Stochastic Events and Dynamics of a Mangrove Root Epifaunal Community

B. L. Bingham & C. M. Young

1Shannon Point Marine Center, Western Washington University, 1900 Shannon Point Road, Anacortes, WA 98221-4042, USA.
2Harbor Branch Oceanographic Institution, 5600 Old Dixie Highway, Ft. Pierce, FL 34946, USA.

With 9 figures and 2 tables

Key words: Mangroves, epifauna, stability, ascidians, sponges.

Abstract. Submerged roots of red mangroves (Rhizophora mangle) in the Florida Keys were photographed at 1- or 2-month intervals for 38 months to measure population dynamics of the epifaunal invertebrate species. Photographs were analysed for species composition and abundance and information on life spans, persistence, mortality, and seasonality. Larval recruitment to artificial surfaces was used to assess reproductive seasonality. As a measure of stability, populations were tested for narrow stochastic boundedness.

In contrast to reports for a tropical mangrove root community, the Florida Keys root community showed enormous variability despite being dominated by long-lived species with low, largely non-seasonal recruitment. Species composition on individual roots changed dramatically on short time scales. Populations of the major species were not narrowly bounded on most roots and there was little evidence for a closely regulated community.

Variability of this community related to the frequency and intensity of stochastic perturbations. Physical disturbance due to strong tidal flows appeared to be the most important structuring process. Species-specific predation and fragmentation of sponges were also important. These features contribute to the instability of the community by producing dramatic fluctuations in species abundances and preventing competitive processes from producing a more stable, equilibrium community. Temporal measurement scale was an additional important consideration in this habitat. Structuring processes occurred on very short time scales (1–2 months) and analysis on longer time scales gave inaccurate impressions of community dynamics.

Problem

Marine epifaunal or fouling communities often show extreme variability in species composition and abundance. This variability has been attributed to distinct seasonal pulses of larval recruitment (Sutherland, 1976; Sutherland & Karlson, 1977), massive senescence and death of established organisms (Sutherland & Karlson, 1977), or disturbances (Smith et al., 1950; Mook, 1983; Hirata, 1987) which open up bare space. Warner (1984) has suggested that the instability observed in these systems may largely be an artifact of the methods used for their study. Indeed, many studies of epifaunal communities have relied on plates or
panels as representative subunits of the natural habitat. Since plates are often small and not directly attached to the natural substrata they are intended to model, they cannot be influenced by many processes (e.g., overgrowth, predation by benthic organisms, colonization by benthic larvae) which affect the natural community.

Insularity and small size, however, are not characteristics unique to experimental plates. Many natural epifaunal assemblages occur on small, isolated habitats. Keough & Butler (1983) studied invertebrate communities growing on the shells of bivalves (Pinna bicolor) scattered throughout a sandy bay. Osman (1977), Mcguinness & Underwood (1986), and others have studied the sessile invertebrates growing on small rocks or boulders. The dynamics of these communities have been similar to those seen on experimental plates, supporting Warner's (1984) argument that small isolated communities are naturally variable.

A notable exception to the general pattern of high variability was seen in the epifaunal community associated with roots of red mangrove trees (Rhizophora mangle) in Bahia de Buche, Venezuela (Sutherland, 1980). Despite being on small habitat islands, these communities showed remarkable stability, with species abundances and community composition changing little over an 18-month period. Sutherland (1980) hypothesized that this surprising stability resulted primarily from a lack of seasonality in the tropics and the consequent absence of heavy recruitment pulses or seasonal adult senescence and death.

In this paper, we present data from another mangrove root epifaunal community; this one located in south Florida. Our goal was to determine if mangrove root communities are inherently stable or if this habitat would show dynamics more typical for insular island communities. We recognize that the term stability can be defined in many ways; community ecologists have long struggled for a consensus (MacArthur, 1955; Margalef, 1969, 1975; Holling, 1973; May, 1973; Sutherland, 1981). To permit comparison with the results of Sutherland (1980), we adopt an operational definition implying constancy over time. A stable community, therefore, is one in which fluctuations of a variable away from an average value (equilibrium) are small.

