EFFECTS OF ALGAL TURF ON MASS TRANSPORT AND FLOW MICROHABITATS OF ASCIDIANS IN A CORAL REEF LAGOON

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ABSTRACT

We measured effects of calcareous algal turf (*Halimeda opuntia*) on water flow and transport of materials to/from compound ascidians (*Lissoclinum patella*) in a shallow coral reef lagoon in Palau. Velocity profiles along *L. patella* colonies in patches of *H. opuntia* did not differ from those along colonies on bare substratum, both when measured in the field and in flume experiments. We used a dye-tracking technique to quantify transport and mixing in the lagoon on spatial scales of meters to tens of meters; horizontal advection was slow (~3cm/s) and dispersion was highly anisotropic (about ten-fold greater parallel to the direction of water flow) at our shallow sites. Turbulent mixing coefficients and advective velocities were not affected by algal turfs or by vertical position in the water column. *L. patella* pump water through themselves, but only process a small proportion of the water moving across their habitat.

INTRODUCTION

Sessile benthic organisms can be dislodged or broken by hydrodynamic forces, yet they also depend on ambient water motion for the transport to their vicinity of dissolved substances (e.g. gases, nutrients) and particulate food, the removal of wastes, the transport of gametes (of spawners), and the dispersal of propagules (e.g. planktonic larvae, spores) (reviewed in Koehl 1984; Nowell and Jumars 1984; Roughgarden et al. 1987; Okubo 1992; Koehl et al. 1993). Areas of coral reef systems where mass exchange may be a problem for sessile organisms are those characterized by slow water movement, such as calm lagoon sites. Common benthic animals in shallow regions of such lagoon sites in the tropical Indo-West Pacific are didemnid ascidians bearing prokaryotic symbionts, *Prochloron* (e.g. Kott 1982; Lewin and Cheng 1989). In this study we focused on the didemnid *Lissoclinum patella* in shallow regions of a calm bay in the Palau lagoon, where colonies were abundant in mats of the calcareous alga *Halimeda opuntia*, and also occurred on coral rock and sand (Swift and Robertson 1991). Canopies of aquatic macrophytes modify ambient water flow and can alter the flux of water-borne materials to and from the organisms living within them (reviewed by Koehl 1986; Worcester 1995). The purpose of this study was to assess the effects of *H. opuntia* turfs on the flow microhabitats of *L. patella* and the mass transport to and from these animals by ambient currents.

Ambient water movement determines the dispersal of the larvae of benthic animals (reviewed in e.g. Koehl et al. 1993; Koehl and Powell 1994). Many sessile animals (e.g. ascidians, bryozoans, many cnidarians) have short-lived larvae. The larvae of *L. patella* in the field remain in the water column <10 minutes and disperse distances <10m (Olson and McPherson 1987). The ecological and evolutionary consequences of such short larval dispersal are reviewed by Davis and Butler (1989). Although the role of large-scale hydrodynamics in the dispersal of coral reef animals with long-lived larvae is well-studied (e.g. Wolanski 1993; Leis 1994), mass transport on the smaller spatial and temporal scales relevant to ascidians and other animals with short-lived larvae has not received much attention in reef systems. One goal of our study was to assess the effects of *H. opuntia* turfs on mass transport on the scale of meters and minutes that is relevant to the dispersal of *L. patella* larvae.

Ascidians use the cilia of their pharyngeal baskets to pump water through their bodies for respiration, filter feeding, removal of excreta, and discharge of gametes (e.g. Fiala-Médioni 1978a; Charriaud 1982). Such pumping must also affect the flux of materials to and from the symbiotic *Prochloron* living in the cloacal cavities of *L. patella*;

Prochloron photosynthesize and contribute to the nutrition of *L. patella* (Pardy and Lewin 1981; Alberte et al. 1987), and *Prochloron* in *L. patella* fix N_2 (Paerl 1984). Filter feeding by dense populations of benthic ascidians can sometimes have a significant impact on phytoplankton populations and on the concentration of suspended organic particles in the water column (Peterson and Riisgård 1992). Another objective of this study was to compare the flux of water through a population of *L. patella* relative to the flux of water across their habitat.

