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# Composition, Export and Faunal Utilization of Drift Vegetation in the Salt River Submarine Canyon

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Submarine canyons may be particularly important in the transport process of drift seagrasses and seaweeds from highly productive shallow lagoon areas to deeper water. We studied the composition, export, and faunal utilization of shallow, nearshore benthic vegetation as it was transported to offshore areas via the Salt River submarine canyon on the island of St Croix, U.S. Virgin Islands. The study was conducted using a saturation diving system (NULS-1: Hydrolab) during two missions in April and August, 1980. Using bottom drifters deployed in Salt River Bay and the submarine canyon, we recorded net benthic current flow up to 2 cm $s^{-1}$ moving out of the lagoon and down the canyon to deeper water. Using bottom nets set up at the canyon head and at the 29 m isobar, and from transect surveys and drift clump samples, we determined drift plant export rates and drift clump biomass and species composition. The dominant drift plants were *Thalassia testudinum* and *Syringodium filiforme* and algae in the genera *Dictyota*, *Dictyopterus*, and *Dilophus*. During the second mission, the seagrass *Halophila decipiens* became more abundant, both in the drift and in large patches along the canyon floor. In both missions, more drift was collected in the nets during high wind conditions than during calmer days. Calculated turnover times ranged from 0·01 to 4·4 days for algae in the order Dictyotales and 4·4 to 18 days for *Thalassia* blades. Total exported biomass of drift vegetation varied between 1·4 to 65·1 kg wet wt $day^{-1}$. Samples of drift vegetation contained mostly juvenile forms of both invertebrates and fishes, but in relatively low numbers. Faunal numbers were most strongly related to rate of drift movement.

## Introduction

The occurrence and widespread distribution of seagrass blades, primarily *Thalassia testudinum*, on the ocean floor from 1000–8000 m have been well documented using deep-sea photography (Menzies *et al.*, 1967; Menzies & Rowe, 1969). This abundant organic material provides a significant food source and habitat to the deep-sea benthos (Moore,

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1963; Wolff, 1976; 1979), and the distribution of some organisms may be directly related to the availability of drift vegetation (Menzies & Rowe, 1969). In addition to seagrasses, marine algae such as *Halimeda*, *Sargassum*, and kelp have been observed either on the bottom or within guts of deep-sea animals (Wolff, 1962; Okutani, 1969; Schoener & Rowe, 1970).

The export of drift vegetation from lagoons and estuaries provides most of the macrodetrital material observed in the deep sea and in some cases, it may be transported over 1000 km before deposition on the sea floor (Menzies *et al.*, 1967). The abundance of deep-sea detrital material has been correlated with storm and hurricane events which export large amounts of vegetation from the coastal zone (Moore, 1963). Recent studies by Zieman *et al.* (1979) in Tague Bay, St Croix and Thayer and Bach (personal communication) in North Carolina have documented export rates from seagrass beds under normal weather conditions. The percent of primary production exported from the embayments varied from 1% for *Thalassia* to 1–20% for *Zostera marina* and to 60–100% for *Syringodium filiforme*. *Thalassia* blades were exported as bedload, whereas *Zostera* and *Syringodium* blades floated to the surface and were exported by wind-driven surface flow.

Large floating rafts of drift vegetation are frequently observed at sea and are suggested as the primary source for the macro-detritus observed on the ocean floor. Slumping and down-slope movement along the continental slope and turbidity currents associated with submarine canyons have also been suggested as mechanisms for the transport of drift

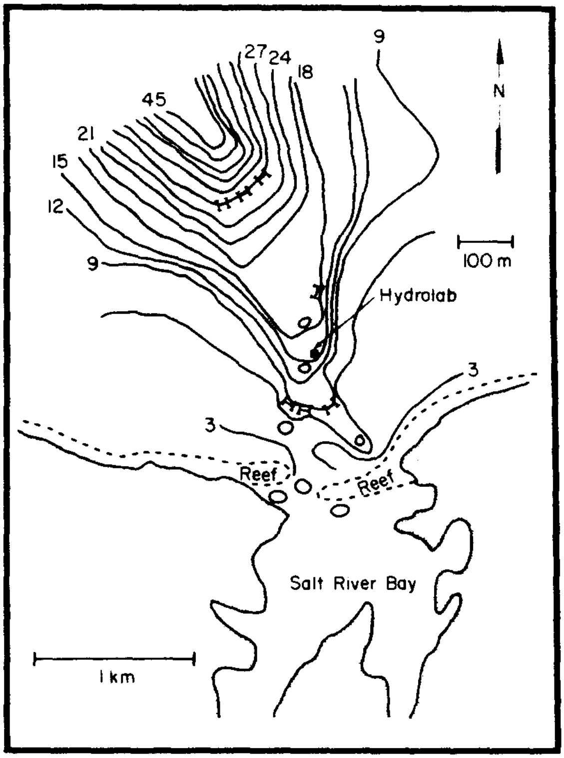

Figure 1. Map of Salt River Bay and offshore submarine canyon (note difference in map scale). Positions of Habitat (HYDROLAB), bottom nets (⊢⊣), and drifter release sites (○) indicated. Isopeths in meters.

vegetation (Heezen, 1955; Menzies & Rowe, 1969). Net down-valley currents have been observed in many submarine canyons (Shepard *et al.*, 1979) and are probably responsible for the export of materials from shallow water. Diving and photographic evidence has shown considerable concentration of drift material in submarine canyons (Shepard & Dill, 1966; Cailliet & Lea, 1977) and in areas immediately offshore from canyons (T. Suchanek, personal communication). No data are available, however, which quantitatively estimate rates of drift movement through submarine canyons.

Shallow-water animals may also be exported with drift vegetation, particularly drift seaweeds. The entangled filaments of many drift seaweeds such as *Hypnea, Laurencia,* and *Cladophora* offer an important habitat to many small invertebrates and fishes. In embayments containing both seagrasses and drift algae, greater numbers of animals are often associated with the seaweed (Gore *et al.*, 1981; Kulczychi *et al.*, 1981). In addition, Cailliet & Lea (1977) discovered a fish once thought rare which is abundant within drift kelp in the Monterey Submarine Canyon. The dissemination of shallow-water animals, particularly to the deep sea, has been suggested as a possible mechanism for the colonization of the ocean floor (Menzies *et al.*, 1967; 1973).