**Material and Methods**

The study site was a small Rhizophora mangle island located near Big Pine Key, Florida (24°44'N, 81°26'W; see map in Bingham & Young, 1991a). The island, located in one of the numerous channels that connect Florida Bay and the Straits of Florida, experiences bi-directional tidal flow with current speeds reaching at least 20 cm·s⁻¹ (Bingham & Young, 1991a). Water temperatures between June and September stay near 31°C, then drop to mid-January lows near 15°C (based on 1987/1988 temperature recordings by N. P. Smith). Salinity ranges from 40% in mid-summer to 32% in the winter months (N. P. Smith, pers. comm.). The western side of the study island is deep undercut, and diverse assemblages of sessile invertebrates grow on the subtidal portions of unanchored R. mangle prop roots (Fig. 1). Water depth at the site ranges from 1.5 to 3 m.

Fig. 1. Rhizophora mangle habitat and root epifaunal community in the Florida Keys study site. A. Mangrove trees with prop roots hanging down into the water. B. Tedania ignis (fire sponge) and Botryllus sp. attached to the submerged roots. C. Haliclona manglei. Note the long sponge tendrils. D. Chondrilla nucula (chicken liver sponge) and T. ignis. Scaled frame width of the lower panels is 8.5 cm.
In January 1986, nylon cable ties with numbered plastic labels were fastened to 30 submerged roots. Because of root and tag loss, additional roots were marked on several later occasions (25 roots in March 1986, 21 roots in July 1986, 17 roots in January 1987, and 30 roots in November 1987). From January 1986 to April 1987, marked roots were photographed monthly on Kodachrome slide film using a Nikonas V underwater camera equipped with a 28-mm lens and a close-up lens with framer that encompassed an area 144 x 216 mm. Between April 1987 and March 1989, the sampling interval was increased to 2 months (with the exception of one 3-month interval between October 1987 and January 1988). On each date, the same root segment was photographed from the same angle by placing the numbered root label directly in the top center of the framer. It should be noted that only a portion of each root was photographed. Therefore, when a sponge or ascidian colony disappeared from a series of photographs, we could not determine whether it had gone extinct on the root or had simply experienced a dramatic change in size.

Photographs were analysed by transmitting them through a video camera to a monitor screen interfaced with a personal computer and a digitizing tablet. Using Microcomp image analysis software, boundaries of the epifaunal invertebrates were digitized and areas and percent covers were calculated. Due to difficulties in accurately digitizing very small or highly-branched organisms, we omitted hydroids and sea anemones from the measurements. Data collected from the photographs were used to characterize the structure and dynamics of the root community. In particular, we tested the hypothesis that the root communities were stable, with only small fluctuation in species composition and abundance over time.

Species abundance. We first examined abundances on a community-wide level by calculating, at each sampling interval, the overall mean abundance of each major species. If the community is stable, and if the study roots represented a true cross section of the community, individual population abundance should remain fairly constant and fluctuations in overall abundances should be small. These results were examined graphically by plotting mean abundances over the 38-month study.

We used a 'Runs up and down test' (Sokal & Rohlf, 1981) to test for seasonal patterns in species abundances. The number of runs observed for each species (where a run is a series of abundance measurements with at least one increase and no decreases or at least one decrease and no increases) was compared to the expected number (calculated from the number of samples collected). Significantly fewer than expected runs indicated a systematic trend in the data (such as might be produced by a seasonal effect). Significantly more than the expected number of runs indicated a short-term cyclic phenomenon.

The concept of 'narrow stochastic boundedness' (Chesson, 1978; Kay & Butler, 1983; Keough & Butler, 1983) was used to quantify and statistically test variability in species abundances on individual roots. With this technique, a variable (in this case percent cover of a species) shows 'narrow stochastic boundedness' (roughly comparable to deterministic stability in a non-deterministic environment?) if fluctuations in that variable stay within pre-defined boundaries and show no long-term trends. Definition of those boundaries requires the arbitrary designation of two values, $\omega$ and $\varepsilon$, where $\omega$ is a predetermined percentage of the mean ($\bar{Y}$) within which fluctuations are considered small (i.e., fluctuations are narrowly bounded if they do not exceed $\pm \omega$) and $\varepsilon$ is the probability of exceeding the boundaries. To permit comparisons with the results of Kay & Butler (1983), values of $\omega = 0.2$ and $\varepsilon = 0.05$ were adopted (see Keough & Butler, 1983 for discussion of the rationale for choosing these values). A species, therefore, was 'bounded' on a root if 95% of the measured percent cover values fell within $\pm 20\%$ of the mean. If fluctuations in cover exceeded that level, the null hypothesis of boundedness was rejected.

