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NOTE

Effects of water velocity on NH_4 and PO_4 uptake and nutrient-limited growth in the macroalga *Dictyosphaeria cavernosa*

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ABSTRACT: *Dictyosphaeria cavernosa* is a spatially dominant macroalga on coral reefs in Kane'ohe Bay, Hawai'i, USA, and occupies a range of habitats from low energy reef slopes to a high energy barrier reef flat. Previous studies demonstrated that *D. cavernosa* growth is limited by the availability of dissolved inorganic nitrogen (DIN) in Kane'ohe Bay, and that, on protected reef flats and slopes, the rate at which DIN is supplied to thalli from the water column is too low for sustained growth. Under these conditions, DIN released from sediments into the water-filled chambers beneath thalli is used for growth. At exposed sites such as the barrier reef, nutrient-rich sediments do not accumulate but *D. cavernosa* is abundant, suggesting that high levels of water motion supply nutrients from the water column to thalli at rates high enough for sustained growth. To test the hypothesis that nutrient acquisition by *D. cavernosa* increases with increasing water velocity, rates of NH_4 and PO_4 uptake were measured at a range of water velocities within the range measured in *D. cavernosa* habitats (0.02 to 0.13 m s^{-1}). Rates of uptake for both nutrients were positively correlated with velocity and with concentration. Results from the uptake experiments were used to construct a simple model to predict the combinations of nutrient concentration and water velocity at which the nitrogen and phosphorus requirements for growth can be met by uptake from the Kane'ohe Bay water column. The model predicts that, at sites in Kane'ohe Bay where average water velocities are higher than 0.05 m s^{-1}, DIN supplied to thalli from the Bay water column can support the specific growth rate measured in the field. At sites where average water velocities are less than 0.05 m s^{-1}, thalli must utilize DIN supplied from benthic sources in addition to water column nitrogen to maintain growth rates at field levels. Similarly, at sites where water velocities are higher than 0.01 m s^{-1}, PO_4 supplied to thalli from the water column can support growth at field levels, while thalli at sites with lower water velocities must utilize PO_4 supplied from benthic sources.

KEY WORDS: Coral reef · *Dictyosphaeria cavernosa* · Growth · Macroalgae · Nitrogen · Phosphorus · Uptake · Water velocity

Coral reef systems characterized by nutrient-poor surface waters often support high rates of gross primary productivity. Several mechanisms have been proposed to explain this observation. One is that efficient nutrient recycling takes place within and between benthic organisms (Johannes et al. 1972, Muscatine & Porter 1977). Another possible mechanism is the acquisition of dissolved nutrients from benthic sources in addition to the overlying water column (Entsch et al. 1983, Stimson et al. 1996). Benthic algae that have horizontally oriented thalli or form mats over sediment have access to 2 major sources of dissolved nutrients. One is the water beneath thalli which is often enriched with sediment-derived nutrients (Lapointe & O'Connell 1989, Lavery & McComb 1991a, Krause-Jensen et al. 1996, Stimson et al. 1996, Larned & Stimson 1997). The other nutrient source is the well-mixed water column above the thalli. Although nutrient concentrations in the water column are generally lower than concentrations beneath algal thalli, water velocities are generally higher, so nutrient supply rates may be as high or higher than those beneath thalli. The nutrient supply rate (the product of nutrient concentration and water velocity), rather than concentration per se, determines the availability of dissolved nutrients to macroalgae and other autotrophs (Fujita & Goldman 1985, Atkinson 1988). At sites where nutrient supply rates from the water column are low, growth in some algal mats and thalli can only be sustained when the algae utilize benthic nutrient sources (Lavery & McComb 1991a, Larned & Stimson 1997). The relative contributions of nutrients derived from the overlying water column and from the benthos to the nutrient requirements of macroalgae have not been evaluated. The purpose of this paper is to determine the conditions of nutrient concentration and water velocity under which the thallose macroalga *Dictyosphaeria cavernosa* (Forskål) Børgesen can acquire sufficient amounts of nitrogen and phosphorus from the overlying water column to sustain long-term growth, and

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the conditions under which nitrogen and phosphorus supplied from the benthos must be utilized in addition to water column nitrogen and phosphorus.

