or included in the Lindeman spines (Fig. 2).

The Lindeman spines (Fig. 2) summarise trophic structure after collapsing of the system to simple linear transfers between trophic categories. They summarise several salient differences among the models, viz. the greater 'size' of the coral-dominated system; increased flows to detritus from primary producers in the algae-dominated state, particularly if grazers do not respond to the increase in algal production; and, in comparing between the 2 algae-dominated scenarios, differences in flows from plants to grazers to higher order consumers are rapidly damped (largely because of low trophic efficiency of trophic category II; Table 2) so that flows from trophic categories III→IV are similar in the 2 models, and flows to higher trophic categories are essentially identical.

Despite the large number of trophic levels, the average level of feeding of all trophic groups in all models is always <4 (Table 3). The effective trophic level (ETL) of grazing fish (which inadvertently feed on demersal zooplankton; Polunin 1988, Klumpp & Polunin 1989) and the higher order consumers of zooplankton, planktivorous fish and piscivorous fish, declines with decreasing coral abundance (Table 3). This indicates that in the coral-dominated state carbon fixed by zooxanthellae is eventually utilised by higher order consumers in significant amounts and that in the transition to an algae-dominated system, the average number of steps from photosynthetically fixed carbon to consumers decreases. However, the decline in the ETL of zooplankton with loss in coral cover is, in one sense, artificial since the link from corals to zooplankton describes the reproductive output of corals and does not indicate that zooplankton feed directly on corals (although zooplankton

feed indirectly on corals by consuming coral mucus in the water column; see Appendix 1; Gottfried & Roman 1983). Transfer from corals to fish is largely via the contribution of coral gametes and larvae to zooplankton, but there are some links via production of mucus and its loss to the water column as detritus. The ETLs of compartments in trophic chains involving microbes, detritivores, and invertebrates (and therefore invertivorous fish) are largely unaffected by the transition from coral- to algae-dominated (Table 3). The exception is the ETL of water column protozoa which increased from 1.54 to 3, but this reflects only that imports of column protozoa are not required to balance the algae-dominated networks.

Trophic efficiencies of trophic categories II and III distinguish between the 2 scenarios for the algae-dominated system (Table 2). Compared to the coral-dominated system, the trophic efficiency of trophic category II decreases in the algae-dominated state if the increase in algal carbon is lost to detritus, but increases

Table 2. Trophic efficiencies (%) of each trophic category for each of the 3 models. '↑ algal C': increase in algal carbon in the shift from a coral- to an algae-dominated system

Trophic category	Coral dominated	Algae dominated	
		↑ algal C to detritus	↑ algal C to grazers & detritus
II	5.7	4.5	6.7
III	16.8	15.9	10.4
IV	18.0	15.6	15.3
V	0.5	5.1	5.2
VI	16.5	4.2	4.1
VII	0.0	0.0	0.0
Average	11.5	9.06	8.34

Table 3. Effective trophic levels of each trophic compartment for each model; values for autotrophs and detrital compartments = 1 by convention. '↑ algal C': increase in algal carbon in the shift from a coral- to an algae-dominated system

Compartment	Coral dominated	Algae dominated	
		↑ algal C to detritus	↑ algal C to grazers & detritus
Grazing fish	2.19	2.06	2.03
Grazing invertebrates	2.00	2.00	2.00
Corals (heterotrophic)	2.00	2.01	2.01
Zooplankton	2.94	1.57	1.57
Carniv/detrit inverts	2.00	2.00	2.00
Invertivorous fish	3.00	3.00	3.00
Piscivorous fish	3.47	3.15	3.08
Planktivorous fish	3.46	2.43	2.43
Meiofauna	3.13	3.13	3.13
Sedimentary protozoa	3.00	3.00	3.00
Sedimentary bacteria	2.00	2.00	2.00
Water column bacteria	2.00	2.00	2.00
Water column protozoa	1.54	3.00	3.00

when about half of algae net production is consumed by herbivores. Trophic efficiencies of category III decrease with decline in coral cover, but the decrease is greatest when grazers increase their total consumption of algal carbon. Trophic efficiencies also highlighted differences among the coral- and algae-dominated states. Efficiencies of trophic categories V and VI are lower and higher respectively in the coral-dominated state than in the algae-dominated configurations.

Trophic dependencies

Dependency coefficients reveal marked differences among the 3 models (Table 4). With loss of coral cover the dependence of all trophic groups on coral-derived carbon (both zooxanthellae and the heterotrophic component), including groups ostensibly remotely connected (e.g. meiofauna, invertivorous fish, carnivorous and detritivorous invertebrates), decreases markedly (Table 4). This result emphasises the fundamental importance of corals in fixing carbon that is utilised by most of the system.

In the transition to increased algal cover, the dependence of second order consumers on algal carbon increases considerably, the only exception being piscivorous fish in the situation where the increase in algal production is lost to the detritus pool. When increases in algal biomass are channeled into the system by increased herbivory (algae-dominated Scenario 2), piscivorous fish become more dependent on algae-derived carbon and less dependent on planktivorous fish and zooplankton-derived carbon. Not surprisingly, the importance of grazers (particularly grazing fish) in trophic transfers to most other consumers in the network is greatest when they respond to increased availability of algae, e.g. grazing invertebrates become more important and detritivorous and carnivorous invertebrates less important as sources of carbon for invertivorous fish.

Dependency on phytoplankton carbon is relatively low for all groups in all models, although in the algae-dominated states transfers to zooplankton from phytoplankton (via direct and indirect circuits) attain nearly 10% of the total intake. With declining coral cover, dependency of sedimentary microbes, invertebrates and invertivorous fish on phytoplankton carbon declines considerably. Similarly, most groups are less dependent on zooplankton when algae dominate, particularly when grazers respond to the increased availability of algae. In part this reflects the reduced contribution of coral reproductive propagules to zooplankton as coral cover declines.

Dependency of higher organisms on flows from microbes (bacteria, protozoa, microzooplankton and

meiofauna) is low, although clearly there are strong dependencies within the subnetworks of water column microbes and sedimentary microbes. All sedimentary microbes demonstrate strong dependency on carnivorous and detritivorous invertebrates, which make the single largest contribution to the sedimentary detritus pool at the base of the sedimentary microbe subnetwork. The large increase in dependency of water column protozoa and microzooplankton on water column detritus and bacteria for the algae-dominated scenarios reflects that some water column protozoa are imported in the coral-dominated state but imports are not required to balance the algae-dominated networks.

DISCUSSION

The models: gross properties and comparison with other schemata

The overriding feature of carbon flux on the shallow front of Davies Reef is the dominance of exogenous inflows and exports, not because of high standing concentrations of carbon in the water column but by virtue of high flow rates and thus transport of large volumes of water. Moreover, our estimates of exogenous inputs do not include water moving into the reef front zone and then around the reef without passing over it, which greatly exceeds volumes flowing over the reef flat from the front zone (Hamner & Hauri 1981, Hamner & Wolanski 1988, Hamner et al. 1988). Although a portion of the carbon exported from the reef front zone will be utilised by organisms of the reef flat (Ayukai in press), lagoon and back reef, it is clear that the paradigm of low advective inputs and the importance of relatively tight and efficient recycling of inorganic nutrients (e.g. Muscatine & Porter 1977, Erez 1990, see also D'Elia & Wiebe 1990) does not apply to all organic elements, and certainly not to organic carbon. Compared to larger temperate marine systems, e.g. the Baltic Sea (Wulff & Ulanowicz 1989) and Chesapeake Bay, USA (Baird & Ulanowicz 1989), carbon flux on Davies Reef is dominated to a greater degree by exogenous transfers; but, carbon of exogenous origin comprises a much smaller amount of the total internalised flux, and recycling of carbon is higher on the reef than in these temperate systems (26 to 32% of total flux recycled on Davies Reef versus 22% in the Chesapeake and Baltic systems).

The models presented here are not directly comparable to previous schemata (cf. Polovina 1984, Wilkinson 1987, Sorokin 1990b) as our models contain a greater number of trophic compartments and there is

Table 4. Dependency coefficients (%) for each of the 3 models. These give the fraction (%) of total carbon intake of one compartment (in the rows) that is contributed by another (in the columns), including direct, indirect and recycled flows. This is shown as 'Dependency OF (↓):' groups in rows 'ON: (← →)' groups in columns. Top values (normal type) are for the coral-dominated state; middle values (italics) are for the algae-dominated state where the increase in production of algal carbon is lost to detritus (Scenario 1); lower values (bold) are for the algae-dominated state where the increase in production of algal carbon flows to detritus and grazers in equal proportions (Scenario 2). Cpt: Compartment