In practice, the test was done following Keough & Butler (1983) by calculating coefficients of variation (CV) and standard errors of the coefficients of variation (SECV) for the arcsine-transformed percent cover data according to the following formulae:

$$CV = \frac{\sigma}{\bar{Y}} \times 100$$

$$SE_{cv} = \left( \frac{CV}{\sqrt{2n}} \right) \left( 1 + \left( \frac{CV}{100} \right)^2 \right)$$

where $\sigma$ = standard deviation, $\bar{Y}$ = mean, and $n$ = number of observations. This was repeated for each species on each root and results were used to calculate the $t$ statistic:

$$t = \frac{CV - 10.2}{SE_{cv}}$$

which could be compared to table values with $(n - 1)$ degrees of freedom.
This process allowed us to test the null hypothesis (H$_0$: CV $\leq$ 10.2%) against the alternate hypothesis (H$_a$: CV $>$ 10.2%), where 10.2 is based on the pre-chosen values of $w$ and $e$. To maintain sufficient power for valid statistical tests, roots for which fewer than eight samples were available were not tested (see Keough & Butler, 1983). Where species were unbounded, we calculated critical $w$ values. These values are the lowest values of $w$ that would result in retention of the null hypothesis and represent, therefore, the boundary widths that would be required to consider the population stochastically bounded.

**Species composition.** We used cluster analysis to determine whether species composition on individual roots changed significantly over time. Percent cover measurements of all epifauna on 30 roots were clustered with data collected from the same roots 6 months later. An unweighted centroid cluster algorithm (Ludwig & Reynolds, 1988) produced Euclidean distances for every possible pair of roots (including samples of the same root taken 6 months apart). If the species composition on a given root did not change substantially in 6 months, the distance between two samples from that root should have been smaller than the distance between any two randomly chosen roots in the habitat (*i.e.*, a root should have been more similar to itself than to other roots in the community).

To test this, the Euclidean distance between two samples of the same root (taken 6 months apart) was compared to the distribution of distances for all other possible root pairs. If the calculated distance fell in the lower 5% of the distribution, the root showed high temporal similarity to itself and it was concluded that the composition of the epifaunal community had not changed significantly in the 6-month study period. To look at longer-term changes, samples from the same roots taken 12 months apart were clustered and analysed in the same way.

**Species characteristics.** To characterize individual species and to permit comparison with Sutherland’s (1980) study, several other measurements were extracted from root photographs. Persistence and longevity of each species were determined by examining serial photographs of a root. Probabilities of continued occurrence were determined for 12, 18, 24, and 36 months after initial tagging. Colony sizes, shapes, and locations were carefully examined in each photograph to ensure that single colonies were actually persisting and not simply being replaced by other recruits of the same species.

To measure larval supply and to test for seasonal recruitment, 30 15 x 15 cm unglazed ceramic tiles were placed in wood racks directly beneath the study roots. The tiles rested face down, 20 cm off the bottom. From January to April (1987), tiles were replaced monthly and individual recruits were counted. From May 1987 to January 1988, the sampling interval was increased to 2 months. After 2 months, it was impractical to count individual recruits, so percent cover measurements were taken. Twenty-five additional tiles were suspended vertically within the root canopy. These tiles were photographed in place on each sampling date between January 1986 and October 1987. Photographs were examined for the appearance of new sponge and ascidian colonies. Because ceramic tiles were used for recruitment surfaces, results cannot be extrapolated directly to the root community. Instead, they serve only as rough indicators of larval availability.