Scales at which to measure water flow

To answer the questions posed above, flow encountered by *L. patella* both in and outside *H. opuntia* mats had to be characterized at the appropriate spatial and temporal scales. The important scales for *L. patella* are: 1) the individual scale (ambient water flow encountered by a colony, and water pumping by a colony — mm's to cm's, seconds), and 2) and the dispersal scale (dispersal of larvae and transport of water-borne material to/from the vicinity of colonies — meters, minutes).

On the individual scale, benthic organisms can be in flow microhabitats that are quite different from the mainstream flow at sites where they occur (reviewed in Koehl 1984, 1986), not only because of their position with respect to local topography and neighboring organisms, but also because of their height relative to the velocity gradient (benthic boundary layer) that develops along the substratum. The steepness of this velocity gradient determines the flux of momentum, dissolved substances, and particles between the water and the benthos (e.g. Nowell and Jumars 1984).

The effects of water flow on a variety of biological processes of coral reefs and lagoons is reviewed by Hamner and Wolanski (1988). Most investigations of flow in tropical lagoons have concentrated on multi-kilometer scales, much larger than the dispersal scale on which we have focused (although Wolanski (1993) has noted the potential importance of flow processes occurring at smaller scales to phenomena occurring at the multi-kilometer scale). For example, in the Great Barrier Reef system of Australia, the coupling of water flow to important biological processes such as larval transport and connectivity of reefs, lagoon flushing, and benthic algal productivity have been studied at the multi-kilometer scale (e.g. Frith et al. 1986; Wolanski et al. 1988; Dight et al. 1990; Ridd et al. 1990; Wolanski and King 1990; Black and Moran 1991; and others reviewed by Wolanski, 1994).

Our study focused on the effects of *H. opuntia* turf on the velocity profiles encountered by *L. patella* (mm to cm scale) and on the advection and mixing of water-borne material in their vicinity (m to 10m scale). We compared the latter to pumping rates of *L. patella* to estimate their effect on water exchange within the lagoon.

MATERIALS AND METHODS

Study sites and transects

The field measurements described below were conducted at two shallow sites in Iwyama Bay, Palau (7°30'N, 134°30'E), West Caroline Islands. A patch of *Halimeda opuntia* turf and an adjacent patch of bare substratum (coral rock and sand) were chosen for study at each site; transects (9m long) were run parallel to the shore across these patches and the neighboring area. The longest dimension, width, and height of each *Lissoclinum patella* colony touched by the transect were measured to the nearest 1cm using a ruler. The diameter of each *H. opuntia* patch crossed by the transect was also measured to the nearest 1cm. The proportion of substratum area covered by *L. patella* was estimated for each turf patch and each bare patch crossed

by the transect by dividing the sum of the distances along the transect that crossed *L. patella* colonies by the total distance along the transect of the patch. Photographs of haphazardly-selected undisturbed *L. patella* colonies taken by a snorkler floating above them were projected onto a Jandel 2210 digitizing tablet; colony areas were measured to the nearest 1mm^2 using Sigma Scan 3.01 software, and the number of open atrial siphons per colony area was determined.

Measurement of velocity profiles in the field
Velocities of water motion were measured at different heights above the substratum. A post (2mm thick) was held vertically with one end touching the substratum; horizontal rods (diameter = 2mm, length = 15cm) attached to the post at measured heights above the substratum, pointed downstream. A small puff of seawater marked with fluorescein dye was released from a syringe near the upstream end of each rod (at the same height as the rod, but displaced 2cm laterally so the rod did not interfere with the flow), and the time for the dye to travel a distance of 10cm (indicated by two marks on the rod) was timed to the nearest 0.1s using a digital stopwatch. Six puffs were timed at each height above the substratum and used to calculate the mean velocity at each height. Profiles were done above *L. patella* in turfs and on bare substrata within a few minutes of each other.

