Effects of Plant Size and Distribution on the Numbers of Invertebrate Species and Individuals Inhabiting the Brown Alga *Pelvetia fastigiata*

F. C. Gunnill

Scripps Institution of Oceanography, A-001; La Jolla, California 92093, USA

Abstract

The invertebrates living on specimens of the brown alga *Pelvetia fastigiata*, growing in the intertidal zone at La Jolla, California (USA) in November 1975 were enumerated. Within 7 collecting sites, larger plants generally shelter more animal species and individuals than smaller plants. The number of species on a given plant can be described as an equilibrium number; numbers of species and individuals can become similar on defaunated and transplanted algae of comparable sizes placed at the same experimental site. Such equilibria are site-specific because the colonization, immigration and loss rates of animals differ among the sites studied. Relationships between plant size and the number of animal species and individuals on *P. fastigiata* also differ among the collecting sites. The between-site differences are related to tidal level, to habitat diversity and to habitat patch-size. Small isolated plants without epiphytes shelter few species. The faunas of larger isolated plants at mid-tide levels generally include many thallus-dwelling, tubiculous, vagrant and epiphyte-dwelling species, but few such species commonly inhabit plants within aggregations of *P. fastigiata*. Within aggregations, the plants host relatively few epiphytes and thus lack habitat diversity, and the net emigration rates of many animals including epiphyte-dwellers are relatively high. Plants within aggregations, however, usually shelter more animal individuals than isolated plants. Thus, faunal diversity is reduced, not increased within the largest patches of *P. fastigiata*.

Introduction

Benthic and terrestrial communities have been described as mosaics of habitat patches (Johnson, 1970; Root, 1973). Within such mosaics, patches of a given type differ in age, size and/or isolation and thus appear to be habitat islands (Janzen, 1968; Levin and Paine, 1974). The number of species on islands generally increases with increasing island size (Preston, 1962a, b; Connor and Simberloff, 1978). MacArthur and Wilson (1967) relate such species-area relationships to the colonization, immigration and extinction rates of species and predict that the number of species on each island varies about an equilibrium number. Although aspects of theories for island biotas remain unproven (May, 1975; Simberloff, 1976a; Gilbert, 1980), both species-area relationships and equilibrium numbers of species within patches would be significant to the faunas of habitat patches (Levin and Paine, 1974; Opler, 1974).

The application of island biogeographic principles to habitat patch biotas has been supported by several studies of the numbers of species within patches (e.g. Seifert, 1975; Abele and Patton, 1976) or the distributions of individual species (Smith, 1974; Gunnill, 1982). Other studies, however, report deviations from island predictions resulting from the transience of the animals or patches examined (Tepedino and Stanton, 1976; Beaver, 1977) or from faunal variations with patch size (Osman, 1977; Ogden and Ebersole, 1981). Within habitat-patch mosaics, variations in the distributions or relative abundances of species with increasing patch size can be important to community structure (Root, 1973; Atsatt and O'Dowd, 1976). Therefore, the present study compares assemblages of invertebrate animals inhabiting a wide size range of patches formed by an intertidal alga with predictions for the faunas of islands and patches within mosaics.

The perennial brown alga *Pelvetia fastigiata* forms distinct patches in the mid-intertidal zone at La Jolla, California (Gunnill, 1980a, 1982). Small patches (< 1 m²) are formed by non-contiguous (isolated) plants; large patches are formed by dense aggregations of contiguous plants. For the present study, specimens of *P. fastigiata* have been collected from 2 aggregations and from 5 locations with isolated plants. Relationships between plant size and the number of animal species or individuals per

plant are described and compared among the 7 sites. Then, experiments with defaunated or transplanted algae have elucidated the colonization, immigration and loss rates of animals. In addition, longer-term experiments have determined whether the faunas of *P. fastigiata* are equilibrium faunas. Finally, the distributions of animals in groups of species differing in behavior and/or host plant specificity are compared among collecting sites.

Materials and Methods

Collecting Stations

The 7 collecting stations included bedrock exposures and cobbles or boulders deposited on an intertidal erosional platform in the Bird Rock region of La Jolla, California (see Gunnill, 1980b, 1982). At 2 sites, aggregations of *Pelvetia fastigiata* cover 100% of the rock surface and, at 5 sites, isolated plants cover an average of only 6% of the rock surface (Table 1). The *bank-site aggregation* is formed by plants growing on inshore ridges. The following 3 sites with isolated plants are adjacent to the bank aggregation: (1) *high-isolated* (which includes plants on the crest of a ridge), (2) *near-channel,* and (3) *sand-channel* (which both include plants growing on rocks in troughs beside the high-isolated ridge). The *mid-bank aggregation* is on an outcrop on a small peninsula. The *mid-isolated* plants are a minimum of 8 to 10 m from the mid-bank and other areas inhabited by *P. fastigiata*. Plants at the *cove site* are 150+ m from the nearest *P. fastigiata*. All collecting stations are at mid-tide levels (+0.7 m) except for the upper mid-intertidal high-isolated site (+1.4 m).

Experimental Sites

The 5 experimental sites are at increasing distances from decreasing quantities of *Pelvetia fastigiata* (see present Table 1; and Gunnill, 1982): The *bank-* and *near-sites* are

on the periphery of the bank-aggregation collecting station. Plants at the bank-site are contiguous with, and those at the near-site (a man-made clearing) are ≤ 0.3 m away from, unmolested plants in the aggregation. The *mid-site* lies between and a minimum of 3 to 5 m away from plants at the mid-bank and mid-isolated collecting stations. The *cove-site* is 5 m from the cove collecting station. The *far-site* is 56 m from the mid-site and 30 m from the nearest unmolested *P. fastigiata*. All experimental plots are at the same mid-tide level (+0.7 to +0.8 m).

Although *Pelvetia fastigiata* generally does not grow in contact with other plant species, animals that inhabit it can also live on other macrophytes growing in the Bird Rock area. Several brown algae (e.g. *Egregia menzii, Eisenia arborea* and *Cystoseira osmundacea*) grew in low intertidal/subtidal areas ≤ 30 m from all but not within any study sites. The brown alga *Sargassum muticum* grew in or near most sites, but was relatively common only at the sand-channel site (see Gunnill, 1980b). The green alga *Codium fragile* also grows at mid-tide levels and, before they were removed, individuals grew at several experimental sites. Coralline algae (e.g. species of *Jania* and *Corallina*) and associated red algae (e.g. species of *Pterocladia* and *Laurencia*) commonly cover intertidal platforms but not rocks inhabited by *Pelvetia fastigiata*. Red algae were most abundant at the cove collecting site and several experimental sites and were rare at the mid-isolated and (except *Endocladia muricata*) high-isolated sites. In addition, although the other red algae can grow under aggregated *P. fastigiata,* only small tufts of coralline algae grew under the aggregations studied.

Red algae that grow on coralline algae can also grow as epiphytes at the bases of *Pelvetia fastigiata*. In addition, filamentous epiphytes such as *Ectocarpus* spp. can grow near the distal ends of *P. fastigiata* fronds. With few exceptions, filamentous epiphytes were less abundant than red algal epiphytes. Both types of epiphytes were most frequent and abundant on large isolated *P. fastigiata* at mid-tide levels; some small plants at such sites also sup-

Table 1. *Pelvetia fastigiata.* Distribution and average densities within 7 collection sites at Bird Rock, La Jolla, California. Aggregated (Aggr) but not isolated (Isol) plants are contiguous with other *P. fastigiata.* Plant densities are averages in m² quadrats along line transects surveyed in November 1975. Percent cover by *P. fastigiata* is estimated from ranges of plants in 4 size classes counted in the field and determined for plants collected from mid-isolated and bank sites. Aggregations by definition cover 100% of the rock surface

Site	Tide height (m)	Plant dispersion	No. plants m⁻² > 80 g	No. plants m⁻² Total	% cover	Site area (m²)
High-isolated	+1.4	Isol	1.0	5.8	6	23.0
Bank	+0.7	Aggr	22.0	41.1	89	50.0[a]
Mid-bank	+0.7	Aggr	29.0	49.0	108	3.5
Near-channel	+0.7	Isol	1.5	10.5	15	15.0
Sand-channel	+0.7	Isol	1.1	4.5	7	130.0[a]
Mid-isolated	+0.7	Isol	0.4	4.0	4	150.0[a]
Cove	+0.7	Isol	0.5[a]	4.0[a]	4	35.0[a]

[a] Estimations from incomplete records

ported epiphytes. During the present study, however, epiphytes were not common either on plants within aggregations or on isolated plants at upper mid-intertidal levels.

Collections

On 1 November 1975, 141 *Pelvetia fastigiata* were cut ≤ 1 cm above their holdfasts and preserved in Formalin. The exclusion of holdfasts does not exclude a holdfast fauna because *P. fastigiata* has discoid holdfasts. The preserved algae were rigorously washed over 0.09 and 1.0 mm sediment sieves and then the size of washed algal specimens was measured as damp dried wet weight = damp weight (see Gunnill, 1982). The animals were hand-sorted from debris; most animals were enumerated at the species level, but difficult taxa such as nematodes and mites were enumerated at higher taxonomic levels termed operational taxonomic units (OTU's; Schoener, 1974 a). My OTU's can underestimate numbers of species only where the taxa are abundant and thus cannot change the conclusions to be drawn. Although copepod nauplii can represent species, they are excluded when numbers of individuals are compared because they were not enumerated in all samples. Otherwise, my abundance data are whole-sample counts of all animals collected on the sieve screens.

The animals inhabiting *Pelvetia fastigiata* are divided into groups of species differing in taxonomy, feeding behavior, vagility and/or host-plant specificity as determined by their gut contents, their distributions among plant species, dispersal experiments and/or literature on similar species (e.g. Colman, 1940; Glynn, 1965; Hagerman, 1966; Gunnill, 1979; Hicks, 1980). Island and habitat-island studies often examine a single group of taxonomically related species. May (1975) reports that the slopes of species-area relationships for related taxa may be limited to Preston's (1962a) predicted values by the additivity of non-interacting species. Although species-area relationships for guilds of potentially interacting, but often unrelated, species need not encounter the additivity constraint (e.g. Opler, 1974; Seifert, 1975), the best use of such relationships may still be to examine biotic similarities or differences. In the present study, analog species- (and individuals) area relationships are primarily used for such comparisons.