**Results**

1. **Species abundance and composition**

Although many sessile invertebrate species were present on the mangrove roots, the community was dominated by massive sponges. The fire sponge, *Tedania ignis*, was the most abundant species, with an average community-wide coverage of 16.7 ± 5.2% (Fig. 2). *Chondrella mucula* and *Halichondria magniconulosa* were the next most abundant sponges (6.5 ± 4.3% and 5.3 ± 3.5% cover, respectively). *Tedania ignis* and *H. magniconulosa* often formed enormous colonies (some greater than 1 m in diameter) which engulfed and occasionally monopolized roots. Several other sponge species were present but were not particularly abundant and never dominated roots (*i.e.*, *Lissodendoryx isodictyalis*: 1.3 ± 1.4% cover, *Haliclona ma-
Fig. 2. Abundances of the sponges *T. ignis*, *C. nucula*, and *H. magniconulosa* in the mangrove root community. Standard errors are shown. The vertical dotted line indicates the date that Hurricane Floyd struck the study area.

*gla ris*: $1.6 \pm 0.9\%$ cover, *Clathrina coriacea*: $0.3 \pm 0.2\%$ cover; Fig. 3). Ascidians were the next most common taxon. However, except for *Ecteinascidia turbinata* which briefly dominated some roots, their abundance was generally low (*E. turbinata*: $9.6 \pm 5.2\%$ cover, *E. minuta*: $2.6 \pm 2.4\%$ cover, *Botryllus* sp.: $1.2 \pm 0.7\%$ cover, Fig. 4).

All these epifaunal species examined showed great temporal variability (Figs 2–4). The sponges *Tedania ignis* and *Clathrina coriacea* were most abundant in the winter months, while populations of the ascidian *Ecteinascidia minuta* peaked in late summer. There was, however, statistical evidence for repeated seasonality only in the abundance patterns of *T. ignis* (Table 1). *Chondrilla nucula* showed more than the expected number of runs and these seemed to represent regular short-term cycles (1–2 months). All other species showed random fluctuations in abundance.
Boundedness

All species tested deviated significantly from narrow stochastic boundedness as defined for this study. Seven of the nine major epifaunal species were 'unstable' on most of the roots examined (Figs 5, 6), indicating large temporal variability in epifaunal cover. Maximum fluctuations were seen with the ascidian Ecteinascidia turbinata, which was unbounded on 37 of the 38 roots examined. Smallest fluctuations were seen with the small calcareous sponge Clathrina coriacea (unbounded on 6 of 16 roots).

Critical $\omega$ values calculated for all unbounded cases averaged from 0.43 (C. coriacea) to 0.68 (H. magniconulosa). These results confirm the variability; the coefficients of variation often exceeded by 2 to 3 times the level that would be
Fig. 4. Abundances of ascidians on the Rhizophora roots. Symbols are as described for Fig. 2.

Table 1. 'Runs up and down' testing for epifaunal seasonality. Significant negative values (i.e., fewer than the expected number of runs) indicate systematic trends as might be produced by seasonal effects. Significant positive values (i.e., more than the expected number of runs) indicate regular short-term cycles. *: P < 0.05.

<table>
<thead>
<tr>
<th>epifaunal species</th>
<th>observed runs</th>
<th>expected runs</th>
<th>z</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tedania ignis</td>
<td>11</td>
<td>16.3</td>
<td>-2.62*</td>
</tr>
<tr>
<td>Chondrilla nucula</td>
<td>23</td>
<td>16.3</td>
<td>3.28*</td>
</tr>
<tr>
<td>Halichondria magniconulosa</td>
<td>17</td>
<td>16.3</td>
<td>0.32</td>
</tr>
<tr>
<td>Lissodendoryx isodictyalis</td>
<td>11</td>
<td>13.6</td>
<td>-1.44</td>
</tr>
<tr>
<td>Haliclonia manglaris</td>
<td>13</td>
<td>16.3</td>
<td>-1.64</td>
</tr>
<tr>
<td>Clathrina coriacea</td>
<td>16</td>
<td>16.3</td>
<td>-0.16</td>
</tr>
<tr>
<td>Ecteinascidia turbinata</td>
<td>18</td>
<td>16.3</td>
<td>0.82</td>
</tr>
<tr>
<td>Ecteinascidia minuta</td>
<td>13</td>
<td>15.6</td>
<td>-1.34</td>
</tr>
<tr>
<td>Botryllus sp.</td>
<td>13</td>
<td>14.3</td>
<td>-0.70</td>
</tr>
</tbody>
</table>
considered bounded with this technique. Levels of unboundedness were similar whether roots were initially sampled in January, March, July, or November (Figs. 5, 6).