Boundary shear velocity (u_*) is a measure of the steepness of the velocity gradient in the benthic boundary layer (e.g. Nowell and Jumars 1984). For each profile of mean velocity as a function of height above the substratum, u_* was calculated as described by Koehl and Alberte (1988).

Measurement of velocity profiles in a flow tank
The field technique described above did not permit measurement of details of the velocity profiles (on the scale of mm's) just above the surfaces of *L. patella* colonies, hence such profiles were measured in a laboratory flow tank. Intact sections of *H. opuntia* turf containing *L. patella* colonies were collected and placed on the floor of a flow tank (Vogel and LaBarbera 1978) (Fig. 1,A). Motor speeds were chosen and collimators were adjusted in the flow tank to produce velocity profiles that mimicked those measured in the field. A vertical plane parallel to the flow direction along the middle of the tank was illuminated by a strobotac (GenRad #1531-A) flashing at known frequencies through a slit in the opaque ceiling of the tank. Long-exposure photographs (e.g. Fig. 1,B) captured the position of natural particles in the water on successive flashes of the strobotac. Digitization of such images permitted velocity profiles to be calculated, as described in Koehl and Alberte (1988). After the flow over *L. patella* in *H. opuntia* turf was thus photographed, the algae were removed while the ascidians were left in place on bare substratum, and the velocity profiles over them were assessed again.

Measurement of advection and mixing in the field
Advection and turbulent diffusion of parcels of fluid were estimated using a dye tracking technique (Koehl et al. 1993; Koehl and Powell 1994). Blobs of dye (fluorescein solution in seawater) were released above *H. opuntia* turfs and above adjacent bare substratum at various matched times during the tidal cycle at both sites. Each 60ml blob of dye was released from a syringe without a needle. "Surface" blobs were released approximately 5cm below the air-water interface, and "bottom" blobs were released approximately 5cm above the substratum. Timed photographs of the dye were taken from the top of an adjacent steep hill; the angle of the camera from the horizontal was measured and used to correct the digitized images for parallax, as described by Koehl et al. (1993). The blobs were photographed until they moved out of view, which took from 5 to 19 minutes; this time scale corresponds to the duration of *L. patella* larval swimming measured in the field (Olson and McPherson 1987). Slides were digitized and advective velocities and turbulent mixing coefficients were calculated using the techniques described by Koehl et al. (1993) and summarized below.

Dye-tracking techniques are a direct way of measuring the movement of water and waterborne materials in the ocean

(e.g. Pritchard and Carpenter 1960; Okubo 1971). The motion of any parcel of fluid is composed of: 1) a translation of the center of mass (advection); 2) a rotation about the center of mass (vorticity); and 3) a deformation of the parcel (expansion or contraction along three mutually perpendicular axes). The blobs we tracked expanded as dyed water mixed with surrounding undyed water by "turbulent diffusion" (not to be confused with molecular diffusion due to the random thermal motion of molecules). At our shallow sites dye mixed between the surface and the bottom in a few seconds, so we assumed the dye to be well-mixed vertically and we only estimated the horizontal motion and expansion of dye patches. We also made the simplifying assumption that dye was uniformly distributed within a patch, and used the x,y coordinates of all the pixels within the perimeter of a digitized patch to calculate the position of its centroid at successive times, t_n and t_{n+1}. If the centroid of the blob moved a distance Δs_n, then $\bar{U}_n$, the advective speed during this n^{th} time interval, is given by