The purpose of our study was to measure the movement and faunal utilization of drift vegetation in the Salt River submarine canyon on the island of St Croix in the U.S. Virgin islands. The study was conducted using an underwater habitat (NULS-1, formerly HYDROLAB) located on the canyon floor. Two seven-day missions were undertaken in April (mission 1) and August (mission 2) 1980. The study was designed to measure three components: (1) the net bottom current flow in the canyon responsible for drift vegetation movement; (2) the types and movement of drift vegetation; (3) the fauna associated with the drift material.

## Materials and methods

### *Study site*

The Salt River Canyon is a small submarine canyon located offshore from Salt River Bay (Figure 1). A small intermittent stream empties into the bay, which is surrounded by mangroves (*Rhizophora mangle*) and sand beaches. Seagrasses (*Thalassia testudinum* and *Syringodium filiforme*) and the macroalgae *Hypnea musciformis, Penicillus* sp., *Halimeda* sp. and members of the order Dictyotales, form the dominant benthic vegetation within the shallow (1–3 m) embayment. A narrow coral reef barrier separates the bay from the ocean, except for a small gap adjacent to the western head of the canyon. An eastern branch of the canyon extends up to the reef front itself. The canyon extends seaward 8 km from the reef gap and terminates at a depth of 3500 m on the St Croix shelf.

The habitat is located at 15 m depth on a sandy bottom. A description of the habitat is given by High *et al.* (1973). The excursion depths for the habitat divers ranged from 9 to 40 m. Within this range, the canyon has a fairly constant width of approximately 120 m and is bounded by a vertical wall on the west side and a gradual slope along the eastern margin. The bottom of the canyon consists of coarse sand with isolated seagrass beds (*Halophila decipiens*) and mounds due to the burrowing shrimp, *Callianassa* (T. Suchanek, personal communication). Clumps of drift vegetation are also frequently observed throughout the canyon.

### *Net bottom current flow*

Net bottom flow from Salt River Bay to the submarine canyon was studied using weighted bottom drifters (Kahlsico 233WA200, El Cajon, CA) and perforated ping-pong balls. The drifters were deployed during both missions, whereas the ping-pong balls were used during the August study only. Numbered drifters (200) and colour-coded ping-pong balls (400) were released at three sites behind the reef in the lagoon, at both canyon heads, and at three depths (12, 15, 21 m) within the canyon (see Figure 1). The position of the drifters and balls in the canyon was plotted from two daily surveys and whenever else they were observed during diving activities. Current speeds from artificial drifter resightings were calculated by dividing the estimated linear distance travelled for each drifter by the time between original deployment or previous sighting and resighting. The residence time of water in the canyon was calculated from average current speeds divided by the axial length of the canyon from its head to the 29 m excursion line limit.

### *Biomass and export of drift vegetation*

The movement of drift into and out of the canyon was estimated from stationary net collection. Nets 1 m tall and 3 m wide were constructed from $\frac{3}{8}$-inch mesh netting. The nets consisted of two 1 × 1 m side panels and a central 1 × 1 m pocket to trap drift moving down-canyon. They were erected with steel bars and held in place by sand anchors. Three nets were set up at the head of the canyon at 8 m depth and three nets at the base of the diver excursion limit at 29 m depth (Figure 1). A seventh net was placed along the eastern edge of the canyon at 20 m to record any drift moving in from the east slope. The nets were sampled twice daily and the drift sorted ashore to species level and wet weights taken. During the August mission, Hurricane Allen (maximum winds 240 kph) came within 320 km of St Croix, and high winds and waves required aborting the saturation mission. However, net collections and bottom sampling were continued by diving from the surface.

The daily import and export of drift vegetation were calculated from the two nets at the west canyon head and the three nets at the 29 m excursion line limit, respectively. The shallow nets occupied 13% of the width of the canyon and the deep nets occupied 8%. Total daily biomass collected in the canyon head and deep nets was divided by these respective percentages to calculate import or export. Nets were sampled twice daily; however, periods of slack or up-canyon currents did reverse the nets so that material was undoubtedly lost. This was particularly true for the nets along the east slope and in the east canyon head, so these collections were not considered in our calculations. Furthermore, observations of drifters in the east canyon head indicated that this area acted as a cul-de-sac rather than a major channel for drift import. Wave action probably affected the collection efficiency of our shallow nets by causing reversing water movement on the bottom. Thus, estimated import is one to several orders of magnitude below export. Since the biomass of drift in the canyon did not decrease during each mission, we assume that our import calculations are underestimates. We have greater confidence in the export estimates as reversing current flow and wave action were not prevalent at the lower depths.

The distribution and biomass of drift vegetation within the canyon were determined along line transects. Randomly chosen transects were established perpendicular to the main axis of the canyon at depths between 20 and 40 m, since drift vegetation at shallower depths was very sparse during our study. Sampling units consisted of 2 m wide and 5 m long rectangles along the transect lines. Most of the drift material was found as clumps, usually in small depressions in the sand bottom. The number of drift clumps were counted in each sampling unit and the size (< 10, 10–20 and 20 cm diameter) and major species present recorded.

The biomass and composition of drift clumps were determined by sorting randomly chosen clumps from each size class. The number of clumps sorted was determined from a plot of species number against increasing sample size. The point at which few new species were recorded with additional samples was used to estimate optimal sample size and ranged between three and thirteen samples, depending on clump size and date. Samples were sorted into species categories for all vegetation and separate wet weights determined. Voucher specimens are deposited at the San Francisco State University herbarium.

Turnover times for drift vegetation in the canyon were calculated from estimated biomass and export rates. Biomass estimates for each species were calculated from frequency data multiplied by the average wet weight for each species within a clump. This was summed for all clump sizes and multiplied by the area surveyed ($1{\cdot}6 \times 10^4$ m$^2$) to estimate the total biomass for each species. Portions of the canyon bottom not surveyed by transects consisted largely of bare sand and would not contribute to additional overall canyon biomass. Because of uncertainty over import calculations, only export rates were used to calculate turnover as biomass divided by export. The effect of including import estimates to calculate net export would increase turnover times by $< 5\%$, in most cases.