Relationships between the numbers of animal species or individuals on *Pelvetia fastigiata* and plant size are described with least-squares regressions. Such relationships can be expressed by a variety of methods based on logarithmic, semi-logarithmic or untransformed data (e.g. May, 1975; Connor and McCoy, 1979). I selected logarithmic ($\log_{10}$) regressions to normalize variances; such regressions exclude zeros, but log $Y + 1$ mode regressions are not good descriptors when small plants consistently are not inhabited. Although regressions are consistent, objective descriptors of log-linear trends in the data from each site, my data need not represent singular, monotonic func-

tions (see also Whitehead and Jones, 1969; Dony, 1977). Therefore, the data as well as the regressions are used for between-site comparisons.

Manipulation Experiments

In all experiments, plants were cut from their holdfasts and mounted at preselected sites by tightening hose clamps around their basal ends to nails set into rock. Some algae were transplanted to new sites with minimal disturbance, but others were defaunated in freshwater and then placed at new sites (see Gunnill, 1982). Experiments were conducted in October and November of 1975 and in January and February of 1976. Plant specimens were collected on predetermined schedules and treated as described above. Since experimental plants can have faunas similar to those of unmolested plants, neither defaunation nor transplantation *per se* limits the faunas of experimental plants (see also Gunnill, 1979, 1982). Thus, faunal differences reflect differences in the immigration and emigration rates of animals.

Between-site comparisons of the numbers of species or individuals on algae placed in the field for the same number of days are made with Kruskal-Wallis tests with honest significant difference discrimination of rank averages. Data from all manipulation experiments are combined in such analyses. Effects of plant size are examined with sign tests (see Gunnill, 1982). Temporal trends in the faunas of defaunated or transplanted algae are described with logarithmic regressions. Such regressions are analogous to colonization and relaxation (transplantation) curves (Simberloff and Wilson, 1969; Diamond, 1972), but include increases or decreases in the numbers of individuals as well as species on experimental algae. Colonization and relaxation curves may be described with either exponential or power functions (see Sheldon, 1977), but neither can be used as the sole criterion for the definition of "equilibrium" (MacArthur and Wilson, 1967). Exponential functions presume that such equilibria exist, whereas power functions assume that they do not exist. In the present study, three criteria will be used to define equilibria; the approach and intersection of colonization and relaxation regressions, the overlapping of data, and the maintenance of similar averages in the colonization and relaxation experiments.

Results

Numbers of Species and Individuals on Unmolested *Pelvetia fastigiata*

The numbers of animal species and individuals on algae collected from 7 sites at Bird Rock are presented in Figs. 1 and 2, respectively. As expected, small plants generally shelter fewer species and fewer individuals than large plants. Therefore, regressions describing relationships be-
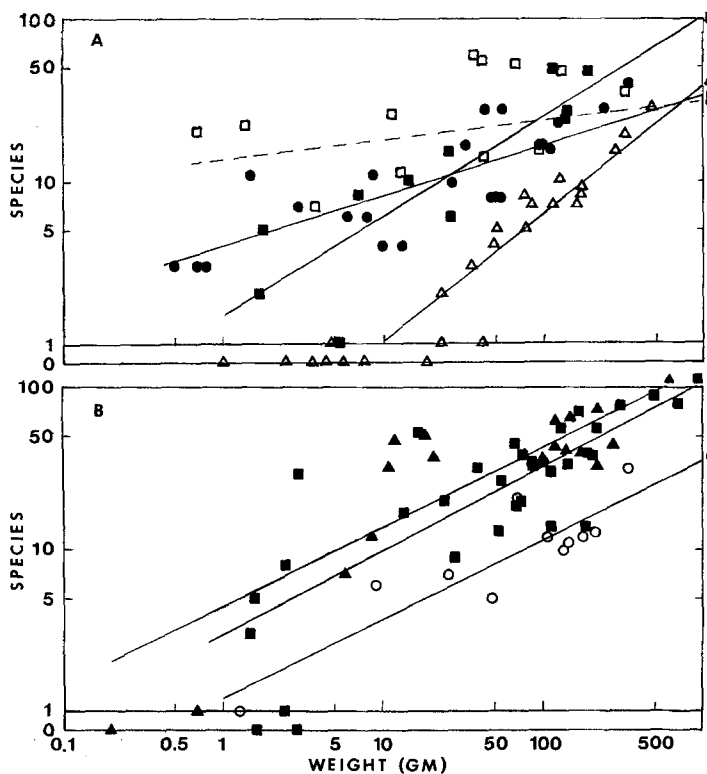
Fig. 1. Relationships between numbers of invertebrate species and size (damp wt) of *Pelvetia fastigiata* at the 7 collection sites at Bird Rock. (A) triangles = high-isolated; circles = bank aggregation; filled squares = near-channel; open squares = sand-channel. (B) circles = mid-bank aggregation; squares = mid-isolated; triangles = cove. Lines keyed at frame margins are logarithmic regressions given in Table 2 (continuous line = $p < 0.05$; dashed line = not significant)

Table 2. Numbers of animal species and individuals on unmolested *Pelvetia fastigiata* from the 7 collection sites. Regressions of form $\log y = a + b \log x$ describing relationships with plant size at 7 sites. N: number of occupied samples; 95% CL: 95% confidence limits of b; r: correlation coefficient; p: probability level (NS = not significant; $* = p < 0.05$; $** = p < 0.001$) in F-tests. isol: isolated; chan: channel. Since log regressions exclude zeros, N can differ from the numbers of samples in Figs. 1 and 2

Site	N	a	b	95% Cl	r	p
Number of species						
High-isol	19	− 0.7890	0.7907	0.1815	0.91	**
Bank	23	0.5977	0.3069	0.1067	0.79	**
Mid-bank	11	0.0836	0.4910	0.1927	0.79	**
Near-chan	11	0.1811	0.6142	0.2730	0.86	**
Sand-chan	9	1.1381	0.1165	0.2267	0.42	NS
Both chan	20	0.7012	0.3318	0.2190	0.60	*
Mid-isol	30	0.5701	0.4762	0.1493	0.78	**
Cove	17	0.6476	0.4949	0.2043	0.80	**
Total number of individuals						
High-isol	19	− 1.3605	1.6480	0.3180	0.94	**
Bank	23	1.1708	1.0020	0.1833	0.93	**
Mid-bank	11	− 0.1533	1.2782	0.4607	0.90	**
Near-chan	11	− 0.3599	1.4297	0.5048	0.91	**
Sand-chan	9	1.5441	0.3586	0.7098	0.41	NS
Both chan	20	0.6801	0.8292	0.4793	0.65	*
Mid-isol	31	0.4010	1.1097	0.2550	0.86	**
Cove	17	1.0015	0.8831	0.3052	0.85	**
Number of individuals other than *Scutellidium lamellipes* and *Ampithoe tea*						
High-isol	19	− 0.1446	0.7805	0.2858	0.81	**
Bank	21	0.3576	0.5098	0.2291	0.73	**
Mid-bank	10	− 0.0103	0.5020	0.1471	0.94	**
Near-chan	11	− 0.0217	0.9268	0.3866	0.88	**
Sand-chan	9	1.7132	0.0422	0.4440	0.08	NS
Both chan	20	0.9200	0.4233	0.2921	0.58	*
Mid-isol	31	0.4734	0.8087	0.2822	0.74	**
Cove	17	1.0335	0.7289	0.3592	0.74	**

tween the numbers of species or individuals and plant size are highly significant at 6 sites (Table 2). Such regressions for sand-channel site plants are not significant because small plants at that site often shelter relatively high numbers of animals. Regressions combining data from both channel sites are significant, although variance among the faunas of smaller plants is high. Similar variance occurs within collections from the mid-isolated and cove sites.

Species-plant size relationships differ between sites (Fig. 1). Regression slopes are lowest for *Pelvetia fastigiata* in the bank aggregation and highest for high-isolated plants, but confidence intervals on the slopes overlap between sites (Table 2). Numbers of species on algae of a given size, however, are not equal at the 7 sites. At the high-isolated site, small plants are not inhabited but the largest plants can shelter as many species as plants within aggregations. At mid-tide levels, isolated plants in channels near the bank aggregation tend to have numbers of species and regression slopes between those of aggregated and more distant isolated plants. In general, aggregated and upper mid-intertidal plants shelter fewer species than comparable isolated plants at mid-tide levels.