$$\bar{U}_n = (\Delta s_n)/(t_{n+1} - t_n) \qquad (1)$$

To separate the expansion of a patch of dye from its rotation, we determined the two horizontal principal axes of the patch at each time: "A", the "major" axis of greatest spread of the patch, and "B", the "minor" axis perpendicular to "A". A practical way to identify the axes, A and B, of a patch is to conduct a principal components analysis (PCA) using x,y coordinates of all the pixels within the blob perimeter; σ_A^2 and σ_B^2, the variance associated with the principal components (principal axes) A and B provide a measure of the dispersion of the patch along each axis (e.g. Presendorfer 1988; Chatfield 1980). For programming efficiency, we utilized a mathematically equivalent
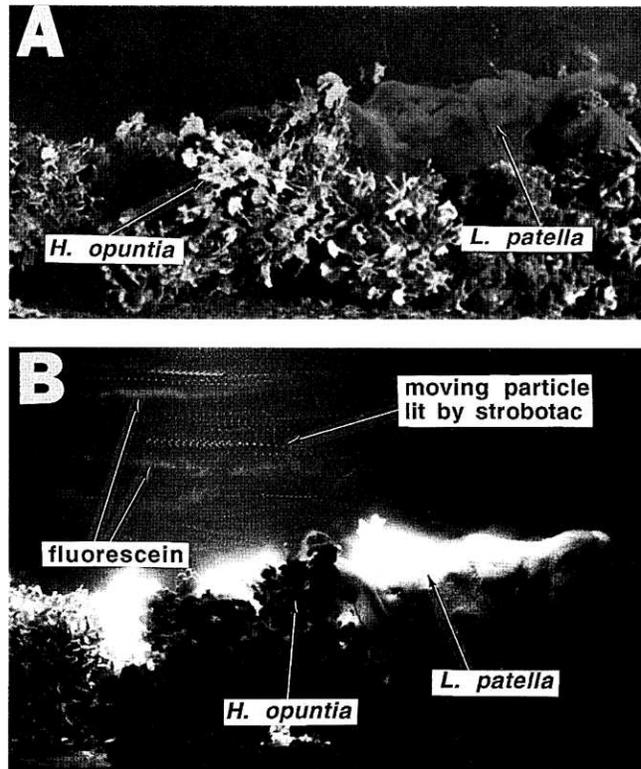

Fig. 1: A. Section of *Halimeda opuntia* turf containing *Lissoclinum patella* colonies that was collected intact in the field and subsequently placed in a flow tank. B. The same section of *H. opuntia* turf as in A, but illuminated by a sequence of flashes from a strobotac in a single vertical plane parallel to the direction of flow. The fluorescein dye was released upstream of the turf at several heights above the substratum.

formulation to PCA, "the equivalent ellipsoid" technique due to Poinsot (Marion 1970).

Measuring the rate of spread of the patch along the principal axes gives an estimate of the turbulent diffusion in the fluid during the patch motion. Thus,

$$K_A = 0.5 \, d(\sigma_A^2)/dt \qquad (2)$$

$$K_B = 0.5 \, d(\sigma_B^2)/dt \qquad (3)$$

That is, K_A and K_B are the slopes of the curves of σ_A^2 and σ_B^2 as a function of time, and can be obtained using linear regression.

Measurement of *L. patella* pumping rates in the field

The pumping rates of *L. patella* were assessed in the field. The time required for a small puff of dye released from a syringe at the atrial siphon to travel a distance of 5cm was measured with a digital stopwatch to the nearest 0.1s and used to calculate exit velocity; six replicate measurements were made per colony and used to calculate a mean velocity. The diameter of the circular artrial siphon was measured to the nearest 5mm using vernier calipers, and the volume pumped per time through the siphon was estimated as the product of the siphon cross-sectional area and the exit velocity, as described by Fiala-Médioni (1978a).

Statistical analyses

Statistical analyses were done using Systat 5.04 software.

RESULTS

Organisms and water flow at the study sites

Both study sites were characterized by patches of *H. opuntia* turf (Table 1) surrounded by areas of bare coral rock and sand with occasional shoots of the seagrass *Enhalus acoroides*. The most abundant sessile animals were *L. patella* (measurements summarized in Table 1); smaller didemnid ascidians, *Trididemnum cyclops*, also occurred in the turf. *L. patella* colonies in turf were similar in length and width to colonies on bare substratum, but their percent cover in *H. opuntia* patches, although quite variable, was about three times greater than on bare substratum. The upper surfaces of colonies in turf were flush with the top of the turf (Fig. 1,A); the height of such colonies in *H. opuntia* patches was significantly greater than of colonies on bare substratum (Student's t, p = 0.000005).