### *Faunal associates*

The invertebrate and fish fauna associated with drift vegetation were examined from both net collections and clump collections. On the first mission, associated fauna were collected by hand from the drift after it was treated with a fish anaesthetic, quinaldine. An airlift sampler with a 1 mm mesh net was used on the second mission, and appeared to be more efficient at capturing the more motile forms within the drift clumps. The drift clumps, the sand directly beneath the clumps, and an equivalent area of bare sand adjacent to the clumps were sampled separately. The animals were sorted ashore from the drift, preserved in 10% formalin and identified to the lowest possible taxonomic level. The samples are deposited both at San Francisco State University (invertebrates) and Moss Landing Marine Laboratories (fishes). In addition, frequent observations were made of drift clumps while diving.

## **Results**

### *Currents*

During mission 1, the aquanauts relocated 44 of the drifters with a total of 65 observations. During mission 2, 39 of the drifters were relocated with a total of 87 observations. In both cases, most of the observations were made during the first two days following deployment. The net drifter movement was down-canyon to deeper water, but some tidal activity was noted. The decline in observations after two days indicates a rapid dispersal, especially for those drifters deployed within the canyon. The sighting of east lagoon drifters indicates that bottom transport and potential drift movement occur between Salt River Bay and the submarine canyon. No west lagoon drifters in the canyon were recovered in either the canyon or the lagoon and their movement remains uncertain.

From plots of drifters observed on more than one occasion, a general bottom current pattern became apparent (Figure 2). The drifters generally moved down the central axis of the canyon head and then toward the eastern slope. Those drifters observed along the 29-m excursion line were found primarily toward the west wall, indicating a major bottom movement toward the west below the 20-m isobar, in addition to the general down-canyon net movement.

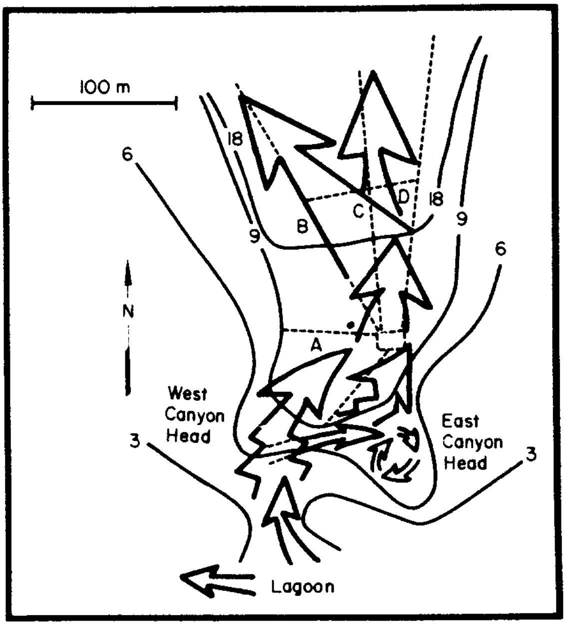

Figure 2. Generalized net bottom current direction determined from diver observations of bottom drifters. Relative magnitude of arrows indicative of frequency of drifter observations. Dotted lines and letters refer to bottom navigation grid used by saturation divers. Isopeths in meters.

Although the net current movement was toward deep water down the canyon, periods of reversed movement were observed. Observations from both the habitat window and the collecting nets indicated up-canyon currents associated with flooding tides (data from the Tides and Water Level Division, National Marine Fisheries Service) and high swell conditions on the surface. Also, some drifters were retrieved by us on shore.

The ping-pong balls tended to exhibit very similar patterns of dispersal to the drifters (see Figure 2), but also tended to remain in specific locations longer, therefore acting more like drift clumps of seagrasses and algae than the drifters. Ping-pong balls placed in the east canyon head were concentrated at the reef sand interface and they remained there throughout the mission.

During the spring saturation dive, the first two days were calm, followed by strong northeasterly winds and 1·5 to 2·1-m swells over the canyon. Diver visibility was very poor (3·0 m) and strong reversing currents were noted.

Expressed as means, currents were slower for the first two calm days before windy conditions in both missions than they were during such conditions (Figure 3). Also, current speeds down-canyon were higher during mission 2 than mission 1, a fact which might be explained by tides, storm conditions (Hurricane Allen) and/or water density differences (D. Hubbard, personal communication).

### *Drift vegetation: net collections*

The amount of drift vegetation collected in the net was extremely variable and highly dependent upon time of collection. On several occasions, especially during mission 1, the

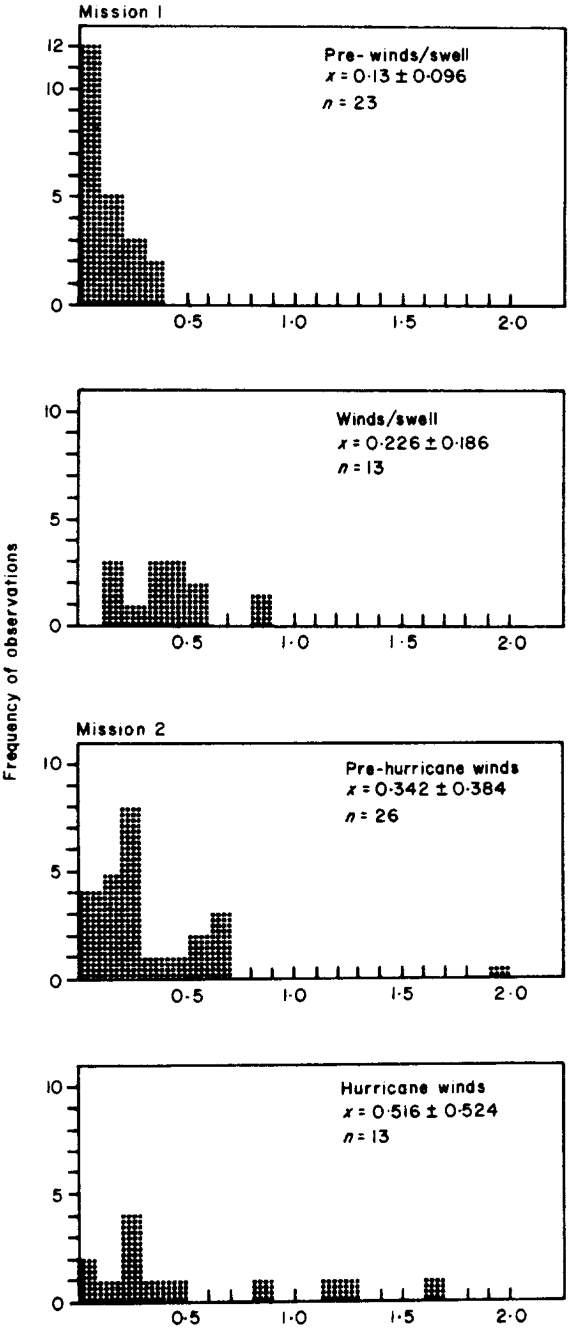

Figure 3. Frequency of observed net bottom current speeds (cm $s^{-1}$) as determined from successive locations of marked bottom drifters. All net current speeds are downcanyon. Observations for mission 1 and mission 2 separated for periods of calm to near calm and periods of strong winds.

