

6 *Flow*

INTRODUCTION

Hydrodynamic force is a direct environmental factor, but water motion also affects other factors including: nutrient availability, light penetration (turbidity), and temperature and salinity changes (Lobban and Harrison 1994). Most algae are attached by a holdfast to the substrate, which prevents their being swept away by waves and tide. Unlike most plants, seaweeds do not need to be rooted as their nutrients are derived primarily from the surrounding water, not the substrate. Communities of unattached macroalgae are commonly found in calm coastal waters (Norton and Mathieson 1983).

Flow and Morphology

Studies on the influence of water flow on macroalgae have predominantly focused on the mechanical stress of drag and the effects of diffusion limitation through boundary layers (Lüning 1990). For most sessile benthic algae these are the two major hydrodynamic forces of importance (Mann and Lazier 1996). The trade-off between too much water motion imposing drag, and too little imposing diffusion stress and nutrient limitation, results in modifications of algal form and function (Lobban and Harrison 1994).

The mechanical stress of currents and waves impose drag, especially important to large algae (e.g., kelps) on rocky coastlines where they are exposed to high-energy environments. Elasticity of stipes and blades is a common adaptation, allowing kelps to survive in the upper sublittoral zone on wave-beaten shores, and may allow the thalli to bend parallel to the flow, bringing them closer to the bottom boundary layer where the flow

is reduced (Lüning 1990). Flexibility is an important means of reducing drag and allowing growth to greater sizes (Denny *et al.* 1985). The long flexible blades of kelps may actually be advantageous in that growth beyond a certain length, which exceeds the product of average water speed and half the wave period, will not further increase the drag force pulling on the holdfast (Koehl *et al.* 1991; Vogel 1994). Many macroalgal kelps in temperate rocky shores are sufficiently long for the phenomenon to be significant; they go the great lengths to avoid drag (Vogel 1994).

Another adaptation to drag are the smooth and narrow fronds found in individuals from high-energy environments, whereas broader fronds with undulate ruffled margins tend to be restricted to individuals found in areas with lower currents (Koehl and Alberte 1988). Plants from exposed sites were found to have only a quarter the drag per unit surface area of plants from more protected sites; the flat narrow blades stack tightly in higher flows, reducing drag (Koehl and Alberte 1988; van Tuessenbroek 1989). The undulate margin reduces the deleterious effects of self shading and enhances uptake of dissolved nutrients in low-energy environments (Gerard and Mann 1979). This plasticity in morphology allows a balance between the twin constraints of diffusion stress and drag forces.

Similar intra-specific differences were recorded by de Paula and de Oliveira (1982) in the tropical alga, *Sargassum cynosum*. In sheltered environments with low drag forces, plants grew five times as high and had over five times the biomass, yet had holdfasts with nearly 40% less bottom area; plants from exposed locations invested 47% of the dry weight in the holdfast, while plants from sheltered areas invested only 11%, clearly demonstrating the impact of drag on morphology. What especially needs to be emphasized is the complexity of intra-specific tuning of morphology, and reconfiguration with habitat based on increasing hydrodynamic forces (Lobban and Harrison 1994).

Flow and Boundary Layers

In the previous chapter the importance of boundary layer effects on nutrient uptake was alluded to. The viscosity effects of water at the scale of boundary layers limits diffusion rates of gases and ions (Lüning 1990; Vogel 1994). Viscosity causes the average speed of flow to decrease from the open water to zero at the boundary, the no-slip condition (Denny 1988). As turbulent eddies also decrease to zero at the boundary, the efficient transport of nutrients and wastes by turbulence is replaced by slow molecular transport at a rate according to Fick's law, a restriction known as the diffusion limitation of metabolism (Vogel 1994; Mann and Lazier 1996). The thickness of the boundary is reduced by the speed of the water flowing over it (Vogel 1994). For seaweeds this can be achieved by attachment in locations with tidal currents and wave action. It has been shown by numerous investigators that nutrient uptake and photosynthesis tend to increase with increasing water motion (see list of reviews in Lüning 1990 and Mann and Lazier 1996).

The rate of nutrient transport depends on the thickness of the diffusion boundary layer, with thickness determined by turbulent mixing and water flow (Lüning 1990). For nitrate and phosphate nutrients in seawater, the diffusion boundary layers are only about one-eighth the thickness of the velocity boundary layer (Lobban and Harrison 1994). Morphological adaptations like marginal outgrowths, undulated margins, and holes in the thallus may enhance turbulence in laminar flow, or hair-like projections may penetrate the boundary layer, thereby reducing diffusion limitation (Raven 1981; Lüning 1990). Plants can therefore modify their hydrodynamic micro-habitats by adjusting their morphologies (Wheeler 1988).

In many tropical macroalgae, thalli are composed of cylindrical branches, rather than fronds or blades, presenting quite a different hydrodynamic micro-environment. The flow here is over and through a series of narrow, closely spaced, rod-like surfaces. At all velocities the thallus as a whole will dampen large-scale turbulence, and water passing through the thallus will exhibit smoothed flow. At flow speeds of 6-12 cm·s⁻¹ (depending

on the diameter and spacing of the branches) micro-turbulence will occur, which is important for gas and nutrient exchange (Anderson and Charters 1982; Lobban and Harrison 1994). The optimum range of water velocity lies in the range 10-20 $\text{cm}\cdot\text{s}^{-1}$ because algae can get the maximum benefit from a turbulent velocity boundary layer and thus enhanced diffusion of nutrients, while having minimal effects on drag (Wheeler 1988; Lobban and Harrison 1994).

Drifting macroalgae may experience diffusion boundary layer stresses akin to phytoplankton in that they are also moving passively with the water column, and therefore less likely than attached algae to have a rapid flow of water past the thallus. This can lead to potential nutrient limitation, which may be overcome by sinking through the water column as algae are slightly denser than seawater (Norton and Mathieson 1983), or by settling in areas with moderate flows that are insufficient to remobilize the drift clump.

A final consideration on boundary layers is that the benthos-water column interface is also characterized by a boundary layer (Vogel 1994; Mann and Lazier 1996), which may become especially important to algae in low-flow situations. Drift aggregations frequently result in extensive mats covering the benthos in areas of low flow (Norton and Mathieson 1983). In the absence of water flow, tissues within these mats can quickly become nutrient limited because of poor exchange processes between the interstitial water and the water column above the mat (Stimson and Larned 2000). In this case nutrients derived from decomposition (Zimmerman and Montgomery 1984; Hanisak 1993) or exchange with sediment porewaters (Raven 1981; Williams 1984) may be of greater importance than nutrient exchange with the overlying water column.

Flow and Spatial Distribution

From initial model runs performed after I measured data on light, temperature, salinity, and nutrients, I came to suspect that hydrodynamic flow may play an important role determining distribution and abundance of drift algae in the Bay, with low-energy sites

retaining mats of algae and high-energy sites transporting algae. This means that net accumulations of drift algae may occur at low-flow canal sites and net flux of algae can occur through high-flow oceanic cuts.

Clumps of drift macroalgae in seagrass systems in Florida vary in size (10-50 cm diameter) and most typically are comprised of rhodophyte (red algae) taxa (Bell and Hall 1997). Drift algae can originate from hard substrates located outside seagrass beds or alternatively break off *in situ* after epiphytic growth on seagrass blades (Norton and Mathieson 1983; Bell and Hall 1997). Regardless of the original source, drift algae are moved via wind and water currents. Passive movement of drift algae implies that the hydrodynamic regime of a body of water may be critical in determining the distribution of areas of algal retention or accumulation. Bell and Hall (1997) found that spatial variation in drift distribution was highly correlated with the local energy regime in Tampa Bay, with passive transport and deposition of algal clumps strongly linked to the bay-wide hydrodynamic regime. Algal movement was heavily dictated by winds and currents, with hydrodynamically less active environments favoring accumulation of drift at a greater rate than sites with high current velocity (e.g., inlets) or extensive exposure to waves.

At a local scale, drift algae display highly aggregated distributions within seagrass beds. Some seagrass beds may retain more drift algae than others because of blade morphology (Virnstein and Carbonara 1985); thus, the spatial distribution of algae may be closely linked to seagrass species composition and spatial distribution. Transport of drift algae was greatest in shallow-water seagrass beds with short canopies during periods of wind induced or tidal currents (Madley and Bell 1996). Higher amounts of drift biomass (3.5-18.5 times as much) were found in large seagrass patches, compared to smaller patches, in accordance with patterns expected if algae accumulate in zones of attenuated water flow (Bell *et al.* 1995). Dissimilar algal accumulation may also be related to the location of source populations relative to seagrass patches, patch orientation relative to

flow, and the route of dispersal between these positions, *i.e.*, flow direction and magnitude.

To test the hypothesis that hydrodynamic flow within Biscayne Bay is affecting distribution of drift algae, there are a number of questions that needed to be addressed:

- What are the circulation patterns of tidal flows within Biscayne Bay?
- Are drift algae entering the Bay through tidal inlets, and if so, what are the abundance and composition of this drift?
- What flow speeds are required to transport clumps of drift algae?
- How does substrate type (complexity) influence transport rates?
- What is the persistence time of drift algae under different flow regimes, and how does this compare with measurements taken at the field sites within the Bay?

METHODS

A number of aspects of hydrodynamic transport were examined, including the forcing functions based on simulation models and sediment characteristics, and responses by drift clumps to flow. Responses of interest included the composition and biomass of drift entering into the Bay, flow rates required to transport drift algae, the effects of substrate type on transport speeds, and the persistence time of algae in a given location under various flow scenarios.

Hydrodynamic Regime

Hydrodynamic flows from tidal and wind driven circulation were obtained for Biscayne Bay using the output of a hydrodynamic model (Wang *et al.* 2001). Supporting arguments for Bay-wide circulation patterns were developed from maps of bathymetry (S. Tosini, pers. comm.) and sediment depth and composition, as proposed by Bell and Hall (1997).

Sediment depths were measured at 222 sites in Biscayne Bay during periodic seagrass and hard-bottom surveys conducted by CMEA scientists. From these data I plotted a map of sediment depths using ArcView's Spatial Analyst extension (see spatial interpolation methods in Chapter 5, Appendix).

Drift Algal Responses

Many of the experiments in this section were conducted near the University of Miami's Rosenstiel School of Marine and Atmospheric Science (RSMAS) boat dock. RSMAS is located on Virginia Key, FL, with the docks facing south into Bear Cut. This Cut, like many others between barrier islands on the eastern side of Biscayne Bay, has a significant tidal flow from the Atlantic Ocean to the Bay. With the tidal frequency twice daily, the RSMAS docks are subjected to strong currents ($50\text{-}70\text{ cm}\cdot\text{s}^{-1}$) four times per day. Experiments One and Two were performed near the RSMAS docks in a seagrass bed dominated by *Syringodium filiforme*. The bed was located about 10-20 m offshore and between 5-10 m from the outer pilings (OP) of the docks (Fig. 1). The seine net used in Experiment One was tied between OP 2 and OP 3, just beyond the offshore edge of the seagrass bed, which is located between OP 1 and OP 2 (Fig. 1).

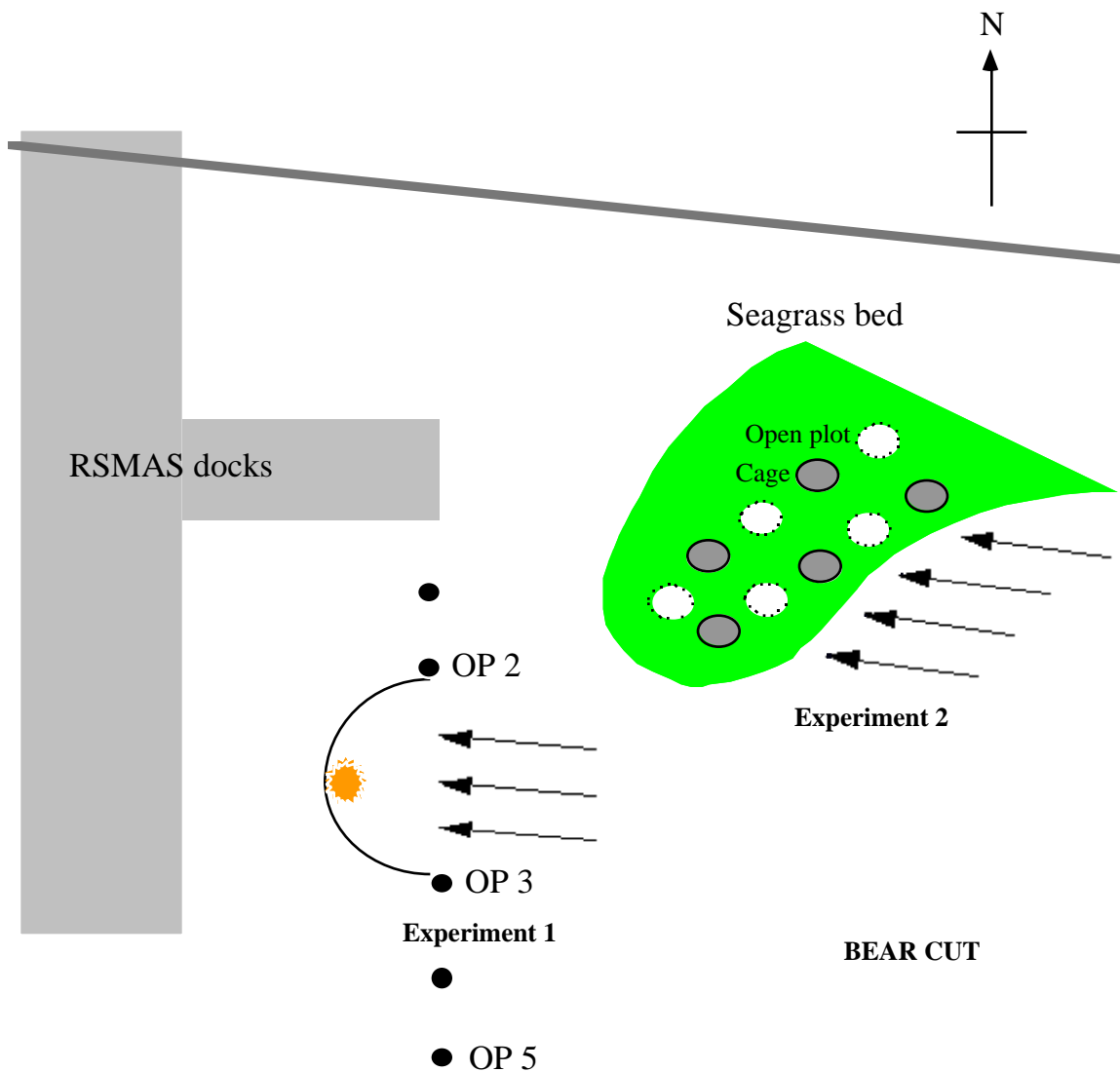


Fig. 1: Schematic of the two experiments at the Bear Cut study site near the RSMAS docks, not to scale.