Growth rates of *Dictyosphaeria cavernosa* thalli from Kane'ohe Bay, O'ahu, Hawai'i, USA are limited by the availability of dissolved inorganic nitrogen (DIN) (Larned & Stimson 1997). Thalli cultured in flowing unenriched seawater from the Kane'ohe Bay water column did not sustain positive growth rates. The DIN concentration in this seawater is 0.43 ± 0.36 µM (mean ± 1 standard deviation, N = 75 samples from January 1994 to August 1996). *D. cavernosa* thalli sustained positive growth in culture at DIN concentrations ≥0.75 µM, and thalli exposed to the nutrients released from coral reef sediment patches also sustained positive growth (Larned & Stimson 1997). On protected reef slopes and flats in Kane'ohe Bay, *D. cavernosa* overgrows coral and occupies gaps between corals, creating water-filled chambers beneath the thalli in which fine sediments accumulate. On exposed, high energy reef flats, fine sediments do not accumulate, and *D. cavernosa* thalli adhere closely to the substrata and do not form large chambers. See Stimson et al. (1996) for details of the natural history of *D. cavernosa* in Kane'ohe Bay. DIN concentrations within *D. cavernosa* chambers on protected reefs are significantly higher (1.90 ± 1.14 µM, mean ± 1 standard deviation, N = 21) than concentrations in the water column above the chambers. Larned & Stimson (1997) suggested that *D. cavernosa* can persist and grow on protected reefs because thalli utilize the DIN released from sediments and trapped within chambers.

Although sediments appear to be an important nutrient source for *Dictyosphaeria cavernosa*, the possibility remains that nutrient advection from the water column is of equal or greater importance in regions of Kane'ohe Bay where levels of water motion are higher than those in previous field and laboratory experiments (Larned & Stimson 1997). Water velocity was held constant in the earlier experiments, and the effects of velocity on growth or nutrient uptake were not measured. In the present study, we consider the effects of water velocity on the DIN (as NH_4) and PO_4 uptake capacity of *D. cavernosa*. Results from these uptake experiments are used to predict the combinations of water column nutrient concentrations and velocities at which the nitrogen and phosphorus requirements for tissue growth may be met by uptake from the water column.

Methods. ***Dictyosphaeria cavernosa collection and preparation:*** *Dictyosphaeria cavernosa* thalli were collected from the slopes of patch reefs (2 to 3 m depth) in southern Kane'ohe Bay. Three collections of thalli were made during the study, each from a different reef. Large thalli (20 to 100 cm across) were removed from the coral substrata and transported in seawater to the Hawai'i Institute of Marine Biology. The thalli were held overnight in large tanks with flowing unfiltered seawater from the Kane'ohe Bay water column, and transferred the following morning to an oval flume (24 m long by 0.4 m wide) in which they were arranged in a single layer 2.8 m^2 in area (7 m long and 0.4 m wide, approximately 3 kg dry weight). A description of this flume is given in Baird & Atkinson (in press). Unattached *D. cavernosa* thalli are buoyant, so the thalli in the flume were held in place with vinyl-covered steel mesh (2.5 cm mesh width). Thalli were left in the flume to acclimate for 18 h with flowing seawater before starting the experimental runs.

Rates of dissolved inorganic nutrient uptake by coral reef primary producers have been shown to increase with surface roughness or rugosity (Thomas & Atkinson 1997). Surface roughness causes increased friction (dissipation of energy), and boundary layer thickness decreases with both increasing friction and increasing velocity (Nowell & Jumars 1984). Therefore, differences in the roughness of thallus surfaces among collections of *Dictyosphaeria cavernosa* could have confounded the effects of water velocity on nutrient uptake. To determine whether the thalli from the 3 collections were of comparable roughness, a set of measurements of the heights of thalli above the bottom of the flume were made using a pin frame with a single row of 100 steel pins spaced 1 cm apart. Two sets of pin frame measurements parallel to the long axis of the flume were made on each collection of thalli. Roughness was calculated as the standard deviation of the 200 height measurements for each collection of thalli (Baird & Atkinson in press). Roughness varied between collections by less than 10% (roughness value for collection 1:3.23 cm; for collection 2:3.10 cm; for collection 3:2.91 cm).

Experimental procedure: Prior to the start of each flume experiment, inflow water was turned off and the water depth in the flume was lowered to 20.0 cm. Water volume, corrected for the volume of thalli, was approximately 2.2 m^3. Water motion in the flume was provided by a propeller on a 12 V motor submersed in a well at one end of the flume. Flow straighteners (3 concentric 180° curves made of acrylic) were placed in both turning sections of the flume to dampen turbulence produced by the motor and the endwalls. Three water velocity ranges were used during experimental runs with each collection of thalli: 0.02 to 0.03, 0.06 to 0.08 and 0.12 to 0.13 m s^{-1}. During the 6 h runs, velocities were measured at 30 to 60 min intervals by timing the passage of a drogue over the thalli.