The most individuals occurring on plants of any given size generally are found within the bank aggregation (Fig. 2). Although steep regression slopes (> 1.0) indicate that densities of animals often increase with the size of isolated *Pelvetia fastigiata*, even large plants at the high-isolated and near-channel sites tend to shelter relatively few individuals. Moderately large plants (e.g. 100 g) at the cove and mid-isolated sites can shelter as many animals as similar plants in the mid-bank aggregation and large plants can harbor numbers of individuals comparable to
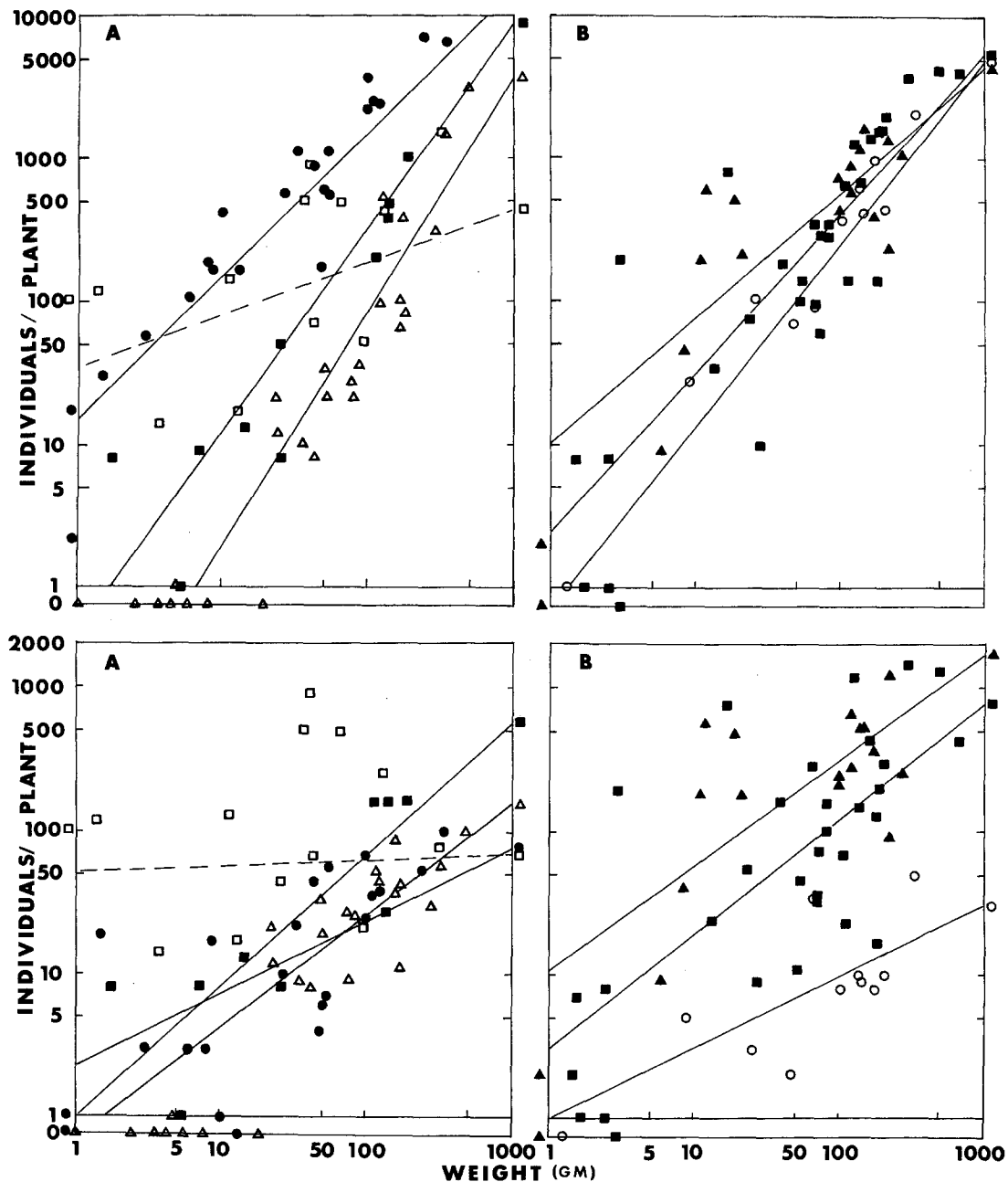
Fig. 2. Relationships between total number of individuals (top graphs) and number of individuals other than *Scutellidium lamellipes* and *Ampithoe tea* (bottom graphs) and size (damp wt) of *Pelvetia fastigiata* at the 7 collection sites. Data exclude copepod nauplii. Symbols and lines in (A) and (B) as in Fig. 1

those on plants in the bank aggregation. Nevertheless, isolated plants at mid-tide levels generally shelter more species but fewer individuals than plants within aggregations.

The faunas of *Pelvetia fastigiata* include two species that typically inhabit only *P. fastigiata* and many animals that commonly inhabit other plant species in the study area. The first two species, the copepod *Scutellidium lamellipes* and the amphipod *Ampithoe tea* represent from 0% of the total number of individuals on small isolated plants to an average of 99 + % of the individuals on plants within aggregations (Fig. 2). The summed abundances of other animals often increase significantly with increasing

plant size (Table 2, Fig. 2). Larger plants at the high-isolated and bank sites shelter similar numbers of individuals, but the densities of animals on plants there are low in comparison to those on plants at the mid-isolated and cove sites. Thus, if individuals of the first two species are excluded, aggregated plants tend to shelter both fewer species and fewer individuals than comparable isolated plants at mid-tide levels.

Colonization, Immigration and Faunal Equilibrium

Colonization and immigration, respectively, refer to the arrival of species and individuals on an alga. In this study,

the first animal of a given species arriving on an alga is both a colonist and an immigrant. Similarly, local extinctions can occur by either the emigration or the death of individuals. The initial colonization and immigration rates of animals were measured on defaunated algae placed at 5 sites for 1 d. Net colonization, immigration and emigration rates were measured on defaunated and transplanted algae placed in the field for 5 d.

The colonization and immigration rates of animals differed between the 5 experimental sites (Table 3). After 1 d, numbers of invertebrate species colonizing defaunated plants were greatest at the bank- and cove-sites and least at the far-site ($p < 0.05$). The total numbers of individuals on such plants were greatest at the bank- and near-sites because immigration rates of *Scutellidium lamellipes* and *Ampithoe tea* decrease significantly with increasing distance from *Pelvetia fastigiata* (see Gunnill, 1982). After 1 d of immigration, summed abundances of other species were similar on plants at most sites. After 5 d, however, experimental plants at the bank-site generally sheltered more individuals than defaunated plants placed at other sites ($p < 0.005$). In 5 d, the numbers of species increased on experimental plants at the bank-, near- and mid-sites, but mid- and especially far-site plants still sheltered relatively few species ($p < 0.025$). Since many animals on cove plants were associated with drifting red algae, the

colonization and immigration rates of dispersing individuals tended to be greatest within the bank aggregation and to decrease with increasing distance from areas occupied by *P. fastigiata*.

When algae growing in the bank aggregation were transplanted elsewhere, numbers of species on the plants generally remained within the range of control plants collected from the aggregation (cf. Table 3 and Fig. 1). Although there were no significant between-site differences, algae transplanted to the mid- and far-sites tended to shelter fewer species than other plants. After 5 d, algae transplanted to the bank-site sheltered more animals (excluding *Scutellidium lamellipes* and *Ampithoe tea*) than plants placed at other sites ($p < 0.05$). Exceptionally high numbers of animals on some bank-site transplants coincided with drifting sand. However, the suggestion that net losses of species occur where colonization and immigration rates are reduced is confirmed by longer-term experiments described below.

Experiments at the near- and far-sites examined if the faunas of *Pelvetia fastigiata* are equilibrium faunas. In colonization studies, faunal equilibrium can be declared if numbers of species cease to increase and begin to vary about an average (e.g. Schoener, 1974b). Such equilibria could occur within each colonization or relaxation (transplantation) experiment of the present study. The present

Table 3. Colonization and relaxation within the faunas of defaunated and transplanted *Pelvetia fastigiata* placed at the 5 experimental sites for 1 or 5 d. A: number of species; B: number of individuals; C: number of individuals other than *Scutellidium lamellipes* and *Ampithoe tea*. Dash = no data

Site	Colonization Day 1			Colonization Day 5			Relaxation Day 5		
	A	B	C	A	B	C	A	B	C
October and November 1975									
Bank	10	130	7	20	1 615	47	34[a]	4 312[a]	92[a]
	16	196	13	26	1 104	42	43	2 849	107
Near	15	53	11	13	387	12	20	1 372	37
	9	222	6	18	524	15	25	2 882	78
	7	127	5	19	537	19	12	1 613	11
Mid	13	24	14	16	25	13	–	–	–
	5	8	6	10	30	10	–	–	–
	6[a]	21[a]	7[a]	5	7	4	–	–	–
	6[a]	14[a]	11[a]	11[a]	46[a]	12[a]	–	–	–
Cove	16	26	22	14	32	15	–	–	–
	24	50	45	21	90	57	–	–	–
Far	2	1	1	3	2	2	16	388	24
	7	11	8	2	1	1	22	295	38
	3	2	2	10	10	8	11	203	11
January and February 1976									
Bank	11	459	7	11	691	19	24	2 614	27
	20	508	18	18	1 486	40	18	2 816	21
Near	23	318	36	11	208	23	12	410	23
	11	49	8	13	66	14	12	255	17
Mid	8	22	8	8	21	11	12	329	27
	3	3	3	–	–	–	12	52	9
Far	6	10	7	4	4	4	10	22	15
	11	19	14	5	5	4	–	–	–

[a] Large plant (~ 200 g) not included in standard analyses
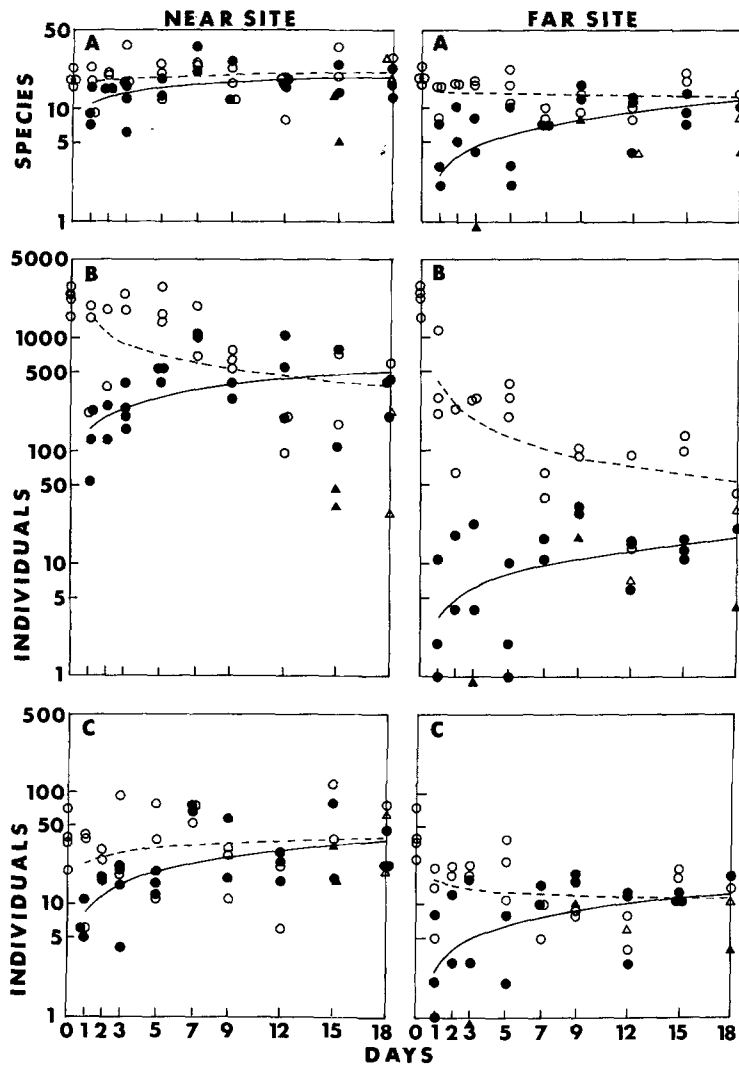
Fig. 3. Number of species (A), total number of individuals (B), and number of individuals other than *Scutellidium lamellipes* and *Ampithoe tea* (C) on defaunated (filled symbols) and transplanted (open symbols) *Pelvetia fastigiata*, placed at near- and far-experimental sites, as a function of time. Circles = approximately 100 (70 to 130)g plants; triangles = < 50 g plants. Small plants are excluded from the regressions given in Table 4 (continuous line = $p < 0.05$; dashed line = not significant)