Dependency OF (↓):	ON: (← →)																		
	Cpt 1	Cpt 2	Cpt 3	Cpt 4	Cpt 5	Cpt 6	Cpt 7	Cpt 8	Cpt 9	Cpt 10	Cpt 11	Cpt 12	Cpt 13	Cpt 14	Cpt 15	Cpt 16	Cpt 17	Cpt 18	Cpt 19
Grazing fish (Cpt 5)	0.6 <i>0.9</i> 0.4	8.6 <i>1.7</i> 0.8	48.4 <i>48.9</i> 53.1	41.5 <i>41.8</i> 42.5	0.1 <i>0.2</i> 0.2	0.0 <i>0.0</i> 0.0	10.2 <i>2.8</i> 1.3	10.3 <i>10.3</i> 4.8	0.0 <i>0.0</i> 0.0	0.0 <i>0.0</i> 0.0	0.0 <i>0.1</i> 0.0	0.1 <i>0.1</i> 0.0	0.0 <i>0.0</i> 0.0	0.0 <i>0.0</i> 0.0	0.0 <i>0.0</i> 0.0	0.0 <i>0.1</i> 0.0	0.1 <i>0.1</i> 0.0	3.53 <i>2.4</i> 1.1	0.0 <i>0.0</i> 0.0
Grazing invertebrates (Cpt 6)	0.8 <i>0.1</i> 0.1	13.3 <i>1.2</i> 0.6	80.8 <i>84.8</i> 91.5	0.5 <i>3.0</i> 1.4	0.4 <i>1.0</i> 1.2	0.1 <i>0.2</i> 0.2	15.6 <i>1.9</i> 1.0	1.7 <i>1.0</i> 0.5	11.6 <i>11.6</i> 6.2	0.0 <i>0.1</i> 0.0	0.2 <i>0.4</i> 0.4	0.3 <i>0.6</i> 0.3	0.0 <i>0.0</i> 0.0	0.0 <i>0.0</i> 0.0	0.1 <i>0.1</i> 0.0	0.1 <i>0.3</i> 0.1	0.1 <i>0.1</i> 0.0	20.0 <i>20.0</i> 10.7	20.0 <i>20.0</i> 10.8
Corals (heterotrophic) (Cpt 7)	5.1 <i>4.3</i> 4.3	84.9 <i>61.9</i> 61.9	1.3 <i>7.8</i> 6.7	0.8 <i>4.9</i> 4.3	0.7 <i>1.7</i> 3.6	0.1 <i>0.3</i> 0.6	30.5 <i>4.7</i> 4.7	8.9 <i>7.8</i> 7.8	0.1 <i>0.1</i> 0.1	0.1 <i>0.1</i> 0.2	0.3 <i>0.7</i> 1.2	0.5 <i>1.0</i> 1.0	0.0 <i>0.0</i> 0.0	0.0 <i>0.0</i> 0.0	0.0 <i>0.0</i> 0.0	0.3 <i>0.7</i> 0.7	0.5 <i>0.4</i> 0.4	33.2 <i>32.6</i> 32.6	0.1 <i>0.1</i> 0.1
Zooplankton (Cpt 8)	6.1 <i>9.0</i> 9.0	83.5 <i>16.8</i> 16.8	1.4 <i>5.7</i> 5.1	0.9 <i>3.6</i> 3.3	0.8 <i>1.5</i> 3.2	0.1 <i>0.2</i> 0.4	98.4 <i>27.2</i> 27.2	8.8 <i>2.8</i> 2.8	0.1 <i>0.2</i> 0.2	0.1 <i>0.2</i> 0.2	0.3 <i>0.5</i> 1.0	0.5 <i>0.8</i> 0.8	0.0 <i>0.0</i> 0.0	0.0 <i>0.0</i> 0.0	0.0 <i>0.0</i> 0.0	0.3 <i>0.9</i> 0.9	0.5 <i>0.7</i> 0.7	34.1 <i>23.1</i> 23.1	0.1 <i>0.2</i> 0.2
Carn/detritiv invertebrates (Cpt 9)	4.0 <i>0.7</i> 0.7	66.3 <i>5.8</i> 5.8	4.2 <i>24.0</i> 20.9	2.5 <i>15.0</i> 12.9	2.2 <i>5.0</i> 10.8	0.7 <i>1.2</i> 2.3	78.1 <i>9.4</i> 9.4	8.2 <i>4.8</i> 4.8	57.7 <i>57.8</i> 57.8	0.2 <i>0.4</i> 0.5	0.9 <i>2.0</i> 3.8	1.4 <i>3.2</i> 3.2	0.1 <i>0.1</i> 0.1	0.0 <i>0.0</i> 0.0	0.4 <i>0.4</i> 0.4	0.6 <i>1.3</i> 1.3	0.4 <i>0.3</i> 0.3	99.7 <i>99.7</i> 99.5	99.9 <i>99.9</i> 99.8
Invertivorous fish (Cpt 10)	3.1 <i>0.6</i> 0.4	50.7 <i>4.5</i> 3.5	26.7 <i>41.8</i> 52.1	1.9 <i>11.5</i> 7.8	1.7 <i>3.9</i> 6.6	29.9 <i>30.3</i> 45.5	59.7 <i>7.2</i> 5.7	6.3 <i>3.7</i> 2.9	74.0 <i>74.0</i> 58.6	0.1 <i>0.3</i> 0.3	0.7 <i>1.5</i> 2.3	1.1 <i>2.4</i> 1.9	0.1 <i>0.1</i> 0.0	0.0 <i>0.0</i> 0.0	0.3 <i>0.3</i> 0.3	0.4 <i>1.0</i> 0.8	0.3 <i>0.3</i> 0.2	76.3 <i>76.3</i> 60.2	76.4 <i>76.4</i> 60.4
Piscivorous fish (Cpt 11)	1.7 <i>2.2</i> 1.1	24.1 <i>4.3</i> 2.3	38.4 <i>40.8</i> 48.3	32.4 <i>33.9</i> 38.0	77.6 <i>77.9</i> 88.4	0.7 <i>0.8</i> 0.8	28.3 <i>7.0</i> 3.7	23.9 <i>23.7</i> 12.5	1.7 <i>1.7</i> 0.9	2.2 <i>2.3</i> 1.5	0.1 <i>0.3</i> 0.3	20.6 <i>20.6</i> 10.9	0.0 <i>0.0</i> 0.0	0.0 <i>0.0</i> 0.0	0.0 <i>0.0</i> 0.0	0.1 <i>0.3</i> 0.2	0.2 <i>0.2</i> 0.1	14.8 <i>12.2</i> 6.4	1.7 <i>1.8</i> 0.9
Planktivorous fish (Cpt 12)	5.6 <i>7.0</i> 7.0	79.3 <i>14.1</i> 14.1	2.0 <i>10.2</i> 8.9	1.3 <i>6.5</i> 5.7	1.2 <i>2.4</i> 5.1	0.2 <i>0.4</i> 0.8	93.4 <i>22.8</i> 22.8	77.1 <i>76.3</i> 76.3	0.1 <i>0.2</i> 0.2	0.1 <i>0.2</i> 0.3	0.4 <i>0.9</i> 1.7	0.7 <i>1.4</i> 1.4	0.0 <i>0.0</i> 0.0	0.0 <i>0.0</i> 0.0	0.0 <i>0.0</i> 0.0	0.4 <i>1.0</i> 1.0	0.5 <i>0.6</i> 0.6	50.5 <i>42.2</i> 42.2	0.1 <i>0.2</i> 0.3
Meiofauna (Cpt 13)	4.0 <i>0.7</i> 0.7	66.4 <i>5.8</i> 5.8	4.1 <i>23.9</i> 20.7	2.5 <i>15.1</i> 13.0	2.2 <i>5.1</i> 10.8	0.6 <i>1.1</i> 2.0	78.2 <i>9.4</i> 9.4	8.2 <i>4.8</i> 4.8	57.8 <i>57.8</i> 57.9	0.2 <i>0.4</i> 0.5	0.9 <i>2.0</i> 3.8	1.4 <i>3.2</i> 3.2	0.1 <i>0.1</i> 0.1	13.1 <i>13.1</i> 13.1	100 <i>100</i> 100	0.6 <i>1.3</i> 1.3	0.4 <i>0.3</i> 0.3	99.8 <i>99.8</i> 99.7	100 <i>100</i> 100
Sedimentary protozoa (Cpt 14)	4.0 <i>0.7</i> 0.7	66.4 <i>5.8</i> 5.8	4.1 <i>23.9</i> 20.7	2.5 <i>15.1</i> 13.0	2.2 <i>5.1</i> 10.8	0.6 <i>1.1</i> 2.0	78.2 <i>9.4</i> 9.4	8.2 <i>4.8</i> 4.8	57.8 <i>57.8</i> 57.9	0.2 <i>0.4</i> 0.5	0.9 <i>2.0</i> 3.8	1.4 <i>3.2</i> 3.2	0.1 <i>0.1</i> 0.1	0.0 <i>0.0</i> 0.0	100 <i>100</i> 100	0.6 <i>1.3</i> 1.3	0.4 <i>0.3</i> 0.3	99.8 <i>99.8</i> 99.7	100 <i>100</i> 100
Sedimentary bacteria (Cpt 15)	4.0 <i>0.7</i> 0.7	66.4 <i>5.8</i> 5.8	4.1 <i>23.9</i> 20.7	2.5 <i>15.1</i> 13.0	2.2 <i>5.1</i> 10.8	0.6 <i>1.1</i> 2.0	78.2 <i>9.4</i> 9.4	8.2 <i>4.8</i> 4.8	57.8 <i>57.8</i> 57.9	0.2 <i>0.4</i> 0.5	0.9 <i>2.0</i> 3.8	1.4 <i>3.2</i> 3.2	0.1 <i>0.1</i> 0.1	0.0 <i>0.0</i> 0.0	0.4 <i>0.4</i> 0.4	0.6 <i>1.3</i> 1.3	0.4 <i>0.3</i> 0.3	99.8 <i>99.8</i> 99.7	100 <i>100</i> 100
Water column bacteria (Cpt 16)	4.0 <i>0.7</i> 0.7	66.5 <i>5.8</i> 5.8	3.9 <i>23.8</i> 20.4	2.5 <i>15.1</i> 13.0	2.2 <i>5.1</i> 10.9	0.4 <i>0.9</i> 1.7	78.3 <i>9.4</i> 9.4	8.2 <i>4.8</i> 4.8	0.2 <i>0.4</i> 0.4	0.2 <i>0.4</i> 0.5	0.9 <i>2.0</i> 3.8	1.4 <i>3.2</i> 3.2	0.0 <i>0.0</i> 0.0	0.0 <i>0.0</i> 0.0	0.0 <i>0.0</i> 0.0	0.6 <i>1.3</i> 1.3	0.4 <i>0.3</i> 0.3	100 <i>100</i> 100	0.2 <i>0.4</i> 0.4
Water column protozoa (Cpt 17)	1.1 <i>0.7</i> 0.7	17.9 <i>5.8</i> 5.8	1.1 <i>23.8</i> 20.4	0.7 <i>15.1</i> 13.0	0.6 <i>5.1</i> 10.9	0.1 <i>0.9</i> 1.7	21.1 <i>9.4</i> 9.4	2.2 <i>4.8</i> 4.8	0.0 <i>0.4</i> 0.4	0.0 <i>0.4</i> 0.5	0.2 <i>2.0</i> 3.8	0.4 <i>3.2</i> 3.2	0.0 <i>0.0</i> 0.0	0.0 <i>0.0</i> 0.0	0.0 <i>0.0</i> 0.0	26.9 <i>100</i> 100	0.1 <i>0.3</i> 0.3	26.9 <i>100</i> 100	0.1 <i>0.4</i> 0.4
Water column detritus (Cpt 18)	4.0 <i>0.7</i> 0.7	66.5 <i>5.8</i> 5.8	3.9 <i>23.8</i> 20.4	2.5 <i>15.1</i> 13.0	2.2 <i>5.1</i> 10.9	0.4 <i>0.9</i> 1.7	78.3 <i>9.4</i> 9.4	8.2 <i>4.8</i> 4.8	0.2 <i>0.4</i> 0.5	0.2 <i>0.4</i> 0.5	0.9 <i>2.0</i> 3.8	1.4 <i>3.2</i> 3.2	0.0 <i>0.0</i> 0.0	0.0 <i>0.0</i> 0.0	0.0 <i>0.0</i> 0.0	0.6 <i>1.3</i> 1.3	0.4 <i>0.3</i> 0.3	26.6 <i>6.0</i> 6.0	0.2 <i>0.4</i> 0.4
Sedimentary detritus (Cpt 19)	4.0 <i>0.7</i> 0.7	66.4 <i>5.8</i> 5.8	4.1 <i>23.9</i> 20.7	2.5 <i>15.1</i> 13.0	2.2 <i>5.1</i> 10.8	0.6 <i>1.1</i> 2.0	78.2 <i>9.4</i> 9.4	8.2 <i>4.8</i> 4.8	57.8 <i>57.8</i> 57.9	0.2 <i>0.4</i> 0.5	0.9 <i>2.0</i> 3.8	1.4 <i>3.2</i> 3.2	0.1 <i>0.1</i> 0.1	0.0 <i>0.0</i> 0.0	0.4 <i>0.4</i> 0.4	0.6 <i>1.3</i> 1.3	0.4 <i>0.3</i> 0.3	99.8 <i>99.8</i> 99.7	57.8 <i>57.9</i> 57.9

