Composition, export, and import of drift vegetation on a tropical, plant-dominated, fringing-reef platform (Caribbean Panama)

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Abstract. For 15 months, the composition and abundance of drift vegetation were determined from a plant-dominated fringing reef at Galeta Point, Caribbean Panama. Five nets located downstream of the reef platform continuously sampled 1.0–1.3 ha of reef flat which included 137–202 m of fore reef. Time series and multiple correlation analysis were done to evaluate the dependence of drift biomass on selected physical and biological factors. Export and import rates and turnover times were derived and compared between the dominant species. Floating leaves, branches, and seeds of higher plants were the major components of imported drift with 52% of the dry weight mass, followed by algae and seagrass each with 19%, the water hyacinth *Eichhornia* with 2%, and floating tar with 8%. Exported biomass from the reef platform was higher in the dry-season (late November–March) than in the wet-season (April–early November). Within the 1.0–1.3 ha sampling area, export estimates ranged from 37–294 kg mo^{-1} for the seagrass *Thalassia*, 3–171 kg mo^{-1} for the alga *Laurencia*, and 3–74 kg mo^{-1} for the alga *Acanthophora*. Multiple correlation models indicated that meteorological and hydrographic conditions explained between 31 to 65% of the variance in the drift biomass and that the best predictors of exported biomass were tidal elevation and wind speed (3 week lag). Export rates increased with high tides and strong winds and decreased with elevated water temperatures. Autocorrelations of drift biomass were generally highest at 2 week intervals, suggesting that the quantity of drift removed from the platform was, in part, related to spring and neap tide cycles. Export rates were also affected by the morphology of the vegetation, development of uprights, and location on the reef platform. Import rates of terrestrial-plant debris, the hyacinth *Eichhornia*, the seagrass *Syringodium*, and the brown alga *Sargassum* did not exhibit pronounced seasonal patterns in abundance and averaged 60.2, 1.9, 1.1, and 2.7 g d^{-1}m^{-1}, respectively. Wind speed was negatively correlated with *Sargassum* abundance, suggesting that strong winds depleted it from nearshore waters. Floating tar averaged about 10 g d^{-1} m^{-1}, the highest reported in the Caribbean. The plant-dominated fringing reef at Galeta Point is shown to be a major source, as well as a recipient, of drift vegetation.

Introduction

Drift seagrasses and algae play an intricate part of many pelagic and benthic ecosystems, providing habitat and food for many fish (Lenanton et al. 1982; Kulczycki et al. 1981) and invertebrates (Gore et al. 1981; Koop and Griffiths 1982). Large accumulations of drift affect nutrient cycling (Schramm and Booth 1981; Zimmermann and Montgomery 1984) and may influence the survivorship and recruitment process of many species (Stoner and Livingston 1980; Lenanton et al. 1982; Kingsford and Choat 1985). Drift algae increase habitat complexity which reduces predation rates by fish on invertebrate prey (Heck and Orth 1980; Heck and Thoman 1981); fish and macroinvertebrate abundances are frequently correlated with the amount of drift biomass (Hunter and Mitchell 1967; Mitchell and Hunter 1970; Hooks et al. 1976; Heck and Wetstone 1977; Gore et al. 1981). Recently, the geographic distribution of brooding and broadcasting invertebrates has been related to rafting opportunities (Highsmith 1986).

Free-living seagrasses and algae occur in many temperate, subtropical, and tropical systems: salt marshes and estuaries (Brinkhuis et al. 1976; Hamm and Humm 1976; Bird et al. 1977; Benz et al. 1979; Chock and Mathieson 1979), open coastal systems (Burrows 1958; Womersley and Norris 1959; Josselyn et al. 1983), and oceanic waters (Winge 1923; Parr 1939; Dooley 1972). Zobell (1971) reported 200 cubic yards of drift seaweed per linear mile of shore in California. Virnstein and Carbonara (1985) recorded 164 g (dry wt) m^{-2} as an average

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for 15 ha in the Indian River Lagoon, Florida. Parr (1939) estimated 4–11 million tons (fresh wt) of drift *Sargassum* in the Sargasso Sea. Despite the ecological importance and abundance of drift, the quantity and species composition of drift vegetation removed from or entering into most benthic communities is largely unknown, with the exceptions of tropical studies at Laurel Cay, Puerto Rico (Glynn 1973), St. Croix, Virgin Islands (Zieman et al. 1979; Josselyn et al. 1983), and Enewetak (Johannes and Gerber 1974).

This study documents the seasonal composition and abundance of macroscopic vegetation removed from a plant-dominated, fringing-reef platform at Galeta Point, Panama. Export rates and turnover times were calculated for the dominant reef-flat species. In addition, higher-plant debris (mostly decaying stems, blades, and seeds), tar (pelagic oil), and the brown alga *Sargassum* that drifted onto the reef platform were quantified. Estimates of drift biomass were correlated with meteorological and hydrographic conditions and reef-flat standing crop to determine the dependence of drift biomass on physical and biological variables and to serve as a basis for detecting seasonal cycles.

Methods

Study site. Investigations were made on the reef flat adjacent to the Galeta Marine Laboratory, Smithsonian Tropical Research Institute [S.T.R.I.], at Galeta Point, Republic of Panama (9° 24.3'N, 79° 51.8'W). The reef is about 6 km northeast of Colon, the Caribbean entry into the Panama Canal (Fig. 1). The reef flat supports copious growths of algae, mostly the calcareous green alga, *Halimeda opuntia* (L.) Lamour., the fleshy red algae, *Laurencia papillosa* (Forsk.) Grev., *Acanthophora spicifera* (Vahl) Børg., and *Gelidiella acerosa* (Forsk.) Feldm. and Hamel, and the seagrass, *Thalassia testudinum* Banks ex König and Sims (Kilar et al. 1988). The landward side of the reef is bordered by a lagoon or mangrove swamp, while on the seaward side the reef slope extends down to an abutting sand plain at 13 m depth. The reef flat is usually covered by 0.1 to 0.5 m of water, with tidal fluctuations of 0.7 m (Macintyre and Glynn 1976). The topography of the reef flat is such that the highest elevation occurs in the fore reef and decreases landward. Together with wave-driven forces, there is an almost unidirectional flow of water over the reef surface (Kilar 1984; Kilar et al. 1988). Seawater temperature on the reef flat is generally between 26° and 29 °C, with salinity varying be-

tween 32 and 35 ‰ (Hendler 1976). Galeta reef is considered representative of the fringing reefs that occur on Panama's Caribbean coast (Macintyre and Glynn 1976).