Water flow at both sites was characterized by slow currents. Instantaneous velocities at a point (U) and advective transport (ū) across the habitat were only a few cm's per second (Table 2). Advective velocities were significantly faster during flooding and ebbing tide than at slack tide at site #1 (Kruskal-Wallis, p = 0.04), but not at site #2. Water depth varied with time in the tidal cycle, but was always less than 2m. Mixing in these shallow habitats was highly anisotropic, with K_A (which was parallel to the direction the water was flowing) generally an order of magnitude greater than K_B (Table 2).
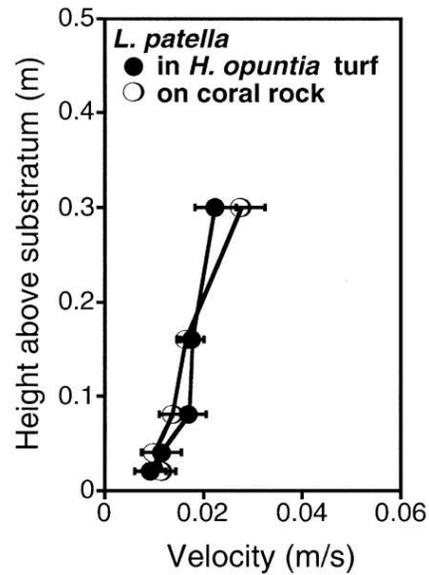

Fig. 2: Velocity profiles measured in the field. Error bars indicate +/- one standard deviation.

Flow microhabitats of *L. patella*

L. patella and *H. opuntia* are short and hence encounter the slowly-moving water near the substratum, as revealed by velocity profiles measured in both the field (Fig. 2) and the lab (Fig. 3). The boundary shear velocities (u.) measured in the field (n = 4) and replicated in the lab (n = 10) were low: 0.001 to 0.003 m/s.

Velocity profiles over *L. patella* on bare substratum and those in *H. opuntia* turf were the same (Figs. 2 and 3). Observations of dye indicated that little water penetrated the dense *H. opuntia* turfs, hence skimming flow (see Nowell and Jumars 1984) occurred over the turf and the *L. patella* colonies flush with the turf's surface. Instantaneous velocities measured in the field 2cm above colonies in turf were not significantly different from those above colonies on bare sand (paired t, p = 0.7). Similarly, velocities measured in the flow tank just a few mm's above the surface of a colony in turf were indistinguishable from those above the same colony after the turf was removed (Fig. 3).

Advection and mixing

Our measurements of advective velocity (ū) and turbulent mixing coefficients (K_A, K_B) are plotted in Fig. 4. There was no significant difference (paired-t test, p ≥ 0.3 for all comparisons) between the ū's, K_A's, and K_B's of dye blobs released above *H. opuntia* turfs versus above bare substratum, both for blobs released near the bottom and for blobs released near the surface. Although we did not quantify vertical mixing, we observed that dye was rapidly dispersed between the surface and the bottom at both of our

Table 1. Measurements of *Lissoclinum patella* colonies and *Halimeda opuntia* patches determined from transects in a coral reef lagoon in Iwyama Bay, Palau. Sample sizes (n's) refer to number of colonies (columns 1-6, 10), number of patches (columns 7-8, 11), or number of photographs (column 9).

	L. patella colonies in *H.opuntia* patches			*L. patella* colonies on coral rock			% cover of *L. patella*		open atrial siphons of *L.patella*		*H. opuntia*
	colony length (cm)	colony width (cm)	colony height (cm)	colony length (cm)	colony width (cm)	colony height (cm)	in *H. opuntia* patches (%)	on coral rock (%)	siphons per colony area (#/m²)	pumping rate per siphon (cm³/s)	patch diameter (m)
mean	6	4	7	6	3	3	22	7	830	0.159	0.72
SD	4	2	3	3	1	2	22	14	591	0.141	0.86
n	41	41	41	22	22	20	6	10	19	13.0	13