nets were reversed by an up-canyon current and any prior material collected was lost. However, the net movement of drift biomass was down-canyon, particularly at depths below 15 m. Between 9 and 29 m, the drift material appeared very mobile. The plants in the net collections were primarily turtle grass (*Thalassia testudinum*) and manatee grass (*Syringodium filiforme*), but in some collections, various algae such as *Dictyota* spp., *Dictyopterus* spp., and *Dilophus* spp. were abundant. During mission 2, algae in the order Dictyotales were far more abundant in the net collections. A primary difference between the mission 1 and mission 2 net collections was the presence of *Halophila* in mission 2, which covered large expanses of the canyon floor. Early in mission 1, *Thalassia* comprised the major vegetation imported to the canyon (Figure 4). However, subsequent to the high wind and swell period, both *Syringodium* and the Dictyotales eclipsed *Thalassia* import. Import of *Syringodium* and the Dictyotales remained high through the mission. Export from the canyon was also high during this period, particularly for *Syringodium* and the Dictyotales. Maximum export occurred on 31 March at 40·7 kg wet wt per day.

A much stronger wind-associated export was noted in mission 2 (Figure 5). Initially, import was less and export similar to rates observed in April. *Thalassia* blades dominated. However, following the strong winds (20–30 knots) and high swell (3·0–3·5 m) on 3–4

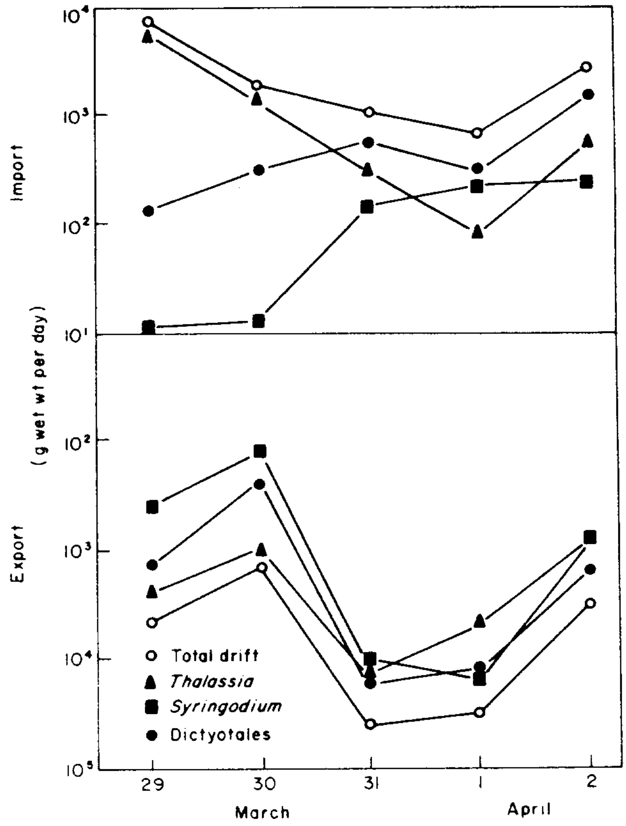

Figure 4. Comparison of daily import and export of drift vegetation in the Salt River canyon for mission 1. Estimates extrapolated from total net catch at head and end of canyon, respectively.

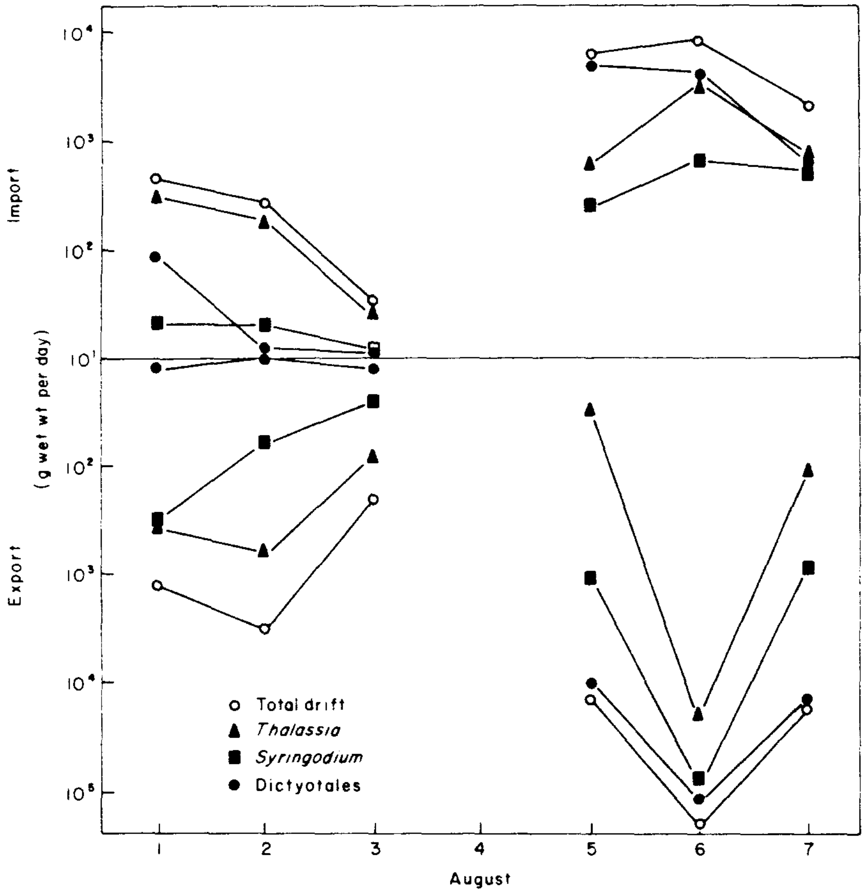

Figure 5. Comparison of daily import and export of drift vegetation in the Salt River canyon for mission 2. No net collections made during Hurricane Allen associated winds.

August, both import and export rates increased dramatically. At this time, *Syringodium* and the Dictyotales dominated the drift vegetation, although *Thalassia* import and export also increased. Maximum export was 250 kg wet wt day$^{-1}$ on 6 August, two days following the strongest wind and swell.