no, or only partial, overlap in the identity of most compartments. However, some useful general comparisons can be made. In terms of gross trophic structure, the ECOPATH model developed for French Frigate Shoals in Hawaii, USA (Polovina 1984, Atkinson & Grigg 1984, Grigg et al. 1984), demonstrates some similarity to our models in that there is some resolution of higher order consumers (however, the top-down approach of ECOPATH is quite different to that employed here). Polovina's (1984) species group of 'reef fishes' closely parallels the sum of the fish groups in our models. However, estimates of the total production of reef fish in our models are over an order of magnitude greater than that predicted by ECOPATH, despite that in both models these fish are feeding at about the same trophic level and that the ecological efficiency of trophic category II is lower on Davies Reef (~6%) than at French Frigate Shoals (20%). This is explained in part by an order of magnitude higher standing biomass of fish (Williams & Hatcher 1983) and higher benthic primary production (algae + corals; see Appendix 1) on mid-shelf reefs in the GBR. Also, in ECOPATH only ~5% of net primary production (NPP) reaches non-benthic predators (Atkinson & Grigg 1984), whereas in our models at least 16.1 to 26.9% of NPP (depending on the model) is utilised by predators (invertivorous fish, piscivorous fish and zooplankton) feeding at trophic level 3. That so little plant-derived carbon reaches higher consumers in the ECOPATH scenario reflects the low trophic efficiencies of trophic categories III and IV (4 and 2% in ECOPATH versus ~17 and 18% respectively for the coral-dominated state on Davies Reef). These differences suggest that many more data are required on flux rates, assimilation efficiencies and other physiological processes at a variety of appropriate temporal and spatial scales and, also, that a critical comparison of top-down and bottom-up approaches to modelling material fluxes is warranted.

Although the overall structure and trophic resolution of Sorokin's (1990b) general model of energy flow on a 'typical' coral reef is simpler than in our models, fundamental differences in the role of bacteria in the 2 schemes warrant discussion. In Sorokin's model detritus is the foundation of the system, and the bulk of primary production enters the network via microbial links. Bacteria account for >70% of the total energy flow, and the second greatest flow is zooxanthellae → coral → detritus. In our model, the total flux of carbon from sedimentary and water column detritus to heterotrophs ($13.5 \text{ g C m}^{-2} \text{ d}^{-1}$) is similar to the transfer from zooxanthellae to corals ($12.6 \text{ g C m}^{-2} \text{ d}^{-1}$), but most of the flux from detritus to heterotrophs is accounted for by corals feeding on POC (49%) and by detritivores (48%), not by bacteria (1.7%). Note that whereas a large proportion (50%) of water column bacteria on

coral reefs may be attached to detrital particles (Moriarty 1979), they likely amount to only a negligible portion (<0.1%) of POC (Coffroth 1990). Also, dependency coefficients (Table 4) suggest that flows via bacteria may be relatively unimportant for higher order consumers.

This discrepancy cannot be accounted for by the different units of the models; how then can such a large and fundamental difference be reconciled? Part of the answer is that Sorokin's estimates of bacterial biomass and production are too high (Ducklow 1990) and that his model is for an entire reef system and not a specific zone dominated by hard substratum. Unlike other reef zones, particularly lagoonal areas, there is relatively little sediment on the shallow front zone of Davies Reef (at 7.5 m only 5% of the benthos is sand; Daniel et al. 1985, Klumpp et al. 1987). Our estimates of total bacterial metabolism are likely to be underestimates because we were unable to take into account utilisation of DOC or the activity of bacteria on hard substrata or on biological surfaces. However, even if we assume that bacterial production is as high on hard substrata (excluding live coral) as it is on sand, our conclusions are unchanged; given 41% cover of hard substratum with surface rugosity of 1.86 (Klumpp & McKinnon 1989), if bacterial production on this substratum is equivalent to that on sand on an areal basis, then the proportion of total flux from detritus → heterotrophs via bacteria increases from 1.7 to 2.0%, which is negligible. Moreover, since much of the hard substrata is coralline algae, which characteristically has regions of thallus with low densities of bacteria (Johnson et al. 1991a, b), the assumption of equivalent production of bacteria on hard substrata as on sand may be an overestimate. Spatial variation in the biomass and production of water column bacteria is unlikely to account for the discrepancy since standing stocks (11.9 mg C m^{-3} for Davies Reef; T. Ayukai unpubl.) are low and do not vary greatly among zones (Moriarty et al. 1985a, Ducklow 1990). Thus, our cautious conclusion is that the importance of microbial links in recycling and flows to heterotrophy are highly spatially variable on coral reefs and appear to be relatively unimportant in areas dominated by corals and strong hydrodynamic flow but much more important in areas with high cover of sediments. However, we add the caveat and echo Sorokin's (1990b) sentiments that much more work is required on the importance of microbes as a food source.

Effects of transition to an algae-dominated state

Extensive replacement of live coral with free-living algae can lead to net erosion of reefs as a result

of depletion of reef-building organisms (Bak 1990, Glynn & Colgan 1992), but the effects of shifts in community structure of this kind on carbon flux and other aspects of system function are poorly understood. Unless loss of corals is extreme, the same kinds of trophic groups and qualitatively identical linkages between them describe both community states, although the precise species complement of any particular trophic group may differ. The question arises whether a particular trophic group functions similarly regardless of its precise species signature (the 'redundancy' hypothesis) or whether changes in the species complement of particular trophic groups incrementally affect the system (the 'rivet' hypothesis; Chapin et al. 1992). Our results show that, even at the coarse level of trophic structure considered in our networks, network properties and the structure of transfers of carbon among trophic compartments in terms of both absolute and relative fluxes are fundamentally affected by shifts in community structure. Moreover, our analysis is conservative in that it assumes no changes in the diversity or relative composition of any trophic compartment other than corals.

Replacement of corals by algae realises decreases in primary productivity, and thus decreases in overall system size and activity (e.g. in *TST* and *A*), although there is an increase in the magnitude of transfers to detritus. The significant decrease in system size is not dependent on our assumption that algae-covered substrata on coral- and algae-dominated reefs are similarly productive, since even with the most optimistic estimates of algal production in the algae-dominated state (see 'Methods'), loss of coral cover realises a large decrease in system size. Decline in size and ascendancy is normally indicative of disturbance to, or stress on, a system (Kay et al. 1989). However, the structure of recycling suggests that the relative magnitude of the 'stress' is not large. Disturbed systems tend toward fewer cycles, short circuit lengths and a preponderance of single-nexus cycles (Baird & Ulanowicz 1989); but, our networks reveal moderate numbers of cycles, including some with long circuit lengths and some large nexuses. Increase in the proportion of total flux that is recycled, as was observed with loss of coral cover, has been reported for other disturbed marine systems (Ulanowicz 1984, Baird & Ulanowicz 1989).

The decrease in *TST* and *A* occurs largely because, in our models, productivity of live coral is greater than that of equivalent dead coral overgrown with epilithic algae. Since this difference in productivity underscores many of the differences in network characteristics between the 2 states, the flux estimates for gross primary production of zooxanthellae and

epilithic algae warrant careful scrutiny. Our values for algal production come from extensive and repeatable measurements at Davies Reef (Klumpp & McKinnon 1989, 1992). Estimates for Davies Reef are nearly identical to those for a variety of other reefs in the GBR system (Klumpp & McKinnon 1992), but may be lower than those for equivalent algal assemblages in the Caribbean (Carpenter 1985). Our value for coral production is more problematic (gross production = $27 \text{ g C m}^{-2} \text{ coral d}^{-1} = 14.8 \text{ g C m}^{-2} \text{ substratum d}^{-1}$; Appendix 1), and is midrange of several estimates for coral outcrops on the GBR (Kinsey 1985). This level of production exceeds the high end of the range suggested by Muscatine (1990; $14 \text{ g C m}^{-2} \text{ d}^{-1}$), but is similar to the high rates recorded for *Pocillopora damicornis* ($28.9 \text{ g C m}^{-2} \text{ d}^{-1}$) by Jokieli & Morrissey (1986). Smith (1981) asserts that rates of gross production of the order of $25 \text{ g C m}^{-2} \text{ d}^{-1}$ can be found in shallow thickets of coral. Our point is that, while Kinsey's (1985) values for productivity of coral outcrops (which will include some algal production) are at the high end of production rates expected of corals, even if these estimates are high by 100%, the same qualitative behaviour in network characteristics would result and our conclusions would not change. For there to be no change in total gross primary production in the shift to dominance by algae, production by coral zooxanthellae would need to be greater than an order of magnitude lower than the estimate used here, which is clearly untenable. Our estimate of total gross primary production (corals + algae = $15.9 \text{ g C m}^{-2} \text{ d}^{-1}$ for the coral-dominated state) is within the normal range for coral-dominated reef areas (e.g. see Smith 1981, Adey 1983, Kinsey 1985).