Experiment 1: Biomass and Composition of Drift Entering Through Bear Cut

Macroalgal biomass and composition were determined from samples caught in a 50' x 0.25" (19.67 m x 1.2 cm²) mesh seine net (C5S2 Minnow Seine, Memphis Net and Twine Co. Inc., Memphis, TN) that was tied securely to two wooden pilings (OP 2 and OP 3) at the RSMAS docks (Fig. 1). The seine net was weighted with 3 pound (1.5kg) dive weights along the bottom margin, and buoyed by additional lobster-trap floats attached by

cable ties along the upper edge, to ensure that the complete vertical extent of the water column was sampled, even during peak flow velocities.

During daylight hours at the end of every tidal cycle, all the biomass in the net was hand collected into a mesh bag during slack tide. Algae were sorted in the laboratory to the lowest taxonomic level (usually species, but occasionally only to genus). Blotted wet weight by Division (Phaeophyta and Rhodophyta) and taxonomic composition were recorded. Samples were collected over a 5-8 day period to determine inter-tidal variance, and sampling was repeated three times over the course of a year (Aug., Dec., May) to determine seasonal differences in the species composition of algae. Separate two-way ANOVAs testing season (random effect) and tide (fixed effect) were performed on the biomass data for each Division.

Experiment 2: Drift Transport and Persistence under a Variety of Flow Regimes

1. Flow: Tidal flow regime in Bear Cut was measured at OP5 in June 1999 and plotted for a 25 day period. Mean velocity of flood and ebb flows, as well as the mean velocity of the strongest 10% of the flows, were determined from these data. Flows at the five outer pilings of the RSMAS docks were determined by T. Jones (pers. comm.). Flow measurements were conducted at the surface only. A floating object was placed near each pylon and timed over a known distance. No flow measurements were made directly at the pylons because of turbulent eddies entraining any object placed directly at the pylon, which would not be indicative of the actual flow velocity past the pylon. A one-way ANOVA was performed on the flow rates obtained.

2. Transport: Movement of drift algae under two flow regimes were experimentally tested in the seagrass bed near the RSMAS docks. Flow velocities were determined at peak incoming tide and approximately half tide with a rotary flow-meter (Model 2030, General Oceanics Inc., Miami FL). Transport rates of clumps of drift algae of a known biomass (100 and 500 grams spun wet weight) were measured at each current velocity by recording

the transit time over one meter distance. Five replicate measurements were taken, and t-tests on transport rates comparing clump sizes at a given current velocity were performed.

3. Persistence: Residence times of drift algae under three flow regimes were compared. The two high-flow regimes were located in Bear Cut, where open and enclosed plots (0.25m²) were set up in the seagrass bed. A no-flow control was set up in one of the CMEA Mesocosms (see Chapter 3 for description of facilities), identical to the enclosed plots in the seagrass bed.

In the grass bed, open plots (= high-flow) were marked at four corners by Rebar stakes pushed into the sediment, and for the enclosed plots (= medium-flow) 1" Vexar mesh was tied to the Rebar stakes, effectively reducing current by almost two-thirds. Plots in the mesocosm had no tidal flows, but otherwise identical physical conditions to the Bear Cut site (depth, light, temperature, water quality, benthic habitat). Flow measurements were taken at each plot and a one-way ANOVA performed on the measured speeds.

Persistence times of drift were recorded for the two flow regimes in Bear Cut and the no-flow control in the mesocosm during the summer (Aug. '99). Control trials were repeated in summer (Aug. '99) and winter (Feb. '00) to determine seasonal differences. Approximately one kilogram wet weight (spun to remove excess water in a salad spinner [Hay 1981]) of drift algae were added to each of the plots. The plots were revisited after the first tide, and all the algae in the open plots had been removed by the current. Remaining biomass (spun wet wt) of drift in the enclosures was measured every 24 hrs after the start of the experiment, until no more algae were present. The influence of flow on persistence of the remaining biomass was analyzed by repeated measures ANOVA with time treated as a blocking variable (Neter *et al.* 1996).

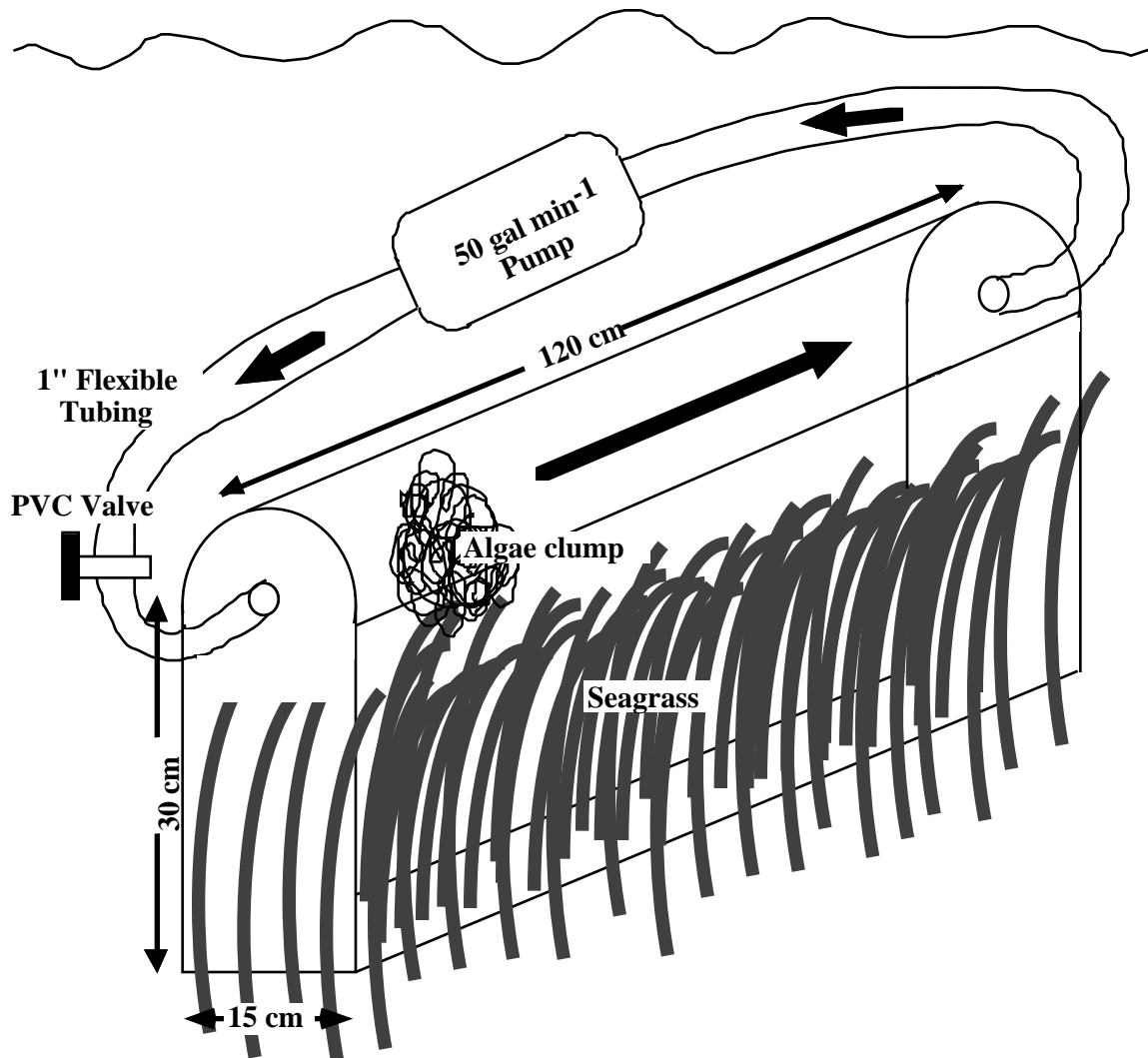


Fig. 2: Design of a flume used to measure transport speeds of drift algae under increasing flow velocities over different substrate types in Experiment 3.

Experiment 3: Drift Transport Rates over Various Seagrass Substrates

A flume was built out of a half-open cylinder of clear acrylic (1.2m long x 15 cm diameter) with glass sides (30 cm high) and placed over four different seagrass substrates: sparse, medium, and dense *Thalassia*, and dense mixed *Thalassia* and *Halodule* in the CMEA mesocosms (see Table 6 for densities). Recirculating flow within the flume was provided by a 50 gallon (189.2 l) min⁻¹ submersible pump (Model 6-CIA, Little Giant

Pump Co., Oklahoma City, OK), regulated by a 1" PVC ball valve to control the flow rate (Fig. 2). Flow velocities used were determined by recording the time it took a front of red dye (Red Food Color, McCormick & Co. Inc., Hunt Valley, MD) to traverse the flume.

A clump of drift algae (<100 g wet wt) was placed in the flume, through a moveable glass panel near the incoming nozzle and transit times measured ($n = 3-7$) under four different flow velocities (0, 7.5, 20, and 50 $\text{cm}\cdot\text{s}^{-1}$ approximately). Data were plotted on a log-log plot of algal transport speed against current velocity in the flume for each of the four seagrass substrate types. Data were analyzed using the Sheirer-Ray-Hare extension of the non-parametric Kruskal-Wallis test, followed by Tukey's post-hoc comparisons to determine like groups.

Experiment 4: Tidal Flow Velocities and Persistence Time of Drift Algae at Field Sites

1. Flow: Numerical output of the Wang circulation model for Biscayne Bay was used to determine separately for flood and ebb tides the mean tidal velocity, the mean velocity of the upper 10 percentile of flows, and peak velocity at the six field sites over the period 1996-1999. Data for Bear Cut were obtained from the flow meter results obtained from OP5 in Experiment Two. t-tests of the absolute values of the mean and upper 10 percentile velocities were compared between incoming and outgoing tides within each site. Flood and ebb tidal velocities were compared across sites by separate one-way ANOVAs.

As the model output for the specific field site locations was not validated, I used chalk block dissolution rates to provide an independent, integrated measure of relative water motion at given a location (Doty 1971; Vogel 1994, pg. 129). The relative water motion (integrated wave motion and tidal current flows) was measured at the surface of the seagrass canopy at five sites (Bear Cut, BC, SK, BKP, FP) in the dry and wet seasons.

Ten dried and pre-weighed carpenter's chalk blocks were placed in mesh bags (1 mm mesh size) and attached to individual wooden dowels, with the chalk blocks positioned just above the seagrass canopy at each of the sites. The chalks were left in the field for 48

hours, retrieved, rinsed in freshwater, dried, and re-weighed. The weight loss of a set of control blocks placed in still water at 35 psu salinity was also determined. Mean final weights of the chalk-blocks were compared among sites using a two-way mixed model ANOVA of site (random effect) and season (fixed effect). Student's t-tests of chalk dissolution in the RSMAS dock-flow experiments were done to compare results of high-flow and no-flow conditions in Experiment 2.

2. Persistence: Residence times of drift algae at four field sites (BKP, FP, BC, SK) were determined from data collected by Irlandi (unpubl. manuscript) from 0.25m² plots during 9/97-8/98. In order to determine the residence time and movement of algae over a plot, five permanent 25 m long transects 10 m apart were established at each site. Each transect line was marked with a subsurface PVC pole at either end, and a polypropylene line ran along the seafloor connecting the two poles. Eight randomly chosen 0.25 m² quadrats were permanently established along each transect line (see Chapter 2, Fig. 2). Half (*i.e.*, four) of these quadrats were cleared of algae in September 1997. At monthly intervals percent cover of algae was determine and the cleared plots re-cleared. The percent cover in the remaining uncleared permanent quadrats was determined on a monthly basis.

In a second experiment I set out arrays of twelve permanent 1 m² quadrats at my six field sites from 8/98 - 8/99. Every six weeks the quadrats were photographed and the percent cover of drift algae in the digitized images was determined (see Chapter 2 methods).

From the resulting percent cover database, the frequency of quadrats surveyed that contained drift was plotted for all sites and months surveyed. In addition mean transition probabilities were determined for a two-state (drift present, drift absent) model of drift dynamics at each site based on the monthly data for each sampling program. The four possible transitions are:

$P(0,0)$ = no drift at t_1 or t_2 ,

$P(0,1)$ = no drift at t_1 changes to drift present at t_2 ,

$P(1,1)$ = drift present at t_1 and persists to t_2 ,

$P(1,0)$ = drift present at t_1 but removed by t_2 .

where t is a monthly time-step.

RESULTS

Hydrodynamic Regime

Flow

Flow-vector outputs from the Wang hydrodynamic circulation model (Wang *et al.* 2001) indicate high flow regions occur at the oceanic cuts along the eastern margin of Biscayne Bay adjacent to the Atlantic Ocean. Tidal flows of some magnitude are predicted by this model, with vectors of magnitudes up to $100 \text{ cm}\cdot\text{s}^{-1}$ or greater found at Bear Cut, the Safety Valve, Caesar Creek, and Broad Creek inlets (J. Wang, pers. comm.). Flows associated with tidal exchange through Broad Creek had velocities up to $40 \text{ cm}\cdot\text{s}^{-1}$ (Fig. 3). Tidal flows decline in magnitude in a westward direction, so that the lowest current speeds ($10 \text{ cm}\cdot\text{s}^{-1}$) are typically found along the western mainland coastline (Fig. 3). Interestingly flows at Fender Point (FP) were net positive during the period analyzed, and there was not a distinct sinusoidal pattern to tidal flows like at the other sites (Fig. 3). The velocities predicted by the model are dependent on the magnitude of tidal exchange with higher tidal volumes during spring tides, and wind driven water circulation patterns within the Bay (Wang *et al.* 2001).