During Panama's dry-season, usually late November to March, northern and northeasterly trade winds blow with a mean velocity of 24 to 27 km h^{-1}, which is about three times the mean velocity occurring in the wet-season, April to early November (Hendler 1976). Waves generated by these strong winds cause considerable turbidity and remove weakly attached organisms. During the wet-season, when calm seas coincide with a high pressure system or with a low spring tide, the reef surface is exposed (Hendler 1977; Cubit et al. 1986) for several days to weeks killing most non-swimming invertebrates and greatly reducing algal and seagrass cover (Glynn 1968; Hendler 1976, 1977; Hay 1981; Kilar 1984; Cubit et al. 1986; Kilar et al. 1988). More detailed lists of species or descriptions of the reef community of Galeta Point are available in Birkeland et al. (1976), Cubit and Williams (1983), Connor (1985), and Kilar et al. (1988), while a survey of the rocky-shore zonation on the Atlantic coast of Panama is given by Brattström (1985). A detailed study of water-level fluctuations and emersion regimes at Galeta Point has been done by Cubit et al. (1986).

Drift biomass. From January 1979 to March 1980 drift materials leaving the reef were collected continuously in 5 cone-shaped nets, with an upstream rectangular, P.V.C.-framed opening of 0.91 m high × 0.46 m wide, and a downstream, 0.25 m diameter opening, joined together by 3 mm Vexar netting (Fig. 2). A removable 0.75 × 1.25 m nylon bag (3 mm mesh) was attached to the downstream end and emptied 1–3 times a week. Nets were positioned to collect drift materials just before entering the Galeta back-reef channel and to maximize the amounts of drift biomass collected and the area of the reef platform sampled. Nets were concentrated in areas adjacent to the lab, outside the reef area affected by water contacting the sea walls of the Galeta marine station (current direction was determined with a fluorescein sodium dye), and spaced at about 10, 20, 40, and 80 m from the first net (Fig. 3). Preliminary observations of reef-flat currents and samples of drift biomass suggested that nets located near the lab would collect more biomass. As most algae (Norton and Mathieson 1983) and the seagrass *Thalassia* (Zieman et al. 1979) are negatively buoyant, the import of reef-flat vegetation occurs infrequently; an observation that has been corroborated from samples collected by a net placed on the outer edge of the fore reef in February, May, August, and November 1979. Materials not on the reef flat, reef slope, or subtidal sand plain (higher-plant debris, tar, and *Sargassum filipendula* C. Ag.) were classified as "imported." All other materials were considered "exported."

To determine the sampling area and the efficiency at which the nets collected drift, tags were released upstream of the five nets. Tags consisted of neutrally buoyant, fluorescent surveyor's tape (about 3 × 3 cm). For every meter of transect, ten labeled tags were released from predetermined locations along fore- (transect no. 1) and mid-reef (transect no. 2)
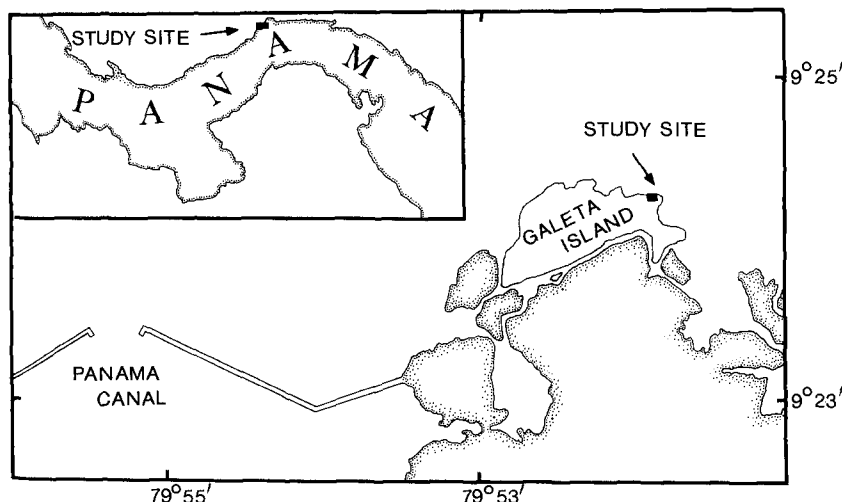

Fig. 1. Study site at Galeta Island (not stippled), Panama, about 6 km northeast of the Caribbean entry into the Panama Canal. Breakwaters define entrance into canal
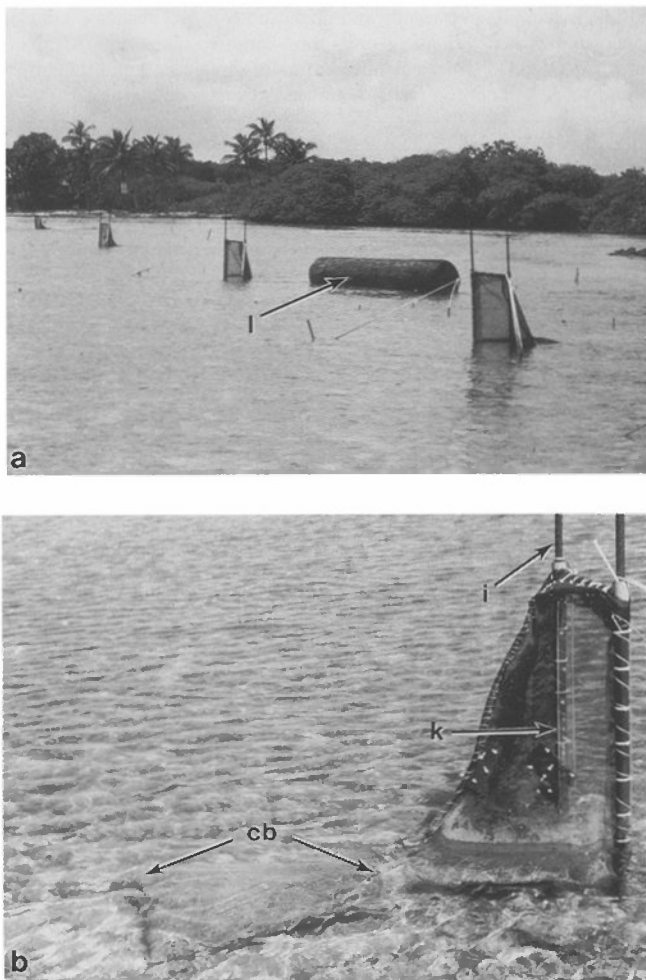
transects (Fig. 3). Two transects were used to determine sampling area, as the flow rate of water across the platform was not uniform (Kilar 1984; Kilar et al. 1988). Tags captured in the nets defined the borders of the sampling area and sampling efficiency. In the first trial, tags were released in calm sea-conditions along only the fore-reef transect. In the three subsequent trials, tags were released along fore- and mid-reef transects in severe (rough), moderate, and calm (light) sea-conditions.