The shift in primary production from domination by zooxanthellae to domination by free-living algae markedly alters the relative importance of pathways in the network, e.g. herbivorous fish and invertebrates account for 2.2% of net primary production (NPP) and coral heterotrophy for 90.3% of NPP when corals dominate, but when algae dominate and grazers respond to increased availability of algae, herbivores and corals account for 36.3 and 24.5% of NPP respectively. Changes in flow structure with loss of corals are indicated by an increased average path length, reduced average trophic level of most of the second order consumers, reduced trophic (ecological) efficiencies of most trophic categories, and marked changes in dependencies on other trophic groups. An unequivocal conclusion is that in the coral-dominated state, carbon fixed by zooxanthellae is used indirectly by most organisms in the system, even those seemingly remotely connected. This is revealed by both the dependency coefficients, which emerge as the measures most sensitive to changes in commu-

nity structure, and the changes in the effective trophic level of higher order consumers.

Carbon flux in the algae-dominated state

The precise details of changes in network properties with loss of coral cover depend on the fate of the additional algae-derived carbon in the system, but published empirical data on this aspect are currently lacking. We considered situations in which the increased production of algae is lost to detritus and grazers do not respond (Scenario 1), and alternatively, where consumption rates of algae increase (Scenario 2). It is possible that either scenario may apply, although the balance of evidence suggests that on the GBR grazing fish do not respond to the increase in algal biomass with loss of coral cover. Williams (1986) examined the effect of increased cover of algae (caused by outbreaks of crown-of-thorns starfish) on grazing fish on several GBR reefs by comparing population abundance estimates made 3 yr prior to starfish infestation with estimates made soon after destruction of corals. Although Williams found that temporal differences in fish populations on impacted reefs with high cover of algae were not detectably different to those on control reefs dominated by corals, his results are equivocal because his tests have low power (given a \log_5 scale measure of abundance and low replication), the time between loss of coral cover and censusing of fish is likely to have been too short for changes in fish population size to occur, and his methods could not detect individual functional responses such as changes in grazing, growth or fecundity rates. However, more detailed recent work has corroborated Williams' conclusions. A study of 6 GBR reefs found that the abundance, biomass, feeding rates, growth rates, and gonad indices of grazing fish are similar on algae-dominated reefs impacted by crown-of-thorns starfish and coral-dominated reefs (T Hart unpubl. data). These findings suggest that grazing fish on the GBR may be recruitment limited (see Doherty & Williams 1989) and not food limited. However, this situation is unlikely to apply to all reef systems. In direct contrast to results for the central GBR, Robertson (1991) recorded increases of 250 and 160% in the population sizes of 2 species of acanthurid in response to increased availability of algae after die off of sea urchins in Panama. Since there was no change in recruitment rates of the fish during the study, Robertson (1991) concluded that the increase in population sizes indicated food limitation.

The response of grazers, both fish and invertebrates, to changes in absolute and relative abundances of

algae and corals requires further resolution. An important component of this question is the response of herbivores to different kinds of algae since in some systems the community structure of algal assemblages changes during the phase transition (Carpenter 1990, Hughes 1994) and different herbivores respond differentially to different algal species (e.g. Hackney et al. 1989, Padilla 1989, Hay 1991). This information is important to the question of network properties since, although the network is considerably more sensitive to wholesale shifts in structure than to our alternative scenarios of the fate of photosynthetically fixed carbon in the algae-dominated state, the 2 scenarios for the algae-dominated state yielded dissimilar values for some parameters. Notably, trophic dependence of higher order consumers on grazers, flow diversity (a log scale), the relative importance of recycling, trophic efficiency of trophic category III, and the effective trophic level of piscivorous fish were sensitive to the relatively small differences in the fate of algal carbon.

This study has shown how community parameters can affect an aspect of ecosystem functioning on a coral reef. Given the diversity of reef forms and variability among reefs in flux processes (e.g. Hatcher 1990), our results are unlikely to apply to all coral reefs. Furthermore, despite the appeals of workers over a decade ago to give more emphasis to whole reef systems and not just to convenient components of them (e.g. Hatcher 1983b), there remains a dearth of system-level information about coral reefs and a poor understanding of how population and community parameters relate to functions at the system level. Given the intensity and extent of anthropogenic impact on coral reef systems (Wilkinson 1993), there is urgent need for this situation to be rectified. An integrated, multidisciplinary and large-scale manipulative (intentional or otherwise) study at the system level will go a considerable way towards achieving this goal.

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Appendix 1. Sources and/or derivation of estimates of carbon flux ($\text{g C m}^{-2} \text{d}^{-1}$) on the front slope of Davies Reef (depth 5 to 10 m, mean depth 7.5 m) when unaffected by crown-of-thorns starfish *Acanthaster planci* and coral cover is 55%. Flows are calculated assuming steady state for each compartment and for the system as a whole. Flows $X \rightarrow Y$ indicate flows from compartment X to compartment Y. The number of decimal places does not indicate the precision of the estimates but are required in some places to balance flows. Exogenous imports consider only water that eventually flows over the reef and not that which flows parallel to the front and around the reef to exit downstream (see 'Methods' for details). AE: assimilation efficiency; C: consumption, COA: coralline algae; dw: dry weight; EAC: epilithic algal community; fw: fresh weight; P_G : gross production, P_N : net production; R: respiration; B: biomass