Bathymetry

Depth of the Bay's basins dictates in part the tidal circulation patterns involved (Hoffmeister 1974). Depth at the central part of the Bay increases to 4-5 m, with shallower margins around the periphery of the Bay (Fig. 4). Featherbed Banks reaches across the

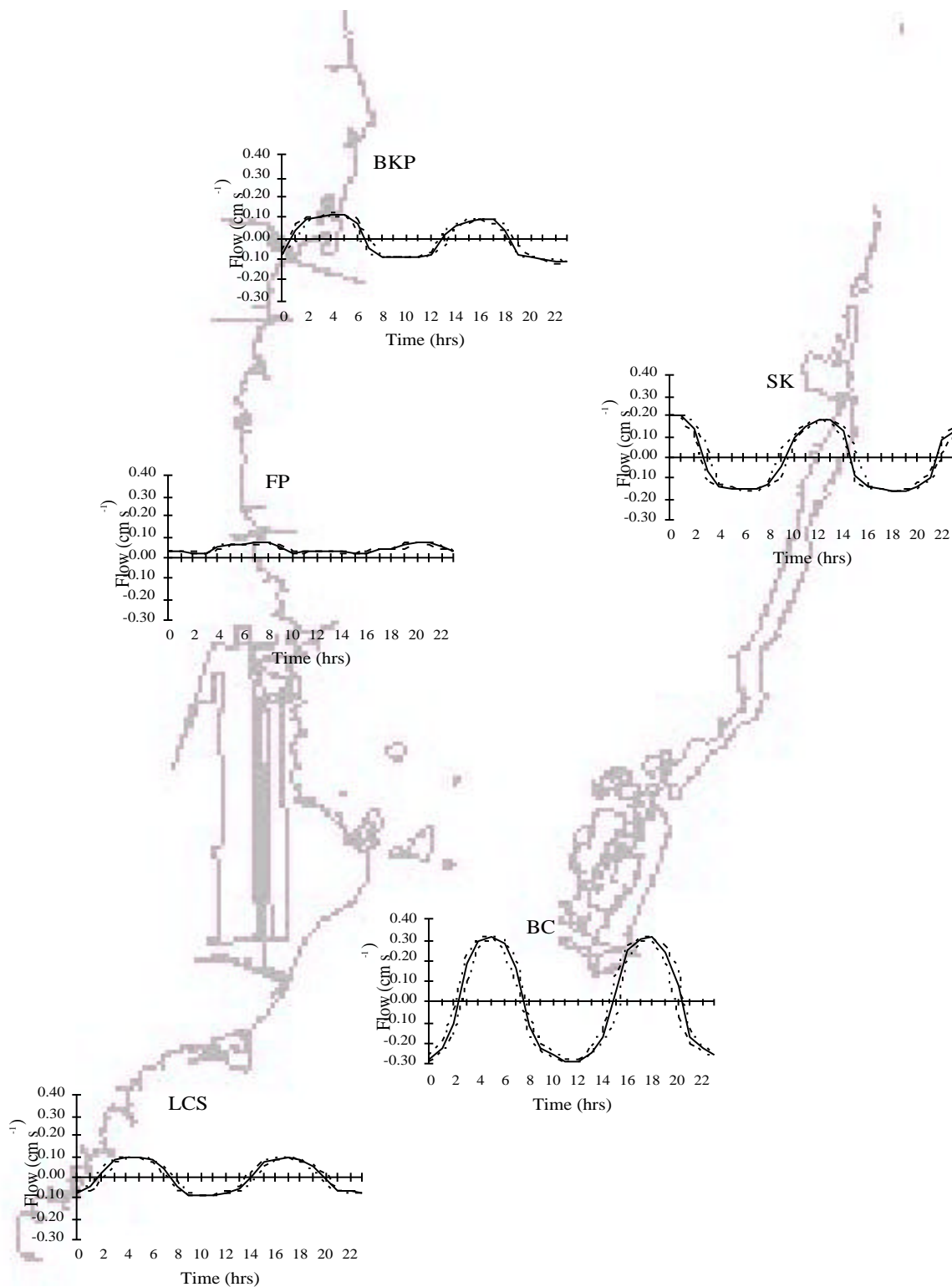


Fig. 3: Median (\pm min., max.) incoming and outgoing tidal flows over 24 hrs for selected study sites in Biscayne Bay. Positive flows denote incoming tides, while negative values indicate outgoing tides. Greater flows are associated with tidal exchange through cuts while weaker tidal currents occur towards the mainland.

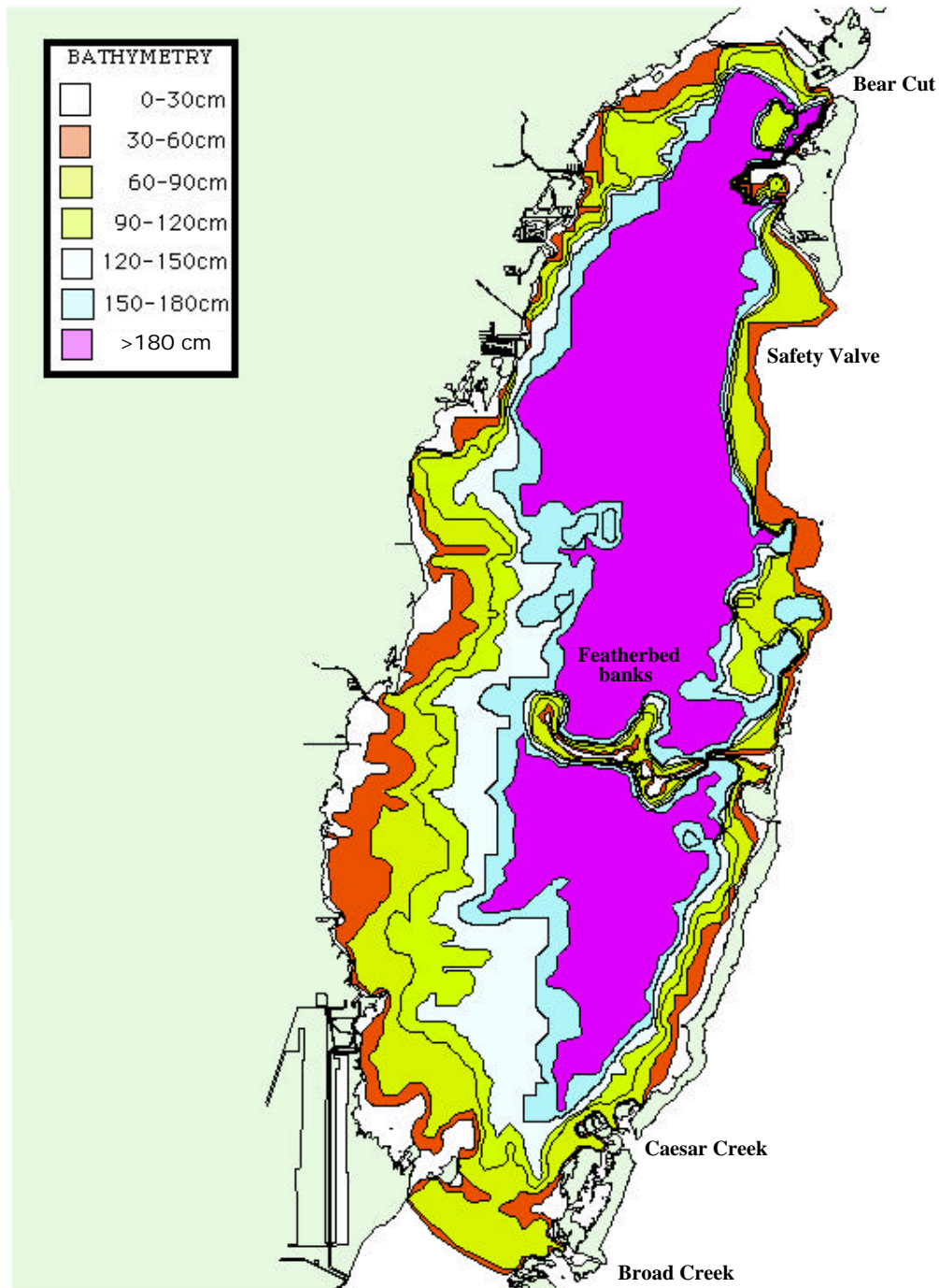


Fig. 4: Biscayne Bay bathymetry, with depths in centimeters. Maximum depth in the center of the Bay reaches approximately five meters. Features mentioned in the text are labeled. Source: S. Tosini, CMEA data.

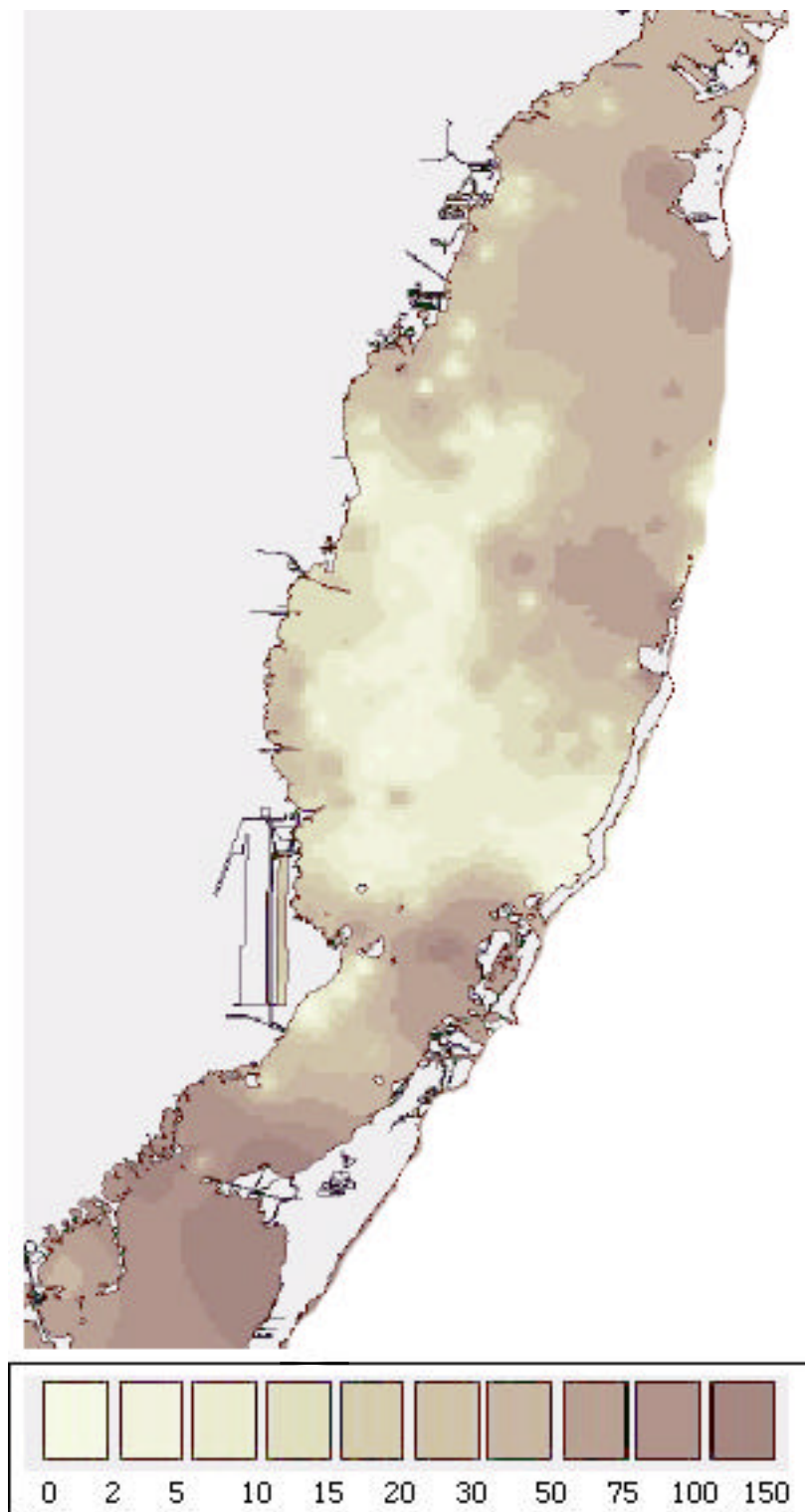


Fig. 5: Mean sediment depths (cm) in Biscayne Bay interpolated from measurements at 222 locations.

center of the Bay in an E-W direction and may influence the tidal circulation resulting in predominantly N-S flows occur along the western margin of the Bay (Figs. 3 and 4).

Sediments

Sediment depth, and the percent fine fraction of the sediments, are often indicative of net depositional environments with low flow-velocities (Gray 1981, Fonseca *et al.* 1982). Sediment depths tend to be high at the Safety Valve, a region of high flows, and low along the western mainland shoreline, where lower flows are indicated by the Wang model (Fig. 5).

This discrepancy can mostly be resolved by the presence of extensive *Thalassia* beds in the Safety Valve (Alleman *et al.* 1995) that bind the sediments to prevent removal by current flows (Zieman 1982). Furthermore, the presence of seagrass aids in the deposition of fine sedimentary particles, which can result in accretion of sediments over time (Zieman 1982). The lack of extensive marine sediments along the western section of the Bay is a result of the geologically recent rise in sea-level resulting in a prograding marine facies over older Everglades-like terrestrial muds (Hoffmeister 1974). The resulting sediments overlying the limestone bedrock are thin with interspersed circular areas of deeper sediments, which often contain a dense cover of *Thalassia* (the terrestrial origin of these patches is speculated on by Zieman 1972).

Drift Algal Responses

Experiment 1: Biomass and Composition of Drift Entering Through Bear Cut

Drift algae transported through Bear Cut was comprised of *Sargassum* (a brown alga) and about 15 genera of red algae (Table 1). At the genus level, composition of the drift algae being transported through Bear Cut is 50% similar to the complement found at the canal sites. The three most common genera at Bear Cut are different from those found at the canal sites (Table 1).