	U at 30cm (m/s)	Ū (m/s)	K_A (m/s)	K_B (m/s)
site 1	0.06 ±0.01 (n = 5)	0.03 ±0.02 (n = 9)	0.001 ±0.001 (n = 9)	0.0001 ± 0.0001 (n = 9)
site 2	0.02 ± 0.01 (n = 5)	0.03 ± 0.02 (n = 12)	0.009 ± 0.008 (n = 12)	0.002 ± 0.003 (n = 12)

shallow sites, hence it is not surprising that there was no
significant difference between the ū's, K_A's, and K_B's
measured over periods of minutes for dye released near the
surface versus dye released near the substratum (paired-t
test, $p \geq 0.3$ for all comparisons). There were significant
differences within a site between ū's measured at different
times in the tidal cycle (Kruskal-Wallis, $p > 0.05$).

Water pumping by *L. patella*

Although the volume of water pumped per time through an
atrial siphon was greater for large colonies than for small
ones (Fig. 5, Kendall Tau, $p = 0.006$), there was no
significant association between colony size and the volume
of water pumped per horizontal plan area of colony (Kendall
Tau, $p > 0.05$). Therefore, we estimated the volume of water
pumped by the *L. patella* on an area of substratum by the
product of the pumping rate per siphon, the number of
siphons per plan area of colony, and the percent cover of
L. patella (Table 1). By dividing this product by the
volume of water advected across an area of substratum per
time, we obtained the proportion of the flux of water
across the habitat that was processed by the *L. patella*
living there (Table 3). These estimates indicate that,
although flow was very slow at the sites we studied, *L.
patella* only processed a tiny fraction of the water moving
past them, even when at high density in *H. opuntia* patches.

DISCUSSION

Flow microhabitats

Benthic ascidians like *L. patella* and turf-forming algae
like *H. opuntia* that hug the substratum are buried within
the benthic boundary layer and encounter flow velocities
lower than freestream. Thus, velocity measurements made
by current meters deployed in the water column do not
reflect the flow microhabitats of such organisms.

Although macrophyte canopies can reduce the water flow
encountered by organisms living in them (e.g. Koehl 1986;
Worcester 1995), *L. patella* colonies in *H. opuntia* patches
are not buried within the turf, but rather have their upper
surfaces at the top of the algae where they encounter
skimming flow over the turf. Therefore, *L. patella* colonies
in patches of *H. opuntia* experience similar boundary shear
velocities (u_*) to those experienced by colonies on
neighboring bare substratum. Since the u_* are similar, the
flux of momentum, dissolved substances, and particles between
the water and the benthic ascidians (e.g. Nowell and Jumars
1984) should be similar for colonies in and outside the
algal patches.

Larval dispersal

Advection and turbulent diffusion measured on kilometer
scales (e.g. Wolanski 1993, 1994) are suitable for modeling
the dispersal of long-lived larvae of fish, coral, or
starfish, but they are not useful for analyzing the dispersal
of short-lived larvae or of gametes spawned into the water
column (e.g. Thomas 1994). Our measurements of ū's, K_A's
and K_B's at the spatial scale of meters and the temporal
scale of seconds to minutes are more appropriate for
quantifying the transport and mixing of gametes and short-
lived larvae.