Estimates of dry weight were derived for species by subsampling the contents of each net. Materials were thoroughly mixed and emptied into 30 to 60, 2 liter, containers. Four subsamples were randomly selected, and the contents were sorted to species. Materials in the remaining containers and the sorted aliquots were rinsed in fresh water and dried to a constant weight at 90 °C. Estimates of the dry weight were summed for the five nets, totaled each month, and divided by the mean efficiency of the nets. Because each net collected vastly different quantities of biomass, net samples were not replicates and could not be used to define confidence limits.

Species-specific export rates standardized to areal coverage were derived each month for the dominant reef-flat species. Export rates were calculated by dividing monthly estimates of captured drift biomass by the net's sampling efficiency (mean) and the species' areal coverage (m^2). Estimates of cover were derived by multipling the occurrence of a species in the sampling area (no. of samples with a given species divided by the total no. of samples) by the sampling area of the five nets. The sampling area was defined by the tags of all release-capture trials, as the sampling efficiency was low (1–3%). Turnover time was calculated by dividing a species' export rate by its standing crop. Standing crop and occurrence samples were taken from Galeta reef concurrently with this study (Kilar et al. 1988). Only samples within the drift sampling area were used to estimate standing crop and occurrence.

Species-specific import rates were calculated for higher plant materials, *Sargassum*, and tar by dividing monthly estimates of biomass or mass by the efficiency (mean) of the five nets, and the linear distance of fore reef in the sampling area. The distance sampled along the fore reef was determined from the tags of all release-capture trials.

Data analysis. Drift biomass was analyzed by time series analysis of Box and Jenkins (1976) and multiple correlation models. Correlations of drift biomass were computed for major drift components at weekly intervals over the 15-month sampling period to determine whether the drift biomass was independent of meteorological and hydrographic conditions. Multiple correlation models were formed, following the recommenda-

Fig. 2. Drift sampler(s): a Four of the five samplers positioned in the back reef. l = log. b A close-up view of the sampler. cb = detachable collection bag; i = iron bar; k = plexiglass knife
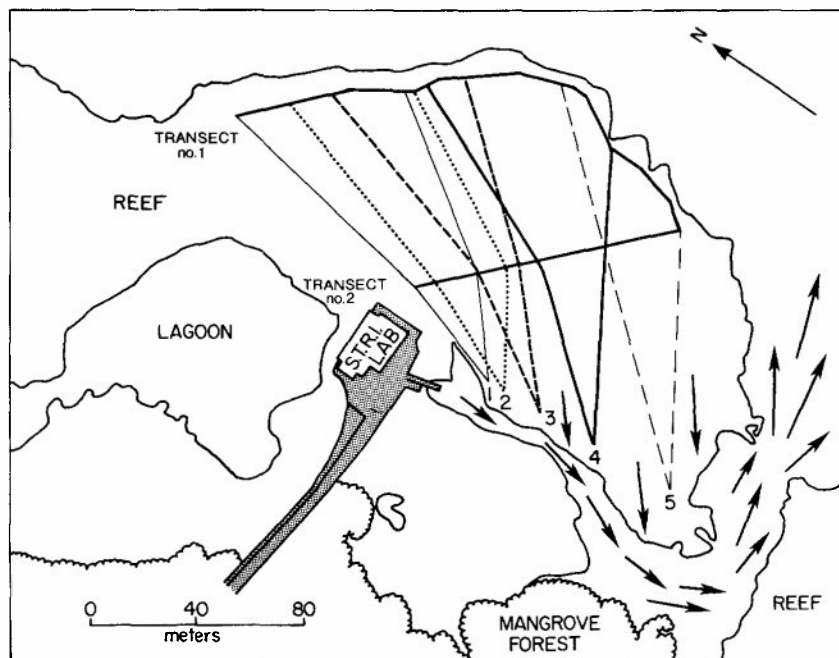

Fig. 3. Location and sampling area of the five drift samplers on the reef platform at Galeta Point, Panama. Tags released along transects 1 and 2 determined the sampling area of each net. Arrows indicate the relative flow of water in the back reef

tions of Montgomery and Peck (1982). Hydrographic and meteorological data for the 15-month sampling period included wind velocity, upstream water temperature, tidal elevation, solar irradiance, and rainfall on a time scale of hours (Cubit et al. 1988). Preliminary models evaluted both the mean, maximum, and minimum values of each variable or, as in the case of tidal elevation, time above the 50 and 60 cm datums or below 30 and 27 cm datums. Because of major gaps in physical data, correlation analyses were limited to the periods of 18 January to 20 September 1979 for wind speed, 18 January 1979 to 31 January 1980 for upstream water temperature, and 15 February 1979 to 27 March 1980 for tidal elevation, and 18 January 1979 to 27 March 1980 for solar irradiance. Within these periods 61, 433, 418, and 188 h of missing data occurred for wind, temperature, tide, and solar data, respectively. These gaps occurred over a 1 to 3 day period and were filled by averaging hourly means from adjacent days. Only once, from 19 to 25 October, was a gap in solar data filled by averaging the data from the preceeding (12–18 October) and succeeding (26 October–1 November) sampling-periods. Cross correlations were computed between physical variables and drift biomass to determine appropriate time lags and between physical variables to determine the degree of multicollinearity. When necessary, models were $\log_{10}$-transformed to satisfy regression assumptions of normality and heteroscedasticity. Outliers were removed only to meet the above assumptions. Correlations between standing crop and export biomass were examined at a time scale of a month, restricting the standing crop data of Kilar et al. (1988) to the drift sampling area.

Results

Sampling area and efficiency

Sampling efficiency averaged 1.8%, ranging from 0.8 to 3.6% (Table 1). No obvious pattern emerged between the sea condition in which tags were released and net efficiency. It was determined that the five nets sampled a maximum of 1.32 ha and a minimum of 1.04 ha of reef flat, which entailed linear distances of 202 and 137 m of the fore reef. Pooling the results of release-capture trials, the sampling area of each net is shown in Fig. 3. Over the 15-month period, samples were lost on only six occasions, representing an error in sampling of 1.7%.