Daily variability in biomass was high, especially of the *Sargassum* fraction, which was often present in the samples in a pulsed mode, *i.e.*, over a few sequential days a large portion of the total biomass contained *Sargassum*. This was observed to hold true for both flood and ebb tides, possibly indicating some back and forth transport of the same biomass on successive tides.

Total biomass collected varied among seasons, with larger average amounts of drift algae collected in May than the other two months sampled (Fig. 6). The late dry season is the period of peak drift algal biomass at most of the study sites in the Bay (see Chapter 2). Analysis of the *Sargassum* and rhodophyte fractions shows that mean biomass of *Sargassum* does not vary significantly either by season or by tide (flood vs. ebb) (Table 2). In contrast there is a significant increase in the biomass of red algae transported through Bear Cut in the month of May (Table 2), coinciding with the peak biomass period found at sites within the Bay, and from observational evidence of seasonal blooms on the reefs outside the Bay (Lirman and Biber 2000). There is also significantly higher biomass of red algae on incoming tides than outgoing tides (Table 2), possibly indicating a net transport of biomass from offshore into the Bay. However, this may be confounded by higher flow rates measured at this site on incoming tides than outgoing tides, although this is not necessarily indicative of flows thorough Bear Cut as a whole.

To remove this potentially confounding effect, I calculated the approximate volume of water filtered through the seine net during flood and ebb tides. The results indicate that during ebb tides a little over two-thirds the volume of water passed through the seine net compared to flood tides (with a total volume filtered of about $2 \times 10^5 \text{ m}^3$). Extrapolating this to the rest of Bear Cut, an initial estimate of total algal biomass entering and leaving through this Cut (one of many) into the Bay shows greater total biomass entering than leaving the Bay for both groups in all months, except *Sargassum* in May, and more biomass of red algae than *Sargassum* moving thorough the Cut in all months sampled (Table 3). From these data an estimate for total algal biomass moving through all the inlets

Table 1: Generic composition of drift algae coming through Bear Cut. Superscripts denote the three most abundant genera by biomass. Similarity at the genus level is 50%.

Algae	Bear Cut	Canal Sites
<i>Acanthophora</i>	X	X
<i>Bostrychia</i>	X	
<i>Ceramium</i>	X	X
<i>Champia</i>	X	
<i>Chondria</i>	X	X ²
<i>Cladophora</i>	X	X
<i>Crouania</i>	X	
<i>Dasya</i>	X ³	X
<i>Dictyota</i>	X ²	X
<i>Digenea</i>		X
<i>Gracilaria</i>		X
<i>Heterosiphonia</i>	X	
<i>Hypnea</i>	X	X
<i>Laurencia</i>	X	X ¹
<i>Polysiphonia</i>		X ³
<i>Sargassum</i>	X ¹	X
<i>Spyridia</i>		X
<i>Wrangelia</i>	X	

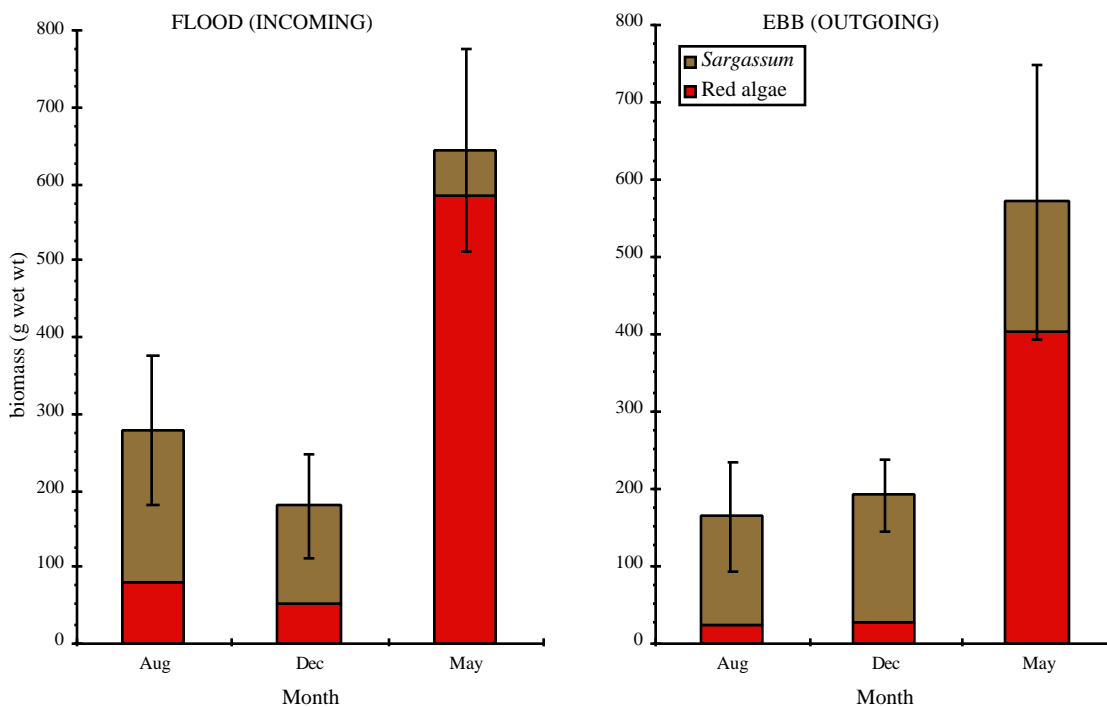


Fig. 6: Mean (\pm SD) biomass (spun wet wt) of drift algae transported by tidal currents through Bear Cut and collected from the seine-net in Experiment 1.

Table 2: Two-way ANOVAs of algal biomass by month (random factor) and tide (fixed factor), presented in Fig. 6. Significant effects are highlighted in bold font, and Tukey's post-hoc comparisons of significant results.

SOURCE	df	SS	MS	F	P
^a <i>Rhodophyta</i>					
Month (M)	2	74.932	37.4659	27.0261	<0.0001
Tide (T)	1	16.042	16.0482	11.5764	0.0016
M x T	2	1.3773	0.6889	0.4969	0.6122
error	39	54.065	1.3863		
	<u>Date</u>	<u>Aug.</u>	<u>Dec.</u>	<u>May</u>	
	Tukey's	B	B	A	
	<u>Tide</u>	<u>In</u>	<u>Out</u>		
	Tukey's	A	B		
^b <i>Sargassum</i>					
Month	2	0.119	0.0593	0.0240	0.9763
Tide	1	0.665	0.6645	0.2694	0.6071
M x T	2	2.141	1.0705	0.4341	0.6514
error	34	83.854	0.5946		

^aRhodophyte data were *ln*-transformed for normality (Shapiro Wilk's $W=0.9668$, $P<0.3331$) and homoscedasticity (Bartlett's $F=1.4048$, $P<0.2189$), with $r^2=0.6286$ for the ANOVA, $n=5-11$. ^b*Sargassum* data were *ln*-transformed for normality (Shapiro Wilk's $W=0.9485$, $P<0.0955$) and homoscedasticity (Bartlett's $F=0.9195$, $P<0.4669$), with $r^2=0.0342$ for the ANOVA, $n=4-10$.

Table 3: Biomass of drift algae calculated coming through Bear Cut into Biscayne Bay. Two major components of the drift, *Sargassum* and red algae are expressed as total biomass (kg) and standardized biomass ($\text{mg}\cdot\text{m}^{-3}$). Biomass of the floating *Sargassum* was calculated on only the upper 0.5m volume of the water column, while for red algae the entire depth was considered.

Month	Flood				Ebb			
	<i>Sargassum</i>		Red algae		<i>Sargassum</i>		Red algae	
	kg	mg m^{-3}	kg	mg m^{-3}	kg	mg m^{-3}	kg	mg m^{-3}
Aug.	26.3	1.0	131.5	0.5	14.0	0.8	35.2	0.2
Dec.	21.5	0.8	131.5	0.5	14.0	0.8	35.2	0.2
May	6.6	0.25	789.0	3.0	19.4	1.1	352.0	2.0

(Bear Cut, Safety Valve, Caesar Creek, and Broad Creek) into the Bay yields about 200 kg *Sargassum* plus 100 kg red algae = 300 kg (Aug., Dec.), or 50 kg *Sargassum* plus 500 kg red algae = 550 kg (May) moving into/out of the Bay per tide (*i.e.*, twice a day); about a half to one ton of biomass per day!

Experiment 2: Drift Transport and Persistence Under a Variety of Flow Regimes

2.1 Flow

Measures of tidal flow velocities were undertaken by Jones (2002) in 1999 at the docks. Comparative tidal velocities in an offshore direction at the five outer pilings (OP) of the RSMAS docks (Fig. 7A) were found to be statistically indistinguishable for the four outermost pilings, with only the one closest to shore (OP1) showing a significant reduction in flow velocities measured (Fig. 7A, Table 4). This is important, as a long-term measure of tidal flows at OP 5 was undertaken by B. Haus (T. Jones, pers. comm.) with a flow meter attached to a datalogger for the month of June 1999. The resulting tidal flow regime is plotted for 25 days (Fig. 7B), showing the changes in flood and ebb flows with the lunar cycle. These data indicate that at the RSMAS docks and immediate surroundings, including the seagrass bed where some experimental studies on drift transport were undertaken, the mean flood tide velocities are almost 50% higher than ebb tide flows (Figs. 7B, and 12). A hand-held flow meter was used to measure the actual flows at each of the plots set up in the seagrass bed, and confirms the higher flood tidal velocities measured at the pilings (Fig. 9A).

An integrated measure of both flow and water motion arising from waves (e.g., boat wakes) can be measured using chalk block dissolution rates. Weight loss in blocks placed out at Bear Cut were almost an order-of-magnitude greater (t-test: $t_{13df} = -8.984$, $P < 0.0001$) than those in the mesocosm, which were close to the weight loss measured in the controls kept in still water at 35 psu (Fig. 8). This is because there is some negligible flow ($<10 \text{ l}\cdot\text{min}^{-1}$ into 3000 l) through the mesocosms, resulting in a complete turnover of the water column about twice in a 12 hour period.

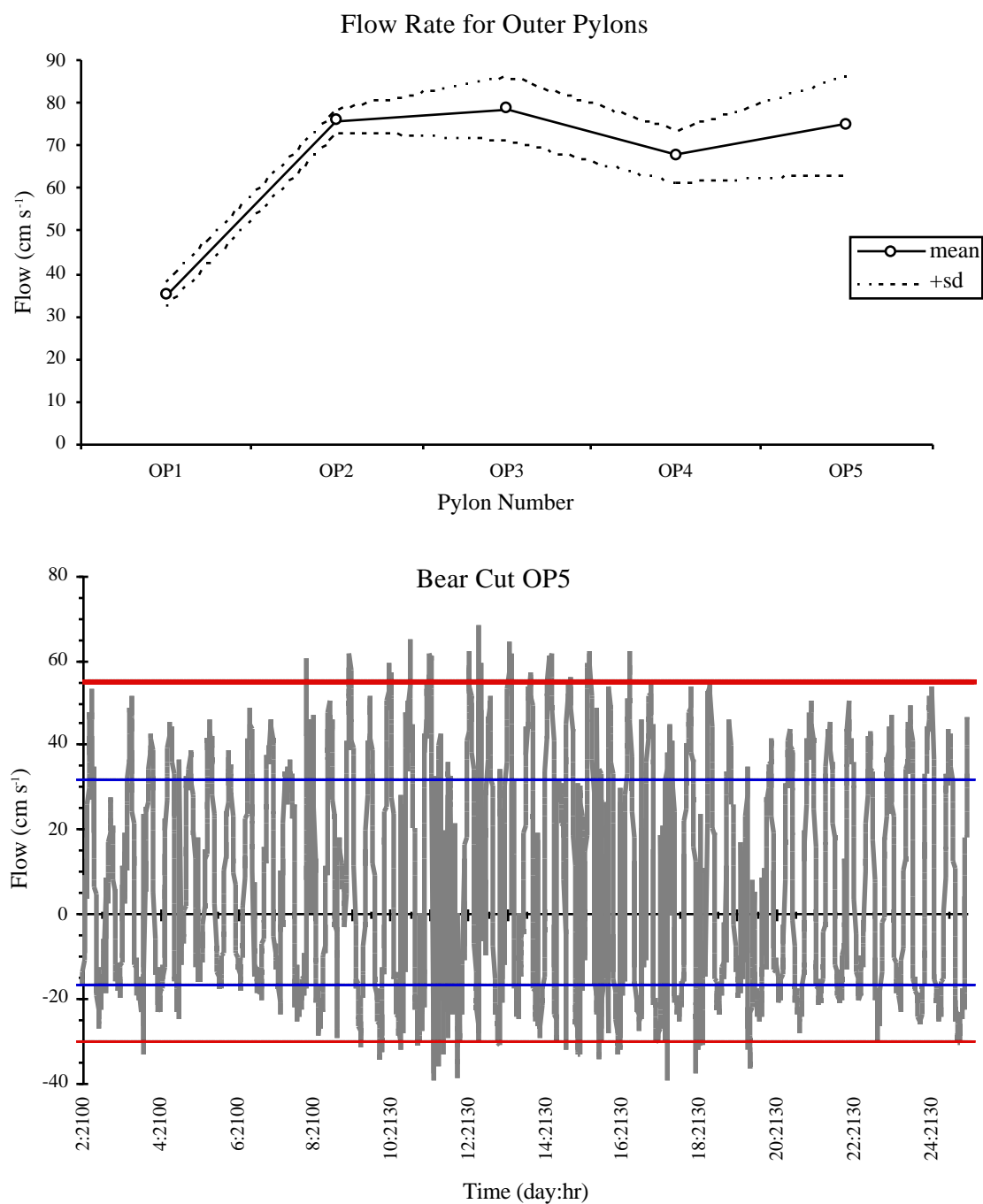


Fig. 7: Tidal flow velocities ($\text{cm}\cdot\text{s}^{-1}$) measured at the Bear Cut study site. A) by timing a float over a known distance at the five pylons (OP1 through OP5) (data from T. Jones). B) using a flow meter to measure tidal fluxes at OP5 over 25 days, blue lines indicate tidal means, red lines are means of upper 10 percentiles (data from B. Haus).