The behavior of *L. patella* larvae has been studied in the
field by Olson and McPherson (1987). *L. patella* release
their tadpole larvae at midday; the larvae first swim up
for about a minute, and then move back down toward the
substratum. Although *L. patella* larvae can swim for over
an hour in the lab, they usually remain in the water column
<10 minutes in the field and are transported distances of
<10m by ambient currents. Our data suggest that the
dispersal distances of larvae released by colonies in *H. opuntia* turf
are similar to those of larvae released by colonies on bare
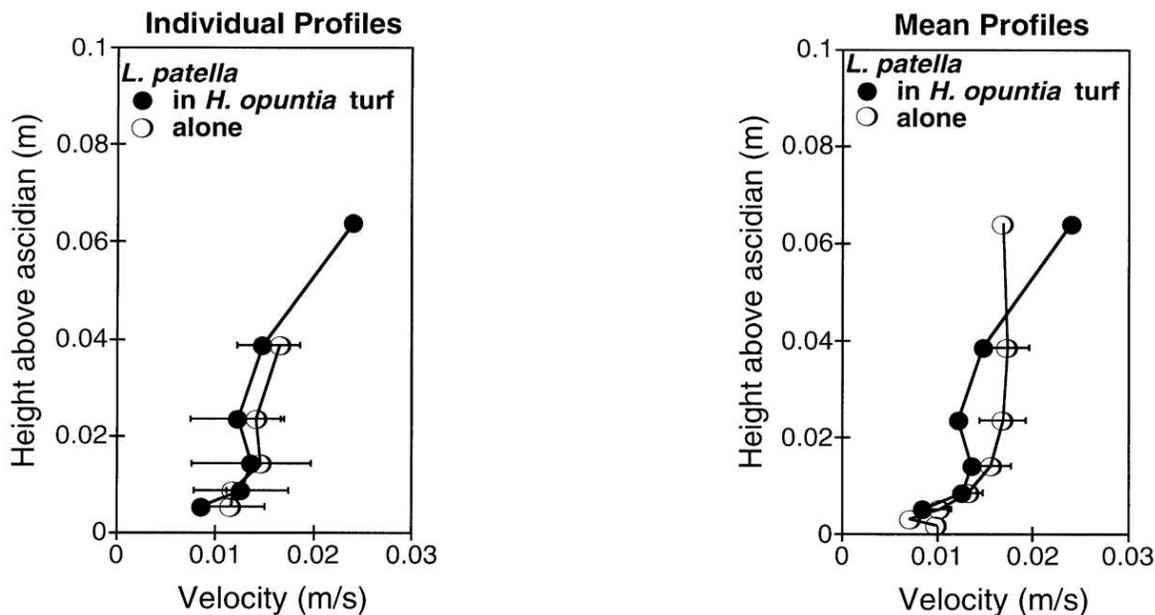substratum. However, since larvae released at midday

Fig. 3: Velocity profiles measured in the flow tank. "Individual profiles" shown in the graph on the left are ex-
amples of measurements made from a single photograph; velocities at each height are the average of all particle tracks
within a depth bin centered at that height. "Mean profiles" in the graph on the right show the mean velocities at each
height averaged over all individual profiles (i.e. all photographs). Error bars are +/- one standard deviation.

Table 3. Percent of ambient water flux processed by the ascidian *L. patella*. The percent cover of ascidians was highest within the patches of *H. opuntia*. The "entire site" values were calculated using the percent cover data for entire transects crossing both sand and turf.

	High Tide	Low Tide
In *H. Opuntia* patches	0.04%	0.69%
In the entire site	0.02%	0.32%

encounter different stages of the tidal cycle from one day to the next, the dispersal distances of larvae released on different days by the same colony should differ. Our data also suggest that the rate of horizontal transport of larvae is the same throughout their trajectory up and then back down in the water column at our shallow, well-mixed sites. In contrast, Worcester (1994) found that ascidian larvae that swam to the air-water interface in a wind-swept estuary with seagrass meadows were transported horizontally more rapidly than those deeper in the water column.

Mass transport on the scale of meters in a shallow lagoon
Our measurements of advection and mixing at the spatial scale of meters in Iwayama Bay can be compared with similar dye measurements made at other types of coastal sites. The slow $\bar{u}$'s (a few cm/s) are comparable to those measured in temperate estuaries subjected to tidal flow, as are the anisotropic mixing coefficients, with K_A's of order 10^{-3} m^2/s (Worcester 1995). Surprisingly, the advective velocities and mixing coefficients measured at our calm lagoon sites were also of the same order as those measured over corals subjected to waves on the leeward side of Lizard Island, Great Barrier Reef (Best et al., unpublished data). Although the instantaneous velocities at the wavy reef were much greater than those in the protected lagoon, net transport across the coral site was slow because water motion in waves is orbital. Because of this back-and-forth water motion in waves, even the advection and mixing measured at
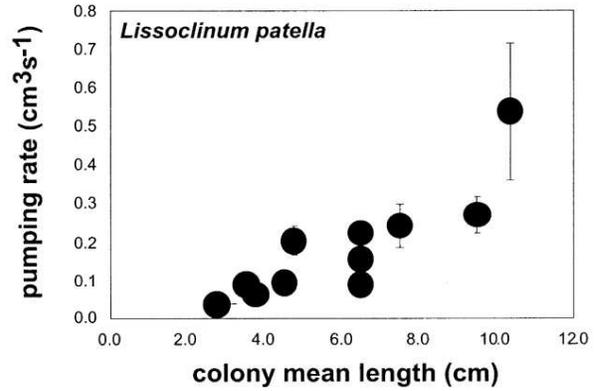