To begin each run, a combined NH_4 and PO_4 spike was added to the flume water at 09:00 h. Nutrient spikes were calculated to raise the NH_4 concentration

in the flume to approximately 20 µM and the PO_4 concentration to approximately 2 µM. Solutions were prepared with reagent grade NH_4Cl and $KHPO_4$. Nutrient spikes were slowly added to the flume water just downstream from the motor and approximately 12 m upstream from the edge of the *Dictyosphaeria cavernosa* test section. Sampling began after waiting 30 min for the nutrient pulse to mix into the flume water. A small siphon hose was used to withdraw water samples from the flume at 10 cm depth into a seawater-washed bucket over about 10 min. These samples were subsampled (100 ml) with an HCl-washed and sample-washed syringe, and filtered (Whatman GF/C) into HCl-washed and sample-washed Nalgene bottles, and then frozen. Water samples were collected every 30 min from 09:30 to 11:00 or 11:30 h, then every hour until 15:00 or 15:30 h. Inorganic nutrient concentrations in the water samples were measured with a Technicon II Autoanalyser by Analytical Services, University of Hawai'i. Water temperature and salinity in the flume were monitored with a Seabird Seacat 19 Profiler CTD. Over the course of each run, water temperature rose from approximately 27 to 30°C, and salinity increased by about 1.5%. At the end of each run, the walls of the flume were scrubbed, inflow water from Kane'ohe Bay was restored and the thalli in the flume were flushed until the following morning (16 h).

A control run was carried out to measure nutrient uptake by phytoplankton and epiphytes on the flume walls and vinyl mesh, and these measurements were used to correct the uptake rates calculated for *Dictyosphaeria cavernosa* thalli. With the vinyl mesh in place, and no thalli in the flume, the same NH_4 and PO_4 spikes used in *D. cavernosa* runs were added to the seawater in the flume. The velocity during the control run was maintained at approximately 0.13 m s^{-1}, and water samples were taken every 2 h for 8 h using the same sampling procedure as in the *D. cavernosa* runs.

Each of the 3 *Dictyosphaeria cavernosa* collections were used for NH_4 and PO_4 uptake measurements at 3 different velocities on consecutive days. Because nutrient pulses were administered to each collection daily for 3 d, the possibility arose that uptake rates in some experimental runs were affected by nutrient loading during previous runs. To minimize this problem, runs took place in order from slowest to fastest, as the slower runs were presumed to result in lower uptake rates and lower levels of tissue loading (Bilger & Atkinson 1995). Two 10 to 15 g wet weight tissue samples were taken from thalli in the field at the time of each collection and from thalli in the flume before each run for nutrient analysis. These samples were analyzed for tissue carbon, nitrogen and phosphorus to determine whether N:C and P:C ratios were increasing between runs. Carbon and nitrogen concentrations in dried, lyophilized tissue samples were measured using a Perkin-Elmer 2400 CHN Analyzer. Tissue phosphorus concentrations were measured after dissolution in 1 M HCl with a Perkin-Elmer 6500 inductively coupled plasma spectrophotometer at the Agricultural Diagnostic Service Center, University of Hawai'i.

Uptake rate calculations from flume experiments and estimated uptake in the field: Uptake rates of NH_4 and PO_4 into coral reef benthic communities are generally proportional to nutrient concentration (Bilger & Atkinson 1995, Thomas & Atkinson 1997):

$$m = SC_b \quad (1)$$

where m is uptake or mass flux to the benthic surfaces (mmol m^{-2} d^{-1}), C_b is the NH_4 or PO_4 concentration in the water column well above the boundary layer (mmol m^{-3}), and S is the first-order uptake rate constant (m s^{-1}). The symbol m is used here for uptake on an areal basis to distinguish it from biomass-specific uptake, usually denoted by V (e.g. Harrison et al. 1989). For each flume experiment, S was calculated as the slope of a linear regression of the ln NH_4 or ln PO_4 concentration versus time, normalized by the ratio of flume volume to planar area of *Dictyosphaeria cavernosa*. This ratio was 0.79 for all runs.

DIN and PO_4 uptake rates required to match long-term growth of *Dictyosphaeria cavernosa* in the field were estimated using the equation

$$m_{field} = \mu C_t n \quad (2)$$

where m_{field} is the uptake rate in the field (mmol m^{-2} d^{-1}), μ is the specific growth rate of thalli in the field (g g^{-1} d^{-1}), C_t is the tissue nitrogen or phosphorus concentration of thalli in the field (mmol N or P g^{-1} dry weight), and n is the dry weight:area ratio for thalli in the field (g dry weight m^{-2}). The following values were substituted into Eq. (2): a specific growth rate of 0.005 g g^{-1} d^{-1} (Stimson et al. 1996); tissue N and P concentrations of 0.74 and 0.024 mmol g^{-1} dry weight, respectively (Larned & Stimson 1997); and a dry weight:area ratio of 1004 g dry weight m^{-2}. Thallus growth rates were calculated from long-term (30 d) measurements made throughout the year. The dry weight:area ratio was determined from a linear regression of the dry weights of 35 thalli on area (R^2 = 0.91, $p < 0.001$). These thalli were collected from the same sites as thalli used in the flume uptake experiments. The estimated field uptake rates have the same units as the flume uptake rates.

To equate DIN and PO_4 uptake with nutrient requirements for growth, m was set equal to m_{field}:

$$m = m_{field} = SC_b = \mu C_t n \quad (3)$$

Values of S were determined at different water velocities, so that Eq. (3) could be used to determine

combinations of water velocity and nutrient concentration sufficient to support the specific growth rate measured in the field.