Table 4. Numbers of species and individuals comprising faunas of defaunated and transplanted *Pelvetia fastigiata* placed at the near- and far-sites. Regressions of form $\log y = a + b \log x$ describing temporal trends. Individuals do not include copepod nauplii. Regressions are depicted on semi-logarithmic axes in Fig. 3. N: number of occupied plants; a, b: 95% CL: 95% confidence limits of b; r: correlation coefficient; p: probability level (NS; $* = p < 0.05$; $** = p < 0.001$) in F-tests

Site	Experiment	N	a	b	95% CL	r	p
Number of species							
Near	Defaun.	24	1.0430	0.1943	0.1549	0.47	*
Far	Defaun.	21	0.3717	0.5487	0.3604	0.59	*
Near	Transpl.	20	1.2323	0.0704	0.2000	0.17	NS
Far	Transpl.	24	1.1434	−0.0398	0.1702	−0.12	NS
Total number of individuals							
Near	Defaun.	24	2.1898	0.4099	0.3052	0.51	*
Far	Defaun.	21	0.5186	0.5647	0.4513	0.52	*
Near	Transpl.	20	3.1765	−0.4711	0.4480	−0.46	*
Far	Transpl.	19	2.6041	−0.6833	0.4123	−0.65	*
Individuals other than *Scutellidium lamellipes* and *Ampithoe tea*							
Near	Defaun.	24	0.9230	0.5080	0.2802	0.62	*
Far	Defaun.	21	0.4412	0.5361	0.4106	0.53	*
Near	Transpl.	20	1.3581	0.1852	0.4247	0.21	NS
Far	Transpl.	19	1.1946	−0.1190	0.3229	−0.19	NS

Table 5. Percentages of *Pelvetia fastigiata* at Bird Rock collection sites occupied by each animal taxon. High: high-isolated; Bank, Mdbk: bank and mid-bank aggregations, respectively; Chan: both channels combined, Mdis: mid-isolated; cove: cove. * = epiphytes present on *P. fastigiata*; dash = animal absent

Plant size:	0 to 66 g (bank-site 0 – 20 g)								> 66 g (bank-site > 20 g)					
Site:	High	Bank	Mdbk	Chan*	Chan	Mdis*	Mdis	Cove	High	Bank	Mdbk	Chan*	Mdis*	Cove*
No. of plants:	13	10	4	10	5	8	6	7	12	13	7	9	18	10
Thallus-dwelling species														
Scutellidium lamellipes	8	90	75	50	–	25	17	14	100	100	100	100	100	100
Scutellidium arthuri	–	–	–	–	–	–	–	–	–	–	–	–	11	10
Scutellidium spp.	–	–	–	–	–	–	–	–	–	–	–	–	11	–
Harpacticus uniremis	–	–	–	60	–	38	–	29	8	38	43	78	50	70
Harpacticus sp. (2)	–	–	–	–	–	–	–	–	–	–	–	33	–	–
Harpacticus ? sp.	–	–	–	30	20	–	–	–	–	8	–	56	11	20
Iodomene armata	–	–	25	20	–	13	–	14	–	23	14	44	17	40
Porcellidium viride	–	–	–	20	–	–	–	–	–	–	14	22	6	60
Porcellidium fimbriatum	–	–	–	–	–	25	17	–	–	–	14	22	44	60
Porcellidium spp.	–	–	–	20	–	13	–	–	17	–	–	33	22	20
Porcellidium spp. juveniles	–	–	–	10	–	–	–	14	–	–	14	33	6	20
Zaus spinatus	–	10	–	20	–	–	–	–	–	23	14	67	17	10
Zaus sp. (2)	–	–	–	–	–	–	–	–	–	–	29	22	6	10
Zaus sp. copepodites	–	–	–	–	–	–	–	–	8	–	–	–	6	–
Lacuna unifasciata	–	30	–	50	20	100	50	86	8	62	71	100	100	100
Tricolia rubrilineata	–	30	–	10	–	13	–	71	–	38	29	44	61	100
Tubiculous amphipods														
Ampithoe tea	–	40	25	50	20	75	17	71	42	100	100	100	100	100
Ampithoe pollex	–	–	–	–	–	13	–	29	–	–	–	22	–	10
Photis spp.	–	–	–	20	–	25	17	29	–	–	14	33	44	70
Corophium spp.	–	–	–	30	–	50	–	29	–	15	29	11	67	70
Aorides columbiae	–	–	–	20	–	50	–	14	–	–	–	33	6	40
Vagile herbivores														
Littorina spp.	8	–	–	10	–	–	–	–	83	–	–	11	–	–
Hyale grandicornis	38	–	–	–	–	–	–	–	100	–	–	56	17	–
Hyale frequens	–	40	–	40	–	63	–	57	8	100	43	67	78	90
Elasmopus rapax	–	–	–	20	–	50	17	–	–	15	14	11	67	50
Vagrant species														
Barnacle cyprids	–	–	–	10	–	63	–	100	8	–	14	11	61	100
Isotoma ? sp.	–	–	–	–	–	–	–	–	–	8	–	22	6	20
Paraclunio sp. larvae	–	–	–	10	–	–	–	14	–	–	43	22	–	10
Other insects	–	–	–	–	–	25	–	29	8	–	29	–	17	30
Dynamella glabra	–	–	–	–	–	13	–	–	–	–	14	11	11	30
Other sphaeromids	–	–	–	30	–	–	–	–	–	–	14	22	17	10
Idotea urotoma	–	–	–	–	–	–	–	–	–	–	–	22	–	–
Ianiropsis kincadi	–	–	–	20	–	13	–	–	8	–	–	33	17	20
Munna ubiquita	–	–	–	–	–	–	–	–	–	–	–	33	11	10
Paranthura elegans	–	–	–	–	–	–	–	–	–	–	–	–	17	70
Colanthura sp.	–	–	–	–	–	–	–	–	–	–	–	11	6	–
Gnathid	–	–	–	–	–	–	–	–	–	–	14	–	–	–
Cryptoniscids	–	–	–	–	–	13	–	14	–	–	–	–	17	40
Anatanais normani	–	–	–	–	–	38	–	29	–	–	–	–	44	20
Leptochelia sp ?	–	–	–	–	–	13	–	–	–	–	–	22	11	10
Undetermined tanaids	–	–	–	10	–	–	–	29	–	–	–	11	11	30
Cumella vulgaris	–	–	–	20	–	–	–	14	–	–	–	–	17	10
Pachygrapsis crassipes juveniles	–	–	–	–	–	–	–	–	8	–	–	11	–	–
Megalops larvae	–	–	–	–	–	–	–	–	8	–	–	11	6	–
Pugettia sp. juveniles	–	–	–	–	–	–	–	–	–	–	–	–	39	20
Pagurus samuelensis	–	–	–	20	–	–	–	–	–	–	–	11	6	–
Stylochus ? sp.	–	–	–	10	–	13	–	–	–	–	14	–	39	10
Allelocoela	–	–	–	–	–	–	–	–	–	–	–	–	28	–
Other flatworms	–	–	–	–	–	–	–	14	–	–	–	–	11	20
"Epiphyte-dwelling" species														
Heterophilias seclusus	–	–	–	–	–	13	–	–	–	8	–	–	6	–
Amphilochidae	–	–	–	–	–	–	–	–	–	8	–	–	17	–
Eophliantidae	–	–	–	–	–	–	–	–	–	–	–	–	17	10

Table 5 (continued)

Plant size:	0 to 66 g (bank-site 0 – 20 g)								> 66 g (bank-site > 20 g)					
Site: No. of plants:	High 13	Bank 10	Mdbk 4	Chan* 10	Chan 5	Mdis* 8	Mdis 6	Cove 7	High 12	Bank 13	Mdbk 7	Chan* 9	Mdis* 18	Cove* 10
Other gammarid amphipods	–	–	–	20	–	25	–	29	–	8	–	44	11	40
Caprella equilibria	–	–	–	10	–	13	–	–	–	–	–	11	6	–
Other caprellid amphipods	–	–	–	–	–	–	–	14	–	–	–	–	–	10
Parathalestris bulbiseta	–	–	–	20	–	13	–	–	–	–	–	22	–	20
Dactylopodia vulgaris	–	–	–	40	–	–	–	14	8	–	–	56	6	20
Alteutha langi ?	–	30	–	10	–	25	17	–	–	23	–	22	6	–
Eupelte ? sp.	–	–	–	–	–	–	–	–	–	–	–	22	6	10
Diarthrodes spp.	–	–	–	40	–	13	–	29	–	31	14	67	50	20
Ectinosoma melaniceps	–	–	25	60	–	63	–	57	8	15	14	67	56	60
Ectinosoma spp.	–	–	–	10	–	13	–	29	–	–	–	33	11	30
Paralaophonte pacifica	–	–	–	30	–	25	–	43	–	–	–	22	17	20
Echinolaophonte armiger	–	–	–	30	–	63	–	71	–	8	43	22	67	70
Parastenhelia spp.	–	–	–	50	–	–	–	29	8	8	14	56	50	30
Lourenia armatus	–	–	–	10	–	–	–	–	–	–	–	11	33	–
Other copepods	–	20	25	100	60	63	–	86	58	69	43	89	94	90
Paradoxostomid (1)	–	–	–	70	40	–	–	29	8	46	–	78	17	80
Paradoxostomid (2)	–	20	25	80	40	100	33	71	8	92	57	100	100	100
Paradoxostomid (4)	–	–	–	50	40	38	–	29	–	23	–	44	61	40
Paradoxostomid (5)	–	–	–	20	–	38	–	–	–	8	71	11	39	70
Paradoxostomid (7)	–	–	–	30	–	13	–	29	–	38	–	56	33	20
Paradoxostomid (8)	–	–	–	10	–	13	–	29	–	8	–	11	6	20
Ostracod (10)	–	–	–	10	–	–	–	–	17	–	–	11	–	–
Cytherids (1)	–	–	–	20	–	25	17	43	–	31	14	56	61	90
Neonesidea phlageri	–	–	–	–	–	–	–	–	–	–	–	–	6	–
Other ostracods	–	–	–	–	–	–	–	43	8	–	–	22	33	50
Sabellid polychaetes	–	–	–	50	40	88	–	57	8	15	29	56	72	80
Platynereis bicanaliculata	–	–	–	–	–	–	–	–	–	–	–	11	39	20
Syllids (1)	–	10	–	40	–	75	–	29	–	–	14	33	72	40
Syllids (2)	–	–	–	20	20	13	–	29	–	–	–	22	50	30
Exogone sp.	–	–	–	–	–	–	–	14	–	–	–	11	6	10
Tacytrypane sp.	–	–	–	–	–	13	17	–	–	–	–	–	28	–
Other polychaetes	–	–	–	10	–	13	–	43	–	8	–	11	33	20
Oligochaetes	–	10	–	10	–	–	–	–	–	–	–	11	11	20
Amphithalamus spp.	–	–	–	10	–	13	–	57	–	8	–	67	33	50
Barleeia spp.	–	–	–	30	–	43	–	–	–	15	14	33	61	100
Caecum californicus	–	–	–	–	–	–	–	–	8	–	–	–	–	10
Other gastropods	–	20	–	50	–	38	–	71	25	38	43	78	83	100
Lasea subviridis	–	10	–	–	–	13	–	–	–	–	–	–	–	–
Hyatella arctica	–	–	–	–	–	–	–	–	–	–	–	–	6	10
Mytilus spp.	–	–	–	–	–	–	–	–	–	–	–	11	6	–
Undetermined pelecypods	–	–	–	10	–	–	–	14	–	8	–	11	17	20
Nematodes	–	10	–	70	40	75	17	71	25	62	43	89	100	100
Rhombognathid mite (1)	–	10	50	40	20	88	–	57	33	77	86	100	100	100
Rhombognathid mite (3)	–	10	25	10	–	–	–	–	25	23	–	44	17	30
Halacarid (2)	–	10	–	40	–	25	17	43	17	15	–	33	67	60
Other Acarinae	15	–	–	70	40	88	–	71	33	23	–	89	78	80