### *Drift vegetation: clump distribution and composition*

Seagrass blades comprised the dominant vegetation in the drift clumps on the canyon floor. Cumulative species curves for each mission indicate that we had sufficient samples to adequately represent the species composition of the clumps. Blades of *Thalassia testudinum* and *Syringodium filiforme* were present in both April and August, whereas *Halophila decipiens* and *Halodule wrightii* were present only in the summer (Tables 1–4). The majority of the drift blades were black to brown in colour, except for *H. decipiens* blades, which were green. This plant was the only seagrass growing on the canyon floor and it was extremely abundant during August.

In April, the three clump sizes were relatively common (Table 1) and the percentage of *Thalassia* and *Syringodium* in each clump size class was stable, with the drift algae comprising only 15% overall (Table 2). Almost all of the drift algae found in clumps and net

TABLE 1. Frequency, size and dominant plants of drift clumps noted in transects. The standard deviation about the mean frequencies are in parentheses

| Mission | No. of transects | Depth range | Length range | Mean frequency per 10 m² size of clumps: < 10 cm | 10–20 cm | > 20 cm | Total | Dominant plants (Percent of samples) |
|---|---|---|---|---|---|---|---|---|
| Mission 1<br>(March–April) | 16 | 20–39 m | 45–55 m | 1·23<br>(0·92) | 0·83<br>(0·62) | 0·44<br>(0·56) | 2·42<br>(1·73) | *Thalassia* (69%)<br>*Syringodium* (13%)<br>*Thal./Syr.* (18%) |
| Mission 2<br>(July–August) | 14 | 20–29 m | 45–60 m | 1·33<br>(0·46) | 0·23<br>(0·22) | 0·004<br>(0·013) | 1·61<br>(0·67) | *Halophila/Thalassia* (79%)<br>*Thalassia* (14%)<br>*Halo./Syr.* (7%) |

TABLE 2. Relative abundance of dominant plants in drift clumps in mission 1

| Plant | Mean biomass of plants (g per clump) for given clump diameter: < 10 cm | 10–20 cm | > 20 cm |
|---|---|---|---|
| *Thalassia* | 10·9 | 21·1 | 44·4 |
| *Syringodium* | 7·5 | 24·3 | 27·3 |
| *Dictyopterus* | 2·8 | 3·2 | 6·2 |
| *Dictyota* | 0·8 | 3·7 | 7·1 |
| *Dilophus* | 0·4 | 0·3 | 0 |
| *Sargassum* | 0 | 0·5 | 0 |
| Total number of species | 12 | 19 | 20 |
| Mean number of species | 4·9 | 5·9 | 7·7 |
| Total mean biomass (g per clump) | 22·4 | 53·1 | 85·0 |
| No. of samples | 9 | 14 | 7 |

collections during April were members of the brown algal order Dictyotales (Tables 2, 4). In August, the clumps were less abundant, mostly smaller than 10 cm in diameter, and often appeared less dense than those in April (Tables 1, 3). The relative abundance of drift seagrass blades to drift algae was similar to April; however, the Dictyotales were far less common and several species of red algae were frequently observed (Table 4). Following the period of high winds associated with Hurricane Allen, the relative abundance of *Syringodium* blades and of species in the Dictyotales increased dramatically. In addition, *Syringodium* blades were widely distributed throughout the canyon in long windrows. These windrows were often associated with ripple features on the sand and the drift vegetation gradually moved down-canyon in the days following the hurricane event.

### *Drift vegetation: turnover time estimates*

Turnover time for *Thalassia* and *Syringodium* was on the order of weeks in April and months in August before the hurricane-associated winds (Table 5). Members of the

TABLE 3. Relative abundance of dominant plants in airlift samples of drift clumps in mission 2, before and after hurricane winds. All clumps were smaller than 10 cm diameter

| Plant | Mean biomass of plants (g per clump) | |
|---|---|---|
| | Before hurricane | After hurricane |
| *Thalassia* | 6·8 | 1·4 |
| *Syringodium* | 5·3 | 13·5 |
| *Halophila* | 8·1 | 3·0 |
| *Halodule* | 0·7 | 0·05 |
| *Dictyota* | 0·1 | 11·7 |
| *Dilophus* | 0 | 1·9 |
| Other | 1·6 | 1·8 |
| Total number of species | 24 | 18 |
| Mean number of species | 7·4 | 9·0 |
| Total mean biomass (g per clump) | 22·6 | 33·4 |
| No. of samples | 11 | 6 |

TABLE 4. Occurrence of drift algae comprising greater than 1% by wet weight of clump or drift collections

| Species | Clumps | | Net collection | |
|---|---|---|---|---|
| | April | August | April | August |
| Dictyotales | | | | |
| *Dilophus alternans* | + | + | + | + |
| *Dilophus guiniensis* | + | | + | + |
| *Dictyopterus deliculata* | + | + | + | + |
| *Dictyota bartayresii* | + | + | + | + |
| *Dictyota dentata* | + | | + | + |
| *Dictyota divaricata* | | + | | |
| *Dictyota jamaicensis* | + | + | + | + |
| *Dictyota linearis* | + | | + | + |
| *Dictyota volubis* | | | | + |
| *Stypopodium zonale* | | | + | + |
| *Padina sanctae-crucis* | | | | + |
| Nemalionales | | | | |
| *Galaxaura subverticillata* | + | + | + | + |
| Gigartinales | | | | |
| *Gracilaria cylindrica* | | + | + | + |
| *Hypnea musciformis* | | | | + |
| Rhodymeniales | | | | |
| *Acanthophora spinifera* | | + | | |
| *Champia parvula* | | | | + |
| *Dasya pedicellata* | | + | | |
| *Dasyopsis antillarum* | | + | | |

Dictyotales were exported rapidly in April and August following high wind and swell. However, all drift material was rapidly exported following the hurricane-associated event. In both missions, estimated turnover times for water were less than those calculated for drift vegetation.