Table 4: One-way ANOVA of flows by pylon (fixed factor) to show that flow at the seagrass bed (OP 2-3) is reasonably approximated by flow at OP5, see Fig. 7. Means that are not significantly different by Tukey's posthoc comparison are indicated by the bar.

SOURCE	df	SS	MS	F	P
Pylon	4	4.2381	1.0595	19.626	0.0001
Error	10	0.5399	0.0539		

Tukey's	OP1	OP2	OP3	OP4	OP5

Data are non-normal (Shapiro Wilk's $W=0.8506$, $P<0.0173$) but homoscedastic (Bartlett's $F=1.0854$, $P<0.3617$), with $r^2=8870$ for the ANOVA, $n=3$.

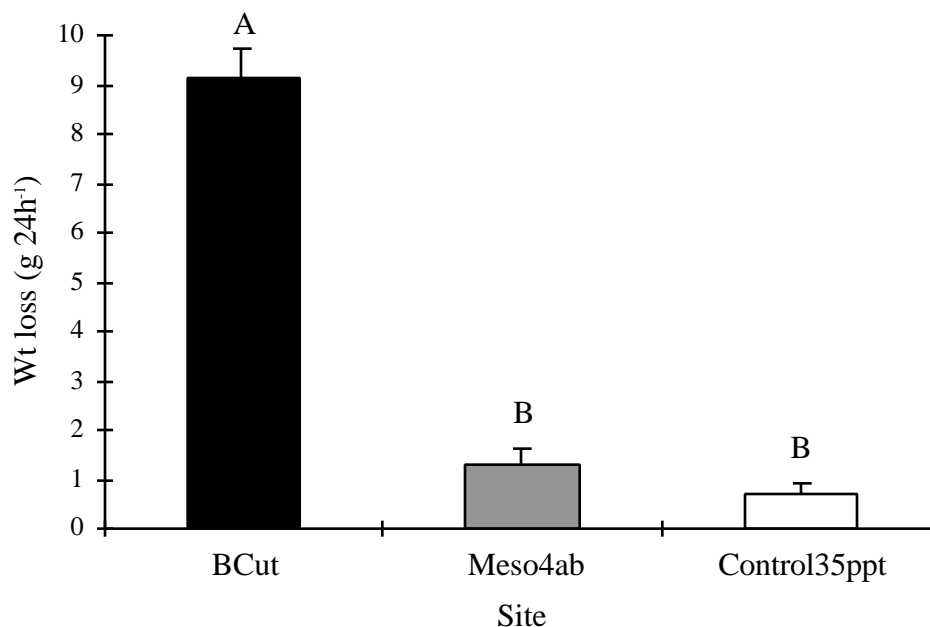


Fig. 8: Mean (\pm SE) dissolution of carpenter's chalk blocks over 24 hours at the RSMAS dock seagrass bed, with Tukey's posthoc analysis indicating means that are significantly different with different letters.

2.2 Transport

This experiment measured both transport speeds and persistence of drift algae in high-, medium-, and no-flow regimes. Flow velocities were significantly different among the three regimes (One-way Model I ANOVA: $F_{2,17} = 83.501$, $P < 0.0001$). Flows measured during peak incoming tidal currents were close to $50 \text{ cm}\cdot\text{s}^{-1}$ (Fig. 9A). The presence of the 1" Vexar mesh enclosures reduced flows by about half, resulting in mean peak incoming

current velocities experienced by the drift algae within the enclosures of 20-25 $\text{cm}\cdot\text{s}^{-1}$ (Fig. 9A). Flows in the mesocosm, the no-flow control were, essentially zero (Fig. 9A).

Transport speeds of drift algal clumps of various sizes in Bear Cut were between 0.5-0.7 of the current velocity (Fig. 9B), with no significant differences among clump sizes (at 25 $\text{cm}\cdot\text{s}^{-1}$: $t_{\text{4df}} = 1,235$, $P = 0.2846$, and at 50 $\text{cm}\cdot\text{s}^{-1}$: $t_{\text{4df}} = -0.373$, $P = 0.7281$).

2.3 Persistence

The persistence time of drift algae in the three flow regimes was significantly different (Table 5), with persistence inversely related to flow velocity (Fig. 9C). In the high-flow regime (the open plots in Bear Cut) persistence time was less than one tide, with algae being transported out of the open, marked plots once flow velocities approached 15-25 $\text{cm}\cdot\text{s}^{-1}$. Algae in the enclosures persisted for up to five days (about 20 tidal cycles), with biomass decreasing exponentially, as the clumps were successively fragmented by the tidal currents (Fig. 9C). Drift algae persisted in the no-flow conditions for somewhat greater than a month in the summer, with a steady decline (Fig. 9C). This decrease in biomass was observed to be related mostly to decay of the thallus tissues, and is probably related to the higher summer time water temperatures ($> 30^{\circ}\text{C}$).

To test this hypothesis, the trial was repeated in winter, when water temperatures are frequently less than 25°C . Not surprisingly (see Chapters 2 and 3), drift algae persisted longer in winter than in summer, although there was no significant difference in biomass over time (Fig. 9C, Table 5). Decline in biomass was observed to be primarily a result of the mats becoming positively buoyant because of trapped air-bubbles from photosynthesis, and floating to the surface of the mesocosm tank, with some loss occurring down the drains of the tank. Also, in one instance of non-demonic intrusion (*sensu* Hurlbert 1984) around day 25, a substantial portion of this floating biomass was inadvertently discarded in routine maintenance activities of the mesocosm facility. For these reasons the persistence

time recorded for the winter is highly conservative, with persistence time potentially on the order of 1.5-2 months, compared to around 1 month in the summer.

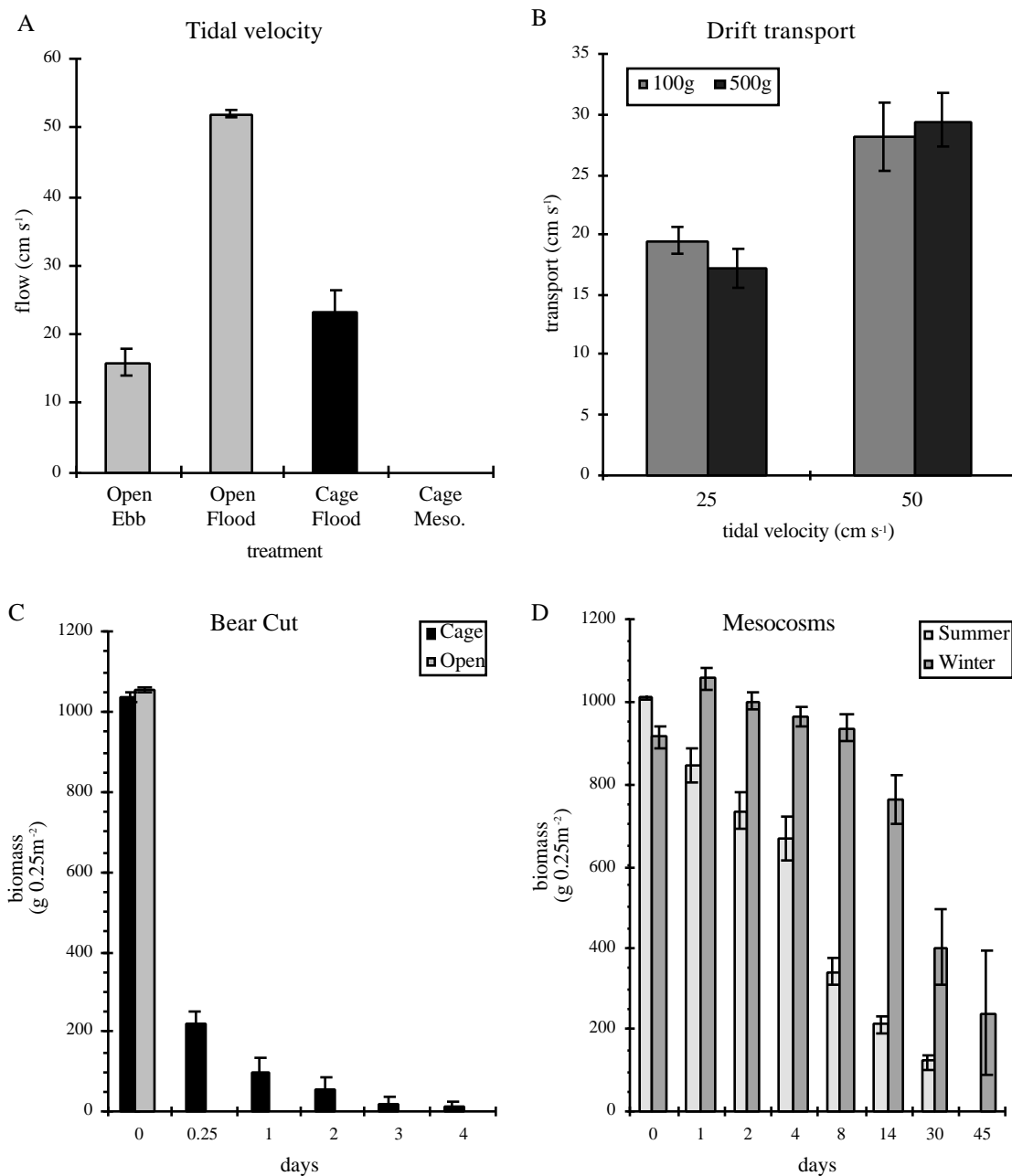


Fig. 9: Results from Experiment Two: A) Mean (\pm SE) flow velocities ($\text{cm}\cdot\text{s}^{-1}$) measured at enclosures in the seagrass bed and in the mesocosm. B) Mean (\pm SE) transport speeds of two different sizes of drift algal clumps in Bear Cut. C) Persistence times of drift algae under three flow regimes, and D) over two seasons in the no-flow regime in the mesocosms.

Table 5: ¹Repeated measures ANOVA on persistence of drift biomass in the three flow regimes (fixed factor) by time (fixed blocking factor) during the summer trial. ²Repeated measures ANOVA on biomass by season (fixed factor) and time (fixed blocking factor) for the no-flow regime in the mesocosms (see Fig. 9).

Source	df	SS	MS	F	P
¹ Flow	2	3762820	1881410	6.736	<0.05
Day	3	6651299	2217099		
error	6	1675791	279298.5		
² Season	1	1197317	1197317	4.907	<0.10
Day	7	8969468	1281353		
error	7	1708035	244005		

¹ANOVA $r^2=0.8614$, $n=5$. ²ANOVA $r^2=0.8562$, $n=5$.

Experiment 3: Drift Transport Rates over Various Seagrass Substrates.

Increasing density and canopy height of seagrass substrates (Table 6) resulted in decreases in drift transport speed for a given flow velocity (Fig. 10). Flow velocity influences transport speed in the water column by a factor of one-half to two-thirds, as was found by the results of Experiment Two. Complexity of the seagrass surface inversely influences transport speed. Over a bare to very sparse substrate, drift transport speeds were greater (but not significantly) than those measured over seagrass at all flow velocities (Fig. 10). As flow velocity increased, transport speeds of the drift algal clumps increased significantly, with transport at $50 \text{ cm}\cdot\text{s}^{-1}$ significantly greater than at $25 \text{ cm}\cdot\text{s}^{-1}$, and this was significantly greater than at $7.5 \text{ cm}\cdot\text{s}^{-1}$ across all substrate types tested (Table 7). Although not significant, seagrass substrate did affect the transport speed as the medium dense seagrass was less of an obstacle to the passage of drift than the two more complex substrates. At $50 \text{ cm}\cdot\text{s}^{-1}$ the slowest transport speed occurred over the dense *Thalassia* bed (Fig. 10), although this rate was not significantly different from the other two dense substrate types. In contrast, in the mixed seagrass bed, transport speed was significantly slower in the $25 \text{ cm}\cdot\text{s}^{-1}$ flow because of the *Halodule* sheaths sticking up into water column, causing the drift algae to become entangled. At the highest flow velocity this did

Table 6: Characteristics of seagrass habitats over which the flume was used. The number of seagrass shoots (each with 2-3 blades on average) per 0.25 m² areas are given, as well as the approximate canopy height.

Grass cover	<i>Thalassia</i>	<i>Halodule</i>	Height (cm)
v. sparse	9		30
v. sparse	8		30
medium	62		45
medium	63		45
dense	91		45
dense	76		45
dense mixed	61	24	55
dense mixed	69	58	55

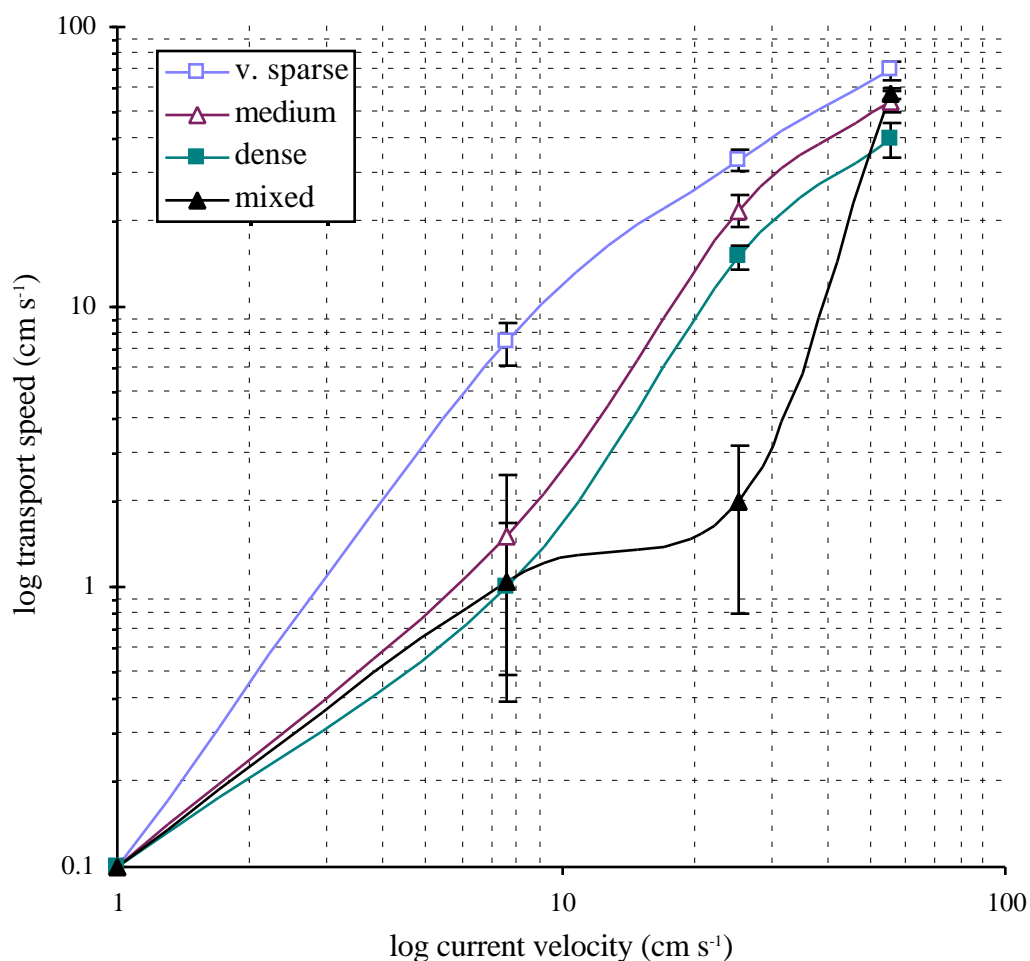


Fig. 10: Mean (\pm SD) drift transport rates under increasing flow velocities in a flume placed over four types of seagrass substrate commonly found in Biscayne Bay .