2. Species characteristics

Persistence and longevity

Cluster analyses provided strong evidence that the species on a single root changed substantially in short time intervals. In samples taken 6 months apart, only 5 of 30 roots clustered more closely with themselves than with other randomly chosen roots (4 roots actually fell in the upper tail of the distribution, indicating that they were significantly less similar to themselves than to other roots). A similar pattern was seen with samples taken 12 months apart: 4 roots fell in the lower tail of the distribution and 4 fell in the upper tail.

Roots which clustered closely with themselves after 6 and 12 months were of two types. Those clustering most tightly were dominated by the sponge *C. nucula* (Euclidean distances ranged from 0 to 5 on a scale from 0 to 120) or were nearly bare (distances from 6 to 14). Roots that changed dramatically in 6 or 12 months
generally held one or more of the large sponge species (T. ignis or H. magniconulosa) or one of the Ecteinascidia species. Euclidean distances for these roots ranged from 61 to 103.

Serial photographs revealed that most species could persist on a root for long periods (Table 2). Tedania ignis, Halichondria magniconulosa, Chondrilla nucula, Lissodendoryx isodictyalis, and Haliclona manglaris all showed consistently high probabilities of resisting displacement from roots on which they were established. The remaining sponge, Clathrina coriacea, appeared less able to hold space in the community, although some individuals did persist for 2 full years. Two ascidians, Ecteinascidia minuta and Botryllus sp., showed low persistence and were unable to effectively hold space. On the other hand, Ecteinascidia turbinata colonies remained on some roots throughout the 3-year period of the experiment.
Table 2. Persistence of *Rhizophora mangle* epifaunal species as measured by serial photographs of individual roots. Data are the percent of the initially chosen roots on which the species was still found. Percent values fluctuated due to differing numbers of original roots relocated at the sample intervals (numbers indicated in parentheses). Question marks indicate that mortality of the individuals was not seen but that none of the original tags could be relocated (generally due to overgrowth).

<table>
<thead>
<tr>
<th>epifaunal species</th>
<th>12 (12)</th>
<th>18 (4)</th>
<th>24 (3)</th>
<th>36 (1)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Tedania ignis</em></td>
<td>92</td>
<td>75</td>
<td>100</td>
<td>?</td>
</tr>
<tr>
<td><em>Chondrilla nucula</em></td>
<td>100</td>
<td>100</td>
<td>?</td>
<td>?</td>
</tr>
<tr>
<td><em>Halichondria magnicornulosa</em></td>
<td>50 (6)</td>
<td>100 (4)</td>
<td>67 (3)</td>
<td>?</td>
</tr>
<tr>
<td><em>Lissodendoryx isodictyalis</em></td>
<td>50 (4)</td>
<td>67 (3)</td>
<td>100 (4)</td>
<td>?</td>
</tr>
<tr>
<td><em>Haliclona manglaris</em></td>
<td>50 (6)</td>
<td>50 (2)</td>
<td>50 (2)</td>
<td>?</td>
</tr>
<tr>
<td><em>Clathrina coriacea</em></td>
<td>43 (7)</td>
<td>33 (3)</td>
<td>33 (3)</td>
<td>0 (1)</td>
</tr>
<tr>
<td><em>Ecteinascidia turbinata</em></td>
<td>71 (17)</td>
<td>50 (8)</td>
<td>13 (8)</td>
<td>50 (2)</td>
</tr>
<tr>
<td><em>Ecteinascidia minuta</em></td>
<td>13 (8)</td>
<td>0 (3)</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Botryllus sp.</em></td>
<td>38 (8)</td>
<td>0 (2)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Unfortunately, due to overgrowth of our tags and dwindling sample sizes, we were unable to determine the total lifespan of most species. With the exception of *C. coriacea*, all of the sponge species still had healthy, viable individuals when sampling had to be terminated due to tag loss. Table 2, therefore, underestimates the lifespans of these species and we can only say that most lived for at least 2 years and that *E. turbinata* lived for at least 3 years. Only the ascidians *E. minuta* and *Botryllus sp.* could be annual species.