study, however, can also determine whether or not the numbers of species and individuals become equivalent on defaunated and transplanted algae placed at the same site.

Equilibrium numbers of species were attained on algae placed at the near-site (Fig. 3A, Table 4). A regression describing the numbers of species on transplanted algae is not significant but is positive in slope, since the average number of species on the algae increased from 18.8 (bank control) through 20.0 (Days 1–5) to 21.2 (Days 7–18). Individual defaunated algae could shelter similar numbers of species within 1 to 3 d but, as indicated by the colonization regression, the average number of species on the defaunat-

ed plants increased more slowly from 0 to 13.5 ($\leq$5 d) to 19.4 ($\geq$7 d). Nevertheless, between the 7th and 18th days of the two experiments, the means and ranges for the numbers of species on defaunated and transplanted algae were similar.

The total numbers of individuals also became similar on defaunated and transplanted *Pelvetia fastigiata* placed at the near-site (Fig. 3B, Table 4). Net emigration was less predictable than net immigration. Following transplantation, numbers of individuals decreased immediately on some algae but not on others. The regression describing the transplantation data, however, is both negative in

slope and significant, because, after 7 d, an average of only 461 animals remained on the transplanted algae. Comparable numbers of individuals could immigrate to defaunated algae in 5 d and an average of 535 animals sheltered in defaunated plants after 7 d in the field. The intersection of regressions for the two experiments after 13 d also suggests that an equilibrium number of individuals was being attained.

The apparent equilibrium number of species for *Pelvetia fastigiata* placed at the far-site is half that of similar plants placed at the near-site (Fig. 3 A). Individual plants could shelter as many species as plants at the bank- and near-sites, but the average number of species on algae transplanted to the far-site decreased to 15.2 (≤ 5 d) and then 12.0 (≥ 7 d). Although 12 taxa could colonize defaunated plants at the far-site in no more than 3 d, and had usually arrived within 9 d (Fig. 3 A), the average number of species on defaunated algae only increased to 9.7 (≥ 7 d). Thus, regressions describing trends in the numbers of species on defaunated and transplanted algae approach without intersecting. Regressions describing the total numbers of individuals on the experimental algae also do not intersect because, after 7 d at the far site, averages of 76 and 17 individuals were living, respectively, on transplanted and defaunated algae. Thus, the numbers of individuals on defaunated and transplanted algae demonstrate that equilibrium faunas were not attained during the far-site experiments (Fig. 3 B).

At the end of the experiments, algae placed at the far-site sheltered fewer species and 6 to 30 times fewer individuals than those at the near-site (Fig. 3 A, B). The between-site differences in the numbers of individuals on experimental plants were primarily caused by two species, *Scutellidium lamellipes* and *Ampithoe tea*. However, the net immigration and emigration rates of other animals also differed between sites (Fig. 3 C). The average number of individuals (excluding *S. lamellipes* and *A. tea*) on algae transplanted to the near-site increased from 37.7 (≤ 5 d) to 46.3 (≥ 7 d). At the far-site, such averages decreased to 19.3 (≤ 5 d) and then 10.8 (≥ 7 d). During colonization, at the near-site, the average number of animals per plant increased to 13.5 (≤ 5 d) and then 38.8 (≥ 7 d). At the far-site, the average number of animals per defaunated plant increased to 5.7 (≤ 5 d) and then 12.8 (≥ 7 d). Thus, at both sites, means and ranges for the numbers of individuals (excluding *S. lamellipes* and *A. tea*) on defaunated algae became similar to those on transplanted algae (Fig. 3 C), but plants at the far-site still sheltered 3 to 4 times fewer individuals than those at the near-site.

Components of the Faunal Assemblage

The structure of the faunal assemblage of *Pelvetia fastigiata* differs with plant size and distribution. Such differences occur not only because the densities of the two invertebrate species that typically inhabit *P. fastigiata* vary with patch size, but also because the frequencies and

abundances of other animals differ between sites (Fig. 2, Table 5). In Table 5, the animals are divided into 5 component groups of species that form the assemblage. In each of these 5 groups, most species were collected on isolated *P. fastigiata* growing at mid-tide levels. Species sheltering on plants within aggregations also shelter on isolated plants, but the converse is not true. Tide level is also significant; plants at the high-isolated site shelter fewer species and, in some instances, different species than plants at mid-tide levels.

The *thallus-dwelling species* listed in Table 5 include harpacticoid copepods and small gastropods that crawl along the surfaces of *Pelvetia fastigiata* and/or other brown algae and surf grass. At most collecting sites, larger *P. fastigiata* shelter more thallus-dwelling species than smaller plants (Fig. 4, Table 6). The abundances of *Scutellidium lamellipes* and the summed abundances of other thallus dwellers also generally increase with increasing plant size (present Fig. 4; and Gunnill, 1982). Although the animal species-plant size relationships are generally determined by copepods, the significant abundance-plant size regressions for thallus dwellers (excluding *S. lamellipes*) on plants at the mid-isolated and cove sites are primarily caused by the gastropods *Lacuna unifasciata* and *Tricolia rubrilineata* (Tables 5 and 6). The regression for plants at the two channel sites is not significant because gastropods are not abundant but copepods (especially *Harpacticus* spp.) are particularly abundant on plants of moderate size (Table 5, Fig. 4). Aggregated algae *per se* shelter relatively few thallus-dwelling species, most of which are represented by single individuals.

Amphipods in several genera attach tubes to *Pelvetia fastigiata*. *Ampithoe* spp. generally live near the distal ends of fronds, while *Photis* spp., *Corophium* spp. and *Aorides columbiae* live near the holdfasts. *Ampithoe tea* inhabits *P. fastigiata* at all sites but, like the other species, generally does not occupy plants at the high-isolated site (Table 5). *Ampithoe pollex* was not collected frequently in November, but tends to occupy isolated plants. The other species are found only as individuals on aggregated plants, but can be abundant (range 0 to 351 individuals species[-1] plant[-1]) on isolated plants at mid-tide levels. Even at the mid-isolated and cove-sites, however, the base dwellers represent an average of less than 5% of the total number of individuals on *P. fastigiata* versus 10 to 30 + % for *A. tea*.

Two *vagile herbivores*, the amphipod *Hyale grandicornis* and *Littorina* spp. (*L. planaxis* plus juveniles), frequently shelter in > 20 or 60 g plants at the high-isolated site (Table 5), where abundances of *H. grandicornis* but not *Littorina* spp. tend to increase with increasing plant size. Although individuals of both the amphipod and the gastropods can shelter in plants at mid-tide levels, their high frequencies and abundances distinguish the faunas of upper mid-intertidal *Pelvetia fastigiata*. Similarly, *H. frequens* is 1 of only 3 species that are frequent and abundant within collections of aggregated *P. fastigiata*. Within the bank aggregation, abundances of *H. frequens* tend to increase with plant size. However, although *H. frequens*
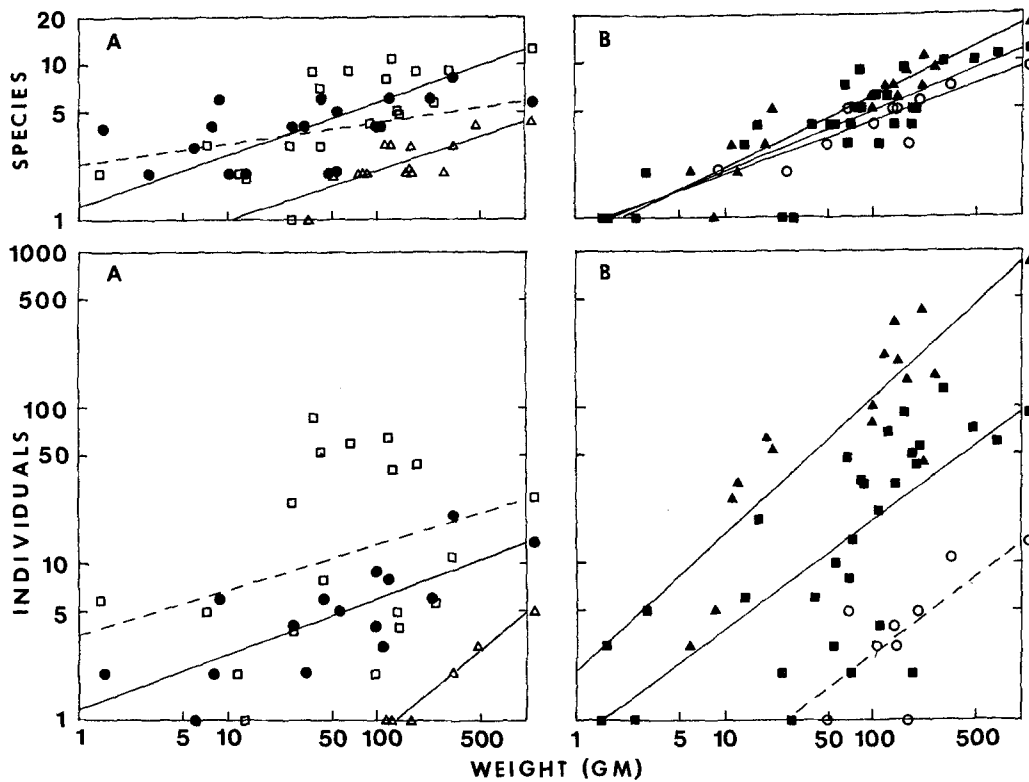
Fig. 4. Relationships between numbers of thallus-dwelling species and individuals and size (damp wt) of *Pelvetia fastigiata*. Lines are logarithmic regressions (continuous line $=p<0.05$; dashed line $=$ not significant) given in Table 6. (A) triangles $=$ high-isolated; circles $=$ bank aggregation; squares $=$ near $+$ sand channels. (B) circles $=$ mid-bank aggregation; squares $=$ mid-isolated; triangles $=$ cove