Water velocities in the field: Relative water velocities were measured at 8 sites in Kane'ohe Bay where *Dictyosphaeria cavernosa* is abundant. These sites represent a range of exposure conditions from protected patch reef slopes to a barrier reef flat subjected to breaking waves. The dissolution of plaster cubes or 'clod cards' were used to measure relative water velocities at the 8 sites over entire tidal cycles, following Larned & Stimson (1997). The use of clod cards for flow characterization has been reviewed by Jokiel & Morrisey (1993) and Thompson & Glenn (1994). To calibrate the clod cards used in the field, the dissolution rates of subsets of each batch of clod cards were measured in the flume at 5 velocities from 0 to 0.2 m s^{-1}. Linear regressions of dissolution rates on water velocity in the flume and inverse predictions from those regressions (Sokal & Rohlf 1981) were used to predict relative water velocities in the field from dissolution rates in the field. Estimated field velocities are 'relative' because clod cards relate multidirectional flow in the field to an equivalent unidirectional flow in the flume. Estimated field velocities fell within the velocity range used for calibration. Field measurements using 10 to 11 clod cards at each of the 8 sites were made in July and December 1995 and March, April and August 1996.

Results. ***Nutrient uptake rates:*** Uptake of NH_4 and PO_4 by *Dictyosphaeria cavernosa* thalli was concentration-dependent as indicated by linear decreases in ln NH_4 and ln PO_4 concentrations over time in each run (Figs. 1 & 2). All linear regressions of these data were significant ($p < 0.05$), and had R^2 values of 0.93 to 0.99 for NH_4 and 0.78 to 0.99 for PO_4.

The uptake rate constants for NH_4, S_N, and for PO_4, S_P, are shown in Table 1. S_N ranged from 6.7×10^{-5} to 14.9×10^{-5} m s^{-1}, and increased with velocity [Fig. 3, regression equation: $S_N \times 10^5 = 5.8 + 64.0$(velocity), $p < 0.01$, $R^2 = 0.88$]. S_P ranged from 2.2×10^{-5} to 4.8×10^{-5} m s^{-1} and increased with velocity [Fig. 4, regression equation: $S_P \times 10^5 = 2.4 + 13.7$(velocity), $p < 0.05$, $R^2 = 0.57$].

Control runs and tissue nutrient analyses: Rates of NH_4 and PO_4 uptake by phytoplankton and epiphytes on the flume walls, floor and wire mesh were measured during the control run (Figs. 1 & 2). The estimated NH_4 uptake rate over the course of the control run, 0.03 mmol m^{-2} d^{-1}, was less than 1% of the NH_4 uptake rate measured for *Dictyosphaeria cavernosa* thalli at similar velocities. The rate of PO_4 uptake during the control run was 0.01 mmol m^{-2} d^{-1}, also less than 1% of the rate measured for *D. cavernosa* thalli at similar velocities.

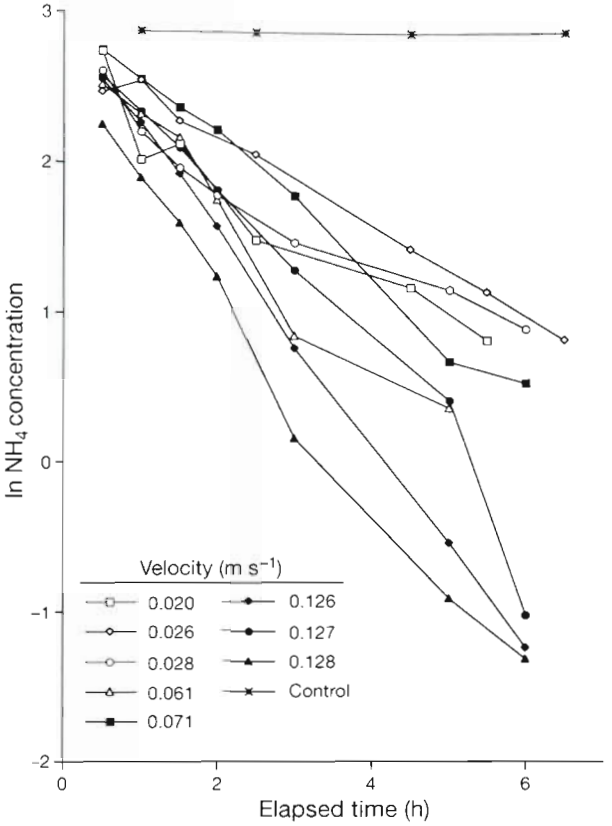

Fig. 1 Natural log-transformed NH_4 concentration in the flume water vs elapsed time during uptake experiments. Experiments ran from 09:00 to 15:00 or 15:30 h. Mean water velocity during the control run was 0.13 m s^{-1}