Compartment	Flow	Magnitude of flow ($\text{g C m}^{-2} \text{d}^{-1}$)	Source/derivation
Phytoplankton (Cpt 1)	Imported	97.20	Phytoplankton in the system is imported; mean surface chlorophyll a of inter-reef waters = 0.27 mg m^{-3} (Furnas et al. 1990), C:chl a = 30:1 (Banse 1977, Chardy & Clavier 1988), at mean depth 7.5 m = $60.75 \text{ mg C m}^{-2}$ substratum. Mean flow over reef crest ca $12000 \text{ m}^3 \text{d}^{-1} \text{m}^{-1}$ of reef front [estimated from mean depth at crest \times water velocity from dye tracers (Barnes & Devereux 1984, Pickard 1986, Barnes 1988), and within range of estimates from current meters; K. Black unpubl. data], \therefore imported phytoplankton = $0.27 \times 30 \times (12000/1000) = 97.2 \text{ g C m}^{-2} \text{d}^{-1}$
	1 \rightarrow 7	0.74	Total consumption of POC by corals = $7.4 \text{ g C m}^{-2} \text{d}^{-1}$ and of this $6.6 \text{ g C m}^{-2} \text{d}^{-1}$ is from detritus (see Cpt 18) and 0.06 from protozoa and other microzooplankton in the water column (see Cpt 19), \therefore by difference flow to corals = $0.74 \text{ g C m}^{-2} \text{d}^{-1}$. This estimate for phytoplankton $> 2 \mu\text{m}$ = 10% of POC available for corals (assuming corals are unable to feed on particles $< 2 \mu\text{m}$), which is close to that of 8.3% of POC estimated for Davies Reef lagoon (Roman et al. 1990)
	1 \rightarrow 8	0.029	Biomass-specific consumption of phytoplankton by zooplankton = $1.728 \text{ mg C mg}^{-1} \text{C d}^{-1}$ (from Roman et al. 1990), \therefore total consumption = $1.728 \times 16.6 = 0.029 \text{ g C m}^{-2} \text{d}^{-1}$ (biomass of zooplankton from Cpt 8)
	R	0	Respiration = 0 since all phytoplankton is regarded as imported
Corals: zooxanthellae (Cpt 2)	Exported	96.431	By difference
	P_G	14.8	P_G from photosynthesis of corals = $27 \text{ g C m}^{-2} \text{d}^{-1}$ (midrange of values for coral outcrops at 6 sites on the GBR; Kinsey 1985). Adjusting to take into account that coral cover on the reef slope at ca 7.5 m is 55% (Daniel et al. 1985), overall $P_G = 14.8 \text{ g C m}^{-2} \text{d}^{-1}$. See 'Discussion' for evaluation of these estimates
	2 \rightarrow 7	12.58	Carbon translocated to zooxanthellae to the animal host = 85% of carbon fixed [midrange of values from Davies (1984), McCloskey & Muscatine (1984), and Edmunds & Davies (1986)] for shallow corals 3 to 10 m depth = $12.58 \text{ g C m}^{-2} \text{d}^{-1}$
Turf algae (Cpt 3)	R	2.22	Assuming growth of zooxanthellae is negligible, then $R_{\text{zooxanthellae}} = 2.22$ (by difference). Thus $R_{\text{zooxanthellae}} = 15\%$ of P_G , which is of the same order as that calculated for <i>Pocillopora eydouxi</i> based on partitioning of energy where $R_{\text{zooxanthellae}} = 10\%$ of P_G (Davies 1984)
	P_G	0.65	P_G of the EAC averaged across seasons = $1.43 \text{ g C m}^{-2} \text{d}^{-1}$ (Klumpp & McKinnon 1989); since EAC occupies 41% of reef slope area (Klumpp & McKinnon 1989) and adjusting for reef surface rugosity factor of 1.86 for reef slope (Klumpp & McKinnon 1989), P_G EAC overall = $1.08 \text{ g C m}^{-2} \text{d}^{-1}$. Since 60% of EAC is turf (Klumpp & McKinnon 1989), P_G turf = $0.6 \times 1.08 = 0.65 \text{ g C m}^{-2} \text{d}^{-1}$ and P_G COA = $0.4 \times 1.08 = 0.43 \text{ g C m}^{-2} \text{d}^{-1}$
	3 \rightarrow 5	0.14	From P_G and R_N for EAC is calculated as $0.6 \text{ g C m}^{-2} \text{d}^{-1}$ (rounded from 0.59; see below for calculations of R), and ca 50% of P_N is lost to grazers (Hatcher 1983a, Klumpp & Polunin 1990, Klumpp & McKinnon 1992), $\therefore 0.3 \text{ g C m}^{-2} \text{d}^{-1}$ is grazed. Now, 60% of EAC is turf algae thus $0.6 \times 0.3 = 0.18 \text{ g C m}^{-2} \text{d}^{-1}$ of turf is lost to all grazers, including both fish and invertebrates, and of this ca 80% ($0.8 \times 0.18 = 0.14 \text{ g C m}^{-2} \text{d}^{-1}$) is accounted for by fish and the remainder ($0.04 \text{ g C m}^{-2} \text{d}^{-1}$) by macroinvertebrates (derived from Hatcher 1983a, Klumpp & Pulfrich 1989, Klumpp & Polunin 1990). Assume all of losses of COA (= 40% EAC) are to fish, which amounts to $0.4 \times 0.3 = 0.12 \text{ g C m}^{-2} \text{d}^{-1}$
	3 \rightarrow 6	0.04	
	3 \rightarrow 18	0.18	By difference
	R	0.29	P_G :R for total EAC = 2.2:1 (Klumpp & McKinnon 1989), $\therefore R = 0.49 \text{ g C m}^{-2} \text{d}^{-1}$ for total EAC and $0.6 \times 0.49 = 0.29 \text{ g C m}^{-2} \text{d}^{-1}$ for the turf component and $0.4 \times 0.49 = 0.2 \text{ g C m}^{-2} \text{d}^{-1}$ for COA
	COA (Cpt 4)	P_G	0.43
4 \rightarrow 5		0.12	See calculations for turf algae (Cpt 3)
4 \rightarrow 18		0.11	By difference
R		0.20	See calculations for turf algae (Cpt 3)
Grazing fish (Cpt 5)	5 \rightarrow 8	0.001	AE = $(P_N + R)/C = 65\%$ (mean of Polunin 1988, Klumpp & Polunin 1989) $\therefore P_N = (AE \times C) - R = (0.65 \times 0.290) - 0.018 = 0.171 \text{ g C m}^{-2} \text{d}^{-1}$ (C = totals from Cpts 3, 4, and 8; see below for derivation of R). Assume 5% of P_N is for mucus production (\therefore to Cpt 18), $\therefore 0.162 \text{ g C m}^{-2} \text{d}^{-1}$ is available for reproduction (i.e. 5 \rightarrow 8) and secondary production (i.e. 5 \rightarrow 11). Now, standing biomass of grazing fish on midshelf reefs = $25.6 \text{ g m}^{-2} \text{fw}$ (Williams & Hatcher 1983) = $8.192 \text{ g m}^{-2} \text{dw}$ since $\text{dw} = 0.32 \times \text{fw}$ (Klumpp & Polunin 1989) = 3.277 g C m^{-2} since $\text{g C} = 0.4 \times \text{dw}$ (Peters 1983, Klumpp & Polunin 1989). Of this biomass, 92% = 3.015 g C m^{-2} constitutes reproductive fish (Doherty 1980). Now, losses of biomass to spawning in herbivorous damselfish are 3% of body mass 9 times yr^{-1} for ϕ (Doherty 1983) = 27% body mass yr^{-1} , \therefore assuming $\sigma:\phi = 1$, = $(3.015/2) \times 0.27 = 0.407 \text{ g C m}^{-2} \text{yr}^{-1}$ for ϕ , and 0.3% of body mass 9 times yr^{-1} for σ (Doherty 1983) = 2.7% body mass yr^{-1} = $(3.015/2) \times 0.027 = 0.041$ for σ , \therefore total P_N to reproduction = $0.448 \text{ g C m}^{-2} \text{yr}^{-1}$ = $0.001 \text{ g C m}^{-2} \text{d}^{-1}$. By difference, P_N to secondary production = $0.162 - 0.001 = 0.161 \text{ g C m}^{-2} \text{d}^{-1}$
	5 \rightarrow 11	0.161	

(Appendix 1 continued on next page)

Appendix 1, continued

Compartment	Flow	Magnitude of flow (g C m ⁻² d ⁻¹)	Source/derivation	
Grazing fish (Cpt 5)	5→18	0.110	By difference; = 0.11 g C m ⁻² d ⁻¹ = 38% of C which is similar to the empirical estimate of ca 35% of total C consumed (mean of Polunin 1988, Klumpp & Polunin 1989)	
	R	0.018	Respiration rate of damselfish = 162 mg O ₂ kg ⁻¹ h ⁻¹ (fw) in summer (Polunin & Klumpp 1989); assume 1/2 this rate in winter, ∴ annual average = 121 mg O ₂ kg ⁻¹ h ⁻¹ (fw). Assume 1/2 of this rate at night, ∴ respiration = 2178 mg O ₂ kg ⁻¹ d ⁻¹ . Now, 1 ml O ₂ = 1.43 mg O ₂ = 20.1 kJ (Peters 1983) = 458 μg C (Jorgensen 1955), ∴ R = 0.697 g C kg ⁻¹ d ⁻¹ (fw), and the standing biomass of grazing fishes on midshelf reefs is 25.6 g (fw) m ⁻² (derived from Williams & Hatcher 1983), ∴ R = 0.0256 × 0.697 = 0.018 g C m ⁻² d ⁻¹	
Invertebrate grazers (Cpt 6)	6→9	0.009	C = 0.04 + 0.01 = 0.05 g C m ⁻² d ⁻¹ , and AE = 50% (Klumpp & Pulfrich 1989), ∴ 6→18 = 0.025 g C m ⁻² d ⁻¹ , and P _N + R = 0.025 g C m ⁻² d ⁻¹ . Assume ca 25% of assimilated C is respired (R. Peters pers. comm.), ∴ R = 0.006 g C m ⁻² d ⁻¹ and P _N = 0.019. Assume production is approximately equally partitioned among invertivorous fish (47%) and carnivorous invertebrates (53%), ∴ 6→9 = 0.47 × 0.019 = 0.009 and 6→10 = 0.53 × 0.019 = 0.01 g C m ⁻² d ⁻¹	
	6→10	0.010		
	6→18	0.025		
	R	0.006		
Corals: heterotrophic (Cpt 7)	7→8	2.65	By difference	
	7→18	7.4	50% of C fixed by photosynthesis is lost to the water column = 7.4 g C m ⁻² d ⁻¹ (assume largely as mucus; Cooksey & Cooksey 1972, Crossland 1980, Crossland et al. 1980, Davies 1984, Muscatine et al. 1984)	
	R	11.28	For whole colony P _G :R = 1.1 (Kinsey 1985), ∴ R _(total) = 13.5 g C m ⁻² d ⁻¹ since P _G = 14.8 g C m ⁻² d ⁻¹ (from Cpt 2), and since R _{zooxanthellae} = 2.22 g C m ⁻² d ⁻¹ then R _{heterotrophic} = 11.28 g C m ⁻² d ⁻¹ , ∴ carbon translocated from zooxanthellae and available for respiration of the animal = 112% of R _{heterotrophic} which is within the range of results for <i>Stylophora pistillata</i> but low for the colonies in shallow water (Muscatine 1990), and is low compared to estimates for <i>Pocillopora eydouxi</i> (Davies 1984) and <i>Porites porites</i> (Edmunds & Davies 1986). Ratio of R _{heterotrophic} :R _{zooxanthellae} = 5.1 which is of the same order measured in <i>P. eydouxi</i> (4.2; Davies 1984)	
Zooplankton (Cpt 8)	Imported	26.4	Import = standing biomass × flow rate. Biomass = 2.2 mg C m ⁻³ on the reef front (Roman et al. 1990), ~ at mean depth of 7.5 m = 16.5 mg C m ⁻² substratum. Flow rate = 12 000 m ⁻¹ d ⁻¹ m ⁻¹ reef front (see Cpt 1) ∴ import = 2.2 × (12 000/1000) = 26.4 g C m ⁻² d ⁻¹	
	8→5	0.03	Cryptofauna, dominated by planktonic forms, occur abundantly in and on coral reef algae (Klumpp et al. 1988) and are consumed inadvertently by grazing fish when they feed (Polunin 1988, Klumpp & Polunin 1989). On the basis of gut analyses showing that cryptofauna in guts of grazers are largely demersal plankters, and preliminary estimates of abundance in the gut (Klumpp & Polunin 1989), assume 10% of ingested C of grazing fish is from zooplankton, ∴ 0.9 × C = 0.14 + 0.12 (from Cpts 3 and 4), ∴ C = 0.29 g C m ⁻² d ⁻¹ , ∴ by difference 8→5 = 0.03 g C m ⁻² d ⁻¹	
	8→7	1.35	Assume 10% of carbon requirements for respiration of coral colonies are met by capture of zooplankton = 1.35 g C m ⁻² d ⁻¹ . This value is an attempted average of a variety of polyp sizes (Porter 1976); it is commensurate with calculations, based on energy, of Porter (1974) and Johannes & Tepley (1974), is midway in the range defined by values estimated by Johannes et al. (1970) and Sorokin (1990a), and is in keeping with the conclusions of Alldredge & King (1977)	
	8→12	0.220	C _{planktivorous fish} = 0.293 g C m ⁻² d ⁻¹ (from Cpt 12), and ca 75% of diet of planktivorous fish is zooplankton (Hamner et al. 1988) = 0.220 g C m ⁻² d ⁻¹	
	8→18	0.043	Assume AE = 50% (approx. mean of values from Omon & Ikeda 1984, Valiela 1984), ∴ loss as faeces = 0.5 × C. ∴ assuming zooplankton feed on phytoplankton (see Cpt 1), detritus (see Cpt 18), and protozoa/microzooplankton (see Cpt 19) = 0.5 × (0.029 + 0.054 + 0.002) = 0.043 g C m ⁻² d ⁻¹	
	Exported	27.4619	By difference	
	R	0.030	Respiration = 1.8 mg C mg ⁻¹ C d ⁻¹ (from Roman et al. 1990), = 1.8 × biomass = 1.8 × 16.5 (see 'import', this Cpt) = 0.030 g C m ⁻² d ⁻¹	
	Carnivorous and detritivorous invertebrates (Cpt 9)	9→10	0.024	Total C _{invertebrates} = 0.024 g C m ⁻² d ⁻¹ (see Cpt 10) and since 0.01 g C m ⁻² d ⁻¹ comes from grazing invertebrates (see Cpt 6), 9→10 = 0.024 g C m ⁻² d ⁻¹ (by difference)
		9→19	3.763	Biomass of invertebrates in live coral matrix = 0.061 g C cm ⁻² and in dead coral matrix = 0.023 g C m ⁻² (derived from Hutchings 1978). Since mean rugosity of massive corals = 3.6 (Keesing 1990) and 55% of reef slope is live coral (Daniel et al. 1985), biomass of invertebrates in live coral = 1213.0 g m ⁻² (fw). Assume dw = 0.25 × fw (Klumpp et al. 1988) and C = 0.4 × dw (Peters 1983), ∴ this is equivalent to 121.3 g C m ⁻² . Since 41% of slope is 'dead' matrix of rugosity 1.86 (Klumpp & McKannon 1989), biomass of invertebrates in this substratum = 17.53 g C m ⁻² . Thus, total biomass = 138.83 g C m ⁻² . Assuming these animals are of similar size and composition to those from substrata at a similar depth in Davies Reef lagoon, overall P _N :B = 3.1 yr ⁻¹ (Riddle et al. 1990, 'deep' site), ∴ P _N = 1.18 g C m ⁻² d ⁻¹ , ∴ by difference 1.18 - 0.024 = 1.156 g C m ⁻² d ⁻¹ is lost to detritus, i.e. assume this proportion of production is animals that die and decompose to sedimentary detritus. Fecal material is lost to detritus, and if AE = 60% (Riddle et al. 1990) then this loss = 0.4 × C = 0.4 × [(P _N + R)/AE] = 0.4 × 6.517 = 2.607 g C m ⁻² d ⁻¹ , ∴ total loss to detritus = 3.763 g C m ⁻² d ⁻¹
R		2.73	B:R = 3048/60 (Riddle et al. 1990), ∴ if B = 138.8 g C m ⁻² d ⁻¹ , R = 2.73 g C m ⁻² d ⁻¹	