Recruitment

Recruitment rates were very low. All three ascidian species recruited to tiles placed beneath the mangrove roots (Fig. 7), but there was rarely more than one recruit per tile and many tiles had no ascidian recruitment at all. Two-month samples showed that *Botryllus sp.*, once established, could rapidly grow and fill available space. The other two ascidians, however, grew very slowly (Fig. 7). None of the major sponge species ever recruited to tiles beneath the root canopy.

Tiles placed directly among the mangrove roots also showed very low recruitment rates. Patchy *Botryllus sp.* recruitment was seen from April to November. *Ecteinascidia turbinata* appeared on a few tiles between January and March, and *E. minuta* colonies occasionally appeared between September and December. In December, the sponge *Clathrina coriacea* recruited to 4 of the 25 tiles. None of the other sponges ever appeared on the tiles. These indications of low recruitment are supported by our observations that bare roots are common in the habitat and roots newly entering the water may remain uncolonized for many months.
Fig. 7. Recruitment to 15 x 15 cm ceramic tiles placed directly beneath the marked mangrove roots. From January to April, tiles were collected and recruits were counted monthly. From May to December, plates were collected after two months and percent cover was determined. None of the major sponge species recruited to the tiles during the year of sampling.

Discussion

1. Community dynamics

Photographic monitoring and analysis of this Florida mangrove root community revealed enormous temporal variability over the 38-month study period. It was common for colonies to appear, disappear, or show substantial size changes after only 1 or 2 months. All species showed significant deviations from stochastic boundedness, indicating that this is a very dynamic community where species interactions are constantly shifting. Fluctuations in species cover were quite large—generally not even confined to boundaries exceeding 100% of the mean (as evidenced by critical \( \omega \) values, Figs 5, 6). This level of variability is similar to that described by Ellison & Farnsworth (1992) for sponges in a Belizean mangrove habitat.

This picture of a dynamic, changing community is dramatically different from the more stable Venezuelan \( R. \ mangle \) root community studied by Sutherland (1980), yet the communities share many fundamental characteristics. For example, sponges (in particular \( Tedania \) ignis) were the most abundant species in both habitats, but colonial ascidians were also important. Although many different species were present in both communities, most were quite rare. Adjacent roots were often dramatically different. Most species were long-lived and showed high persistence. Recruitment rates were low, the dominant species showed some of the lowest recruitment levels, and there was little evidence of seasonality. Given the great similarities in these two habitats, what then destabilizes the Florida Keys community and produces the large fluctuations in epifaunal distribution and abundance?
2. Structuring processes

Equilibrium communities are generally thought to be structured by biotic interactions (primarily competition), while non-equilibrium community dynamics are controlled by physical disturbance and stochastic events (reviewed by DAYTON, 1984; TOKESII, 1993). SUTHERLAND (1980) described the Venezuelan mangrove habitat as a protected, soft bottom bay where temperature and salinity are consistently high (30°C and >32‰ respectively), where hurricanes do not occur, and where predator-related disturbances are unimportant. As predicted by MENG & SUTHERLAND (1987), this stable community appears to be structured primarily by competitive interactions. In contrast, the Florida Keys community shows the high variability more characteristic of a community controlled by disturbances. Based on our observations throughout this study, we propose that the perturbations can be attributed to three sources: 1) physical disturbance resulting from strong tidal flows; 2) species-specific predation; 3) asexual ‘recruitment’.

Physical disturbance

As has been described for intertidal (DAYTON, 1971; SOUSA, 1979), soft bottom (GRASSLE & SANDERS, 1973; THISTLE, 1981), and other fouling communities (OSMAN, 1977; SUTHERLAND & KARLSON, 1977), physical disturbance is probably a major structuring force in the Florida Keys habitat. Although physiological stresses from annual temperature and salinity changes may affect the root species, the greatest impact probably comes from tidal currents. Large sponge colonies commonly disappeared completely between successive photographs of a single root and we often found large sponges lying on the bottom. This can result from current-induced abrasion between roots or simply from sponges growing too heavy to be supported by the root (we sometimes found entire epifauna-laden roots completely broken off).