Table 1. Sampling efficiency and area, and fore-reef distance sampled by drift nets as determined from release-capture experiments. Sampling area was defined from tags released under similar sea conditions from both fore- (*) and mid-reef (**) transects (see Fig. 3)

Relative wave exposure	No. of tags released	No. of tags captured	Efficiency	Sampling area (ha)	Fore-reef distance (m)
Calm	2600*	39	0.015		187
Calm	1150*	22	0.019		137
				1.04	
Calm	800**	17	0.021		
Moderate	1400*	19	0.014		202
				1.32	
Moderate	850**	7	0.008		
Severe	1400*	47	0.036		157
				1.09	
Severe	800**	8	0.010		

$(\bar{x} \pm SD)\ 0.018 \pm 0.009$

Drift composition and abundance

Woody-plant debris was the major component of drift with 52% of the dry weight mass, followed by algae and seagrasses, tar, and the aquatic water hyacinth *Eichhornia crassipes* (Mart.) Solms (Fig. 4a). Of the vegetation exported from the reef, *Thalassia* comprised 54% of the biomass, and *Laurencia* 15%. The percent composition for other major components are shown in Fig. 4b, with the reamining 7% of the biomass consisting of minor reef flat and subtidal species. Subtidal algae, such as the green alga, *Microdictyon boergesenii* Setch. and the red algae, *Cryptonemia crenulata* J. Ag., *Halymenia duchassaignii* (J. Ag.) Kyl., *Ochtodes secundiramea* (Mont.) Howe, and *Peyssonnelia rubra* (Grev.) J. Ag. were occasionally found in drift samples. Drift biomass that was imported onto the platform consisted mainly of woody debris or terrestrial plants, the fucalean brown alga *Sargassum fili-*
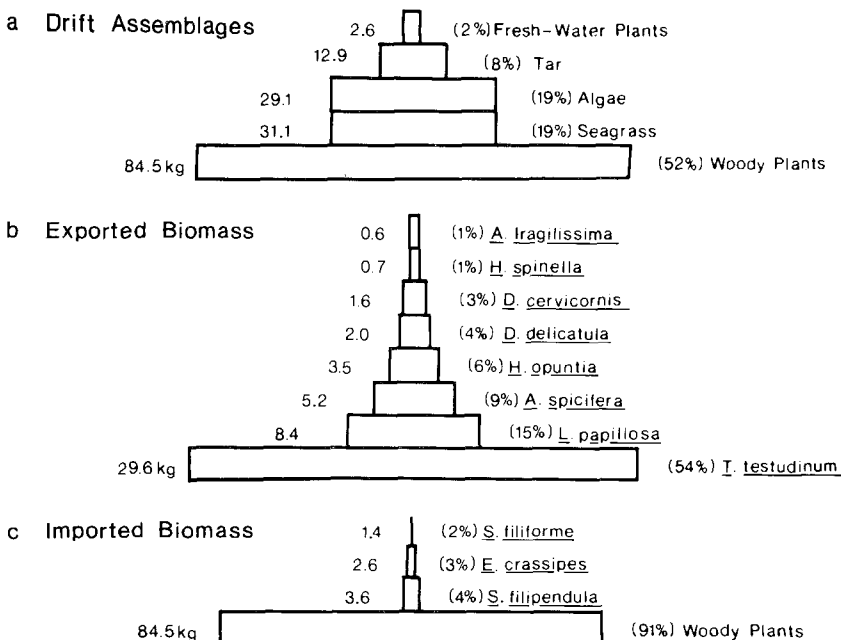

a Drift Assemblages

- 2.6 — (2%) Fresh–Water Plants
- 12.9 — (8%) Tar
- 29.1 — (19%) Algae
- 31.1 — (19%) Seagrass
- 84.5 kg — (52%) Woody Plants

b Exported Biomass

- 0.6 — (1%) A. fragilissima
- 0.7 — (1%) H. spinella
- 1.6 — (3%) D. cervicornis
- 2.0 — (4%) D. delicatula
- 3.5 — (6%) H. opuntia
- 5.2 — (9%) A. spicifera
- 8.4 — (15%) L. papillosa
- 29.6 kg — (54%) T. testudinum

c Imported Biomass

- 1.4 — (2%) S. filiforme
- 2.6 — (3%) E. crassipes
- 3.6 — (4%) S. filipendula
- 84.5 kg — (91%) Woody Plants

Fig. 4. Absolute (kg) and relative (%) magnitudes of drift assemblages (total, exported, imported) collected continuously by the five nets at Galeta Point, Panama, for a 12 month period (January 1979–December 1979). Absolute values are reported to the left of figure

pendula, Eichhornia crassipes, and the seagrass, *Syringodium filiforme* Kütz. Woody-plant debris accounted for 91% of the imported biomass (Fig. 4c).

Seasonal abundance

Estimates of algae and seagrass biomass removed from or drifting into the sampling area were higher in the dry-season than the wet-season, with algae ranging from 29–580 kg mo^{-1} and seagrasses from 37–240 kg mo^{-1} (Fig. 5). Trends of *Thalassia testudinum, Laurencia papillosa, Acanthophora spicifera,* and *Hypnea spinella* (C. Ag.) Kütz. abundance did not differ from the general pattern (Fig. 6), with export rates ranging from 37–294 kg mo^{-1} for *Thalassia,* 3–171 kg mo^{-1} for *Laurencia,* 3–74 kg mo^{-1} for *Acanthophora,* and 1–10 kg mo^{-1} for *Hypnea.* Total terrestrial and fresh-water plant biomass showed no pronounced seasonal trends and averaged about 460 kg mo^{-1} for all but 2 months, March and December (Fig. 5). This pattern differed from those of *Eichhornia, Sargassum,* and *Syringodium* which showed a trend of increasing abundance throughout the sampling period, with intermittent periods of 1–4 months of low or no biomass (Fig. 7). Rafts of *Sargassum* washed ashore in August 1979 and February 1980, depositing 83 and 430 kg, respectively. In March and December 1979, large logs were removed from in front of nets (see Fig. 2) and were not included in estimates of higher-plant drift. Floating tar was highest in January 1979 (280 kg), decreased to immeasurable levels into November 1979, and then increased to 50 kg mo^{-1} by February 1980 (Fig. 5).