Appendix 1, continued

Compartment	Flow	Magnitude of flow (g C m ⁻² d ⁻¹)	Source/derivation
Invertivorous fish (Cpt 10)	10→8	0.0004	Several fluxes are derived by allometry from data for grazing fish. Mean size of individual grazing and invertivorous fish = 63 g (fw) and 75 g (fw) respectively (from Williams & Hatcher 1983); $P_N:B$ ratio for grazing fish = 0.52 yr ⁻¹ (from Cpt 5). ∴ assuming allometric exponent of -0.25 (Peters 1983), $P_N:B_{\text{invertivorous fish}} = (75/63)^{-0.25} \times 0.52 = 0.50 \text{ yr}^{-1}$. Now, standing biomass of invertivorous fish on midshelf reefs = 29.0 g m ⁻² fw (Williams & Hatcher 1983) and $dw = 0.32 \times fw$ (Klumpp & Polunin 1989) and $g C = 0.4 \times dw$ (Peters 1983), ∴ $B_{\text{invertivorous fish}} = 3.712 \text{ g C m}^{-2}$, ∴ from $P_N:B$ ratio $P_N = 1.852 \text{ g C m}^{-2} \text{ yr}^{-1} = 0.005 \text{ g C m}^{-2} \text{ d}^{-1}$. Assume that, as in grazing fish, 0.8% of $P_N = 0.0004 \text{ g C m}^{-2} \text{ d}^{-1}$ goes to zooplankton (i.e. to reproduction)
	10→11	0.0046	The remainder of production = 0.0046 g C m ⁻² d ⁻¹ is lost to piscivorous fish
	10→18	0.010	$C = (P_N + R)/AE$ ∴ assuming AE = 70%, which is slightly greater than for fish feeding on algae, $C = (0.005 + 0.019)/0.7 = 0.034 \text{ g C m}^{-2} \text{ d}^{-1}$, and assume that since AE = 70% then 30% of $C = 0.010 \text{ g C m}^{-2} \text{ d}^{-1}$ is lost as faeces to column detritus
	R	0.019	$R_{\text{grazing fish}} = 0.018 \text{ g C m}^{-2} \text{ d}^{-1}$; $B_{\text{grazing fish}} = 25.6 \text{ g C m}^{-2} \text{ fw}$ (Williams & Hatcher 1983) and $dw = 0.32 \times fw$ (Klumpp & Polunin 1989) and $g C = 0.4 \times dw$ (Peters 1983), ∴ $B_{\text{grazing fish}} = 3.277 \text{ g C m}^{-2}$, ∴ by allometry (Peters 1983) $R_{\text{invertivorous fish}} = (75/63)^{-0.25} \times (3.712/3.277) \times 0.018 = 0.019 \text{ g C m}^{-2} \text{ d}^{-1}$
Piscivorous fish (Cpt 11)	11→8	0.0002	(Note: as for Cpts 10 and 12, reliance is made of empirical estimates for grazing fish) $C = 0.161 + 0.0046 + 0.0427 = 0.2083 \text{ g C m}^{-2} \text{ d}^{-1}$ (from Cpts 5, 10 and 12); $C = (P_N + R)/AE$ ∴ assuming AE = 70% (8% higher than that of grazing fish) then $P_N + R = 0.146$; assume that, as in grazing fish, $P_N:R = 0.26$, then $P_N = 0.030$ and $R = 0.116 \text{ g C m}^{-2} \text{ d}^{-1}$; assume that, as in grazing fish, 0.8% of $P_N = 0.0002 \text{ g C m}^{-2} \text{ d}^{-1}$ goes to zooplankton (i.e. reproduction)
	11→export	0.0298	The remainder of production = 0.0298 g C m ⁻² d ⁻¹ is exported from the system
	11→18	0.0623	Since AE = 70%, 30% of $C = 0.0623 \text{ g C m}^{-2} \text{ d}^{-1}$ is lost to column detritus
	R	0.116	See calculations for 11→8
Planktivorous fish (Cpt 12)	12→8	0.0003	Several fluxes are derived by allometry from data for grazing fish. Mean sizes of grazing fish and planktivorous fish = 63 g and 17 g (fw) respectively (Williams & Hatcher 1983); $P_N:B$ ratio for grazing fish = 0.52 yr ⁻¹ (from Cpt 5), ∴ assume allometric exponent of -0.25 (Peters 1983) $P_N:B_{\text{planktivorous fish}} = (17/63)^{-0.25} \times 0.52 = 0.723 \text{ yr}^{-1}$. Now, standing biomass of planktivorous fish = 168.3 g m ⁻² fw (derived from Williams & Hatcher 1983) and $dw = 0.32 \times fw$ (Klumpp & Polunin 1989) and $g C = 0.4 \times dw$ (Peters 1983, Klumpp & Polunin 1989), ∴ $B_{\text{planktivorous fish}} = 21.54 \text{ g C m}^{-2}$, ∴ from $P_N:B$ ratio $P_N = 15.57 \text{ g C m}^{-2} \text{ yr}^{-1} = 0.043 \text{ g C m}^{-2} \text{ d}^{-1}$. Assume that, as in grazing fish, 0.8% of $P_N = 0.0003 \text{ g C m}^{-2} \text{ d}^{-1}$ goes to zooplankton (i.e. to reproduction)
	12→11	0.0427	The remainder of production = 0.0427 g C m ⁻² d ⁻¹ is lost to piscivorous fish
	12→18	0.088	$C = (P_N + R)/AE$ ∴ assuming AE = 70% (8% greater than for fish eating algae), $C = (0.043 + 0.161)/0.7 = 0.293 \text{ g C m}^{-2} \text{ d}^{-1}$, and assume that, as in grazing fish, 30% of $C = 0.088 \text{ g C m}^{-2} \text{ d}^{-1}$ is lost as faeces to column detritus
	R	0.162	$R_{\text{grazing fish}} = 0.018 \text{ g C m}^{-2} \text{ d}^{-1}$; $B_{\text{grazing fish}} = 3.277 \text{ g C m}^{-2}$ (see Cpts 5 and 10); ∴ by allometry (Peters 1983), $R_{\text{planktivorous fish}} = (17/63)^{-0.25} \times (21.54/3.277) \times 0.018 = 0.162 \text{ g C m}^{-2} \text{ d}^{-1}$
Meiofauna (Cpt 13)	13→9	0.00005	Total number animals in sand on reef front = 50 000 m ⁻² (Hansen et al. 1987) = 26.32 mg C m ⁻² (dw) since 1.0 mg (dw) = 760 animals (derived from mean values for GBR continental shelf meiofauna in Alongi (1989)) and carbon weight = 0.4 × dw (Higgins & Theil 1988). Assume $P_N:B = 15 \text{ yr}^{-1}$ (Alongi pers. comm.), ∴ $P_N = 394.9 \text{ mg C m}^{-2} \text{ yr}^{-1} = 1.082 \text{ mg C m}^{-2} \text{ d}^{-1}$, but not more than 5% of the reef slope at 7.5 m is sand (Daniel et al. 1985, Klumpp et al. 1987), ∴ $P_N = 0.054 \text{ mg} = 0.00005 \text{ g C d}^{-1} \text{ m}^{-2}$ of reef substratum
	13→19	0.00207	By difference
	R	0.00018	$AE_{\text{meiofauna}} = 10\%$ (Alongi pers. comm.), and $R = (C \times AE) - P_N = 0.1 \times 0.0023 - 0.00005 = 0.00018 \text{ g C m}^{-2} \text{ d}^{-1}$
Sedimentary protozoa (Cpt 14)	14→13	0.0003	For front of Davies Reef density of animals = 1.025 × 10 ⁹ m ⁻² (from Hansen et al. 1987), but since not more than 5% of the reef slope at 7.5 m is sand (Klumpp et al. 1987) abundance of protozoa = 51 250 m ⁻² of reef. Ratio of flagellates:ciliates = 12.7 (Hansen et al. 1987), ∴ 47 500 flagellates and 3750 ciliates per m ² of reef = 274.6 and 3.1 μg C m ⁻² respectively [since 1000 nanoflagellates = 5.78 μg C, and 240 ciliates = 0.2 μg C; derived from Ayukai (in press) who estimated conversions as 220 fg C μm ⁻³ for nanoflagellates (Børshøj & Bratbak 1987) and 50 fg C μm ⁻³ for ciliates (Taniguchi 1984) assuming 1 μm ³ = 1 pg fw, $dw = 0.1 \times fw$, carbon weight = 0.5 × dw], ∴ $B = 0.28 \text{ mg C m}^{-2} \text{ reef}$, and assuming $P_N:B = 1 \text{ d}^{-1}$ (Fenchel 1982b), $P_N = 0.0003 \text{ g C m}^{-2} \text{ d}^{-1}$
	14→19	0.0005	By difference
	R	0.0005	Assuming AE = 60% (Fenchel 1982a), $R = (0.6 \times C) - P_N = 0.0005 \text{ g C m}^{-2} \text{ d}^{-1}$