TABLE 5. Turnover times for drift and water in the canyon. For mission 2, BH = before hurricane; AH = after hurricane

| Drift type | Estimated biomass in canyon (kg) | Calculated export (kg day$^{-1}$)—means | | Turnover time (day) | | Water turnover time (day) | |
|---|---|---|---|---|---|---|---|
| Mission 1 (April) | | | | | | | |
| *Thalassia* | 81 | 4·4 | | 18·4 | | | |
| *Syringodium* | 66 | 6·5 | | 10·1 | | | |
| Dictyotales | 27 | 6·2 | | 4·4 | | | |
| Total | 174 | 16·9 | | 10·3 | | 2·3 | |
| Mission 2 (August) | | BH | AH | BH | AH | BH | AH |
| *Thalassia* | 17 | 0·2 | 3·9 | 85·0 | 4·4 | | |
| *Syringodium* | 13 | 0·1 | 19·1 | 130·0 | 0·7 | | |
| *Halophila* (drift) | 20 | 0·9 | 2·8 | 22·2 | 7·1 | | |
| Dictyotales | 0·3 | 0·0 | 34·3 | — | 0·01 | | |
| Other algae | 4 | 0·2 | 5·0 | 20·0 | 0·8 | | |
| Total | 54 | 1·4 | 65·1 | 38·8 | 0·8 | 1·0 | 0·7 |

TABLE 6. Numbers and kinds of animals collected in the canyon head and excursion line nets during mission 1. Data are divided into periods of low drift transport (29 and 30 March) and high drift transport (31 March, 1 and 2 April)

| Animal taxon | 29 and 30 March | | 31 March, 1 and 2 April | |
|---|---|---|---|---|
| | West canyon head | Excursion line | West canyon head | Excursion line |
| Porifera | 2 | 0 | 1 | 9 |
| Annelida | | | | |
| Polychaeta | 3 | 2 | 2 | 10 |
| Mollusca | | | | |
| Gastropoda | 2 | 1 | 1 | 4 |
| Arthropoda | | | | |
| Amphipoda | 6 | 4 | 3 | 8 |
| Natantia (shrimp) | 1 | 0 | 2 | 20 |
| Brachyura (crabs) | 1 | 0 | 2 | 36 |
| Echinodermata | | | | |
| Echinoidea | 0 | 0 | 10 | 104 |
| Holothuroidea | 0 | 0 | 0 | 5 |
| Ophiuroidea | 0 | 0 | 0 | 5 |
| Other | 3 | 2 | 3 | 5 |
| Total organisms | 18 | 9 | 24 | 207 |
| No. of net samples | 4 | 6 | 6 | 9 |

### *Faunal associates: net collections*

The numbers of animals found in the drift collection nets varied with the amount of plant drift material trapped by the nets (Tables 6 and 7). During the period of maximum drift export on 31 March and 1 April, 188 animals were collected from six excursion line samples compared with only nine animals in the previous three days. The August mission was

TABLE 7. Numbers and kinds of animals collected in the canyon head and excursion line nets during mission 2. Data are divided into pre-hurricane (1–3 August) and post-hurricane (5–7 August) periods

| Animal taxon | Pre-Hurricane | | Post-Hurricane | |
|---|---|---|---|---|
| | West canyon head | Excursion line | West canyon head | Excursion line |
| Porifera | 3 | 0 | 8 | 106 |
| Annelida | | | | |
| Polychaeta | 0 | 0 | 6 | 0 |
| Mollusca | | | | |
| Gastropoda | 0 | 0 | 1 | 4 |
| Arthropoda, Crustacea | | | | |
| Amphipoda | 0 | 0 | 9 | 0 |
| Natantia (shrimp) | 2 | 1 | 4 | 6 |
| Paguridae | 6 | 0 | 6 | 40 |
| Brachyura (crabs) | 19 | 1 | 57 | 296 |
| Echinodermata | | | | |
| Echinoidea | 0 | 0 | 71 | 240 |
| Ophiuroidea | 0 | 0 | 1 | 8 |
| Holothuroidea | 0 | 0 | 2 | 0 |
| Chordata | | | | |
| Urochordata | 0 | 0 | 1 | 70 |
| Cephalochordata | 0 | 0 | 0 | 1 |
| Osteichthyes | 0 | 0 | 0 | 7 |
| Other | 0 | 0 | 2 | 7 |
| Total organisms | 29 | 2 | 176 | 784 |
| No. of net samples | 11 | 15 | 6 | 9 |

dramatically divided into a calm pre-hurricane period of low plant drift movement and a large post-hurricane flux of plant material moving down-canyon (Figure 5). Twenty-nine animals were collected in eleven canyon head net samples prior to the hurricane winds and swell, and 176 animals were taken in six net samples collected after sampling resumed on 5 August. Only two animals were collected in 15 pre-hurricane excursion line net samples compared with 764 in nine post-hurricane samples.

In both the spring and summer missions, the faunal samples collected from drift collection nets during periods of maximum plant import and export were dominated by small sea urchins and crabs. The sea urchins were predominantly small individuals (mean test diameter ±95% confidence limits: spring = $4 \cdot 9 \pm 0 \cdot 4$ mm; summer = $7 \cdot 1 \pm 1 \cdot 1$ mm) of the genera *Lytechinus* and *Tripneustes*. The crabs collected during periods of maximum drift movement were also small individuals (mean carapace width ±95% confidence limits: spring = $4 \cdot 4 \pm 0 \cdot 8$ mm; summer = $4 \cdot 0 \pm 0 \cdot 7$ mm) primarily belonging to the families Portunidae and Majidae.

### *Faunal associates: natural drift clump collections*

Thirty clumps were sampled during the first mission and 167 animals were collected from the clumps (Table 8). The clump fauna was dominated by small polychaetes (48), primarily epitokous individuals of the family Syllidae, and amphipod crustaceans (25). The majority

Table 8. Numbers and kinds of animals collected in natural drift clump samples during mission 1. Samples are separated according to clump diameter

| Animal taxon | Clump diameter | | |
|---|---|---|---|
| | < 10 cm | 10–20 cm | > 20 cm |
| Porifera | 1 | 3 | 4 |
| Annelida | | | |
| Polychaeta | 2 | 65 | 3 |
| Mollusca | | | |
| Gastropoda | 0 | 6 | 6 |
| Bivalvia | 0 | 1 | 1 |
| Arthropoda, Crustacea | | | |
| Natantia (shrimp) | 0 | 12 | 2 |
| Paguridae | 3 | 6 | 2 |
| Brachyura (crabs) | 3 | 18 | 5 |
| Amphipoda | 3 | 21 | 1 |
| Echinodermata | | | |
| Echinoidea | 1 | | |
| Chordata | | | |
| Cephalochordata | 0 | 2 | 0 |
| Osteichthyes | 1 | 2 | 2 |
| Other | 1 | 1 | 5 |
| Total organisms | 14 | 125 | 28 |
| No. of clump samples | 9 | 14 | 7 |

of the individuals from the larger-sized invertebrate groups and the fishes were post-larval or juvenile forms.