Fig. 6. Exported biomass (grams dry wt ÷ mean sampling efficiency) of *Thalassia testudinum, Laurencia papillosa, Acanthophora spicifera,* and *Hypnea spinella* removed from the reef flat (1.0–1.3 ha) at Galeta Point, Panama (January 1979–March 1980)
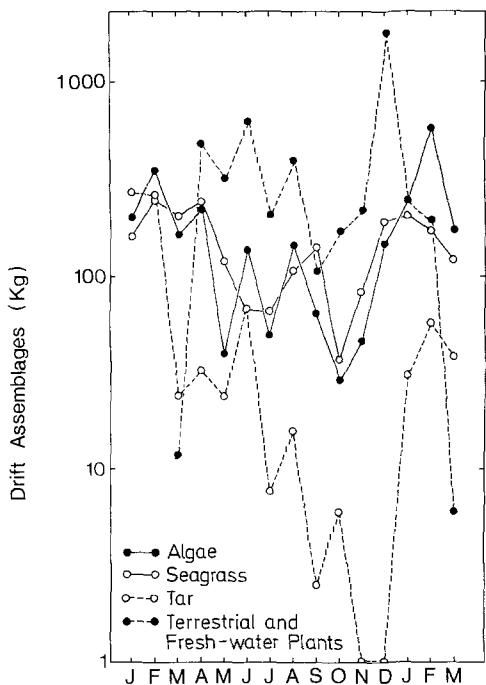

Fig. 5. Estimated mass (grams dry wt ÷ mean sampling efficiency) of terrestrial and fresh water plants, algae, seagrasses, and tar removed from 1.0–1.3 ha of reef flat or traversing 137–202 m of fore reef at Galeta Point, Panama (January 1979–March 1980)
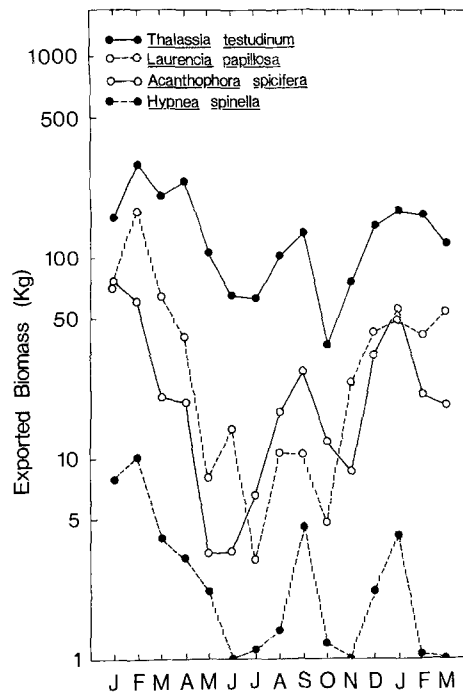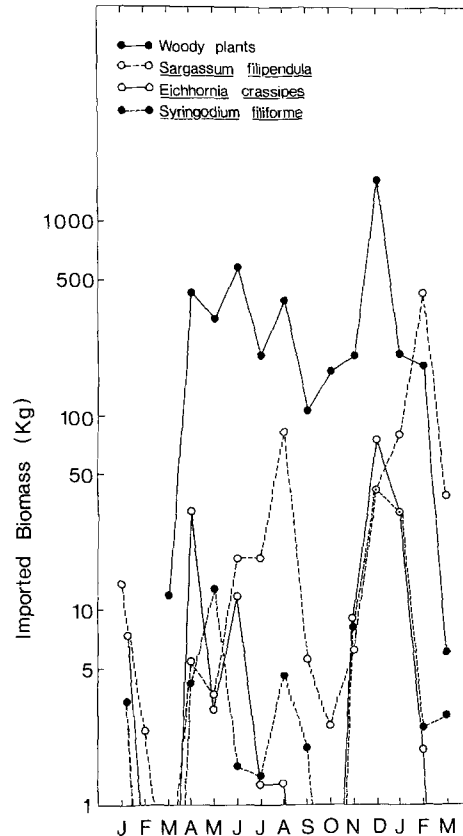

Fig. 7. Imported biomass (grams dry wt ÷ mean sampling efficiency) of woody-plant material, *Sargassum filipendula, Eichhornia crassipes,* and *Syringodium filiforme* traversing 137–202 m of fore reef at Galeta Point, Panama (January 1979–March 1980)

Time series and correlation analysis

Autocorrelations of drift biomass for the major reef-flat species were generally highest at 2 week intervals, suggesting that the quantity of drift removed from the platform was, in part, related to spring and neap tide cycles (Table 2). Those for imported materials (woody-plant debris, *Eichhornia, Sargassum,* and tar) were highest with lags of 1 week. In these analyses, seasonal cycles cannot be determined, as only 15 months of data were collected.

Multiple correlation models for the major drift components are shown in Table 3. These models explained between 31 and 65% of the variance in the drift biomass. Mean tidal elevation and wind speed were determined to be the best predictors of exported biomass. Increases in tidal elevation and wind velocity increased the quantity of biomass removed from the platform. The effect of tidal elevation on drift was virtually instantaneous while that of wind speed had a lag of 3 weeks for most species. In general, wind speed had a greater influence on drift biomass than tidal elevation. *Acanthophora* was the only plant for which water temperature was a better predictor than wind speed of drift biomass. Water temperature was negatively correlated with the exported biomass of *Acanthophora* and with wind speed ($r = 0.910$, $P < 0.001$). Significant negative correlations of temperature and drift biomass were also observed with *Laurencia* ($r = -0.484$, $P < 0.001$), *Thalassia* ($r = -0.437$, $P < 0.002$), *Gelidiella* ($r = -0.337$, $P < 0.010$), and total algae ($r = -0.370$, $P < 0.010$). With imported drift, wind speed was negatively correlated with floating *Sargassum,* and solar irradiance was negatively correlated with higher-plant debris; wind speed and solar irradiance were significantly correlated ($r = 0.633$, $P < 0.001$). Models relating physical variables to the quantity of aquatic macrophytes, total algae, and tar yielded weak correlations ($r \leq 0.038$) which were not significant ($P > 0.05$).

With the exception of *Gelidiella* ($r = 0.637$, $P < 0.020$, $n = 14$), estimates of standing crop and drift biomass for reef-flat species were not significantly correlated ($P > 0.05$).