(Appendix 1 continued on next page)

Appendix 1, continued

Compartment	Flow	Magnitude of flow (g C m ⁻² d ⁻¹)	Source/derivation
Sedimentary bacteria (Cpt 15)	15→9	0.001	$P_N = 28.8 \text{ mg C m}^{-2} \text{ d}^{-1}$ in winter on reef front (Hansen et al. 1987), but $P_{N \text{ summer}} = 5 \times P_{N \text{ winter}}$ (average of Moriarty et al. 1985a, b, Hansen et al. 1992), \therefore annual average = $86.4 \text{ mg C d}^{-1} \text{ m}^{-2}$ of sand (which is within the range for GBR reefs defined by Moriarty et al. 1985b, c) $\approx 4.3 \text{ mg C d}^{-1} \text{ m}^{-2}$ of reef since only ~5% of reef slope at 7.5 m is sand (Daniel et al. 1985, Klumpp et al. 1987). Assume 20% of $P_N = 0.001 \text{ g C m}^{-2} \text{ d}^{-1}$ is consumed by detritivores (Moriarty et al. 1985c). This estimate is for unconsolidated sediment only; see 'Discussion'
	15→13	0.002	Average ratio of carbon biomass of bacteria consumed d ⁻¹ by meiofauna: carbon biomass of meiofauna = 1.8 (Montagna 1984), \therefore bacteria consumed = $26.32 \text{ mg C m}^{-2} \times 0.05\% \times 1.8 = 0.002 \text{ g C m}^{-2} \text{ d}^{-1}$
	15→14	0.0013	Assume 30% of $P_N = 0.0013 \text{ g C m}^{-2} \text{ d}^{-1}$ consumed by sedimentary protozoa (Moriarty et al. 1985)
	15→19	0.0084	By difference
	R	0.004	Average benthic community respiration = $183.5 \text{ mg C m}^{-2} \text{ d}^{-1}$ (Hansen et al. 1992); assume 70% of this = $129.9 \text{ mg C m}^{-2} \text{ d}^{-1}$ is due to bacteria (Alongi pers. comm.), \therefore since average production of benthic bacteria is $139.3 \text{ mg C m}^{-2} \text{ d}^{-1}$ (Hansen et al. 1992), $P_N:R = 1.072$, $\therefore R = 4.3/1.072 = 0.0040 \text{ g C m}^{-2} \text{ d}^{-1}$
Water column bacteria (Cpt 16)	Import	142.8	Seasonal average of bacterial biomass on front of Davies Reef = 11.9 mg C m^{-3} (Ayukai in press) \times flow rate of $12000 \text{ m}^3 \text{ water d}^{-1} \text{ m}^{-1}$ reef front (see Cpt 1) = $142.8 \text{ g C m}^{-2} \text{ d}^{-1}$
	16→17	0.0212	Assume $AE_{\text{column protozoa}} = 0.6$ (Fenchel 1982a), $\therefore C_{\text{column protozoa}} = (P_N + R)/0.6 = 0.0212 \text{ g C m}^{-2} \text{ d}^{-1}$ (see Cpt 17)
	16→18	0.032	Seasonal average of $P_N:R_{\text{column bacteria}}$ at Davies Reef = 0.6 (Ducklow 1990), $\therefore P_N = 0.6 \times B = 0.6 \times 0.0119 \times 7.5 = 0.0536 \text{ g C m}^{-2} \text{ d}^{-1}$, \therefore by difference, production to column detritus = $0.0536 - 0.0212 = 0.032 \text{ g C m}^{-2} \text{ d}^{-1}$
	Export	142.9038	By difference
	R	0.050	Assume same $P_N:R$ ratio as for sedimentary bacteria = 1.072, $\therefore R = 0.0536/1.072 = 0.050 \text{ g C m}^{-2} \text{ d}^{-1}$
Water column protozoa and other micro-zooplankton (Cpt 17)	Import	7.176	Mean standing biomass (averaged over summer/winter) = 11.96 mg m^{-3} (fw) (Ayukai 1991) = $0.598 \text{ mg C m}^{-3}$ since $dw = 0.1 \times fw$ and carbon weight = $0.5 \times dw$ (derived from Taniguchi 1984). Flow rate = $12000 \text{ m}^3 \text{ d}^{-1} \text{ m}^{-1}$ reef front (see Cpt 1) = $7.176 \text{ g C m}^{-2} \text{ d}^{-1}$
	17→7	0.060	Coral clearance rate = $36.72 \text{ m}^3 \text{ d}^{-1} \text{ m}^{-2}$ of coral surface (see Cpt 18) = $99.8 \text{ m}^3 \text{ d}^{-1} \text{ m}^{-2}$ of reef given mean coral rugosity factor of 4.94 and cover of corals at 7.5 m = 55% (see Cpt 18). Thus total intake = $99.8 \times 0.598 = 0.060 \text{ g C m}^{-2} \text{ d}^{-1}$
	17→8	0.002	Assume zooplankton consume protozoa and microzooplankton at the same rate as phytoplankton, \therefore proportional to the standing biomass of phytoplankton (see Roman et al. 1990) = $0.598 \times (0.029/8.1) = 0.002 \text{ g C m}^{-2} \text{ d}^{-1}$
	17→18	0.0085	Assume $P_N:R = 1 \text{ d}^{-1}$ (Fenchel 1982b); $B = 0.598 \text{ mg C m}^{-3} \times 7.5 \text{ m depth} = 4.485 \text{ mg C m}^{-2}$, $\therefore P_N = 4.485 \text{ mg C m}^{-2}$. Assume $AE = 0.6$ (Fenchel 1982a), $\therefore C = (P_N + R)/0.6 = 0.0212 \text{ g C m}^{-2} \text{ d}^{-1}$. Assume all metabolic waste to detritus, $\therefore C = P_N + R = 0.0085$
	Export	7.1185	By difference; export < import follows observations of Ayukai (1991, unpubl.) that standing stocks decrease from reef front to reef flat
	R	0.0082	Assume same $P_N:R$ ratio as for sedimentary protozoa = 0.55, $\therefore R = 0.0045/0.55 = 0.0082 \text{ g C m}^{-2} \text{ d}^{-1}$
Water column detritus (Cpt 18)	Import	795.6	Assume total POC at reef front = 88.4 mg C m^{-3} (see calculations for 18→7 below) of which 75% = 66.3 mg C m^{-3} is detritus. Flow rate over a 1 m tract of reef front = $12000 \text{ m}^3 \text{ d}^{-1}$ (see Cpt 1), \therefore import = $795.6 \text{ g C m}^{-2} \text{ d}^{-1}$
	18→7	6.6	Mean clearance rate of corals measured by Lewis (1976) ca $90 \text{ ml h}^{-1} \text{ cm}^{-2}$ coral tissue (10 of 15 species were between 9.5 and $150 \text{ ml h}^{-1} \text{ cm}^{-2}$). However, clearance rates of <i>Acropora agarites</i> increased from 99.5 to $171 \text{ ml h}^{-1} \text{ cm}^{-2}$ (= 172% increase) with increasing current velocity from 1.4 to 3.4 cm s^{-1} (Lewis 1976); similar increases over a similar range of current velocities in the rate of zooplankton capture by the branching <i>Madracis decactis</i> have been noted (Sebens & Johnson 1991). Since currents on the front slope of Davies Reef at 5 to 10 m are typically 5 to 10 cm s^{-1} (Barnes & Devereux 1984, Pickard 1986, Hamner et al. 1988, K. Black unpubl. data), assume the 170% increase applies, \therefore mean clearance rate = $153 \text{ ml h}^{-1} \text{ cm}^{-2} = 36720 \text{ l d}^{-1} \text{ m}^{-2}$ of coral surface. Now, average POC in Davies Reef lagoon = $104 \text{ } \mu\text{g C l}^{-1}$ (Roman et al. 1990, Klumpp et al. 1992) but only 35% of this amount = $88.4 \text{ } \mu\text{g C l}^{-1}$ is expected on the shallow reef slope which is relatively more influenced by incoming oceanic water (Marshall 1968, Qasim & Sankaranarayanan 1970, Hatcher 1983b). Of this, 16% is <2 μm and \therefore unavailable to corals, \therefore only $74.3 \text{ } \mu\text{g C l}^{-1}$ POC is available, $\therefore 74.3 \times 36720 = 2.73 \text{ g C d}^{-1} \text{ m}^{-2}$ of coral surface is consumed. Now, the mean rugosity factor of a variety of common reef slope corals = 4.94 (Keesing 1990), but coral cover over 5 to 10 m averages only 55% (Daniel et al. 1985), so total POC consumed by corals = $2.73 \times 4.94 \times 0.55 = 7.4 \text{ g C d}^{-1} \text{ m}^{-2}$ of reef. Since only 89% of this is detritus (Roman et al. 1990), total consumption of detritus by corals = $6.6 \text{ g C m}^{-2} \text{ d}^{-1}$