Dictyosphaeria cavernosa tissue nitrogen and phosphorus concentrations and C:N and C:P ratios are shown in Table 2. Tissue nitrogen and phosphorus did not increase during successive flume runs and it is

Table 1. *Dictyosphaeria cavernosa*. Summary of results from NH_4 and PO_4 uptake experiments. Collections refer to *D. cavernosa* thalli collected at a single time and used in more than 1 experimental run. S_N and S_P are the first-order rate coefficients for NH_4 and PO_4 uptake, respectively; St_m(N) and St_m(P) are the calculated Stanton numbers (see 'Discussion') for NH_4 and PO_4 uptake, respectively. Errors shown for S_N and S_P are standard deviations

D. cavernosa collection	Velocity (m s^{-1})	S_N (10^{-5} m s^{-1})	St_m(N) (10^{-4})	S_P (10^{-5} m s^{-1})	St_m(P) (10^{-4})
1	0.026	7.1 ± 0.3	27.3	2.2 ± 0.3	8.5
2	0.020	8.9 ± 1.8	44.5	2.9 ± 1.5	14.5
3	0.028	6.7 ± 0.9	23.9	2.6 ± 0.7	9.3
1	0.071	9.3 ± 0.6	13.0	4.8 ± 0.6	6.8
3	0.061	9.4 ± 0.6	15.4	3.0 ± 0.3	4.9
1	0.126	14.9 ± 0.2	11.8	4.0 ± 0.5	3.2
2	0.128	14.7 ± 1.2	11.5	4.5 ± 0.6	3.5
3	0.127	12.8 ± 1.4	10.1	3.5 ± 0.1	2.8
Control	0.127	0.1 ± 0.01	0.1	0.3 ± 0.2	0.2

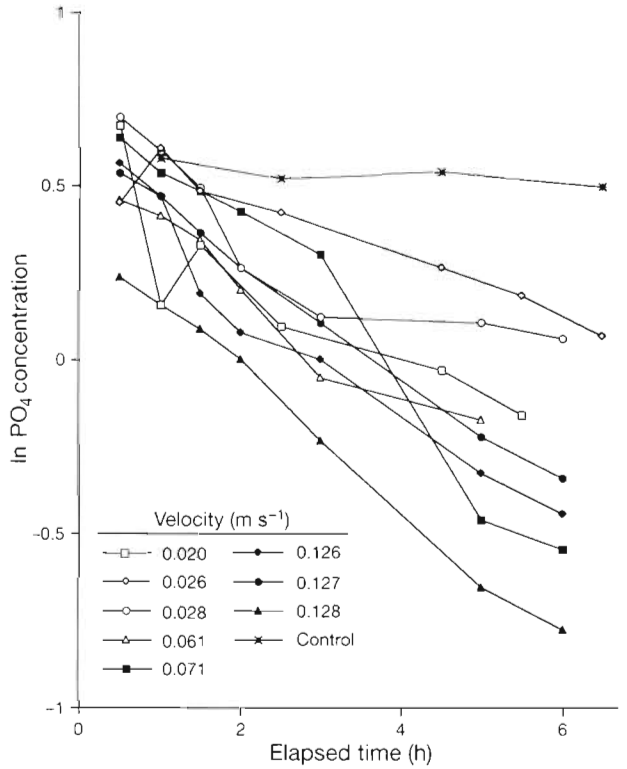

Fig. 2. Natural log-transformed PO_4 concentration in the flume water vs elapsed time during uptake experiments. Experiments ran from 09:00 to 15:00 or 15:30 h. Mean water velocity during the control run was 0.13 m s^{-1}

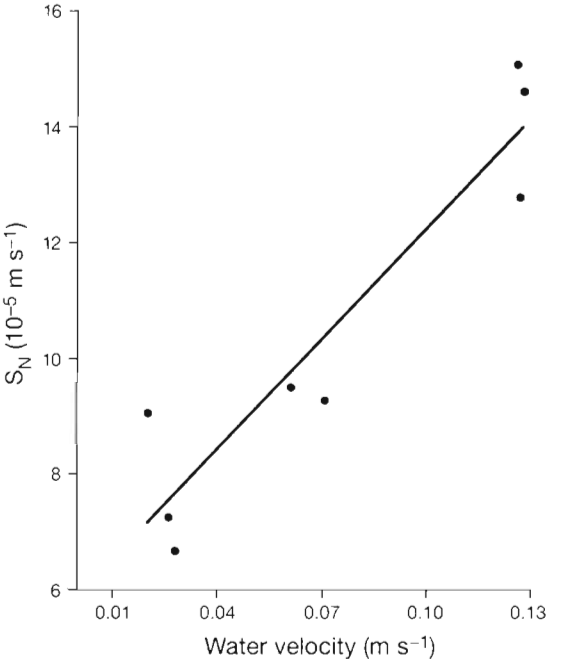

Fig. 3. *Dictyosphaeria cavernosa*. Rate constant for NH_4 uptake (S_N) vs water velocity for the experiments shown in Fig. 1. Line is from the least-square regression ($p < 0.01$, $R^2 = 0.88$)

therefore unlikely that nutrient loading during early runs affected uptake rates in subsequent runs. In previous studies, 10 to 12 d of NH_4 enrichment at a loading rate of ≥60 mmol N g^{-1} wet weight d^{-1} was required to significantly reduce the C:N of *D. cavernosa* tissue (Larned & Stimson 1997).