During periods of high drift transport and reduced drift residence time, fewer motile animals were found associated with the drift. The eighteen drift clumps collected on 29 March, a day of low drift transport (Figure 4) had an average of 5·3 animals and contained 13 shrimp, 7 crabs, and 5 juvenile fishes. The six clumps collected from the same areas on 31 March, a day of high drift transport, had an average of 2·2 animals per clump and contained no shrimp or fishes and only a single crab.

The drift clumps, the sand directly beneath the clumps, and an equivalent area of bare sand adjacent to the clumps were dominated by epifaunal forms, chiefly brachyuran crabs (54) and shrimp (37) (Table 9). The samples from beneath the clumps and the bare sand control samples contained a greater proportion of infaunal animals. Thirteen fishes were found in the drift clumps and in the sand beneath the clumps; none were found in the bare sand controls. All but two of the fishes were larval or young juvenile forms, chiefly gobies. The two adult fish were pipehorses, *Amphelikturus dendriticus*.

No significant differences in mean animal number per sample were found in any sample category comparison. The average number of animals per sample found in the sand beneath the clumps and in the bare sand control samples were also found not to differ significantly. In both the pre- and post-hurricane samples, the combined clumps and sand samples contained significantly greater numbers of animals per sample than did the bare sand controls. Pre- and post-hurricane clumps differed in that five fishes and no urchins were found in the pre-hurricane samples.

TABLE 9. Numbers and kinds of animals collected in natural drift clump samples during mission 2. Sample categories include animals: within the clumps; in the sand beneath the clump; and in the bare sand control samples. Data are divided into pre-hurricane (1–3 August) and post-hurricane (5–7 August) periods

| | Within clumps | | Sand beneath clumps | | Bare sand controls | |
|---|---|---|---|---|---|---|
| Animal taxon | Pre | Post | Pre | Post | Pre | Post |
| Porifera | 2 | 2 | 1 | 0 | 0 | 0 |
| Annelida | | | | | | |
| Polychaeta | 4 | 1 | 7 | 5 | 5 | 6 |
| Mollusca | | | | | | |
| Gastropoda | 9 | 2 | 14 | 2 | 11 | 0 |
| Bivalvia | 1 | 0 | 13 | 7 | 6 | 4 |
| Scaphopoda | 1 | 0 | 8 | 1 | 5 | 1 |
| Arthropoda, Crustacea | | | | | | |
| Amphipoda | 9 | 5 | 5 | 2 | 3 | 9 |
| Ostracoda | 2 | 0 | 5 | 0 | 0 | 0 |
| Natantia (shrimp) | 23 | 4 | 7 | 3 | 2 | 2 |
| Paguridae | 6 | 1 | 0 | 0 | 2 | 1 |
| Galatheidae | 12 | 0 | 5 | 0 | 0 | 5 |
| Brachyura (crabs) | 32 | 24 | 14 | 4 | 3 | 1 |
| Sipuncula | 0 | 2 | 3 | 8 | 2 | 3 |
| Echinodermata | | | | | | |
| Echinoidea | 0 | 5 | 0 | 0 | 0 | 0 |
| Chordata | | | | | | |
| Cephalochordata | 0 | 1 | 4 | 3 | 1 | 5 |
| Osteichthyes | 6 | 0 | 3 | 0 | 0 | 0 |
| Other | 1 | 0 | 1 | 0 | 0 | 0 |
| Total organisms | 108 | 47 | 90 | 35 | 40 | 37 |
| No. of clump samples | 10 | 4 | 9 | 3 | 10 | 3 |

## Discussion

Little is known about rates of movement of drift vegetation in submarine canyons since most observations have been incidental to the deployment of current meters by geologists (Shepard & Marshall, 1978). Shepard *et al.* (1979, p. 1) state that in canyons off southern California great masses of kelp and seagrasses are carried down-canyon by the currents 'entangling the instruments, stopping their operation, and frequently causing current meters to be swept away'. Despite such biological hazards, they were able to collect 25 000 hours of current speed and direction for canyons in southern California and 16 other areas of the world, including the Salt River canyon.

Their study in the Salt River canyon included current measurements at 30 m and 49 m which approximate the depth of our deep canyon nets. They recorded oscillating currents of up to 25 cm $s^{-1}$ punctuated with long, random length periods of either up or down canyon flow. One record at 3 m above the bottom at 49 m showed an almost constant down-canyon current for five days with an average velocity of approximately 10 cm $s^{-1}$. In our study, the drifters floated at approximately 0·5 m off the bottom resulting in calculated net current speeds two orders of magnitude less than those recorded by Shepard *et al.* (1979). We did not calculate net current speeds using the ping-pong ball sightings, but would expect even slower rates as the balls were often lying in sand pockets for several days acting much like drift vegetation. Since most of our resightings of drifters occurred in areas where there was higher diver activity, such as the shallow end of the canyon, our current rate calculations may be biased toward water movement typical of the head of the canyon rather than the deeper end. Divers did experience both up-canyon and down-canyon currents; however, they were unable to record absolute current speeds and duration. Attempts to correlate these observations with tidal data were not successful. Similarly, Shepard *et al.* (1974) were unable to relate tidal periods to oscillating current flows until reaching depths in excess of 200 m. We observed net down-canyon movements during periods of both calm and strong wind events. Stream flow into Salt River Bay is extremely low and evaporation high. As a result, salinities in the bay are equal to or slightly higher than offshore waters. The dominant trade winds are from the northeast and breaking waves on the reef crest probably transport water into the lagoon and higher density water exits through the channel and flows down the canyon (D. Hubbard, personal communication). Many of the bottom drifters deployed in the lagoon during August floated to the surface and required heavier weights suggesting that the density of the lagoon water was greater than it had been in April. In addition, we recorded higher net down-canyon currents during the summer. During both missions, strong winds and the accompanying waves were observed to increase net down-canyon flows. Overall, water residence time in the canyon was on the order of one to two days.