Appendix 1, continued

Compartment	Flow	Magnitude of flow (g C m ⁻² d ⁻¹)	Source/derivation
Water column detritus (Cpt 18)	18→8	0.052	Even assuming very high $P_N:B = 0.7 \text{ d}^{-1}$ for small tropical zooplankton (Newbury & Bartholomew 1976), P_N for zooplankton is low and $= 0.7 \times 16.5$ (biomass from Cpt 8) = $11.55 \text{ mg C m}^{-2} \text{ d}^{-1}$. Now, $C = (P_N+R)/AE = (11.6 + 29.7)/0.5$ [see Cpt 8] = $0.083 \text{ g C m}^{-2} \text{ d}^{-1}$, and consumption of phytoplankton = $0.029 \text{ g C m}^{-2} \text{ d}^{-1}$ (Cpt 1) and of protozoa and other microzooplankton = $0.002 \text{ g C m}^{-2} \text{ d}^{-1}$ (Cpt 17), \therefore consumption of detritus = $0.083 - 0.031 = 0.052 \text{ g C m}^{-2} \text{ d}^{-1}$, which follows observations of Roman et al. (1990) that ingestion of detritus by zooplankton = 2 times ingestion of phytoplankton
	18→12	0.073	$C_{\text{planktivorous fish}} = 0.293 \text{ g C m}^{-2} \text{ d}^{-1}$ (from Cpt 12), and $8 \rightarrow 12 = 0.220 \text{ g C m}^{-2} \text{ d}^{-1}$ (from Cpt 8), $\therefore 18 \rightarrow 12 = 0.293 - 0.220 = 0.073 \text{ g C m}^{-2} \text{ d}^{-1}$
	18→16	0.207	$AE_{\text{bacteria}} = 50\%$ (Ducklow 1983), $\therefore C = (P_N+R)/0.5 = 0.207 \text{ g C m}^{-2} \text{ d}^{-1}$ (from Cpt 16)
	18→19	2.75968	By difference (balancing values for Cpt 19)
	Export	793.97712	By difference (balancing values for Cpt 18)
Sedimentary detritus (Cpt 19)	19→6	0.01	Assume that in grazing 'micro' turf algae 20% of C intake of invertivorous grazers is detritus, $\therefore = 0.2 \times (0.04/0.8) = 0.01 \text{ g C m}^{-2} \text{ d}^{-1}$ [see Cpt 3]
	19→9	6.50695	Total consumption by detritivorous/carnivorous invertebrates = $6.517 \text{ g C m}^{-2} \text{ d}^{-1}$ (see Cpt 9). Of this 0.009, 0.00005, and 0.001 g C m ⁻² d ⁻¹ comes from grazing invertebrates, meiofauna, and sedimentary bacteria respectively (Cpts 6, 13 and 15), \therefore by difference $19 \rightarrow 9 = 6.50695 \text{ g C m}^{-2} \text{ d}^{-1}$
	19→15	0.0167	$AE_{\text{bacteria}} = 50\%$ (Ducklow 1983), $\therefore C = (P_N+R)/0.5 = 0.0167 \text{ g C m}^{-2} \text{ d}^{-1}$ (from Cpt 15)

Appendix 2. Summary of derivations of estimates of carbon flux (g m⁻² d⁻¹) on the front slope of Davies Reef (depth 5 to 10 m, mean depth 7.5 m) for the algae-dominated state after destruction of corals by crown-of-thorns starfish *Acanthaster planci*. Two scenarios are given: (1) coral cover is reduced to 2% (Keesing 1990) but grazers do not respond to the increased availability of algae (e.g. Williams 1986) so the increase in production of algal carbon flows to water column detritus, and (2) coral cover is reduced to 2% and grazers respond to increased availability of algae (e.g. Robertson 1991) so that losses of algal carbon to grazers and losses to detritus are in the same proportion (ca 1:1) as occurs in the coral-dominated state (see 'Discussion'). In these models it was assumed that production of the epilithic algal community (EAC) [coralline algae (COA) + turf algae] per unit area of algae-covered substratum on starfish-affected reefs is identical to that on coral-dominated reefs (see 'Methods'), although the amount of algae-covered substratum is clearly greater on starfish-affected reefs. Flows are calculated assuming steady state for each compartment and for the system as a whole. Flows X → Y indicate flows from compartment X to compartment Y. The number of decimal places does not indicate the precision of the estimates but is required in some places to balance flows. Note that exogenous imports consider only water that eventually flows over the reef but not that which flows along the front and around the reef to exit downstream (see 'Methods' for details). Abbreviations as for Appendix 1

Scenario 1. Coral cover is 2%, excess in production of algal carbon flows to detrital pathways. Fluxes for corals (i.e. ingestion, losses to column detritus, reproduction (i.e. the flux from coral → zooplankton) and respiration) and zooxanthellae (production and respiration) were scaled down from the coral-dominated configuration by a factor of $55/2 = 27.5$. Compartments for phytoplankton, zooplankton, water column detritus, and water column protozoa were balanced by adjusting exports. Assuming dead coral skeletons are colonised by EAC (turf algae + COA), production and respiration of these groups was scaled up by a factor of $(41\% + 53\%)/41\% = 2.29$ to account for their increase in cover. In this scenario, there is no increase in grazer activity so the increase in net algal production is lost as detritus. Magnitudes of flows are summarised.

Scenario 2. Coral cover is 2%, fate of algal production is 50% lost to grazers and 50% exported as detritus. Fluxes for corals (heterotrophic) and zooxanthellae, and gross production and respiration of other heterotrophs were determined as described for Scenario 1. However, net production was apportioned among flows to grazers and detritus in the same proportion as in the coral-dominated state. This carbon was then allowed to flow through the system in such a way as to maintain the characteristic assimilation efficiencies, P:R ratios, etc. of each trophic compartment. Magnitudes of flows are summarised

Compartment	Flow	Scenario 1 magnitude of flow (g C m ⁻² d ⁻¹)	Scenario 2 magnitude of flow (g C m ⁻² d ⁻¹)
Phytoplankton (Cpt 1)	Imported	97.20	97.20
	1→7	0.027	0.027
	1→8	0.029	0.029
	R	0	0
	Exported	97.144	97.144
Corals: zooxanthellae (Cpt 2)	P_G	0.54	0.54
	2→7	0.458	0.458
	R	0.082	0.082
Turf algae (Cpt 3)	P_G	1.49	1.49
	3→5	0.14	0.33
	3→6	0.04	0.083
	3→18	0.645	0.412
	R	0.665	0.665
COA (Cpt 4)	P_G	0.986	0.986
	4→5	0.12	0.264
	4→18	0.407	0.263
	R	0.459	0.459
Grazing fish (Cpt 5)	5→8	0.001	0.002
	5→11	0.161	0.347
	5→18	0.11	0.236
	R	0.018	0.039
Invertebrate grazers (Cpt 6)	6→9	0.009	0.017
	6→10	0.01	0.019
	6→18	0.025	0.046
	R	0.006	0.011
Corals: heterotrophic (Cpt 7)	7→8	0.096	0.096
	7→18	0.27	0.270
	R	0.41	0.410
Zooplankton (Cpt 8)	Imported	26.4	26.4
	8→5	0.03	0.03
	8→7	0.049	0.049
	8→12	0.22	0.220
	8→18	0.043	0.043
	Exported	26.2089	26.2103
	R	0.03	0.03

(Appendix 2 continued on next page)

Appendix 2, continued

Compartment	Flow	Scenario 1 magnitude of flow (g C m ⁻² d ⁻¹)	Scenario 2 magnitude of flow (g C m ⁻² d ⁻¹)
Carnivorous and detritivorous invertebrates (Cpt 9)	9→10	0.024	0.024
	9→19	3.763	3.770
	R	2.73	2.736
Invertivorous fish (Cpt 10)	10→8	0.0004	0.0005
	10→11	0.0046	0.0059
	10→18	0.010	0.0126
	R	0.019	0.024
Piscivorous fish (Cpt 11)	11→8	0.0002	0.0005
	11→18	0.0623	0.1187
	11→export	0.0298	0.0574
	R	0.116	0.219
Planktivorous fish (Cpt 12)	12→8	0.0003	0.0003
	12→11	0.0427	0.0427
	12→18	0.088	0.088
	R	0.162	0.162
Meiofauna (Cpt 13)	13→9	0.00005	0.00005
	13→19	0.00207	0.00207
	R	0.00018	0.00018
Sedimentary protozoa (Cpt 14)	14→13	0.0003	0.0003
	14→19	0.0005	0.0005
	R	0.0005	0.0005
Sedimentary bacteria (Cpt 15)	15→9	0.001	0.001
	15→13	0.002	0.002
	15→14	0.0013	0.0013
	15→19	0.0084	0.0084
R	0.004	0.004	
Water column bacteria (Cpt 16)	Import	142.8	142.8
	16→17	0.0212	0.0212
	16→18	0.032	0.032
	Export	142.9038	142.9038
	R	0.050	0.050
Water column protozoa and other micro- zooplankton (Cpt 17)	Import	7.176	7.176
	17→7	0.002	0.002
	17→8	0.002	0.002
	17→18	0.0085	0.0085
	Export	7.1765	7.1765
R	0.0082	0.0082	
Water column detritus (Cpt 18)	Import	795.6	795.6
	18→7	0.24	0.24
	18→8	0.052	0.052
	18→12	0.073	0.073
	18→16	0.207	0.207
	18→19	2.75968	2.75768
	Export	793.96912	793.80012
Sedimentary detritus (Cpt 19)	19→6	0.01	0.01
	19→9	6.50695	6.51195
	19→15	0.0167	0.0167

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