Table 2. *Dictyosphaeria cavernosa*. Tissue nutrient analyses. Collections refer to *D. cavernosa* thalli collected at a single time and used in more than 1 experimental run. Values shown are averages of 2 samples from thalli in the field at the time of each collection and 2 samples from the flume before each experimental run

Collection		C:N molar ratio	C:P molar ratio	% N by dry weight	% P by dry weight
1	Field conditions	26.4	631.3	0.99	0.04
1	Run 1	27.6	682.5	0.71	0.03
1	Run 2	24.3	616.9	0.85	0.03
1	Run 3	24.0	573.5	1.02	0.04
2	Field conditions	23.9	604.8	0.80	0.03
2	Run 1	24.2	672.5	0.96	0.03
2	Run 2	24.2	662.2	0.89	0.03
3	Field conditions	23.5	625.1	0.81	0.03
3	Run 1	22.7	616.9	0.96	0.04
3	Run 2	23.1	608.3	0.93	0.04
3	Run 3	22.9	637.6	0.99	0.04

Estimated DIN and PO_4 uptake in the field: The estimated nutrient uptake rates required for long-term growth in the field (m_{field}) were 3.71 mmol DIN m^{-2} d^{-1} and 0.13 mmol PO_4 m^{-2} d^{-1}. The estimate for DIN uptake assumes that NH_4 and NO_3 are taken up at the same rate (see 'Discussion'). These uptake rates were substituted into Eq. (3) ($m_{field} = SC_b$), and a range of water velocities and nutrient concentrations were determined which satisfied the equality. Curves plotted from those water velocities and nutrient concentrations are shown in Figs. 5 (for DIN) & 6 (for PO_4). Because there were a limited number of water velocities used in the experimental runs, the values of S_N and S_P that correspond to the velocities shown in Figs. 5 & 6 were determined from the regression lines shown in Figs. 3 & 4, respectively.

Water velocities in the field: Relative water velocities at reef flat and reef slope locations in southern Kane'-ohe Bay ranged from <0.01 to 0.19 m s^{-1}, based on 6 sampling dates from July 1995 to August 1996. The lowest velocities, <0.01 to 0.04 m s^{-1}, were measured on 3 patch reef slopes and the leeward slope of the barrier reef. The highest velocities,

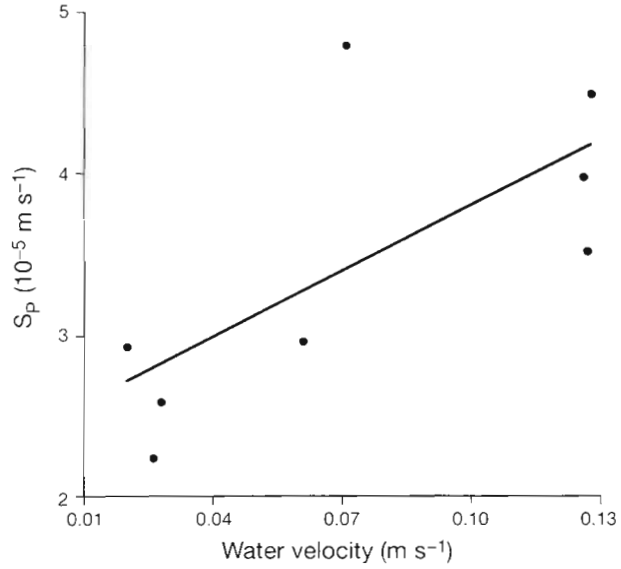

Fig. 4. *Dictyosphaeria cavernosa*. Rate constant for PO_4 uptake (S_P) vs water velocity for the experiments shown in Fig. 2. Line is from the least-square regression ($p < 0.05$, $R^2 = 0.57$)

0.1 to 0.19 m s^{-1}, were measured on the barrier reef flat. Intermediate velocities, 0.02 to 0.08 m s^{-1}, were measured on 3 patch reef flats.