The lack of stochastic boundedness in large, long-lived sponges probably results from such disturbances. This is evidenced by the fact that the most massive sponges (i.e., Halichondria magnificolosa and Tedania ignis) showed the greatest departures from stability, while smaller sponges such as Chondrilla nucula and Clathrina coriacea showed stability on a greater proportion of the root sections. Random disturbances could contribute to the constant reshuffling of species as physical impact damaged or stripped colonies from roots. This could prevent strong competitive hierarchies and intense competitive mechanisms from being established here. Indeed, BINGHAM & YOUNG (1991b) found that sponges in the Florida Keys site show none of the competitive allelopathic effects suggested for sponge-dominated communities in a more moderate tropical habitat (GOODBODY, 1961).

In October 1987, we had the opportunity to observe the effect of a major physical disturbance when the eye of Hurricane Floyd passed directly over the Florida Keys. Although it was a weakening storm by the time it reached that area, wind gusts of 42 m·s⁻¹ (93.9 mph) were reported on Cudjoe Key approximately 7 km from the study site (CASE & GERRISH, 1988). We expected to see major changes in the epifauna due to colony damage and detachment or root breakage. However, subsequent samples (including one taken just 3 days after the hurricane) showed
few obvious effects (Figs 2–4). The impacts of the high winds and waves were barely discernible above background levels of variability inherent in the community, indicating that disturbance and colony damage are common events.

Predation

KEOUGH & DOWNES (1982), CAFFEY (1985), SVANE (1987), OSMAN et al. (1989, 1992), and others have shown that predators can strongly impact communities of sessile invertebrates. However, KEOUGH & BUTLER (1983) and YOSHIOKA (1975) showed that predation may be relatively unimportant in the dynamics of insular epifaunal communities. We believe this generally to be true in the Florida mangrove root community. Asteroids (Echinaster grammicola) were occasionally seen feeding on sponges that had fallen to the seafloor, but were unable to reach intact roots suspended above the bottom. Many fish species lived among the roots and in the adjacent seagrass beds, but in over 270 h of diving, none was ever observed feeding on sponges or ascidians, and no obvious signs of fish predation were ever seen. RANDALL & HARTMAN (1968) examined 212 common West Indies fish species and found only 11 that fed regularly on sponges; none of those species was ever seen in the mangrove habitat where this study was done.

Despite the apparent lack of predator effects in this community, the great instability of Ecteinascidia turbinata populations may result from specialized predation by an inconspicuous polyclad flatworm (Pseudoceros crozieri). When P. crozieri locates an E. turbinata colony, it may stay there feeding on zooids until only basal stolons remain (pers. obs.). Such barren stolons were frequently seen at the study site. These predation-induced colony size fluctuations may be compounded by natural cycles of zooid senescence and regression. Many ascidian species are capable of regenerating zooids from basal stolons (reviewed by BERRILL, 1975; MILLAR, 1971; see also DAVIS, 1988) and this occurs with E. turbinata (Fig. 8). This could explain why E. turbinata shows such enormous temporal variability (93.6% of roots examined were not stochastically bounded—the greatest percentage of any species measured) despite its long life span and high probability of being relocated on the same root. The fluctuations may represent predation (or regression) to basal stolons followed by a re-emergence of healthy zooids.

This resilience of E. turbinata populations has important implications given its recently discovered importance as a source for the potent anti-tumour compound, ecteinascidin 743 (RINEHART et al., 1990; WRIGHT et al., 1990; SAKAI et al., 1992). Study of the compound requires significant harvesting of E. turbinata. Prudent collection methods (i.e., without damaging the stolons) may permit exploitation of the compound without irreversibly impacting wild populations of the species.