Export rates and turnover time

Reef-flat species, such as *Thalassia, Laurencia, Acanthophora,* and *Halimeda,* lost considerable biomass from the estimated 1.0–1.3 ha sampling area, totaling 1659, 444, 269, and 203 kg year^{-1}, respectively (Table 4). Annual export rates of *Thalassia, Hypnea musciformis* (Wulf.) Lamour., and *Acanthophora* were among the highest; however, monthly rates were highest for *Thalassia, Centroceras,* and *Dictyota.*

Turnover times were calculated for *Thalassia* (blades), *Laurencia,* and *Acanthophora,* the dominant,

Table 2. Autocorrelation of biomass or mass for the major drift components at Galeta Point, Panama (February 1979 – March 1980). Only significant correlations are displayed

Species	r	n (weeks)	Lags (weeks)
Spermatophyta			
Thalassia testudinum	0.285*	62	2
Eichhornia crassipes	0.451**	62	1
Terrestrial (woody) plants	0.601**	53	1
Rhodophyta			
Acanthophora spicifera	0.489**	62	1
	0.560**	62	2
	0.250*	62	3
Gelidiella acerosa	0.249*	62	2
Hypnea musciformis	0.294*	62	1
Laurencia papillosa	0.302*	62	1
	0.590**	62	2
Phaeophyta			
Dictyota cervicornis	0.591**	62	1
	0.401**	62	2
	0.259*	62	3
Sargassum filipendula	0.280*	62	1
Other			
Tar	0.334*	62	1

* Correlations are significant at $P < 0.05$
** Correlations are significant at $P < 0.001$

Table 3. Correlation models of drift biomass versus meteorological and hydrographic conditions for major drift components at Galeta Point, Panama. x_1 = mean tidal elevation; x_2 = mean wind velocity; x_3 = mean upstream water temperature; and x_4 = mean solar irradiance. Time scale in weeks. All regression models significant at $P \leq 0.001$

Species	r^2	n	$y = b_0 + b_1 x_1 + b_2 x_2$ or $y = b_0 + b_1 x_1$	Lags (weeks) x_1	x_2	x_3	x_4
Spermatophyta							
Thalassia testudinum	0.511	32	$Log_{10}y = 1.24 + 0.022x_1 + 0.023x_2$	0	3	–	–
Terrestrial (woody) plants	0.334	55	$Log_{10}y = 5.26 - 0.001x_4$	–	–	–	0
Rhodophyta							
Acanthophora spicifera	0.563	49	$Log_{10}y = 11.7 + 0.040x_1 - 0.421x_3$	0	–	1	–
Gelidiella acerosa	0.520	32	$Log_{10}y = -0.218 + 0.029x_2$	–	3	–	–
Hypnea musciformis	0.311	34	$Log_{10}y = 0.048 + 0.042x_2$	–	3	–	–
Laurencia papillosa	0.653	30	$y = -249 + 4.16x_1 + 11.60x_2$	0	3	–	–
Phaeophyta							
Dictyota cervicornis	0.482	30	$Log_{10}y = -0.631 + 0.090x_2$	–	3	–	–
Sargassum filipendula	0.433	33	$Log_{10}y = -3.900 + 0.205x_1 - 0.163x_2$	0	4	–	–

Table 4. Species-specific export and import rates for major drift components standardized to areal coverage or linear distance of fore reef at Galeta Point, Panama (February 1979 to January 1980). $n=12$ months. Confidence limits represent $\bar{x}\pm 95\%$ C.I.

Species	Drift export[a] or import (kg/year)	Species-specific export rate		Turnover time (d)	Species-specific import rate (g/d/m)
		(g/year/m²)	(g/d/m²)		
Spermatophyta					
Thalassia testudinum[b,c]	1659	308	0.918 ± 0.446	223 ± 112	
Eichhornia crassipes	144				1.940 ± 2.270
Syringodium filiforme	82				1.101 ± 1.225
Terrestrial (woody) plants[2]	4512				60.20 ± 44.90
Rhodophyta					
Acanthophora spicifera	269	174	0.451 ± 0.189	207 ± 127	
Amphiroa fragilissima	34	8	0.020 ± 0.009		
Centroceras clavulatum	24	107	0.677 ± 0.565		
Gelidiella acerosa	15	21	0.069 ± 0.069		
Hypnea musciformis	22	185	0.355 ± 0.437		
Hypnea spinella	35	139	1.552 ± 2.106		
Laurencia papillosa	444	112	0.292 ± 0.236	1603 ± 1237	
Phaeophyta					
Dictyota cervicornis	77	149	0.590 ± 0.364		
Sargassum filipendula	202				2.710 ± 2.410
Other					
Tar	716				9.960 ± 1.058

[a] Biomass ÷ net efficiency
[b] Data from March 1979 to February 1980
[c] Data represents only _Thalassia_ blades

perennial species. For other species, turnover times were not derived as monthly estimates of standing crop or exported rate were, for some months, questionable (i.e. low sample size or very little biomass collected). The average turnover time of _Laurencia_ was about 8 times longer than that of _Thalassia_ and _Acanthophora_ (Table 4). The contribution of species to drift biomass was not always proportional to their standing crop on the reef platform (Fig. 6). _Thalassia, Acanthophora, Dictyopteris_, and _Centroceras_ lost proportionally more biomass to drift than _Halimeda opuntia, Amphiroa, Penicillus_, and _Gelidiella_. Some drift material of _Dictyopteris_ may have possibly originated from subtidal habitats.

Large quantities of terrestrial-plant material drifted over the reef platform, averaging about $60\ \mathrm{g\ d^{-1}m^{-1}}$, while _Sargassum_ averaged $3\ \mathrm{g\ d^{-1}m^{-1}}$, _Eichhornia_ $2\ \mathrm{g\ d^{-1}m^{-1}}$, and tar $10\ \mathrm{g\ d^{-1}m^{-1}}$ (Table 4).

Discussion

Physical factors

We have demonstrated that meteorological and hydrographic events are correlated with the amounts of exported biomass. Previously, Moore (1963), Zieman et al. (1979), Josselyn et al. (1983) and Ballantine (1984) have reported that storm and hurricane events can cause extensive damage and appear to be correlated with the amounts of vegetation exported from coastal regions. At Galeta, tidal cycles (spring-neap tides and seasonal events) are correlated with drift biomass, affecting reef assemblages instantaneously. On the other hand, wind

speed is best correlated with drift biomass at a lag of 3 weeks. It follows that wind speed is probably related to one or more physical variables, like temperature, light, nutrients, or water motion (see Schwenke 1971, for review of water motion on plants) that affect plant growth. Wind speed is negatively correlated with upstream water-temperature, suggesting that an increase in wind velocity accompanys the cooling of nearshore surface-water. Lower temperatures can impact upon algal standing crop. For example, temperature optima for _Laurencia_ and _Acanthophora_ productivity are at approx. 25 °C which is near the lower end of the Galeta's temperature range (Kilar 1984). Despite the absence of a strong correlation between monthly estimates of standing crop and drift biomass for most species, we believe that these variables are closely related and that time scales on the order of weeks or days may be necessary to test this relationship. As tides and wind velocities and plant standing crop are highest in the dry-season and lowest in the wet-season (Hendler 1976; Cubit et al. 1986, 1988; Kilar et al. 1988), seasonal cycles in drift biomass are a likely occurrence.