Table 7: Sheirer-Ray-Hare extension of the non-parametric Kruskal-Wallis test on drift transport rates by flow velocity and substrate type (both fixed factors) presented in Fig. 10. The appropriate chi-square test is SS/MS_{total} (Sokal and Rohlf 1995). Significant results at $\alpha = 0.05$ are highlighted in bold. Tukey's post-hoc comparison for significant results indicate groups with like means by the same letter.

SOURCE	df	SS	MS	χ^2	P
Substrate (S)	3	542.063	180.688	5.6347	<0.10
Flow (F)	2	3362.042	1681.021	34.9478	<0.001
F x S	6	217.625	36.271	2.2622	<0.75
error	36	399.750	11.104		
total	47	4521.480	96.202		
	<u>Flow</u>	<u>7.5 cm·s⁻¹</u>	<u>25 cm·s⁻¹</u>	<u>50 cm·s⁻¹</u>	
	Tukey's	C	B	A	

not occur as frequently, as the velocity of the water column was fast enough to discourage settling of the clumps, thereby reducing the possibility of algal entrapment by *Halodule*. Additionally, at the high flow velocity of 50 cm·s⁻¹, even the stiffer *Halodule* sheaths tended to bend, thereby further reducing the possibility of the drift algae becoming snared as it barreled over the grass bed at 1.8 km/h!

Experiment 4: Tidal Flow Velocities and Persistence Time of Drift Algae at Field Sites

4.1 Flow

As flow velocities have been demonstrated to be inversely related to drift transport, or by corollary, proportional to settlement of drift algae in the previous two experiments, it behooves us to investigate the actual flow regime at the seven study sites, to determine whether the observed distribution of drift algae correlates with flow regime. From the synoptic maps of tidal flows, bathymetry, and sediment characteristics, I hypothesized that Bay-wide circulation patterns may be partly responsible for the distribution of drift algae observed within the Bay, with higher abundance of algae in low-flow regimes, and scarcity of drift algae at oceanic cuts where flow velocities are high and encourage transport, rather than settling of drift algae.

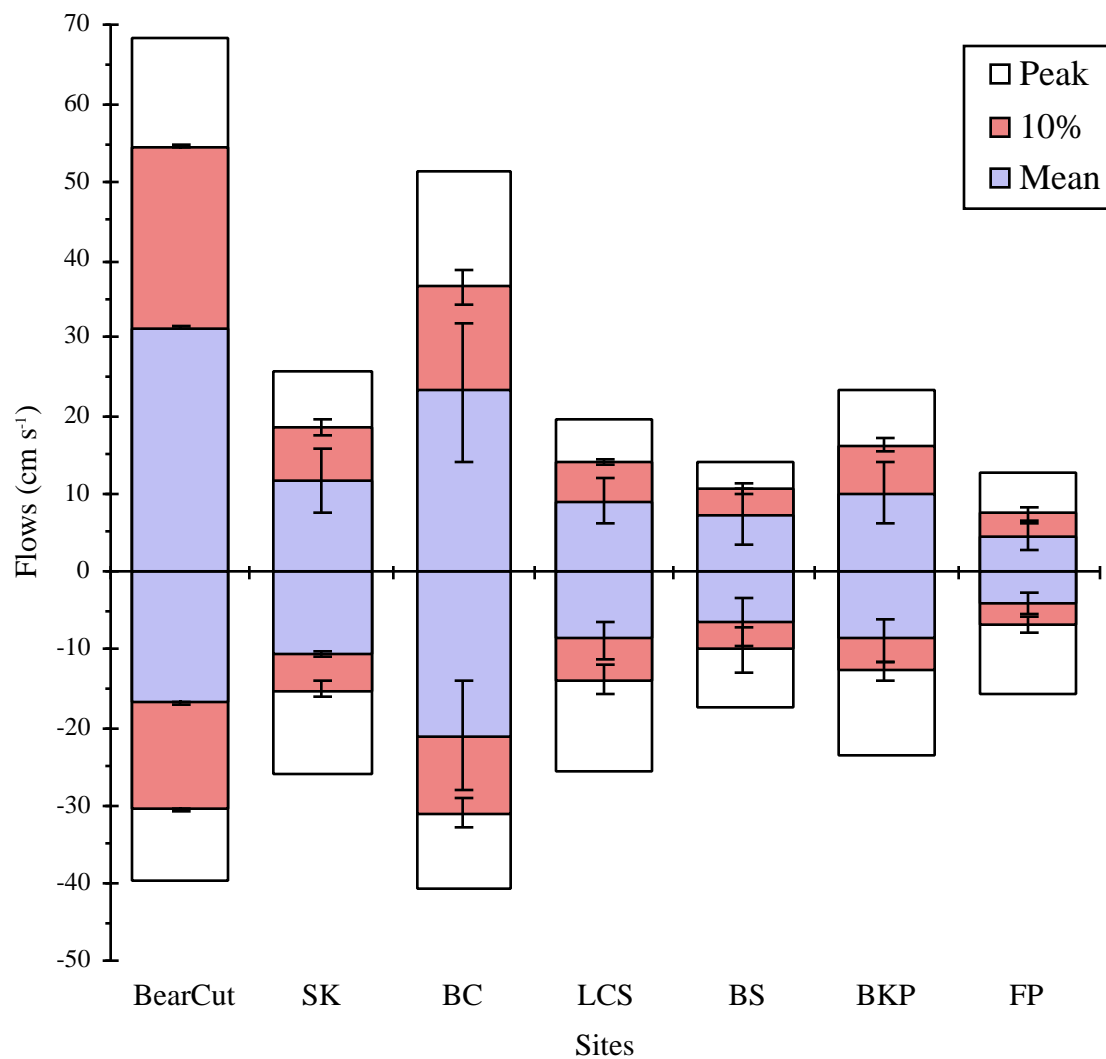


Fig. 11: Mean (\pm SE) tidal flows, mean (\pm SE) peak 10% flow velocities, and maximum flows at study sites in Biscayne Bay calculated from output of the Wang circulation model for 1996-1999. Bear Cut data came from flow measurements at the RSMAS docks.

Table 8: Non-parametric Kruskal-Wallis tests on mean flows by site presented in Fig. 11, with Tukey's post-hoc comparisons across sites.

TIDE	df	χ^2	P				
IN	6	934.239	<0.0001				
OUT	6	901.252	<0.0001				
IN	<u>BearCut</u>	<u>SK</u>	<u>BC</u>	<u>LCS</u>	<u>BS</u>	<u>BKP</u>	<u>FP</u>
Tukey's	A	C	B	DE	D	D	E
OUT	<u>BearCut</u>	<u>SK</u>	<u>BC</u>	<u>LCS</u>	<u>BS</u>	<u>BKP</u>	<u>FP</u>
Tukey's	B	C	A	D	D	D	E

Table 9: t-test results on in vs. outgoing flow velocities at each site shown in Fig. 11, n=5000.

SITE	mean: t	P	peak 10%: t	P
BearCut	17.131	0.001	70.511	0.001
SK	9.235	0.001	2.200	0.05
BC	20.667	0.001	31.824	0.001
BKP	5.933	0.001	45.085	0.001
FP	5.280	0.001	11.426	0.001
LCS	7.800	0.001	0.750	0.5
BS	1.810	0.1	4.787	0.001

The flow velocities at the seven sites investigated are characterized by higher mean and peak flows at the oceanic cuts (Bear Cut, SK, BC) than the mainland coastline sites (LCS, BS, BKP, FP). Mean flow velocities at the oceanic sites are 15-30 $\text{cm}\cdot\text{s}^{-1}$, and are significantly greater than at the canal and sheet flow sites, where mean currents drop to 5-10 $\text{cm}\cdot\text{s}^{-1}$ (Fig. 11, Table 8). At all sites, except Barnes Sound (BS), mean flow velocities were significantly greater on incoming tides than at ebb tide, and mean peak flows differed significantly between tides, except at Little Card Sound (LCS) (Table 9).

Chalk block dissolution rates are indicators of relative water motion and therefore should mirror the flow velocities determined from model output, provided no other factors inducing water motion are locally important. The seasonal weight loss in the chalk blocks placed out at five of the seven sites in two seasons were reasonable estimators of the relative distribution of tidal flow velocities at the three oceanic sites, but over-estimated tidal

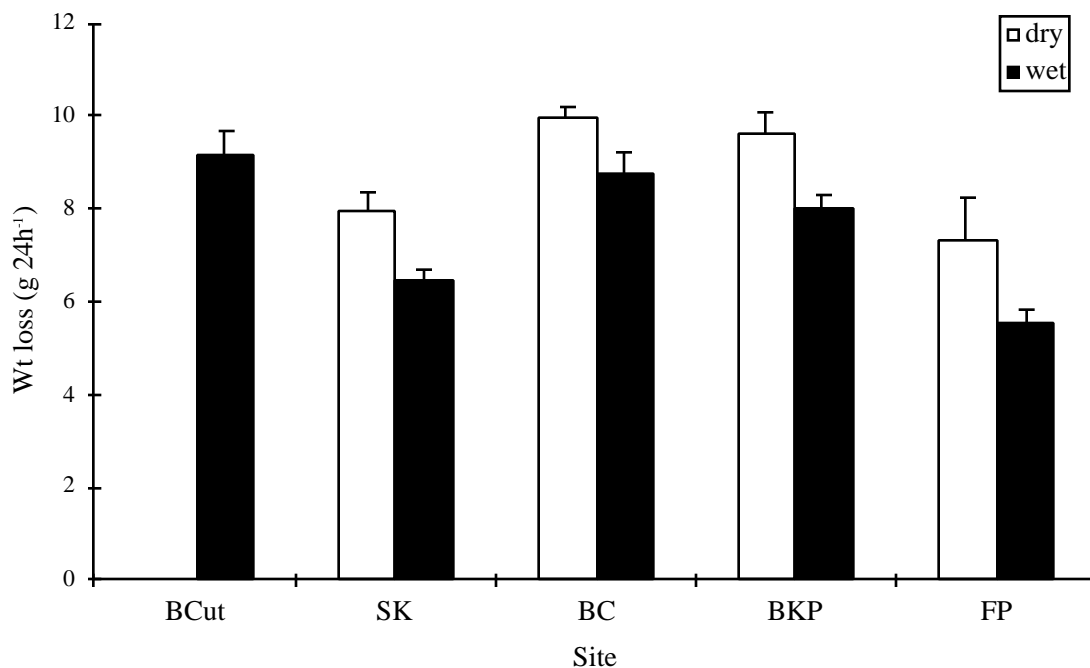


Fig. 12: Mean (\pm SE) dissolution of carpenters chalk blocks over 48 hours at five field sites in two seasons.

Table 10: ¹Two-way ANOVA of chalk block dissolution by site (random factor) and season (fixed factor) on the chalk data for four sites (SK, BC, BKP, FP). ²One-way ANOVA for site (random factor) in the wet season. Significant results followed by Tukey's LSD comparisons, with non-significant groups denoted by like letter-groups (see Fig. 12).

SOURCE	df	SS	MS	F	P
¹ Site (S)	3	164.1608	54.7203	18.5865	<0.0001
Season (Se)	1	66.5397	66.5397	22.6011	<0.0001
S x Se	3	1.6797	0.5599	0.1902	0.9029
error	139	409.2276	2.9441		

Site	SK	BC	BKP	FP
Tukey's	B	A	A	B
Season	dry season		wet season	
Tukey's	A	B		

² Site	BCut	SK	BC	BKP	FP
error	4	4.305	1.0763	17.3446	<0.0001
	112	6.950	0.0620		
Tukey's	A	B	A	A	B

¹Data are normal (Shapiro Wilk's $W=0.9698$, $P<0.0532$) and homoscedastic (Bartlett's $F=3.5284$, $P<0.0509$), with $r^2=0.4259$ for the ANOVA, $n=10-29$. ²Data were \ln -transformed for normality (Shapiro Wilk's $W=0.9744$, $P<0.2184$) and homoscedasticity (Bartlett's $F=1.2415$, $P<0.2908$), with $r^2=0.3825$ for the ANOVA, $n=10-29$.

flow at the two canal sites (Fig. 12). Specifically, during the wet season the dissolution measured at BKP (8.02 g) was significantly higher than at SK (6.42 g) (Table 10), and at FP (5.57 g) was higher than expected, being close to weight loss measured at SK in the same 48 hour period (Fig. 12). The higher than expected dissolution rates at the canal sites could be increased local water motion from fetch-waves, or lower salinities and associated pH changes (E. Irlandi, pers. comm.). Winter dissolution rates are significantly higher than in the summer (Fig. 12, Table 10), indicating waves and chop from frontal weather patterns are more important than low salinity.