Fig. 4: The advective speed, $\bar{u}$, and mixing coefficients, K_A and K_B, measured at the bottom and the surface in water above *H. opuntia* turf and above bare substratum (coral rock and sand). Site #1 is represented by triangles, and site #2 by circles.

Fig. 5: Mean pumping rate for an individual atrial siphon, as a function of colony size. The colony mean length is 0.5(L+W), where L is the colony length, and W is the colony width.

very exposed wave-swept rocky shores of North America (instantaneous velocities of 5 to 10 m/s) were only tenfold greater than we measured at our shallow lagoon sites in Palau (Koehl et al. 1993; Koehl and Powell 1994).

Pumping by *L. patella*
The flux of water through *L. patella* was only a fraction of a percent of the flux of water through our study sites. Therefore, these ascidians were not in danger of depleting the water of resources, even when in high densities in *H. opuntia* turf (Table 3). They and their *Prochloron* were also unlikely to have much effect on the chemistry of the water in the lagoon. However, other *Prochloron*-bearing ascidians, *Didemnum molle*, in Iwayama Bay processed over 10% of the water moving across their habitat (Koehl and Powell, unpubl. data). In contrast, pumping rates of various solitary temperate ascidians are about three orders of magnitude faster than those we measured for the compound didemnid species in Palau (Fiala-Médioni 1978a, 1978b; Charriaud 1982), and dense populations of such solitary ascidians can have a profound effect on the water column (Petersen and Riisgård 1992).

Conclusions
Calcareous algal turf (*Halimeda opuntia*) did not affect the velocity profiles encountered by ascidians (*Lissoclinum patella*) in a shallow coral reef lagoon in Palau, nor did the algae affect advection and mixing on a scale of meters. Mixing in such shallow sites is highly anisotropic, being greatest parallel to the direction of water flow. *L. patella* pump water through themselves, but only process a small proportion of the water moving across their habitat.

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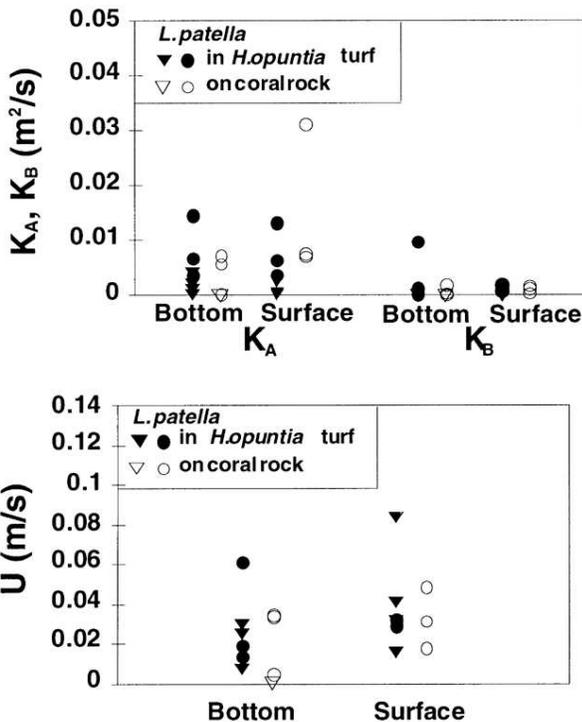
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