Wind speed is negatively correlated with import rates of _Sargassum_ at a lag of 4 weeks. A weak positive correlation occurred between imported biomass and wind speed when no lags were imposed. However, when adding lags of wind speed to the model, correlations became negative and coefficients (r) greatly increased. Thus, strong winds appear to deplete _Sargassum_ from nearshore waters. We believe a very similar situation occurs with terrestrial-plant debris. Cross correlations of wind speed and terrestrial-plant debris displayed a similar pat-

tern to that of *Sargassum*, but were weakly correlated. As to what factors control the seasonal abundance of *Sargassum* and higher-plant debris, we are not certain at this time. The autecology and distribution of *S. filipendula* is poorly understood for this area as are the major sources of higher-plant debris. Many pieces of wood captured by nets had extensive colonies of the goose barnacle, *Lepas*, suggesting that there is a long-range, oceanic, drifting component to some of this material (Gosner 1978).

Water temperature is a better predictor of the exported biomass of *Acanthophora* than is wind speed. During the wet-season, elevated water temperatures accompany periods of low water (Hendler 1976; Cubit et al. 1986, 1988) that decrease algal standing crop on the platform (Glynn 1968; Hendler 1977; Hay 1981; Kilar 1984; Cubit et al. 1986). As algae tend to "dissolve" in the seawater after prolonged exposures in air (Kilar personal observation), the prediction of the model follows that water temperature is negatively correlated with exported biomass. Significant negative correlations between temperature and drift biomass occur with all major reef-flat species. Cubit et al. (1986) have noted that "Emersion of reef flats during extreme low tides is probably the most severe perturbation of physical origin experienced by the organisms in reef flat communities, other than damage from hurricanes and tropical storms." In retrospect, the relatively strong relationship between exported biomass and physical variables suggests that the export of drift biomass from off the reef platform is a predictable, seasonal event.

Effects of life-history strategies

Export rates of *Thalassia, Centroceras, Dictyota, Hypnea* and *Acanthophora* are among the highest on the reef platform (Table 4). The explanation for their high export rate can be attributed, in part, to their life-history strategies. Mshigeni (1978) was first to recognize the ability of *Acanthophora spicifera* to colonize space by vegetative fragmentation. At Galeta Point, Kilar and McLachlan (1986) have demonstrated that *Acanthophora* in the fore reef gives rise to fragments that colonize back-reef habitats. Furthermore, from the same habitat, they have noted that *Acanthophora* lost a greater percentage of its biomass to drift than the non-fragmenting *Laurencia*. Other species thought to reproduce by vegetative fragmentation include *H. musciformis* (Mshigeni 1978), *Centroceras* (Lipkin 1977), and *Dictyota* (Kilar and McLachlan 1986). With *Thalassia*, older blades are constantly released into the water, representing the end of a developmental cycle. Old blades degenerate and are torn from the plant by reef-flat currents (Zieman et al. 1979). Losses to drift are also high for some wave-zone species. Macrophytes, like *H. spinella*, that are restricted to fore-reef habitats lose a larger proportion of their biomass to drift than those in the back reef, like *Penicillus capitatus* Lamk., or species that develop a tough thallus (e.g., *Gelidiella*) or dense "turf construction" of branches (Hay
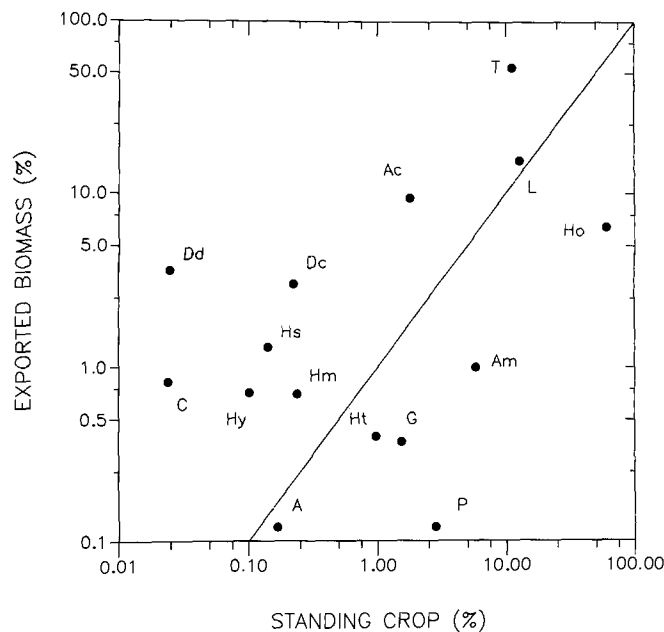

Fig. 8. Logarithmic plot of exported biomass (dry wt) versus standing crop (dry wt) for major reef-flat species. Line indicates the position along X, Y coordinates where the relative abundance of a species on the reef equals its relative contribution to exported biomass. A = *Anadyomene stellata*; Ac = *Acanthophora spicifera*; Am = *Amphiroa fragilissima*; C = *Centroceras clavulatum*; Dc = *Dictyota cervicornis*; Dd = *Dictyopteris delicatula*; G = *Gelidiella acerosa*; Hm = *Halimeda monile*; Ho = *Halimeda opuntia*; Hs = *Hypnea spinella*; Ht = *Halimeda tuna*; Hy = *Hypnea musciformis*; L = *Laurencia papillosa*; P = *Penicillus capitatus*; T = *Thalassia testudinum*

1981), like *Laurencia*. Export estimates of the calcareous algae, *Halimeda opuntia* and *Amphiroa*, are underestimated, as small fragments are relatively heavier and quickly sink. Differences in the turnover times (Table 4) and in the relative proportion of biomass contributed by reef-flat species to drift (Fig. 8) suggest that life-history strategies are important in determining species-specific export rates.