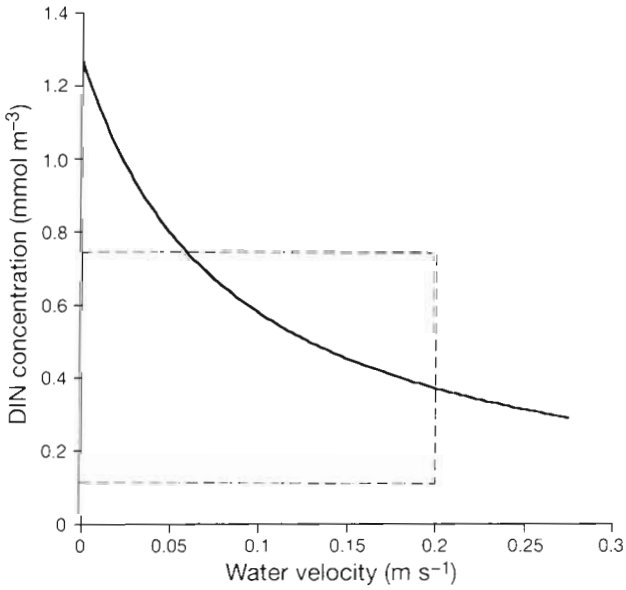

Fig. 5. *Dictyosphaeria cavernosa*. Estimated DIN uptake for long-term growth based on field growth measurements, field tissue nitrogen levels and velocity-specific uptake rate constants for ammonium. Box represents the DIN concentrations (mean ± 1 standard deviation: 0.43 ± 0.31, n = 75) and the range of water velocities measured in regions of Kane'ohe Bay where *D. cavernosa* is abundant. Area above the curve: DIN supply rate is higher than uptake rate required for growth at field levels. Area below the curve: DIN supply rate is lower than uptake rate required for growth at field levels

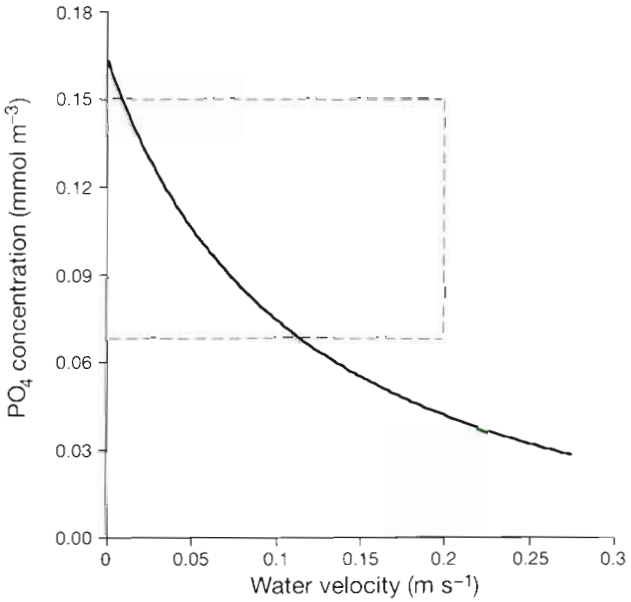

Fig. 6. *Dictyosphaeria cavernosa*. Estimated PO_4 uptake for long-term growth based on field growth measurements, field tissue phosphorus levels and velocity-specific uptake rate constants for PO_4. Box represents the phosphate concentrations (mean ± 1 standard deviation: 0.11 ± 0.04, n = 75) and the range of water velocities measured in regions of Kane'ohe Bay where *D. cavernosa* is abundant. Area above the curve: PO_4 supply rate is higher than uptake rate required for growth at field levels. Area below the curve: PO_4 supply rate is lower than uptake rate required for growth at field levels

Discussion. Under conditions of low water velocity (<0.05 m s^{-1}) and low DIN concentrations (<0.4 µM), uptake of DIN from the water column above *Dictyosphaeria cavernosa* thalli appears to be insufficient for sustained growth at field levels (Fig. 5). These conditions frequently exist on the protected patch and fringing reef flats and slopes in Kane'ohe Bay where *D. cavernosa* is abundant. On the barrier reef flat, however, water velocities rarely fall below 0.1 m s^{-1} and it is likely that uptake of DIN from the barrier reef water column is sufficient for sustained growth (Fig. 5). In contrast, uptake of PO_4 at water velocities as low as 0.01 m s^{-1} is sufficient for sustained growth at field levels (Fig 6). For thalli at low energy sites, access to DIN released from sediments below the thalli, in addition to DIN from the overlying water column, may be a requirement for growth in *D. cavernosa*. DIN and PO_4 are released into the water from reef slope sediments adjacent to and beneath *D. cavernosa* thalli at rates of about 0.5 mmol DIN m^{-2} d^{-1} and 0.1 mmol PO_4 m^{-2} d^{-1}, respectively (n = 20 efflux rate measurements; J. Stimson & S. Larned unpubl. data). Support for the hypothesis that sediment-derived DIN is required for growth at low water velocities comes from field ex-

periments in which DIN supplied by sediment efflux and water column advection resulted in sustained growth, while thalli isolated from sediments did not grow (Larned & Stimson 1997).