Table 6. Thallus-dwelling species, vagrant species and epiphyte-associated species on *Pelvetia fastigiata* at Bird Rock collection sites. Regressions of form $\log y = a + b \log x$ describing relationships between numbers of species or individuals and size of *P. fastigiata*. Number of thallus-dwelling species includes *Scutellidium lamellipes* and copepod nauplii but numbers of individuals do not. Abbreviations as in Table 2

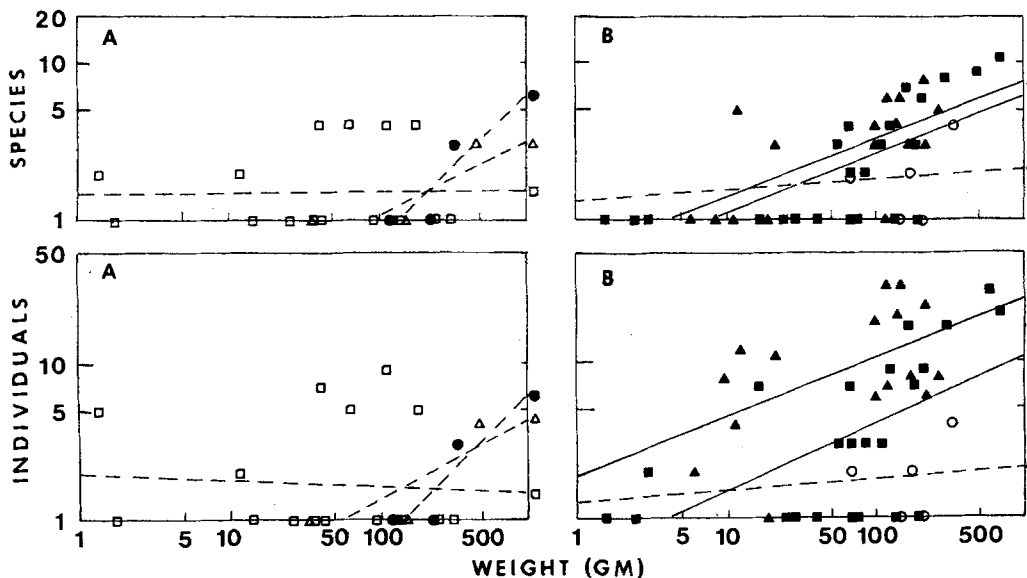| Site	Number of species						Number of individuals				
	N	a	b	95% CL	r	p	a	b	95% CL	r	p
Thallus-dwelling species											
High-isol	14	− 0.3456	0.3286	0.2020	0.72	*	− 1.7150	0.8052	0.3561	0.97	*
Bank	20	0.3646	0.1313	0.1412	0.42	NS	0.0666	0.3543	0.2186	0.71	*
Mid-bank	10	− 0.0806	0.3460	0.1779	0.85	*	− 1.0108	0.7135	1.1161	0.54	NS
Both chan[a]	18	0.0836	0.3373	0.1896	0.69	*	0.5449	0.2893	0.4989	0.29	NS
Mid-isol	29	− 0.0796	0.3800	0.1007	0.83	**	− 0.1032	0.6867	0.2742	0.70	**
Cove	16	− 0.1204	0.4494	0.1163	0.91	**	0.3046	0.8757	0.3243	0.84	**
Vagrant species											
High-isol	3	− 0.6863	0.3934	3.5685	"0.81"	NS	− 0.8662	0.4965	4.5078	"0.81"	NS
Bank	3	− 2.0181	0.9330	10.1683	"0.76"	NS	− 2.0181	0.9330	10.1683	"0.76"	NS
Mid-bank	5	− 0.1154	0.0678	0.3092	"0.37"	NS	0.1154	0.0678	0.3092	0.37	NS
Both chan[a]	17	0.1694	0.0046	0.2099	0.01	NS	0.3141	− 0.0486	0.2922	0.09	NS
Mid-isol	23	− 0.3346	0.3752	0.1787	0.69	**	− 0.2469	0.4267	0.2738	0.58	*
Cove	16	− 0.2059	0.3632	0.2476	0.64	*	− 0.2832	0.3717	0.3448	0.53	*
Epiphyte-associated species											
High-isol	14	− 0.8220	0.6314	0.3293	0.76	*	− 0.8446	0.6734	0.4883	0.66	*
Bank	17	0.3186	0.3570	0.2460	0.62	*	0.3503	0.4193	0.3461	0.56	*
Mid-bank	10	0.3181	0.2038	0.4648	0.34	NS	0.1383	0.3211	0.6493	0.37	NS
Both chan[a]	20	0.8275	0.2142	0.2245	0.43	NS	1.0694	0.3837	0.4952	0.36	NS
Mid-isol	29	0.5293	0.4225	0.1634	0.71	**	0.5536	0.6879	0.3154	0.65	**
Cove	16	0.9018	0.2791	0.2587	0.53	*	1.3994	0.3627	0.5413	0.36	NS

[a] Combined data

Fig. 5. Relationships between number of vagrant species and individuals and size (damp wt) of *Pelvetia fastigiata*. Symbols and lines as in Fig. 4

can be abundant on individual plants, neither *H. frequens* nor *Elasmopus rapax* consistently occupies isolated plants at mid-tide levels.

Motile predators, herbivores and omnivores such as flatworms, isopods and crabs were not uniformly distributed among sites (Table 5). Moreover, *vagrants per se* were rare on aggregated and upper mid-intertidal *Pelvetia fastigiata*. At such sites, only a few species and individuals were found on the largest plants (Fig. 5). Vagrants frequently were present on plants at the channel sites, but neither the numbers of species nor the numbers of individuals correlated with plant size (Tables 5 and 6). At the mid-isolated and cove-sites, the numbers of species and individuals increased significantly with plant size (Fig. 5) but,even at those sites, all vagrants represented an average of less than 3% of the total number of individuals on *P. fastigiata*.

The fifth group in Table 5, "*epiphyte dwellers*", includes animals widely distributed among algal species, especially within assemblages of coralline and other red algae (where some are associated with sand trapped by the algae). Such animals often were sorted from red algal epiphytes growing on *Pelvetia fastigiata*. A few others (*Parathalestris bulbiseta, Dactylopodia vulgaris* plus *Ampithoe pollex*) inhabit filamentous epiphytes. Nematodes, rhombognathid mites and several copepods and ostracods were sorted from both types of epiphytes and also inhabited *P. fastigiata* without epiphytes; several were also on the tubes of the polychaete *Platynereis bicanaliculata* which, itself, is not directly associated with epiphytes. Many epiphyte dwellers, however, were recorded only on *P. fastigiata* with epiphytes (Table 5).

Epiphyte dwellers usually contribute substantially to the total numbers of animal species on *Pelvetia fastigiata* (Figs. 1 and 6). The numbers of species and the summed abundances of epiphyte dwellers increase significantly with the size of *P. fastigiata* at several sites (Table 6). However, most species on aggregated and upper mid-intertidal plants were represented by single individuals. Where epiphyte dwellers were abundant, they often were the taxa causing variance about species- and individuals-plant size relationships for the whole faunas of *P. fastigiata* (Figs. 1, 2 and 6). Such variance is most evident at the mid-isolated and channel sites, where some small plants supported substantial growths of epiphytes and others were epiphyte-free.

Table 7 enumerates the frequencies at which animals in the 5 groups described previously occurred on defaunated and transplanted algae placed at the 5 experimental sites and on algae of similar size obtained from several collecting sites. Few species were both common and evenly distributed among the experimental plants. In the 18 d experiments (Fig. 3), only a few species such as *Scutellidium arthuri, Hyale grandicornis*, and the isopod *Dynamella glabra* were collected most frequently at the far site. Although individuals of more species colonized algae placed at the near-, mid- and cove-sites than at the far site, plants at such sites tended to shelter fewer species and individuals than plants at the bank site (Tables 3 and 7). At mid-tide levels, however, more species inhabit isolated plants than inhabit plants within aggregations (Fig. 2, Tables 5 and 7).

Frequent colonists of the experimental plants often were "epiphyte dwellers" that inhabit *Pelvetia fastigiata* growing at most collecting sites (Tables 5 and 7). Other frequent colonists were vagile herbivores and vagrants that generally did not inhabit small isolated plants. Thus, it appears that the latter species actively select larger plants (but not plants within aggregations). Because small experimental plants (< 50 g) and especially very small plants

(< 20 g) tend to shelter relatively few species and individuals (Fig. 3, triangles), it appears that high emigration rates of the widely distributed colonizing species also reduce the numbers of species on such small isolated *P. fastigiata*. However, plant size alone does not account for between-site differences in the faunas of moderate-sized experimental and unmolested plants.