Fig. 8. Serial photographs of a single study root taken in A. March 1986, B. September 1986, C. January 1987, D. April 1987, E. January 1988, and F. May 1988. The arrows in B, D, and F indicate positions of E. turbinata colonies. Debris was often found floating among the roots. The seagrass blades (Thalassia testudinum) in panel C have been torn loose from the bottom and are floating in the water column. Scaled frame widths are 8.5 cm.
Recruitment

Larval recruitment in this mangrove habitat was generally low and it is unlikely that the community is ever destabilized by the heavy recruitment and annual sloughing reported for temperate fouling communities (Sutherland & Karlson, 1977). Recruitment of several sponge species was never observed. Yet, on occasion, after only a 1-month period, newly established sponges were found on some study roots. Analysis of the photographs and observation of sponges in the habitat revealed an unusual process of ‘asexual recruitment.’ In some seasons, *Haliclona manglaris* and *Lissodendoryx isodictyalis* produced numerous fine tendrils (Fig. 1C). These bits of sponge eventually broke off, drifted away, and became entangled in other roots. Such fragmentation may be a method of invading an area where small larval recruits would be unable to survive but where larger colonies can persist. A similar dispersal process may occur for *E. turbinata* (Bingham & Young, 1991a). While fragmentation appeared to be somewhat seasonal, the location and frequency of attachment and the potential modification of overgrowth patterns and space allocation are largely stochastic events.

3. Scale

Dayton & Tenger (1984), Levin (1992), Tokeshi (1993), and others have emphasized the importance of scale in assessing marine community dynamics. Farnsworth & Ellison (1996) found that dynamics of a mangrove root epifaunal community in Belize were scale dependent (short-term dynamics were controlled by larval supply, while physical factors controlled longer-term processes). To examine the effects of temporal sampling scale on our data, we plotted the percent cover data for Ecteinascidia turbinata, *Lissodendoryx isodictyalis*, and *Haliclondria magniconulosa* on an arbitrarily chosen root using 12-month, 6-month, and 1–2-month intervals (Fig. 9). At the 12-month interval, the community appeared to undergo a steady transition from a nearly bare root to a completely sponge-dominated assemblage (a small *E. turbinata* colony appeared to go extinct in the first sampling interval). As the sampling interval was decreased to 6 and then to 2 months, however, additional important information was gained. Most notable was the enormous variability, including percent cover values of *E. turbinata* approaching 65%, that would have gone unnoticed had sampling been done at intervals greater than 2 months. A much more dynamic community is perceived at the shorter sampling interval.

We do not know if 2 months was the optimum sampling interval in this habitat; perhaps higher frequency sampling would produce additional insights. It is obvious, however, that in this dynamic mangrove habitat, important ecological processes occur on short-time scales. The frequency of perturbation controls the temporal scale at which ecological transitions take place. In stable environments where biotic interactions are more important structuring agents, longer sampling intervals may be appropriate. However, in the rapidly changing *R. mangle* root community we studied, frequent stochastic events (physical damage to colonies and roots, species-specific predation, and asexual ‘recruitment’) destabilize the species assemblage
Fig. 9. Effects of sampling interval on abundance measurements. Percent covers of two sponges (*H. magniconulosa, L. isodictyalis*) and an ascidian (*E. turbinata*) on a single *R. mangle* root are shown. The same data appear in all three panels except that the sampling interval is decreased from 12 months (top panel) to 1–2 months (bottom panel).

and prevent longer-term ecological processes (*e.g.*, competition) from structuring a more stable community.

**Summary**

This study suggests that mangrove root communities in the Florida Keys are extremely dynamic. The communities show significant deviations from narrow
stochastic boundedness. Changes in this community are associated with processes that occur on short time scales (i.e., 1–2 months). Stochastic perturbations, particularly physical disturbance, predation, and asexual ‘recruitment’ disrupt species interaction and prevent longer-term equilibrium processes (e.g., competition) from stabilizing the community.

Acknowledgements

The authors thank J. L. Cameron for valuable field assistance and W. Herrnkind, D. Mariscal, D. Simberloff, for comments on earlier versions of the manuscript. Thanks also to C. Diaz and M. Maldonado who assisted with sponge identifications. N. Smith allowed us to use temperature and salinity data collected near the study site. This work was supported by grant No. OCE-8916264 to C. M. Young and is Harbor Branch Oceanographic Institution contribution No. 1105.

References


Epifaunal community dynamics