Two assumptions should be noted regarding the use of Eq. (3) to plot the curves shown in Figs. 5 & 6. First, nutrient uptake is assumed to be positively correlated with growth. Numerous studies have demonstrated that nutrient uptake can be temporarily uncoupled from growth, due either to 'luxury uptake' or to growth supported by stored nutrients under conditions of low nutrient availability (eg. Ramus & Venable 1987, Björnsäter & Wheeler 1990, Lavery & McComb 1991b). Over the long term, however, nutrient uptake should be correlated with growth because tissue accumulated during growth contains nutrients. Results from laboratory culture experiments indicate that the nitrogen storage capacity of *Dictyosphaeria cavernosa* thalli is very limited, i.e. when external nitrogen concentrations are near growth-saturating levels, little nitrogen is allocated to reserve pools (Stimson et al. 1996, Larned & Stimson 1997). The second assumption is that, in order to estimate the DIN uptake rate required to match the growth rate of *D. cavernosa* in the field, uptake of NH_4 and NO_3 occur at similar rates. If DIN uptake rates are limited by boundary layer transport, as appears to be the case (see below), then this assumption is probably valid, because NH_4 and NO_3 have similar diffusivities in seawater: 19.8×10^{-6} cm^2 s^{-1} for NH_4 and 19.0×10^{-6} cm^2 s^{-1} for NO_3 at 25°C (Li & Gregory 1974).

There is a positive relationship between NH_4 and PO_4 uptake and both components of advection: concentration (Figs. 1 & 2) and velocity (Figs. 3 & 4). The positive relationship observed between uptake and water velocity is consistent with mass transport limitation, i.e. the rate limiting step for NH_4 and PO_4 uptake is diffusion through NH_4- and PO_4-depleted boundary layers. This relation arises because the thickness of the depleted boundary layer, and thus the resistance the boundary layer imposes on nutrient transport, decreases with increasing velocity (Bilger & Atkinson 1992, Dade 1993). The rate constant for nutrient uptake, S, can be partitioned into 2 variables, velocity and the Stanton number, St_m. Stanton numbers are dimensionless coefficients describing heat and mass transfer from fluids to solid surfaces (Kays & Crawford 1993), and have been used to compare nutrient uptake rates with advection rates under varied conditions of velocity, nutrient concentration and surface roughness (Bilger & Atkinson 1992, Thomas & Atkinson 1997). Stanton numbers were calculated for NH_4 and PO_4 uptake by *Dictyosphaeria cavernosa* in the flume experiments as

$$St_m = S/U \quad (4)$$

where U is velocity. Use of Eq. (4) assumes that uptake at environmentally realistic nutrient concentrations is a first-order reaction, i.e. uptake does not 'saturate' as represented by Michaelis-Menton-type models (Bilger & Atkinson 1995). Field and flume experiments indicate that NH_4 and PO_4 uptake by Kane'ohe Bay reef communities and individual coral species are first-order reactions (Atkinson 1987, Atkinson & Bilger 1992, Thomas & Atkinson 1997). The positive linear relationship between velocity and S_N and S_P indicates that the same is true for *D. cavernosa*. That uptake is generally first-order is due to low nutrient concentrations at organism surfaces relative to uptake potential (Bilger & Atkinson 1995).

Stanton numbers for NH_4 and PO_4 uptake by *Dictyosphaeria cavernosa* (Table 1) are similar to Stanton numbers for corals of comparable roughness (Thomas & Atkinson 1997), and corroborate the general finding that rates of dissolved nutrient flux from the water column to the shallow benthos of coral reefs are orders of magnitude slower than rates at which dissolved nutrients are advected past the benthos (Atkinson 1987, Atkinson & Smith 1987, Thomas & Atkinson 1997). Hatcher et al. (1987) scaled DIN and dissolved inorganic phosphorus (DIP) turnover rates, i.e. concentration-specific uptake or release rates, to seawater exhange or advection rates for 4 coral reef flats including Kane'ohe Bay. The resulting ratios are much less than unity (0.03 for DIN, 0.003 for DIP), indicating that nutrient flux on these reef flats is dominated by advection, rather than by uptake, remineralization, nitrogen fixation or other biologically controlled processes. The ratios reported by Hatcher et al. (1987) are consistent with the Stanton numbers presented in Table 1. Under conditions of lower water velocities, ratios of DIN uptake:advection will increase and sources of DIN in addition to the water column, such as nitrogen fixation (Smith 1984, Hatcher et al. 1987) and sediment efflux (Larned & Stimson 1997), may be required for net primary production. Thus, attempts to determine the dominant pathways for DIN and PO_4 cycling in coral reef systems must consider velocity-dependent rates of uptake. From the results presented in this paper, we conclude that while advection supplies sufficient DIN and PO_4 to *D. cavernosa* under conditions of high water velocities, DIN and PO_4 supplied by sediment efflux is required for sustained growth under conditions of low water velocities.

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