The majority of the drift material observed on the canyon floor was derived from seagrasses, primarily *Thalassia testudinum* and *Syringodium filiforme*. Large underwater meadows of these seagrasses were present in Salt River Bay, but were not observed outside the reef. The canyon floor was barren of live vegetation except for the summer growth of *Halophila decipiens*, a few patches of a blue-green alga (*Oscillatoria*), and some macroalgae attached to guide ropes. Diving excursions east and west of the canyon failed to uncover any large vegetated areas. In addition, any material entering via long shore currents would most likely be rapidly consumed by herbivores inhabiting the reef areas on either side of the canyon floor. The observed movement of drifters from the lagoon to the canyon floor and the absence of any nearby sources support the conclusion that Salt River Bay is the primary source of the detrital material.

The detachment and export of *Thalassia* and *Syringodium* blades have been related to leaf senescence, storms, and herbivore action (Zieman *et al.*, 1979). In Tague Bay, just 16 km east of Salt River Bay, these authors found that *Thalassia* tended to be exported by bedload transport, while *Syringodium* with its relatively larger internal air spaces (lacunae) was exported by surface currents. The *Syringodium* blades on the Salt River canyon floor were black and probably had been detached long enough for the trapped internal air to be depleted by microbial degradation resulting in the blades sinking. Data on the relative percentage of seagrass blades in drift net catches showed a greater contribution of *Syringodium* blades in the deep nets compared to the shallow canyon head nets (Hurley *et al.*, 1981) supporting the conclusion that this seagrass is exported by surface flows and sinks over the canyon floor and adjacent nearshore areas. *Thalassia* blades, on the other hand, were the dominant detrital component observed in canyon head nets except during the strong wind/storm events. During the Hurricane Allen associated storm, large amounts of *Syringodium* were exported in excess of its calculated biomass in the canyon. Divers observed that *Syringodium* was more easily resuspended than *Thalassia* blades so that strong down-canyon currents may export accumulated *Syringodium* blades both from within the canyon and adjacent nearshore areas.

Bedload export of *Thalassia* blades from Tague Bay was estimated at 12 kg day$^{-1}$ for a study period in March (Zieman *et al.*, 1979). On an areal basis, 0·02 gm dry wt m$^{-2}$ day$^{-1}$

is exported. Our estimate for export of *Thalassia* through the canyon during a similar period is 4·4 kg wet wt day$^{-1}$ or approximately 0·6 kg dry wt day$^{-1}$. On an areal basis this equals 0·001 gm dry wt m$^{-2}$ day$^{-1}$, an order of magnitude less than Tague Bay. The areas of the two Bays are roughly equivalent (62 hectares for Tague Bay; 57 hectares for Salt River Bay); however, Salt River Bay is more turbid due to the fine bottom sediments accumulated from land runoff. The bottom sediments in Tague Bay are primarily calcareous and less susceptible to prolonged resuspension. Therefore, primary production is probably less in Salt River Bay. Nevertheless, in the Tague Bay study, only 1% of the *Thalassia* production was exported, the remaining being utilized in the seagrass bed itself or fragmented and exported as particulate matter.

Macroalgal export was not considered in the Tague Bay study, but for Salt River Bay it can equal or exceed that of the seagrasses, particularly following strong wind events. The species of algae collected were primarily epiphytic or attached to small rocks and shells and therefore could be easily dislodged by heavy bottom surge. Like *Syringodium*, the density of the macroalgal material is close to that of seawater and they are easily resuspended and transported through the canyon. Their residence time in the canyon under all conditions was an order of magnitude less than any of the seagrasses. The drift algae in the canyon were live compared with the decaying seagrass blades. On the other hand, once removed from the photic zone, the algae rapidly decompose or are consumed by invertebrates (Tenore, 1977). Rarely have deep water cameras photographed macroalgae among the masses of detrital seagrass blades, however, their rapid export in live condition may provide a significant food source to the benthos.

Members of the brown algal order Dictyotales were the major algae observed in the canyon although many species of red algae were seen in Salt River Bay as drift, notably *Acanthophora spinifera, Hypnea musciformis*, and *Gracilaria cylindrica*. In a study of herbivore feeding preferences on a reef at the nearby island of St John, Earle (1972) observed that species of *Dictyota* were able to thrive under heavy grazing pressure near reefs, although they were eaten by several species of fish and invertebrates. At the same location, Mathieson *et al.* (1975) observed that although *D. bartayresii* was eaten by herbivorous fish, it was not as preferred as *Gracilaria cylindrica*. Targett & Mitsui (1979) discovered a very strong hemolysis reaction in fish erythrocytes caused by extracts of *Dictyota dichotoma* suggesting that herbivores unable to detoxify the causative compounds in the alga would avoid it. Thus, the relatively greater abundance of *Dictyota* in the canyon compared to the lagoon may be due to preferential feeding behaviour by herbivores.

The relationships between certain fish and invertebrates with drift vegetation has been recently investigated (Heck & Wetstone, 1977; Kulczychi *et al.*, 1981; Gore *et al.*, 1981). Drift algal clumps or mats are particularly important in providing habitat complexity and shelter. In several cases, strong relationships have been observed between certain animals and the abundance of drift algae. We were unable to note specific associations of animals with the drift vegetation because of a limited number of samples. However, greater numbers of both epifauna and infauna were associated with drift clumps as compared with bare sand. Given the small size of the clumps and their short residence time, the associated invertebrate community must either remain with the drift and be transported to deep water or be continually colonizing new drift material. During periods of longer drift residence time in the canyon, increased numbers of invertebrates and fish were associated with clumps indicating that some attraction was taking place. The fish were post-larval forms and may use the clumps as protection from larger predators or as a food source for smaller prey. However, evidence from the net collections suggests that many of the associated invertebrates are simply unfortunate passengers. During periods of maximum drift export from the lagoon, the drift vegetation contained large numbers of young urchins and crabs. They may be transported rapidly to deeper waters or consumed by predators in the canyon.

Limited utilization of drift vegetation in shallow portions of the canyon must be balanced with the significant food source the drift material and its associated fauna provide to deep sea environments. It has long been recognized that abyssal biomass decreases with distance from land, and presumably decreasing food availability (Ekman, 1953). The studies by Wolff (1976; 1979) document the large amount of seagrass blades on the deep sea floor and the apparent utilization of this material by macrofauna. Recent submersible dives in deep water off the Salt River canyon discovered large accumulations of seagrass blades (T. Suchanek, personal communication). The net down-canyon currents and occasional storm events which transport shallow water detritus through the canyon appear to provide a significant contribution to deep sea food availability.

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