The flow and chalk block data indicate an environment favorable to induce settling of drift algae at canal and sheet-flow sites. To bolster this hypothesis further, it is now necessary to look at the residence time of drift algae *in situ* at these sites, and determine whether a correlation exists between predicted tidal flow regime and persistence of algae, as was demonstrated to occur in Experiment Two.

4.2 Persistence

To look for a correlation between tidal flows and algal accumulations at the six study sites within the Bay, I determined whether differences in the frequency of occurrence of drift algae existed. Locations where drift algae are frequently encountered in permanent quadrats could be indicative of environments that are favorable to the persistence of drift algae. For two separate datasets collected in two consecutive years using different methods, drift algae were found to be less common at oceanic sites than canal sites, with sheet-flow sites intermediate (Fig. 13). For instance, both BKP and LCS have intermediate flow speeds (Fig. 11), yet have quite different drift algal coverage, with BKP having a high abundance of drift, and LCS having very little (Fig. 13). Obviously, tidal flow regime may not be the only variable important for determining the abundance of drift within a site. However, FP and BS are both sites with high levels of drift cover (Fig. 13),

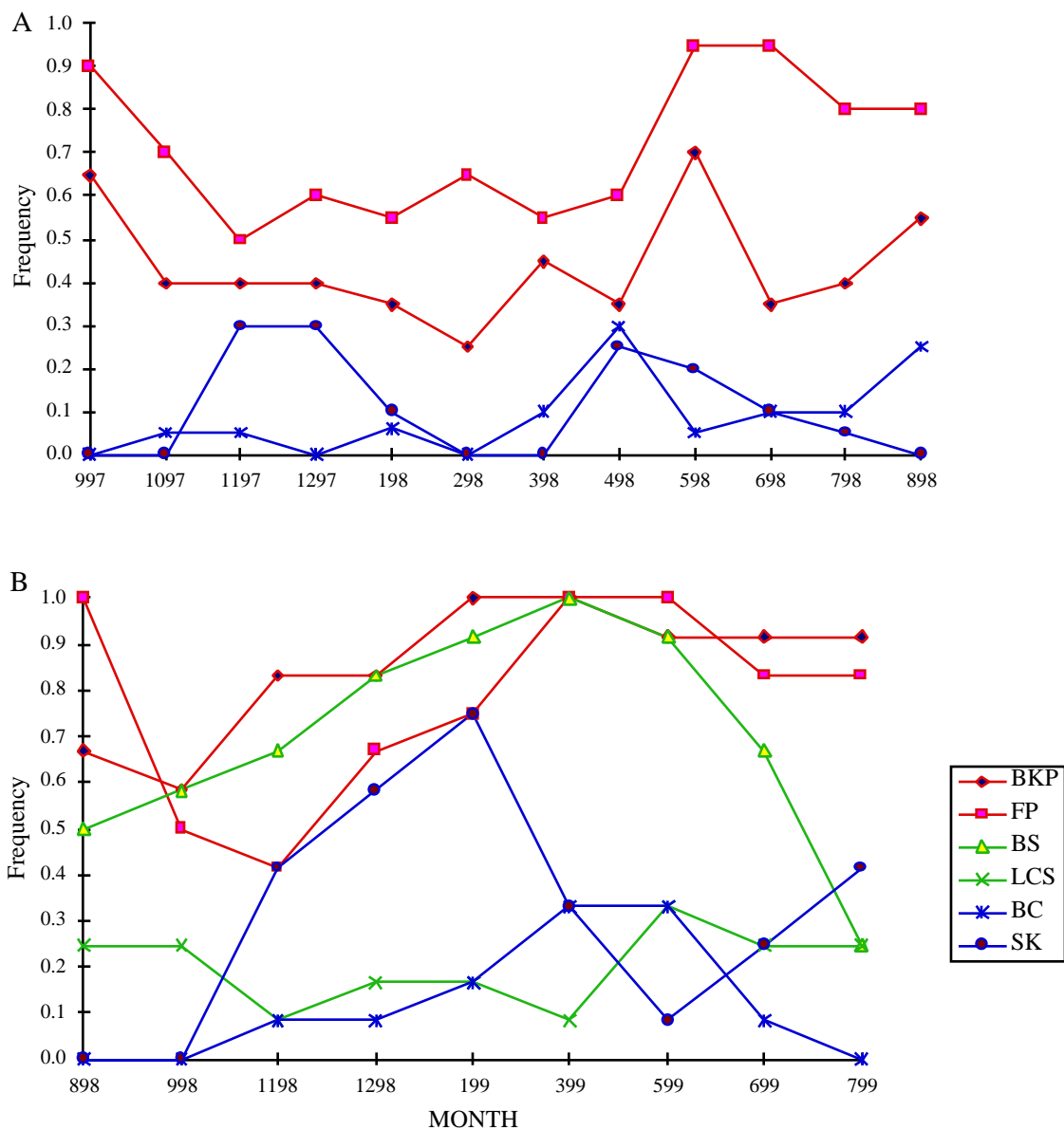


Fig. 13: Frequency of drift algae covering fixed quadrats over two one year sampling programs. For A) 1997-98 quadrat size is 0.25 m², n = 20, and for B) 1998-99 quadrat size was 1 m², n = 12. Abundance is always greater at canal than oceanic sites.

Table 11: Mean monthly transition probabilities for a two phase model of drift dynamics. Data from Sept. 1997 - Aug. 1998 from Permanent vs. Cleared 0.25 m² quadrats at two regimes (canal = FP, BKP vs. oceanic = BC, SK) and from Aug. 1998 - Aug. 1999 from Permanent 1 m² quadrats in three regimes (same as above and sheet-flow = LCS, BS). The transition probability with the highest magnitude is highlighted.

Site	P(0,0)	P(0,1)	P(1,1)	P(1,0)
<u>'97/98 Permanent Q.</u>				
BC	0.83	0.08	0.03	0.06
SK	0.80	0.08	0.03	0.09
FP	0.17	0.12	0.58	0.13
BKP	0.43	0.14	0.28	0.15
<u>'97/98 Cleared Q.</u>				
BC	0.74	0.26		
SK	0.72	0.28		
FP	0.15	0.85		
BKP	0.57	0.43		
<u>'98/99 Permanent Q.</u>				
BC	0.81	0.05	0.05	0.09
SK	0.54	0.16	0.20	0.10
LCS	0.67	0.13	0.07	0.13
BS	0.13	0.11	0.61	0.15
FP	0.11	0.11	0.64	0.14
BKP	0.09	0.06	0.81	0.04

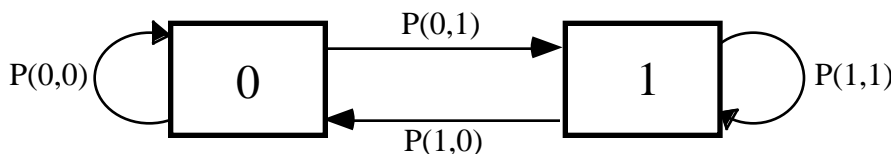


Fig. 14: Diagram of two state model of drift dynamics used to determined transition probabilities. The two possible states a quadrat can have are: drift absent (state 0), or drift present (state 1). Transitions between monthly time intervals (t_x) are therefore: P(0,0) = no drift at t_1 or t_2 ; P(0,1) = no drift at t_1 changes to drift present at t_2 ; P(1,1) = drift present at t_1 and persists to t_2 ; P(1,0) = drift present at t_1 but removed by t_2 .

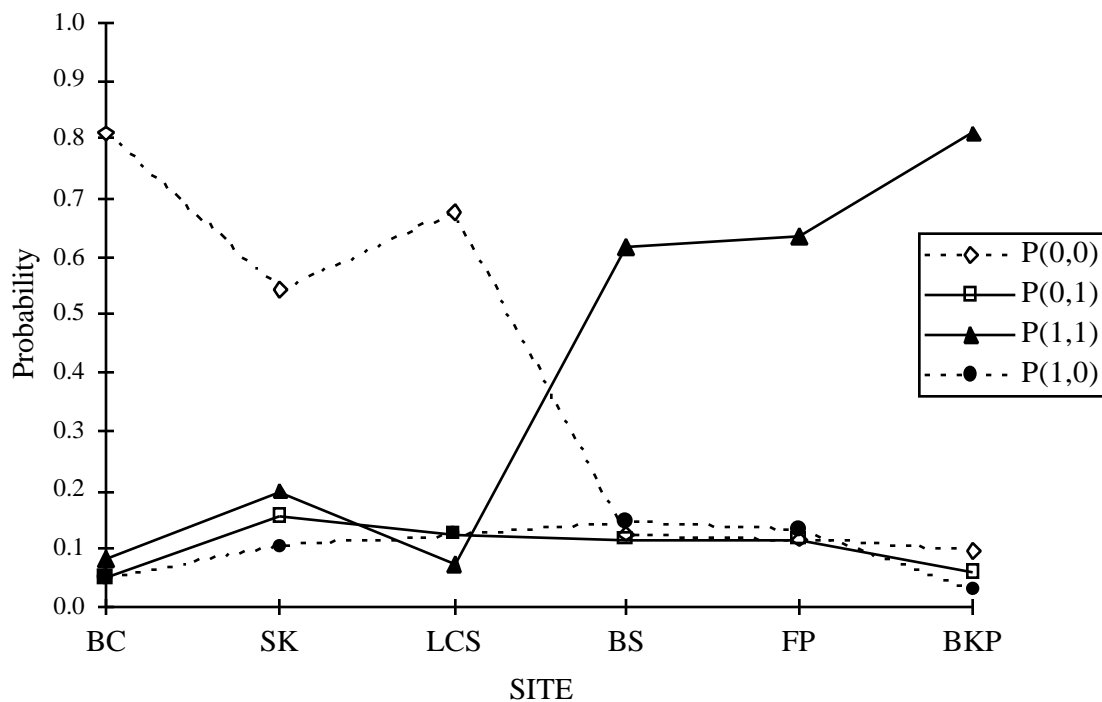


Fig. 15: Transition probabilities at six sites in Biscayne Bay for the period Aug. 1998 - Aug. 1999 based on percent cover estimates from photographic records of 1 m² quadrats, n = 12. P(0,0) are quadrats that remained free of drift algae; P(0,1) were initially free and then became covered; P(1,1) remained covered by algae; and P(1,0) were initially covered and were then cleared by water movement.

and are both characterized by the lowest mean and peak flows of all the sites investigated (Fig. 11). The fact that the three sites (FP, BKP, BS) with the most drift algae are also sites at the lower end of the flow spectrum indicates that low flow velocities within the Bay are probably important in allowing drift algae to settle and persist.

Another indicator of persistence within a set location (a permanent quadrat) is to look at transition probabilities between two alternative phase states: drift algae present or absent (Fig. 14). The permanent, uncleared plots at sites which tend to accumulate algae, should have a high P(1,1) transition probability (*i.e.*, drift cover persists from t_1 to t_2). By corollary, at sites with high flow velocities, transition probabilities for P(0,0) should dominate the system. Indeed, mean monthly transition probabilities at the oceanic sites for 1997-98 are dominated by the P(0,0) transition (> 80%), with only a low probability (

3%) of a quadrat retaining algae over a monthly time step (Table 11). The canal sites FP and BKP further confirm this theoretical prediction with the dominant transition being $P(1,1)$ ranging from 58% at FP in 1997-98, to 81% at BKP in 1998-99. At the canal sites the probability of a quadrat remaining free of drift was low, $P(0,0)$ ranged from 9% at BKP in 1998-99 to a 17% at FP in 1997-98 (Table 11). There is a difference in the results obtained for BKP between 1997 and 1999 sampling periods. Based on the transition probabilities it appears that the occurrence of drift algae increased during 1998 at this site; this is reflected also in the frequency of quadrats containing drift algae (Fig. 13). A reason for this apparent increase in drift coverage could be related to the different methodologies used, especially the difference in quadrat size (see also Chapter 2, Fig. 7). Larger quadrats are more likely to include clumps of drift than smaller quadrats, resulting in an increase in the probability of drift being present at each sampling interval.

Further information can be obtained by comparing the mean monthly transition probabilities between uncleared and cleared permanent plots. In the cleared plots any algae present now equals new algae entering during the time step (*i.e.*, a $P(0,1)$ transition). At the oceanic sites, plots remain predominantly clear of drift ($> 72\%$), although the probability of algae entering a plot is now about three times higher than for the uncleared plots, indicative of a regime where drift algae are being moved around by tidal currents (Table 11). The mean transition probabilities at the canal sites mirror the trends for the uncleared plots, with higher mean probabilities of algae entering a plot (at FP = 85%). At the higher energy canal site, BKP, there was a slightly higher probability of a plot remaining free of algae (57%) than becoming re-covered (43%), within a month of the quadrat being cleared (Table 11).

For data collected from photographic records in the following year (1998-99), the four transition probabilities are plotted against site (Fig. 15). This plot clearly shows the difference among the three sites (BC, SK, LCS) with higher flow velocities and those in the low-flow regimes (BS, FP, BKP). Sites with higher flows are dominated by a $P(0,0)$

transition (plot remains clear of algae, $P = 54-81\%$), while sites with lower flows are dominated by $P(1,1)$ transitions (persistence of drift within a plot, $P = 61-81\%$). Also evident in this graph (Fig. 15) is the similarity among all sites for transitions where drift enter or leave a plot ($P = 5-16\%$). This is similar to the results obtained in the previous year, and indicates that the different behavior of drift algae in the sites studied is likely to be strongly affected by the tidal flow regime present.

To summarize, the results obtained indicate the potential for drift accumulation in low-energy environments, such as occur along the mainland coastline. Drift algae are readily transported by tidal currents, and drift along at speeds between one-half and two-thirds the ambient velocity. Transport speed is a function of substrate type, as more complex bottom topography increases the possibility of entanglement, thereby reducing transport rates. From field data, the probability of drift algae remaining in a small area (1 m^2) is higher at low-energy sites, than at high-energy tidal inlets. The question of whether the drift algae are settling out at the low flow velocities present at the canal sites after net transport across the Bay with tidal currents is still a matter requiring further study.