Export and import rates

Few studies have documented the export or import rates of marine macrophytes. At St. Croix, Virgin Islands, Zieman et al. (1979) report 0.02 g d^{-1}m^{-2} of *Thalassia* and 0.18–0.36 g d^{-1}m^{-2} of *Syringodium* blades removed from Tague Bay, and Josselyn et al. (1983) report 0.001 g d^{-1}m^{-2} of *Thalassia* blades exported from the Salt River submarine canyon. When standardized to sampling area (1.3 ha), our drift estimates of *Thalassia* blades are still an order of magnitude greater (0.35±0.13 g d^{-1}m^{-2}, $\bar{x}$±95% C.I.). Macroalgal export was not considered in the Tague Bay study; however, from the Salt River canyon study algal export, Dictyotales, was estimated as 0.011 g d^{-1}m^{-2} (wet wt). At Galeta Point, the exported algal biomass is considerably larger, 0.30±0.17 g d^{-1}m^{-2} (dry wt), an indication of the copious growth and composition of algae on the reef platform. Johannes and Gerber (1974) report a net im-

port of benthic algal fragments, mainly *Calothrix* and *Asparagopsis*, onto a coral-dominated platform at Enewetak. From their data, we estimate that between 0.6–1.1 mg d^{-1}m^{-2} (wet wt) accumulate onto the reef surface. Our results show that the Galeta reef-flat is a major source rather than a sink of drift biomass.

Tar comprises a significant portion of the mass of materials imported onto the reef flat at Galeta Point. Tar originates from discharge of oil into the sea as bilge water from ships, industrial waste from land (Butler et al. 1973), and occasionally from oil seepages from the sea bottom (Landes 1973). Heavy sea traffic through the Panama Canal and an oil refinery 3–4 km south of the Galeta lab. probably account for the high concentrations. Tar accumulations on sandy beaches of 534 g year^{-1}m^{-1} (Dennis 1959) and 2005 g year^{-1}m^{-1} (Curtis and Saner 1974) are reported from Florida; 1606 g year^{-1}m^{-1} from Texas (Ray et al. 1974); and 190 g year^{-1}m^{-1} from Bermuda (Butler et al. 1973). At 3540 g year^{-1}m^{-1}, Galeta Point, by association, imports two to seven times more than Florida, two times more than Texas, and 19 times more than Bermuda, making Panama's shores, of those monitored to date, the most oil polluted in the Caribbean.

Fate of drift

After breakage, the buoyancy of the drift material determines where it will be deposited. In general, seaweeds without air bladders are negatively buoyant (Norton and Mathieson 1983) and are swept along by currents and deposited in quiet backwaters, on beaches, or into subtidal habitats. At Galeta Point, most algae and blades of *Thalassia* are carried by currents into subtidal habitats (Fig. 3). Tags released on the reef platform occurred frequently on the reef slope on the south side of Galeta reef, the adjacent reef, or the sand plain that joins the two reef systems. Here, Hay et al. (1983) have shown that reef-flat species when transplanted onto the reef slope are readily consumed by herbivorous fish (Scaridae and Acanthuridae), but they are not grazed when placed onto a sand plain. We believe a similar fate awaits most drift algae and seagrass, as numerous fish (Randall 1965; Stoner and Livingston 1980; Kulezycki et al. 1981), gastropods (Paine 1969; Cowper 1978), sea urchins (Ogden et al. 1973; Lowe and Lawrence 1976; Mattison et al. 1977; Russo 1979; Verlaque and Nédelec 1983; Dean et al. 1984), and crabs (Cowper 1978) are known to feed on drift seaweeds and seagrasses. In the dry-season, "tumbleweed-like" aggregates of *Acanthophora*, 0.2 to 0.8 m diameter, and accumulations of *Thalassia* blades occur on the sand plain as bedload. During periods of low light intensities, the algae show signs of decomposition. Otherwise, they appear healthy.

Most floating vegetation, such as woody plants, *Sargassum, Syringodium* and a small percentage of *Thalassia* and algae (e.g., *Acanthophora, Lyngbya*), were observed deposited into the mangrove swamp or sandy beach behind the reef. Previously, Zieman et al. (1979) reports that most *Thalassia* blades remain on the bottom and are transported as bedload, while *Syringodium* with its large air canals are buoyant and transported near the surface. Occasionally, algae have been observed to fragment and float away by entrapping and accumulating nascent oxygen. The hydrodynamic characteristics of floating vegetation are such that the waves and wind force them back onto the shore, concentrating them along the water line and moving them landward with the rising tide. With each successive higher tide, wave, or storm, the drift moves further landward. In the mangroves, several grazers occur along driftlines. In the Galeta mangroves, the gastropod, *Batillaria minima* Gmelin (Birkeland et al. 1976; Macintyre and Glynn 1976) is the most noticeable, occurring in very large numbers. Previous studies of driftlines on sandy shores have observed large concentrations of macrofauna, meiofauna, and insects beneath drift, a response to high food availability in the form of the drift algae and the resulting dissolved organic matter levels (Remane and Schulz 1964; Cheng 1976; Roth and Brown 1976; Joose 1976; Dobson 1976; Simpson 1976; Doyen 1976; Griffiths and Stenton-Dozey 1981; Koop and Griffiths 1982).

Our investigation clearly demonstrates that the algal-dominated platform at Galeta Point is a major source of drift algae and seagrass. Large quantities of marine vegetation are continuously exported from the reef into subtidal habitats. Evidence is presented that suggests that exported biomass from the reef platform is strongly dependent upon meteorological and hydrographic conditions which are predictable, seasonal events. Therefore, organisms may have evolved that specifically utilize drift algae and seagrass for food or habitat, or as a means of dispersal. To illustrate, Highsmith (1986) has hypothesized that the evolution of brooding invertebrates is a response to a lack in rafting opportunities which reduce juvenile mortality among those animals that have pelagic, planktotrophic, or lecithotrophic larvae. Kingsford and Choat (1985) have suggested that the export of large quantities of drift into coastal waters could rapidly alter the distribution patterns of many animals, as they observed 20–25% of the usual numbers of fish had accumulated from surrounding water to previously cleaned drift algae within 5 h. Dean et al. (1984) have proposed that the scarcity of drift algae as food changes the behavior pattern of the red urchin, *Strongylocentrotus franciscanus* A. Agassiz, to form large, motile aggregates or fronts that devastate kelp communities in temperate regions. Further studies are necessary to assess the importance of drift algae and seagrass in structuring and maintaining tropical reefs.

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