The sizes of standard experimental plants in Table 3 did not differ consistently between sites; however, within sites, plant weights varied from 70 to 130 g. Plant sizes tended to be more variable in the winter than in the fall experiments (see Gunnill, 1982). After 1 d of colonization during the winter, the larger isolated plant in each of 3 independent sample pairs sheltered more species and individuals (excluding *Scutellidium lamellipes* and *Ampithoe tea*) than the smaller member of that pair ($p = 0.13$). During the first and fifth days of colonization, larger plants sheltered more species and individuals than smaller plants in 6 of 7 ($p = 0.06$) and 7 of 7 ($p = 0.008$) comparisons, respectively. Thus, net immigration rates tended to increase with increasing plant size. During the fall experiments, however, larger isolated plants did not consistently shelter more species or individuals than smaller plants. The few data from 100 and 200 g plants placed at the mid-site also suggest that neither the initial colonization rates of species nor the immigration rates of animals other than *S. lamellipes* and *A. tea* vary with the size of moderately large plants (Table 3: weights of plant specimens are given in the same sample order in Gunnill, 1982).

The numbers of animal species on isolated *Pelvetia fastigiata* at mid-tide levels are increased by epiphytes and by recruitment over longer periods of time than those examined in the experiments. Epiphytes did not grow on the experimental plants. Immigrating individuals of the colonizing epiphyte-associated animals do not necessarily emigrate from plants without epiphytes; the numbers of such species on defaunated plants increase over time and transplanted algae shelter more species than defaunated algae (averages per plant: near-site 9.6 versus 7.2; far-site 4.2 versus 2.5; see also Table 7). However, the numbers of different species and the average numbers of species and individuals on experimental plants are relatively low in comparison to those on isolated *P. fastigiata* with epiphytes (Fig. 6; Tables 5 and 7). This indicates that epiphytes decrease the emigration of some animal species immigrating to isolated plants; other animal species, particularly those with planktonic larvae, may recruit seasonally. The abundances of tubiculous amphipods, many thallus-dwelling species and even some vagrant species were also relatively low on experimental plants (Tables 5 and 7). Thus, while solitary individuals of such animals on isolated *P. fastigiata* may be transients, the high numbers of species and especially individuals that can occur on large isolated plants require that immigrants remain on *P. fastigiata*. In contrast, relatively high colonization rates but low numbers of species indicate that individuals of these and most other species are transients on plants of all sizes within aggregations.
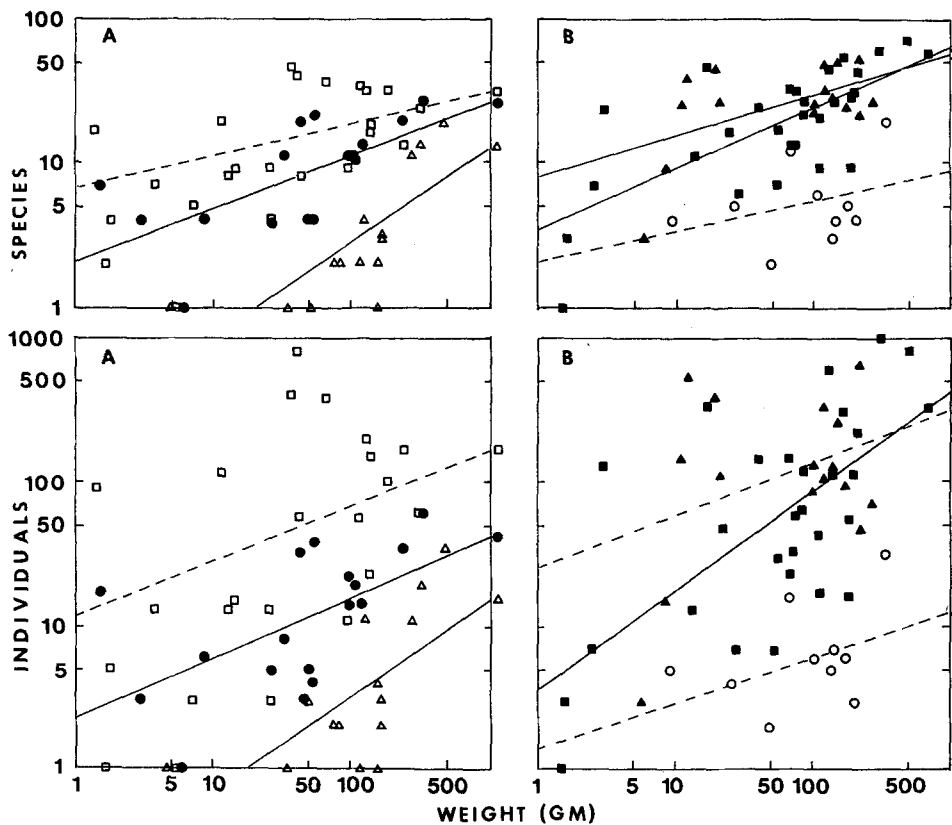

Fig. 6. Relationships between number of epiphyte-dwelling species and individuals and size (damp wt) of *Pelvetia fastigiata*. Symbols and lines as in Fig. 4

Table 7. Invertebrates on 70 to 130 g transplanted (tran), defaunated (def) and unmolested (real) *Pelvetia fastigiata* collected from mid tide level sites at Bird Rock. Individuals on *N* plants have been multiplied to estimate numbers of individuals in each taxon on 10 plant of each type at each site. 0 = present; — = absent

Site:	Near tran	Near def	Far def	Far tran	Bank tran	Bank def	Mid def	Cove def	Bank real	Chan real	Mdis real	Cove real
No. of plants (*N*)	21	24	21	20	2	4	8	4	4	6	10	5
Thallus-dwelling copepods and gastropods												
Scutellidium lamellipes	9 867	3 465	30	1 821	33 820	7 350	91	135	23 323	1 182	1 897	1 870
Scutellidium arthuri	–	–	1	11	–	8	1	3	–	–	–	2
Scutellidium spp.	1	–	–	1	–	–	–	–	–	–	2	2
Harpacticus uniremis	10	2	–	2	25	5	–	3	3	105	17	22
Harpacticus spp.	2	–	1	–	–	–	–	–	–	77	–	4
Iodomene armata	–	0	–	1	–	–	1	–	3	17	2	4
Porcellidium viride	4	2	–	1	5	3	–	20	–	5	1	–
Porcellidium fimbriatum	1	1	–	1	–	–	–	–	–	2	4	8
Porcellidium spp. including undetermined copepodites	4	3	1	1	–	3	–	3	–	10	2	2
Zaus spp.	1	–	–	–	–	–	–	–	5	25	2	2
Lacuna unifasciata	9	3	1	1	10	–	8	25	30	45	179	406
Tricolia rubrilineata	1	–	–	1	30	–	–	–	8	17	46	1 358
Tubiculous amphipods												
Ampithoe tea	358	268	–	104	970	240	30	13	235	343	660	2 010
Ampithoe pollex	1	0	–	–	–	–	–	–	–	2	2	–
Photis, Corophium, + Aorides spp.	5	3	1	4	–	–	3	3	5	37	213	162
Vagile herbivores												
Littorina spp.	1	0	–	1	–	5	–	3	–	2	–	–
Hyale grandicornis	11	7	18	13	10	–	6	5	–	20	1	–
Hyale frequens	15	7	–	2	170	45	–	–	195	50	21	68
Elasmopus rapax	2	0	–	–	–	–	3	3	3	–	3	12
Vagrant species												
Barnacle cyprids	5	2	5	3	2	–	1	5	–	–	11	132
Isotoma ? sp.	34	32	–	2	30	10	1	13	–	2	–	–
Dipteran pupae + larvae	2	5	–	–	–	3	–	–	–	–	–	2
Other insects	3	3	–	–	5	–	1	3	–	–	–	4
Dynamella glabra	2	2	18	30	–	–	10	3	–	–	1	–
Other sphaeromids	1	3	–	–	–	3	–	–	–	3	1	2
Other isopods	1	–	1	1	–	–	–	–	–	5	8	10
Tanaids	–	–	1	–	–	–	–	3	–	3	5	4
Cumella vulgaris	1	–	–	–	–	–	–	–	–	–	2	6
Megalops larvae	1	1	1	–	–	–	–	–	–	2	–	–
Pachygrapsis sp. juveniles	1	3	1	2	5	–	–	3	–	2	–	–
Pugettia sp. juveniles	1	–	1	–	–	–	–	–	–	–	2	2
Pagurus spp.	5	2	–	–	90	3	–	–	–	2	1	–
Flatworms	3	0	–	2	15	3	1	–	–	–	2	2
Epiphyte-dwelling species												
Other gammarid amphipods	5	3	1	–	5	3	–	3	3	7	9	4
Caprella equilibria	1	–	–	–	–	–	–	–	–	3	1	–
Diarthrodes spp.	2	1	–	–	5	–	–	–	3	10	8	8
Ectinosoma melaniceps	2	–	1	6	5	–	–	3	–	43	14	12
Ectinosoma spp.	7	2	3	2	50	10	3	20	–	22	8	10
Paralaophonte pacifica	1	–	–	–	–	–	–	–	–	2	4	4
Echinolaophonte armiger	1	1	–	–	5	3	–	–	3	15	63	74
Parastenhelia spp.	4	2	1	1	5	–	–	3	–	17	41	20
Lourenia armatus	1	–	–	–	–	–	–	–	3	–	12	–
Calanoid copepods	–	0	1	2	–	–	–	3	–	–	–	–
Other copepods	78	40	5	24	115	43	6	38	15	350	180	162
Paradoxostomid (1)	9	4	1	–	–	–	–	13	3	75	1	26
Paradoxostomid (2)	67	20	3	3	110	20	3	40	35	217	135	394
Paradoxostomid (4)	3	1	–	2	10	–	–	–	5	17	12	10
Paradoxostomid (5)	3	0	–	–	10	–	–	–	3	7	2	16
Paradoxostomid (7)	3	0	–	–	5	5	3	–	5	8	3	6
Cytherids (1)	5	4	1	1	–	3	1	3	5	22	46	56

Table 7 (continued)