DISCUSSION

Sources of Drift

Free-living seaweeds are derived from attached populations at some time in the past (Norton and Mathieson 1983). After detachment, algae are exposed to a different environmental regime than the benthic source stock. Detached algae can be classified in relation to their habit: entangled, loose-lying on the substrate, aegagropilous (radial arrangement resembling a spherical ball), embedded in sediments, or free-floating in the water column (Norton and Mathieson 1983). In most cases free-living algae rarely exhibit sexual reproduction, instead propagating by fragmentation. The lack of directional tropisms in continuously tumbling clumps, reverting to a juvenescent state post-detachment, as well as possible nutrient limitation and/or accumulation of exudates in the

parcel of water surrounding the clump as it passively moves with the water column, have all been suggested to be responsible for this lack of initiation of sexual propagules (Norton and Mathieson 1983). Vegetative propagation by dissemination of fragments from the parent clump may serve as an efficient method of dispersal under benign environmental conditions (Norton and Mathieson 1983).

Drift algae are moved by wind and water currents. The abundance of drifting algal mats is governed by the availability of biomass imported from the source(s), and physical forces such as wind, currents, and wave action (Norkko *et al.* 2000). The hydrodynamic setting of a bay is therefore a critical feature in determining algal distribution and abundance (Bell and Hall 1997). As attached algae are rare in seagrass beds, this suggests that drift algae originate from outside the system (Williams-Cowper 1978). Drift algae can originate from hard substrates located outside seagrass bed, or alternatively fragment off epiphytes that originated on seagrass blades (Phillips 1960; Hamm and Humm 1976; Josselyn 1977). A number of species that commonly comprise the drift (e.g., *Laurencia*) are not usually observed as epiphytes on the seagrass blades (Phillips 1960; Hamm and Humm 1976; Williams-Cowper 1978), suggesting external provenance from adjacent hard-bottom areas. Some species found within Biscayne Bay do represent species carried in by water currents (e.g., *Sargassum*), however, most species of red algae (e.g., *Chondria*, *Cladophora*, *Polysiphonia*) found within the seagrass beds studied were not found abundantly elsewhere and probably originated as seagrass epiphytes.

At the small spatial scale within a site, water motion and current flow may not always be directly related to the accumulation of drift algae. Black Point (BKP), a site that experiences moderate water motion with tidal currents, had accumulations of drift algae, while Broad Creek (BC), a site of more rapid current flow, did not.

At BC, clumps of algae were often observed drifting across the site, and PVC poles regularly snagged large mats of algae. This difference in the occurrence of drift algae among sites with tidal current flow may be a result of the source of the drift algae (Fig. 16).

Many of the species that make up the drift algae at canal sites originate as epiphytes growing attached to seagrass leaves. As they increase in biomass, and as the seagrass leaves senesce and are sloughed from the shoots, the algae become part of the drift community. The algae at BKP may have originated there as seagrass epiphytes, with potential nutrient input from canals stimulating algal growth on and amongst the blades (Fig. 16).

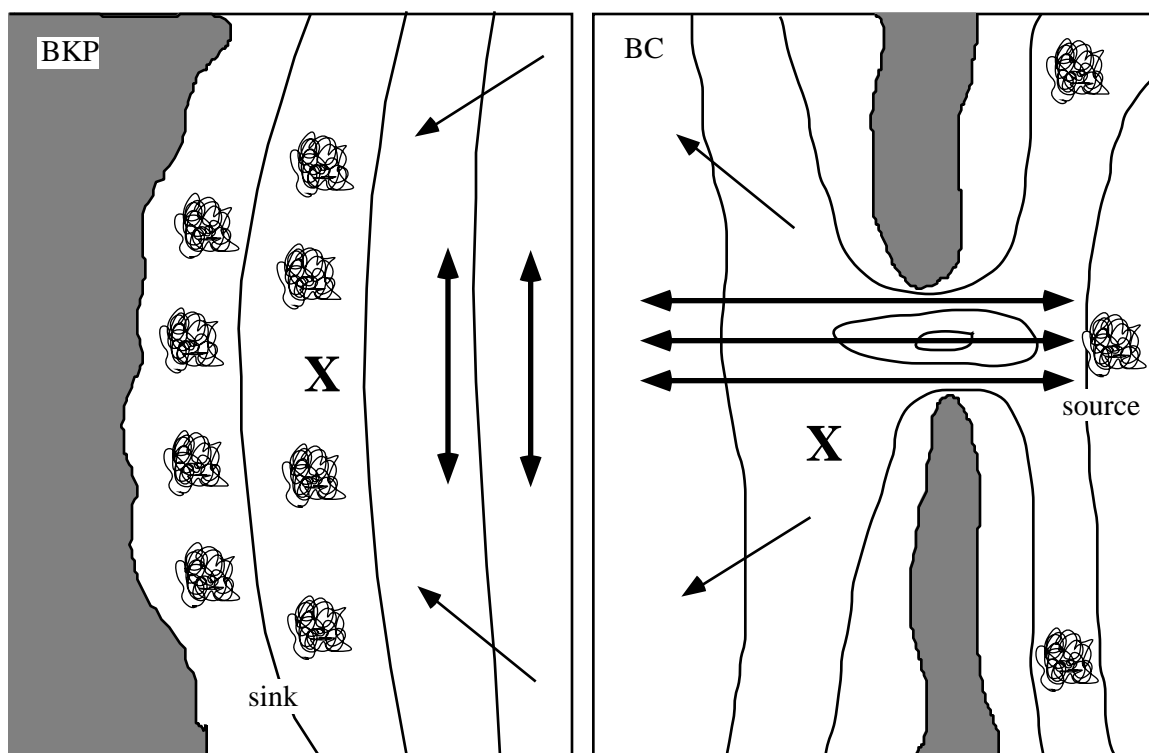


Fig. 16: Schematic showing source-sink relationships for drifting macroalgae at a canal site (BKP) and an oceanic inlet (BC). X marks approximate location of study site in relation to land and predominant tidal flows (heavy arrows). Lighter arrows indicate net transport of drift under tidal and wind-driven water motion.

In contrast, algae drifting through the BC inlet may have originated from outside the Bay, and be passing through with the strong tidal currents (Fig. 16). Accumulation of drift algae occurs at high-energy locales only if currents are locally reduced enough to allow deposition (like the lee of a bank, or depression where current flow is reduced), or if

obstructions entangle passing clumps of algae (such as PVC posts, or more commonly sponges, soft corals, or clumps of the rhizophytic alga, *Halimeda opuntia*).

At the larger spatial scale of Biscayne Bay, the local distribution of *Laurencia poiteaui* in the lower Bay was found to be largely dependent upon water circulation (Josselyn 1977). The greatest biomass of this species was observed in sheltered, shallow, nearshore seagrass beds where masses of loose and drifting algae occurred for long periods of time and continued to grow *in situ* because currents were weak, so that the drifting masses were only occasionally washed ashore or swept out of the seagrass beds after strong wind events. Major accumulations of *L. poiteaui* along the western, mainland coastline can occur because of strong winds during winter cold fronts, which increased the strength and duration of tidal currents in southern Biscayne Bay (Lee and Rooth 1973; Josselyn 1977). In association with the increased water flow, large cylindrical rolling masses of *L. poiteaui* up to 2.4 m long and 0.6 m in diameter were observed moving south and would eventually move into shallow areas and accumulate in large mats (Josselyn 1977).

Transport of Drift

Transport speeds of drift algal clumps measured were somewhat higher than previously reported by Holmquist (1994) in Florida Bay, where algae moved at a rate of about one-half ambient flow by tumbling along, or just above, the surface of the sand or the top of the seagrass canopy. This may be a function of differences in water depth between Florida Bay and Biscayne Bay (M. Harwell, pers. comm.).

The complexity and composition of seagrass beds affect the transport rates of drift clumps, as seen in the flume experiments. At intermediate flow velocities drift algae are transported at reduced speed compared to a bare substrate, however, an increase in transport speeds to values similar to that in the bare substrate at the higher flow velocities occurs over dense seagrass. *Thalassia* has a morphology such that at increasing flow velocities the blades bend over, creating in essence a “smooth surface”, similar to a bare

substrate. Similarly, in a field study, the high density and flexibility of *Thalassia* blades allowed algal clumps being tumbled along by tidal currents to roll over the flattened canopy of blades, at speeds similar to bare substrates (Holmquist 1994).

In the presence of flows $>15\text{-}20\text{ cm}\cdot\text{s}^{-1}$ over seagrass substrate, clumps of *Laurencia* were transported by slowly tumbling over the bottom, rather than drifted in a fixed orientation. Tumbling was caused by the lower portions of the clump contacting the substrate with projecting small branchlets, while the upper portion was pushed forward and over by the current. Clump movement was pulsed, with drifting occurring for a few minutes before settling and the clump becoming enmeshed in the seagrass. After a while the clumps would break free and resume drifting. The algal clump typically tumbled along at, or just above, the surface of the bare sand or seagrass canopy.

Increasing tidal flow velocities reduce the persistence time of drift algae within a seagrass bed. In Bear Cut, drift clumps in sparse beds with shorter canopies were often removed from the bed within <24 hrs by currents, whereas clumps occurring under a canopy in dense seagrass did not readily move, with residence times of up to four days. In a similar study in Florida Bay, only 15% of clumps were moved in seagrass beds with low flow velocities, whereas 95% of clumps were transported over bare substrate under moderate to strong flows (Holmquist 1994). Export of clumps that were not initially entangled in the seagrass was greater, with 85% moving more than 100 m, and in some cases up to 500 m in 24 hrs (Holmquist 1994). Tidal currents dislodged and removed enmeshed algal clumps from seagrass beds a distance of at least 50 m over 20 days (Holmquist 1994).

Spatial and Temporal Patterns

The spatial distribution of unattached benthic drift algae is highly aggregated because of these transport processes (Josselyn 1977; Williams-Cowper 1978; Virnstein and Carbonara 1985), resulting in a high degree of temporal and spatial patchiness over a range of scales

within Biscayne Bay. Accumulations of drift algae tens of centimeters thick can cover large areas, while adjacent areas contain virtually no drift, as has been found for the Indian River Lagoon (Virnstein and Carbonara 1985). Accumulations of high densities of drift algae in the Bay occurred most where seagrass growth was not well developed (bare patches, boat scars), and especially on the lee sides of seagrass patches, as a consequence of reduced current speeds and poor water column mixing (Williams-Cowper 1978; Zieman *et al.* 1989).

Temporal processes of seasonal growth by the macrophytes overlay this spatial pattern. When seagrass beds become denser with growth in the spring and summer, much of the drift algae already present within the beds are apparently trapped by the rapidly growing grass blades and may remain *in situ* for weeks (e.g., Virnstein and Carbonara 1985). These large mats start to decompose in summer with the higher water temperatures. Temperature is important in determining the rate of seaweed decomposition, and therefore persistence time of clumps of algae. Warmer temperatures ($> 30^{\circ}\text{C}$) were found to be the most favorable for decomposition, as reported previously by Hanisak (1987, 1993). These data are consistent with observations that drift biomass in Biscayne Bay drops rapidly during the late summer, and this was also observed to occur in the mesocosm experiments.

The resulting patchy spatio-temporal occurrence of benthic drift algae increases habitat complexity over bare and soft substrate and over seagrasses, providing alternative habitat to benthic fauna, with high abundance of invertebrates recorded associated with drift (Josselyn *et al.* 1983; Virnstein and Carbonara 1985; Holmquist 1994; Vetter 1994, 1995; Norkko *et al.* 2000). Drift algae harbor high densities of animals and at times may be quantitatively more important locally than seagrasses in terms of habitat, nutrient dynamics, and primary production (Virnstein and Carbonara 1985). As benthic drift algae are highly ephemeral in time and space, they can provide a dispersal habitat for mobile benthic macrofauna, providing food and refuge from predators (Kulczycki *et al.* 1981; Virnstein and Carbonara 1985; Virnstein and Howard 1987; Holmquist 1994, 1997). Drifting algae

can therefore affect the distribution of fauna, as some species can use algae as a transport mechanism (Highsmith 1985; Kingsford 1992; Holmquist 1994).

Benthic macroalgal clumps can be important dispersal agents for some invertebrates, especially at small to intermediate spatial scales. Dispersing clumps of algae move up to 0.5 km day^{-1} , and were effective transporters of benthic fauna (Holmquist 1994). Large numbers of fauna, primarily gastropods and crustaceans, were found to remain in the drift clumps during dispersal, with 65-70% of the complement still present after 100 m dispersal distance (Holmquist 1994). The dispersing algal clumps provided a better refuge from predation than direct dispersal over the sand or seagrass habitat (Heck and Thoman 1981; Herrnkind and Butler 1986).

Synopsis of Patterns in Biscayne Bay

The hypothesis of net transport of drift algae within Biscayne Bay westwards by tidal currents and onshore winds, with accumulation of biomass along the mainland coastline appears to be unsupported. Rather, the importance of *in situ* growth of epiphytes on seagrass blades in the nearshore, canal sites is the probable source of much of the drift algae found there. Nutrients entering from canals are likely to support blooms under otherwise favorable environmental conditions. No doubt tidal transport of algal clumps is important in structuring the local distribution of drift accumulations, especially in the lee of seagrass patches, and in bare areas among patches. However, the current velocities present are unlikely to allow long-distance transport of large amounts of biomass. This notwithstanding, observations of large, cylindrical, rolling masses of drift occurring during and after the passage of winter cold-fronts does indicate the importance of water motion in structuring the drift community at certain times of the year. In spring and summer during more quiescent conditions and while temperatures favor the initiation of blooms, drift algae can cover large spatial extents and accumulate in areas of reduced water flow in the lee of seagrass beds. Later in summer, when temperatures increase the decomposition of drift

mats, the spatial coverage of algae is reduced until the winter storms pick up much of the remaining biomass and move it over larger spatial scales.

In contrast to this situation at the low-flow canal sites, high-flow sites at inlets are less likely to accumulate large biomass of drift algae, primarily because the high-flow regime picks up any algae that has been deposited during periods of slack tide. Only in areas with obstructions or depressions, where flow is substantially reduced, are drift algae likely to accumulate. The consequence is that drift are transient, and mostly originate from sources outside the site. These may be located within the Bay itself or at offshore hard-bottom areas in the zone between the barrier islands and the reef tract proper. Unlike the importance of temporal fluctuations in the canal sites, spatial considerations are more important in determining the provenance and fate of drift encountered in the oceanic seagrass beds.