Site:	Near		Far		Bank		Mid	Cove	Bank	Chan	Mdis	Cove
Type of plant:	tran	def	def	tran	tran	def	def	def	real	real	real	real
No. of plants (N)	21	24	21	20	2	4	8	4	4	6	10	5
Other ostracods	1	1	1	–	40	–	–	–	–	5	2	4
Sabellid polychaetes	1	–	1	1	5	–	–	3	–	72	145	124
Syllid polychaetes	1	4	1	2	–	–	–	3	–	7	44	32
Other polychaetes	2	3	1	3	10	–	–	3	–	13	10	14
Oligochaetes	1	–	1	2	–	3	–	–	–	–	–	2
Amphithalamus spp.	4	3	1	–	5	5	–	3	–	17	2	2
Barleeia spp.	1	1	–	1	–	–	–	–	–	5	18	20
Fartulum + Caecum spp.	4	1	1	–	25	3	–	3	–	–	–	2
Other gastropods	12	3	1	3	25	15	3	40	5	20	43	42
Nematodes	28	43	3	5	10	20	5	45	5	293	91	248
Rhombognathid mite (1)	21	6	1	4	55	3	6	3	35	30	227	134
Rhombognathid mite (3)	7	4	–	–	5	3	–	–	5	10	–	–
Halacarid mites (2)	4	3	–	1	15	3	1	–	3	5	17	20
Other Acarinae	10	22	3	11	10	28	1	25	10	43	24	26

Discussion

The numbers of animal species increase with the size of habitat patches formed by plant stands (Ward and Lakhani, 1977; Rigby and Lawton, 1981) and individual plant units (Seifert, 1975; Tepedino and Stanton, 1976; and present study) growing in distinctly different environments. Species-habitat size relationships similar to those described for island biotas suggest but do not prove that principles of island biogeographic theory (MacArthur and Wilson, 1967) apply to the faunas of such plant islands. The theory itself is based on the concept of dynamic equilibrium which predicts that the number of species on a given island will vary about an equilibrium number as colonizing species replace species that become locally extinct. The equilibrium number of species for an island may change with temporal variations in faunal composition, habitat diversity and/or relative isolation (Simberloff and Wilson, 1970; Diamond, 1975; Connor and Simberloff, 1978). Thus, at a given time, the number of species on an island may be varying about an equilibrium number or may be approaching it by either colonization or relaxation (e.g. Simberloff and Wilson, 1969; Diamond, 1972). Such variability presents a practical problem, since deviations from predicted values do not necessarily disprove the equilibrium theory.

In the present study, defaunated and transplanted *Pelvetia fastigiata* simulate islands of similar size and structure undergoing "colonization" and "relaxation" at the same site. The numbers of animal species on the algae increase and/or decrease until they become similar on defaunated and transplanted algae placed within each of two sites. The numbers of individuals also become similar on both types of experimental plants placed at one site. The numbers of species and individuals on the plants, however, differ between sites because the colonization and immigration rates of animals differ between sites. Therefore, the experiments demonstrate that colonization and immigration can maintain relatively constant numbers of species on *P. fastigiata* and that such equilibria can differ between sites.

Dynamic equilibrium theory predicts that turnover will occur in equilibrium biotas as colonizing species replace species that become locally extinct (MacArthur and Wilson, 1967). Colonization curves and between-sample comparisons estimate that, within the faunas of the experimental plants described in the present study, 5 to 40% and up to 60% of the species become locally extinct each day (Gunnill, 1979). Much of the apparent turnover, however, results from the immigration and emigration of individuals of rapidly colonizing species, and thus turnover rates of animals will exceed those on comparable isolated *Pelvetia fastigiata*. Moreover, turnover rates will differ with plant size and distribution. MacArthur and Wilson (1967) predict that, if two islands are similar in habitat structure and isolation, turnover rates of species will be greater on the smaller island. On some marine habitat-islands, turnover rates of animals do decrease as numbers of species increase with habitat size, but the decreases do not necessarily occur for the predicted reasons (Osman, 1977; Ogden and Ebersole, 1981; but see Schoener, 1974a). The results of the present study indicate that the turnover rates of animals on *P. fastigiata* will generally decrease as the size of isolated plants increases, but then will increase on plants in the largest patches (i.e., in aggregations).

During the experiments of the present study, faunas similar to those on some small isolated and aggregated *Pelvetia fastigiata* but not those of larger isolated plants were attained on the defaunated and transplanted algae. Therefore, the equilibrium numbers of species on the experimental plants must be regarded as short-term equilibria (see also Simberloff and Wilson, 1970). Several previous studies have demonstrated that the faunas of small habitat patches can be developed by relatively long-term recruitment of dispersing larvae and/or adults (e.g. Davis, 1975; Osman, 1977). *P. fastigiata* that have grown

to the size of my standard experimental plants are 1 to at least 3 yr old, and individuals can live at least 7 yr (Gunnill, 1979; 1980 a). Since growth rates of individual *P. fastigiata* often are negative (Gunnill, 1979), small plants can also be old plants. Animal species colonizing the experimental plants often are vagrants or apparently transient individuals of widely distributed species that predominate in the faunas of small isolated plants without epiphytes. Individuals of such species, however, may remain on and/or sustain the presence of the species on larger isolated plants (e.g. the "rescue effect": Brown and Kodrick-Brown, 1977). In addition, epiphytes recruiting to and growing on older plants apparently attract and/or retain immigrants of some species. Other animals, particularly tubiculous and thallus-dwelling species, recruit over longer periods of time than those examined. For colonial species, decreasing emigration rates with increasing plant size and *in situ* reproduction can also increase the numbers of species or individuals on large plants (Hughes, 1978; Gunnill, 1982). For the species that live or reproduce on *P. fastigiata* or its epiphytes, patches of *P. fastigiata* can be habitat-islands.

Patches of *Pelvetia fastigiata* are not only habitat-islands but also habitat-patches within a community mosaic (*sensu* Root, 1973). The faunal assemblage includes not only species that typically inhabit *P. fastigiata* but also species that typically inhabit other plant species, are ubiquitously distributed and/or only take refuge in algae. Widely distributed and especially transient species often are excluded from theoretical studies of island and habitat-island biotas (e.g. Lynch and Johnson, 1974). However, it cannot be presumed that single motile individuals on algae do not have breeding potential at or adjacent to a site (e.g. Schoener, 1974 a), that the species would not interact with resident species (e.g. Simberloff, 1976 a), or that individuals of widely distributed, rapidly colonizing species do not remain on plant specimens. Moreover, widely distributed species often predominate in the biotas of small islands (Whitehead and Jones, 1969; Carlquist, 1974; Diamond, 1975) and island transients include predators and seasonal migrants that could compete with resident species (Crowell, 1962; Grant *et al.,* 1975). If island ecology or community structure is of interest, such species cannot be ignored (see also Simberloff, 1976 a).

The present study divides the animals inhabiting *Pelvetia fastigiata* into groups of species differing in taxonomy and behavior; however, the same animals can also be regarded as a single assemblage since they can interact among groups. In sum and often within groups, both the numbers of species and individuals generally increase with increasing plant size. Such relationships can differ between sites (e.g. May, 1975). Moreover, the species-plant size relationships and their between-site differences are partially caused by factors that are believed to govern the numbers of species on islands.

Species-area relationships for island biotas have been attributed to habitable area (e.g. Preston, 1962 a, b; Sim-

berloff, 1976 b), to habitat diversity (e.g. Whitehead and Jones, 1969; Power, 1975), and to passive sampling by which large islands are colonized by more species than small islands (cf. Rigby and Lawton, 1981). At present, it is uncertain whether colonization rates are dependent on island area, and the relative importance of area and habitat diversity has not been resolved (Connor and Simberloff, 1978). All three factors, however, can be significant to the faunas of *Pelvetia fastigiata*. Net colonization rates and the number of different species inhabiting the smallest isolated plants are relatively low. Passive sampling, however, will not account for within- and between-site differences in the faunas of larger plants. Such differences are related to habitat size and/or diversity. The number of species living directly on or sheltering among algal fronds generally increases with the size, hence "area" of isolated plants. Other species are directly or indirectly associated with epiphytes and hence "habitat diversity" (see also Colman, 1940; Hagerman, 1966). The presence or absence of epiphytes coincides with substantial variations in the numbers of species on small plants, and the presence of epiphytes generally coincides with high numbers of species on larger isolated plants at mid-tide (but not upper mid-intertidal) levels.

Reduced habitat diversity is one factor contributing to low numbers of species on aggregated *Pelvetia fastigiata*. Plants within aggregations typically did not support epiphytes. Although many epiphyte-dwelling species were living in tufts of coralline algae growing under the aggregations studied (Gunnill, 1979), few species and few individuals of these species were collected on aggregated plants. This indicates that the species live in the epiphytes on isolated plants but emigrate from aggregated plants. Since epiphytes can grow on and under aggregated *P. fastigiata*, their absence on the plants examined appears to be caused by herbivory. Several grazing gastropods and chitons shelter under aggregated *P. fastigiata*, particularly under the bank aggregation (e.g. Connor, 1978). In addition, 3 species (*Scutellidium lamellipes, Ampithoe tea* and *Hyale frequens*) that were found frequently and abundantly on aggregated plants are grazers (e.g. Glynn, 1965; Hicks, 1980; Gunnill, 1982) but such species also inhabit isolated plants. Moreover, the scarcity of epiphytes cannot account for the low numbers of species and individuals of vagile, vagrant, and most thallus-dwelling animals on aggregated *P. fastigiata*.

Root (1973) predicts that species characteristically inhabiting a host plant will numerically dominate the faunas of large patches of that plant because such species will attain high densities while individuals of other species will drift out or emigrate. On *Pelvetia fastigiata*, the densities of *Scutellidium lamellipes* and *Ampithoe tea* increase with plant size until they represent 50 + % of the faunas of larger isolated plants (Gunnill, 1982, and present study). The same two species represent 96 to 99 + % of the animal individuals (often 96% for *S. lamellipes* alone) on all but the smallest plants within aggregations of *P. fastigiata*. While the other animal species, in sum or individually,

were abundant on large isolated plants, few species were found frequently or abundantly on aggregated plants. Some animals apparently avoid aggregations; relatively high immigration rates but low numbers of species indicate that individuals of most other species are transients that will emigrate from aggregated plants. Thus, although large isolated plants can be habitat islands to a variety of thallus-dwelling, tubiculous and epiphyte-dwelling species, aggregations are habitat islands for only a few species, in particular the two species that characteristically inhabit *P. fastigiata.*

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